To the Graduate Council:

I am submitting herewith a dissertation written by Medhat N. Antonios entitled "Input-Output Analysis of Mathematical Models of Ecosystems." I have examined the final copy of this dissertation for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Doctor of Philosophy, with a major in Mathematics.

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INPUT-OUTPUT ANALYSIS OF MATHEMATICAL MODELS OF ECOSYSTEMS

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ABSTRACT

Necessary and sufficient conditions for the convergence of the solutions of linear and nonlinear time varying compartmental models described by systems of differential equations are reviewed. Similar conditions for discrete models described by systems of difference equations are derived.

For continuous and discrete models, the concept of environ analysis is extended to advanced linear systems and for the first time to systems with time varying coefficient matrices $\overset{\prime\prime}{A}(t)$ and $[\overset{\prime}{A}(t)]^T$. Generalizations to nonlinear models satisfying certain regularity assumptions and to linear systems with time delay are introduced. Output and input environ partitioning flow and storage matrices for a two trophic level aquatic system are derived in the form of integral equations. Also, for the same system, estimates for the deviation of the environ partitions at any time from their asymptotic values are found.

As a step towards the important goal of controlling the eutrophication phenomenon, two phytoplankton population models in natural waters are presented. In the first model, a nonlinear function general enough to include the effects of feeding saturation intraspecific consumer interference, and eutrophication phenomenon is used to present the transfer of material or energy from phytoplankton to zooplankton populations. The model using this grazing rate function is subjected to equilibrium and stability analysis to ascertain its mathematical implications. It is shown that, for a certain range of one of the parameters in this function all equilibrium points of the system become stable even with nutrient enrichment. In the second model, dynamics of both nitrogen and phosphorus cycles are combined. Persistence results for both models are proved and compared.

The influence of direct human control added to different aquatic models is studied in detail. Optimal control theory is used to obtain optimal strategies for the control of these models with several cost functions. It is found that the control program in each problem depends on the model considered and on the function to be optimized. Explicit expressions of singular control in each case are given as functions of the state and costate variables.

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CHAPTER I

ON THE ASYMPTOTIC BEHAVIOR OF SOLUTIONS OF LINEAR AND NONLINEAR SYSTEMS OF DIFFERENTIAL AND DIFFERENCE EQUATIONS

1.1. Introduction

Most of the studies that are published in the field of compartmental and environ analysis are limited to the linear, static case [II.9] .

In the applications area of ecology, all known studies are restricted to linear models. In this chapter, a generalization applicable to more advanced linear and nonlinear systems is presented and studied in detail. First, some results concerning the asymptotic behavior of the solutions of non-homogeneous linear systems of differential equations are reviewed. Then, the relationships between the boundedness and asymptotic behavior of the solutions of the linear differential equation

$$(1.1.1) \qquad \dot{X}(t) = A(t)\ X(t) + Z(t)$$

and of the solutions of the nonlinear equation

$$(1.1.2) \qquad \dot{X}(t) = A(t)\ X(t) + \Phi(X(t);\ t)$$

are explored in Theorems (1.2.1) to (1.2.4). In section 1.3, some results are derived for discrete time systems described by nonhomogeneous linear and nonlinear difference equations [Theorems (1.3.3) to (1.4.1)]. As will be demonstrated, there is a complete parallel to the corresponding results indicated in Section 1.2.

1.2. Dynamic Systems Described by Linear and Nonlinear Differential Equations

Asymptotic Behavior of the Solutions of Nonhomogeneous Differential Equations.

In the linear differential equation

$$(1.2.1) \qquad \dot{X}(t) = A(t)\, X(t) + Z(t)$$

$A(t)$ is an $n \times n$ matrix with complex-valued elements which are measurable and bounded for $t \geq 0$. $Z(t)$ is an n-vector with measurable, complex-valued elements, $\dot{X}(t)$ and $X(t)$ are n-vectors.

Notations and Assumptions

The norm of a vector (matrix) will be denoted by $||\cdot||$ and is defined as the sum of the magnitudes of the elements. A vector (matrix) will be called bounded if its norm is bounded on $t \geq 0$ and convergent if its elements tend to finite limits as $t \to \infty$. We shall denote by $\Phi(t)$ the (nonsingular) fundamental matrix of solutions of the homogeneous equations

$$(1.2.2) \qquad \dot{X}(t) = A(t)\, X(t)$$

for which

(1.2.3) $\Phi(0) = I$, the unit matrix.

Theorem 1.2.1 [T.F. Bridgland 1961]: Every solution of (1.2.1) converges for every convergent $Z(t)$ if and only if

(i) every solution of (1.2.1) is bounded for every bounded $Z(t)$

and

(ii) the matrix

$$W(t) = \int_0^t \Phi(t)\ \Phi^{-1}(\tau)\ d\tau$$

converges. Moreover,

$$\lim_{t\to\infty} X(t) = [\lim_{t\to\infty} W(t)]\ [\lim_{t\to\infty} Z(t)]\ .$$

Perturbed Flow Matrix

Theorem 1.2.2. [T.F. Bridgland 1961]: If every solution of (1.2.1) is convergent for every convergent $Z(t)$, if $D(t)$ is a matrix whose elements are measurable for $t \geq 0$ and if either

(a) $\lim_{t\to\infty} \|D(t)\| = 0$,

or

(b) $\int_0^\infty \|D(t)\|\ dt < \infty$

then every solution of

(1.2.4) $\dot{Y}(t) = [A(t) + D(t)]\ Y(t) + Z(t)$

converges for every convergent $Z(t)$. Moreover,

$$(1.2.5) \qquad \lim_{t\to\infty} Y(t) = \lim_{t\to\infty} X(t) .$$

Corollary 1.2.3. If in (1.2.4) $A(t) = A$, a constant matrix all of whose characteristic roots have negative real parts, then for every convergent $Z(t)$ every solution of (1.2.4) converges to the vector $-A^{-1} \lim_{t\to\infty} Z(t)$; moreover $\lim_{t\to\infty} Y(t) = 0$ when condition (a) is satisfied. (Note: In this case $\Phi(t)\Phi^{-1}(\tau) = \Phi(t - \tau)$.)

The relationship between the boundedness and asymptotic behavior of the solution of the linear and nonlinear differential equation is given in the following theorem.

Theorem 1.2.4. [T.F. Bridgland 1964]: Consider the nonlinear differential equation

$$(1.2.6) \qquad \dot{Y}(t) = A(t)\, Y(t) + \Phi(Y(t);\, t) \quad .$$

If

(i) every solution of (1.2.1) is convergent for every convergent $Z(t)$;

(ii) for sufficiently small $||Y||$, $\lim_{t\to\infty} \Phi(Y;\, t) = \Phi(Y;\, \infty)$;

(iii) for sufficiently small β , $||\Phi(0;\, t)|| \leq \beta$ for $t \geq 0$;

(iv) for $\varepsilon > 0$, there exists $\delta > 0$ and $T \geq 0$ such that

$$||\Phi(Y_1;\, t) - \Phi(Y_2;\, t)|| \leq \varepsilon ||Y_1 - Y_2|| \text{ for } ||Y_i|| \leq \delta ,$$

$$i = 1,\, 2 \text{ and } t \geq T ;$$

then for every vector c for which $\|c\|$ is sufficiently small a unique bounded solution $Y = Y(t; T, c)$ of (1.2.6), satisfying $Y(T; T, c) = c$, exists on $[T, \infty)$ and all such solutions converge to the same limit vector, ξ, which may be determined uniquely as a solution of the equation

$$(1.2.7) \quad \xi = X(\infty)\ \Phi(\xi; \infty) \quad .$$

1.3. Discrete Systems Described by Nonhomogeneous Linear and Nonlinear Difference Equations

Introductory Remarks

The problem generally considered in the modern theory of difference equations is the investigation of analytic solutions of equations of the form

$$(1.3.1) \quad X(k + 1) - X(k) = \Delta\ X(k) = A(k)\ X(k) + w(k)$$

where $\det(A(k) + I) \neq 0$ such that $\Phi^{-1}(k + 1)$ exists or

$$(1.3.2) \quad X(k + 1) - X(k) = \Delta\ X(k) = A(k)\ X(k) + f(X(k); k) \ .$$

where $\Phi(k)$ is the fundamental matrix of the corresponding homogeneous equations.

In this section the behavior of the solutions for large values of k and some relationships between the solutions of the two equations will be investigated. The results will be similar to those obtained for differential equations, and the proofs are simpler. If the elements of A depend on k, it will be supposed that they are defined for

for every k in the range $[0, \infty)$. A direct computation can be used to establish Lemma 1.3.1.

Lemma 1.3.1. The solution of

$$(1.3.1) \quad \Delta X = A(k)\ X(k) + w(k)$$

(where $(A(k) + I)$ is a nonsingular matrix for $k = 0, 1, 2, \ldots$) is given by

$$(1.3.3) \quad X(t) = Y(t) + \sum_{k=0}^{t-1} \Phi(t)\ \Phi^{-1}(k + 1)\ w(k)$$

where $Y(k)$ satisfies

$$(1.3.4) \quad \Delta\ Y(k) = A(k)\ Y(k)\ ; \quad Y(0) = X(0)$$

and $\Phi(k)$ satisfies

$$(1.3.5) \quad \Delta\ \Phi(k) = A(k)\ \Phi(k)\ ;\ \Phi(0) = I \quad .$$

Lemma 1.3.2: Let u be given by the expression,

$$(1.3.6) \quad u(t) = \sum_{\tau=0}^{t-1} \Phi(t + 1)\ \Phi^{-1}(\tau + 1)\ \omega(\tau)$$

$$= \sum_{\tau=0}^{t-1} K(t, \tau)\ \omega(\tau)\ , \quad t \geq 0 \quad ,$$

where K is defined by

$$(1.3.7) \quad K(t, \tau) = \Phi(t + 1)\, \Phi^{-1}(\tau + 1) .$$

If u is bounded as $t \to \infty$ for every input vector ω satisfying one of the conditions

(a) $\|\omega(\tau)\| \leq c_1 < \infty \qquad \tau \geq 0$

(b) $\sum_{\tau=0}^{\infty} \|\omega(\tau)\| < \infty$

or

(c) $\sum_{\tau=0}^{\infty} \|\omega(\tau)\|^2 < \infty$, then the matrix $K(t, \tau)$ satisfies respectively the conditions

(a') $\sum_{\tau=0}^{\infty} \|K(t, \tau)\| \leq c_2 < \infty$, c_2 independent of $t \geq 0$;

(b') $\|K(t, \tau)\| \leq c_3 < \infty$, c_3 independent of $t, \tau \geq 0$;

or

(c') $\sum_{\tau=0}^{\infty} \|K(t, \tau)\|^2 \leq c_4 < \infty$, c_4 independent of $t \geq 0$.

Here the proof will be given in case (a') ; similar proofs can be drived for the other two cases.

Proof of (a')

For fixed t define the linear transformation

$$\Lambda_t : \ell^\infty \to \mathbb{R}^n \quad , \quad \ell^\infty = \ell^\infty(\mathbb{R}^n)$$

where

$$\Lambda_t(\omega) = \sum_{\tau=0}^{t-1} K(t, \tau)\, \omega(\tau)$$

and since $u(t)$ is bounded for all $\|\omega\|_\infty = 1$, then

$$\|\Lambda_t\| = \sup_{\|\omega\|=1} \|\sum_{\tau=0}^{t-1} k(t, \tau)\ \omega(\tau)\| < \infty .$$

Thus, $\{\Lambda_t\}$ is a collection of bounded linear transformation from the Banach space ℓ^∞ into the normed linear space $\mathbb{R}^n$. The Banach Steinhaus Theorem [2] says that either there exists $M < \infty$ such that

(1) $\|\Lambda_t\| \leq M\ \forall t$

or

(2) $\sup_{t \geq 0} \|\Lambda_t(\omega)\| = \infty$

for some ω . Now, if (2) is true, then

$$\sup_{t \geq 0} \|\sum_{\tau=0}^{\infty} K(t, \tau)\ \omega(\tau)\| = \infty$$

or

$$\sup_{t \geq 0} \|u(t)\| = \infty \text{ for this } \omega .$$

But $\lim_{t \to \infty} \|u(t)\| < \infty$ by hypotheses. Hence (1) applies and

(1.3.10) $\|\Lambda_t\| \leq M\ \forall t$.

For a fixed t

(1.3.11) $\|\Lambda_t\| \leq \sum_{\tau=0}^{\infty} \|k(t, \tau)\|$

Now, choose $\omega(\tau)$ such that $\|\omega(\tau)\| = 1$ and

$$\left\| \sum_{\tau=0}^{\infty} K(t, \tau)\, \omega(\tau) \right\| = \sum_{\tau=0}^{\infty} \|K(t, \tau)\| \quad .$$

This choice of $\omega(\tau)$ is in the form

$$(1.3.12) \quad \omega(\tau) = \{\omega_i(\tau)\}_{i=1}^{n} = \{\pm 1\}_{i=1}^{n}$$

where

$$\max_i K(t, \tau)\, \omega(\tau) = \max_i \sum_{j=1}^{n} |k_{ij}(t, \tau)| \ \forall \tau$$

(e.g. if $n = 1$,

$$\omega(\tau) = 1 \ \text{ if } \ K(t, \tau) \geq 0$$

$$\omega(\tau) = -1 \ \text{ if } \ K(t, \tau) < 0 \ ) \quad .$$

It follows that

$$(1.3.13) \quad \|\Lambda_t\| \geq \sum_{\tau=0}^{\infty} \|K(t, \tau)\|$$

From inequalities (1.3.11) and (1.3.13), it follows that

$$\|\Lambda_t\| = \sum_{\tau=0}^{\infty} \|K(t, \tau)\| \leq M \ \forall (t) \ .$$

In case (b) $\Lambda_t: \ell^1 \to \mathbb{R}^n$

and

in case (c) $\Lambda_t: \ell^2 \to \mathbb{R}^n$.

Theorem 1.3.3. Every solution of

$$(1.3.1) \quad \Delta z = A(k)\ z(k) + w(k) \quad \text{with } (A(k) + I) \text{ nonsingular}$$

converges for every convergent $w(t)$ if and only if

(i) every solution of (1.3.1) is bounded for every bounded $w(k)$,

(ii) the matrix

$$Y(t) = \sum_{k=0}^{t} X(t + 1)\ X^{-1}(k + 1)$$

converges. Moreover,

$$\lim_{t\to\infty} z(t) = [\lim_{t\to\infty} Y(t)][\lim_{t\to\infty} w(t)] \ .$$

Proof: We prove first the sufficiency of (i) and (ii). As was indicated before, the solution of (1.3.1) for the initial condition $Z(0) = Y(0) = Z_0$ is

$$z(t) = y(t) + \sum_{k=0}^{t-1} X(t)\ X^{-1}(k + 1)\ w(k)$$

or

$$(1.3.14) \quad Z(t) = y(t) + \sum_{k=0}^{t-1} X(t)\, X^{-1}(k+1)\, e(k) + \sum_{k=0}^{t-1} X(t)\, X^{-1}(k+1) W$$

where we have put

$$\lim_{k\to\infty} w(k) = W$$

and

$$e(k) = w(k) - W \; .$$

In this part of the proof, it will be established that if every solution of (1.3.1) is bounded for every bounded $w(t)$ then

$$\sum_{k=0}^{t-1} \|X(t)\, X^{-1}(k+1)\| \leq M \qquad \forall\, t \geq 0$$

and

$$\lim_{t\to\infty} \|X(t)\| = 0 \; .$$

Let $w(t)$ satisfy $\|w(t)\| \leq C_1 < \infty \;\; \forall\, t \geq 0$; then Lemma 1.3.1 and the assumptions that $y(t) = X(t)\, z(0)$ and the vector, $u(t)$, given by (1.3.6), are bounded as $t \to \infty$ lead to

$$\sum_{k=0}^{t-1} \|X(t)\, X^{-1}(k+1)\| \leq M < \infty \quad \text{as} \quad t \to \infty \; .$$

To establish the asymptotic behavior of X , consider the vector $u(t)$ and the bounded solution of $\Delta X = AX$; this leads to

$$\sum_{k=0}^{t-1} X(t)\ X^{-1}(k + 1)\ X(k + 1) \text{ is bounded as } t \to \infty$$

or

$$X(t)\ (t - 1) \text{ is bounded as } t \to \infty .$$

Now for a given $\varepsilon > 0$ there exists $t_1 \geq 0$ such that for all $t > t_1$, $||e(t)|| < \frac{\varepsilon}{2M}$. From this and (1.3.14), it follows that

$$||\sum_{k=0}^{t-1} X(t)\ X^{-1}(k + 1)\ e(k)|| \leq ||X(t)|| \sum_{k=0}^{t_1-1} ||X^{-1}(k + 1)e(k)|| + \frac{\varepsilon}{2} .$$

Furthermore, there exists $t_2 \geq 0$ such that for $t > t_2$,

$$||X(t)|| < \frac{\varepsilon}{\sum_{k=0}^{t_1-1} ||X^{-1}(k + 1)\ e(k)||} .$$

Hence for $t > \max(t_1, t_2)$,

$$\sum_{k=0}^{t-1} ||X(t)\ X^{-1}(k + 1)\ e(k)|| < \frac{\varepsilon}{2} + \frac{\varepsilon}{2} = \varepsilon .$$

Thus the first two terms on the right side of (1.3.14) tend to zero as $t \to \infty$ and (ii) gives the conclusion.

The necessity of (ii) follows by setting $Y_0 = 0 = Z_0$ in (1.3.14) and replacing $w(t)$ (or in fact W) successively by the columns of the unit matrix. For the necessity of (i) we set $y_0 = 0$ in (1.3.14) and consider the $i^{\underline{th}}$ element of the solution vector

$$(1.3.15) \qquad Z_1(t) = \sum_{j=1}^{n} \sum_{k=0}^{t-1} x_{ij}(t;\, k+1)\, w_j(k) \ , \qquad 1 \leq i \leq n$$

where x_{ij} denotes the $i, j^{\underline{th}}$ element of the matrix $X(t)\, X^{-1}(k+1)$. The function space C of n-tuples $w(k) = (w_1(k), \ldots, w_n(k))$ of complex valued functions measurable for $k \geq 0$ and tending to finite limits as $k \to \infty$ is a Banach space under the norm

$$|w(k)| = \max_{1 \leq i \leq n} \{\sup_{k \geq 0} |w_i(k)|\} \ .$$

For a fixed $k_0 \geq 0$, the transformation $T^i_{k_0}$, defined by

$$T^i_{k_0}\, w(k) = z_i(k_0) = \sum_{j=1}^{n} \sum_{k=0}^{k_0-1} x_{ij}(k_0,\, k+1)\, w_j(k) \ ,$$

$$i = 1, \ldots, n \ ,$$

maps C into the Banach space of complex numbers normed by magnitudes. Simple estimates show that $T^i_{k_0}$ is bounded, hence continuous, on C . Using the vector $\xi_\lambda = (w_1^\lambda(k), \ldots, w_n^\lambda(k))$ where

$$w_i^\lambda(k) = \begin{cases} \operatorname{sgn} x_{ij}(k_0;\, k) \ , & 0 \leq k \leq \lambda \leq k_0 \\ \\ 0 & , \ k > \lambda > k_0 \ , \quad j = 1, \ldots, n \ . \end{cases}$$

where $(\operatorname{sgn} Z = \frac{\overline{Z}}{|Z|})$, we find that a bound of $T^i_{k_0}$ is

$$\sum_{j=1}^{n} \sum_{k=0}^{k_0-1} |x_{ij}(k_0, k+1)| .$$

Indeed, $|\xi_\lambda| = 1$, so that by (1.3.15)

$$\frac{|T^i_{k_0} \xi_\lambda|}{|\xi_\lambda|} = \frac{\sum_{j=0}^{n} \sum_{k=0}^{k_0-1} |x_{ij}(k_0; k+1)| \, |w^\lambda_i(k)|}{1}$$

$$= \sum_{j=1}^{n} \sum_{k=0}^{\lambda-1} |x_{ij}(k_0; k+1)| .$$

All the hypotheses of the Banach-Steinhaus Theorem [2] are fulfilled at this point so we may conclude that there exist $k_i \geq 0$ such that

(1) $\sup_{w \in C; k \geq 0} \{\frac{|T^i_k w(k)|}{|w|}\} = k_i < \infty$, $i = 1, \ldots, n$

or

(2) $\sup_{k \geq 0} \{|T^k_k w(i)|\} = \infty$ for some w .

If (2), then $\sup_{k \geq 0} \{|\sum_{j=1}^{n} \sum_{t=0}^{k-1} x_{ij}(k, t+1) w_j(t)|\} = \infty$, $i = 1, \ldots, n$

or $\sup_{k \geq 0} \|z_i(k)\| = \infty$ for this w . But $\lim_{k \to \infty} \|z(k)\| < \infty$ by hypotheses, hence (1) applies and it follows that

$$\sup_{k \geq 0} \{ \sum_{j=1}^{n} \sum_{k=0}^{t-1} |x_{ij}(t, k+1)|\} < \infty , \quad i = 1, \ldots, n .$$

Hence, that

$$\sup_{k \geq 0} \{ \sum_{k=0}^{t-1} \|X(t) X^{-1}(k+1)\|\} < \infty \quad . \tag{1.3.16}$$

This implies that $Z(t)$ is bounded for every bounded $w(t)$ and the proof is completed.

Theorem 1.3.4. If every solution of

$$(1.3.17)\quad \Delta X(k) = A(k)\,X(k) + w(k)$$

is convergent for every convergent $w(k)$, and if

$$\lim_{k\to\infty} \|D\| = 0 ,$$

then every solution of

$$(1.3.18)\quad \Delta\, y(k) = [A(k) + D(k)]\, y(k) + w(k)$$

converges for every convergent $w(k)$. Moreover,

$$\lim_{k\to\infty} y(k) = \lim_{k\to\infty} x(k) .$$

The proof of this theorem follows from theorem (1.3.1) if we can show that

(i) every solution of (1.3.18) is bounded for every bounded $w(k)$,

(ii) the matrix $Q(t) = \sum_{k=t_0}^{t-1} W(t)\, W^{-1}(k + 1)$ converges where $W(t)$ is the fundamental matrix of the homogeneous system corresponding to (1.3.18).

To prove (i), it suffices to show that there exists $M > 0$, $0 < \beta < 1$ such that

$$||W(t)\ W^{-1}(\tau)|| \le M\ \ \beta^{(t-\tau)}\ .$$

Let $\Phi(t)$ denote the fundamental matrix of the homogeneous system corresponding to (1.3.17). Then by lemma (1.3.1) the solution of the homogeneous system corresponding to (1.3.18) satisfies

$$W(t) = \Phi(t)\ \Phi^{-1}(t_0)\ W(t_0) + \sum_{k=t_0}^{t-1} \Phi(t)\ \Phi^{-1}(k+1)\ D(k)\ W(k)$$

or

$$(1.3.19)\quad W(t)\ W^{-1}(t_0) = \Phi(t)\cdot \Phi^{-1}(t_0) + $$

$$+ \sum_{k=t_0}^{t-1} [\Phi(t)\ \Phi^{-1}(k+1)\ D(k)\ W(k)]W^{-1}(t_0)\ .$$

By hypothesis, the homogeneous system corresponding to (1.3.17) is bounded for every bounded $w(t)$ so that there exists $M_1 > 0$ and $0 < \beta_1 < 1$, such that

$$(1.3.20)\quad ||\Phi(t)\ \Phi^{-1}(\tau)|| \le M_1\ \beta_1^{(t-\tau)}\ ,\quad t \ge \tau \ge 0\ .$$

Using these facts in conjunction with (1.3.19) we obtain the estimate

$$(1.3.21)\quad ||W(t)\ W^{-1}(t_0)|| \le M_1\ \beta_1^{(t-t_0)} +$$

$$+ \sum_{k=t_0}^{t-1} M_1\ \beta_1^{(t-k-1)}\ ||D(k)||||W(t)\ W^{-1}(t_0)||$$

or

$$\beta_1^{-(t-t_0)} \|W(t)\ W^{-1}(t_0)\|$$

$$\leq M_1 + \sum_{k=t_0}^{t-1} M_1\ \beta_1^{(t-k-1)} \|D(k)\|\,\|W(t)\ W^{-1}(t_0)\| .$$

But this implies, by virtue of Lemma 1 (ii) , [Bridgland, 1963],

$$(1.3.22)\quad \beta_1^{-(t-t_0)} \|W(t)\ W^{-1}(t_0)\| \leq M_1 \prod_{k=t_0}^{t-1} (1 + M\ \beta_1^{-1} \|D(k)\|) \quad .$$

Now, assume t_0 is sufficiently large that

$$\sup_{t\geq\tau\geq t_0} \|D(t)\| = C < \frac{\beta_1}{M_1} \quad .$$

Hence, (1.3.22) is reduced to

$$\beta_1^{-(t-t_0)} \|W(t)\ W^{-1}(t_0)\| \leq M_1 \prod_{k=t_0}^{t-1} (1 + \frac{M_1\ C}{\beta_1})$$

$$= M_1\ (1 + \frac{M_1\ C}{\beta_1})^{t-t_0}$$

$$\leq M(2)^{t-t_0} .$$

Thus,

$$(1.3.23)\quad \|W(t)\ W^{-1}(t_0)\| < M\ \beta^{(t-t_0)}\ ,\quad M = M_1\ ,\ \beta = 2\beta_1\ .$$

For the proof of (ii), consider the perturbed system with input $W(t) = I$;

$$(1.3.24)\quad \Delta z = [A(k) + D(k)]\ z(k) + I\ .$$

It is clear that the matrix

$$Q(t) = \sum_{k=0}^{t-1} W(t)\ W^{-1}(k+1)\ ,\quad Q(0) = 0\ ,$$

satisfies (1.3.24) . From lemma (1.3.1)

$$Q(t) = \sum_{k=0}^{t-1} W(t)\ W^{-1}(k+1) =$$

$$= \sum_{k=t_0}^{t-1} \Phi(t)\ \Phi^{-1}(k+1)\ D(k)\ Q(k)$$

$$+ \sum_{k=t_0}^{t-1} \Phi(t)\ \Phi^{-1}(k+1)\ .$$

The first term on the right side converges to zero. To see that this is true, (1.3.20) and (1.3.23) are utilized to obtain

$$\|Q(t)\| \leq \sum_{k=t_0}^{t-1} \|W(t)\ W^{-1}(k+1)\| \leq N\ .$$

Thus,

$$\left\| \sum_{k=t_0}^{t-1} \Phi(t)\ \Phi^{-1}(k+1)\ D(k)Q(k) \right\| \leq N \sum_{k=t_0}^{t-1} M_1\ \beta_1^{(t-t_0)} \|D(k)\|$$

$$= N\ M_1\ \beta_1^{(t-t_0)} \sum_{k=t_0}^{t-1} \|D(k)\|$$

which tends to zero as $t \to \infty$ by hypothesis. Hence

(1.3.25) $$\lim_{t\to\infty} Q(t) = \lim_{t\to\infty} \sum_{k=t_0}^{t-1} \Phi(t)\ \Phi^{-1}(k+1)$$

which is convergent. Thus, the result follows from (1.3.23) and (1.3.25).

1.4. Asymptotic Behavior of the Solutions of Non-Linear Systems of Difference Equations

In this section the significance of the relationship between the boundedness and asymptotic behavior of the solutions of the linear equations

(1.4.1) $$\Delta z = A(t)z(t) + \Phi(t)$$

and the solutions of the nonlinear equation

(1.4.2) $$\Delta z = A(t)z(t) + f(z(t);\ t)$$

is investigated.

In (1.4.1) and (1.4.2), it is required that the $n \times n$ matrix $A(t)$ has elements which are real-valued, continuous and bounded for $t \to 0$ while $\Phi(t)$ and $f(z; t)$ are n-vectors with f having elements which are real valued and continuous for all $t \geq 0$ and all $z \in V$, where V is some neighborhood of $z = 0$ in the space of n-tuples of real numbers. Norms of vectors and matrices are denoted by $\|\cdot\|$ and defined as the sum of the absolute values of the components.

Theorem 1.4.1. If

(i) every solution of (1.4.1) is convergent for every convergent $\phi(t)$;

(ii) for sufficiently small $\|z\|$, $\lim_{t\to\infty} f(z; t) = f(z; \infty)$ exists;

(iii) for sufficiently small β, $\|f(0; t)\| \leq \beta$ for $t \geq 0$;

(iv) for $\frac{1}{M} > \varepsilon > 0$, there exists $\delta > 0$ and $T \geq 0$ such that

$$\|f(z_1; t) - f(z_2; t)\| \leq \varepsilon\|z_1 - z_2\| \quad \text{for} \quad \|z_i\| \leq \delta ,$$

$$i = 1, 2 \quad \text{and} \quad t \geq T ,$$

then for every vector c for which $\|c\| = \|z_0\|$ is sufficiently small a unique bounded solution $z = z(t; T, c)$ of (1.4.2) satisfying $z(T; T, c) = c$ exists on $[T, \infty)$ and all such solutions converge to the same limit vector ξ which may be determined uniquely as a solution of the equation $\xi = Y(\infty)\ \Phi(\xi; \infty)$.

Proof. In Theorem 1.3.3 and Lemma 1.3.2, it is shown that (i) implies the following:

(i') there exists $M > 0$ such that

$$\sum_{\tau=0}^{t-1} \|X(t)\ X^{-1}(\tau + 1)\| < M \quad \forall t \geq 0 ;$$

(ii') $\lim_{t\to\infty} \|Y(t)\| = \lim_{t\to\infty} \sum_{\tau=0}^{t-1} \|X(t)\ X^{-1}(\tau + 1)\|$ exists (as a matrix with finite elements).

The solution of (1.4.2) satisfies

$$z(t) = y(t) + \sum_{\tau=T}^{t-1} X(\tau)\ X^{-1}(\tau + 1)\ f(z(\tau);\ \tau) \ . \tag{1.4.3}$$

It is now shown that $\|z(t)\|$ is bounded for all t.

From (1.4.3)

$$\|z(t)\| \leq \|X(t)\ X^{-1}(T)\|\ \|z(T)\|$$

$$+ \left| \sum_{\tau=T}^{t-1} X(t)\ X^{-1}(\tau + 1)(f(z(\tau);\ \tau) - f(0,\ \tau) + f(0,\ \tau)) \right|$$

$$\leq K\|c\| + \varepsilon\ M \max_{T\leq\tau\leq t} \|z(\tau)\| + M\beta \ .$$

Thus,

$$\max_{T\leq\tau\leq t} \|z(\tau)\| \leq K\|c\| + \varepsilon\ M \max_{T\leq\varepsilon\leq t} \|z(\tau)\| + M\beta$$

or

$$\max_{T \leq \tau \leq t} \|z(\tau)\| \leq \frac{K\|c\| + M\beta}{1 - \varepsilon M}$$

which implies that $\|z(\tau)\|$ is bounded uniformly for $1 - \varepsilon M > 0$ (i.e., $0 < \varepsilon < \frac{1}{M}$) . Let $\lim_{t \to \infty} f(z; t) = F(z)$, $\|z\| \leq \delta$;

$$e(z, t) = f(z; t) - F(z) .$$

Thus,

$$z(t) = y(t) + \sum_{\tau=T}^{t=1} X(t)\, X^{-1}(\tau + 1)\, e(z, t)$$

$$+ \sum_{\tau=T}^{t-1} X(t)\, X^{-1}(\tau + 1)\, F(z) .$$

Next, it will be shown that $\lim_{t \to \infty} \|X(t)\| = 0$. First, it is observed that every solution of (1.4.1) is convergent for every convergent $\Phi(t)$ implies that

$$\sum_{\tau=0}^{t-1} \|X(t)\, X^{-1}(\tau + 1)\| < M < \infty \quad \text{for all} \quad t \geq 0 ,$$

and

$$u(t) = \sum_{\tau=0}^{t-1} X(t + 1)\, X^{-1}(\tau + 1)\phi(\tau)$$

is bounded for every vector satisfying $\|\Phi(\tau)\| \leq c_1 < \infty$. Since every solution of $\Delta X = AX$ is bounded as $t \to \infty$, it follows that $\sum_{\tau=0}^{t-1} X(t)\ X^{-1}(\tau + 1)\ X(\tau + 1)$ is bounded as $t \to \infty$ or $\|X(t)\|$ tends to zero as $t \to \infty$.

Now for a given $\varepsilon > 0$, there exist $t_1 \geq 0$ such that for all $t > t_1$, $\|z\| \leq \delta$ we have

$$\| e(z,\ t) \| < \frac{\varepsilon}{2M} .$$

Thus

$$\begin{aligned} &\| \sum_{\tau=t}^{t-1} X(t)\ X^{-1}(\tau + 1)\ e(z(\tau);\ \tau) \| \\ &\qquad \leq \| \sum_{\tau=T}^{t_1-1} X(t)\ X^{-1}(\tau + 1)\ e(z(\tau);\ \tau) \| \\ &\qquad + \| \sum_{\tau=t_1}^{t-1} X(t)\ X^{-1}(\tau + 1)\ e(z(\tau);\ \tau) \| \\ &\qquad \leq \|X(t)\|\ \| \sum_{\tau=T}^{t_1-1} X^{-1}(\tau + 1)\ e(z(\tau);\ \tau) \| + \frac{\varepsilon}{2} . \end{aligned}$$

Furthermore, there exists $t_2 \geq 0$ such that for all $t > t_2$

$$\|X(t)\| < \frac{\varepsilon}{\sum_{\tau=t}^{t_1-1} \|X^{-1}(\tau + 1) e(z(\tau);\ \tau)\|.}$$

For $t > \max(t_1,\ t_2)$, it follows that

$$\left\| \sum_{\tau=T}^{t-1} X(t)\ X^{-1}(\tau + 1)\ e(z(\tau);\ \tau) \right\| < \frac{\varepsilon}{2} + \frac{\varepsilon}{2} = \varepsilon\ .$$

This implies that the solution of (1.4.2) converges.

CHAPTER II

INPUT-OUTPUT ANALYSIS IN ECOLOGICAL SYSTEMS

2.1 Introduction

Input-output analysis for applications in economics was introduced by Leontief [6] to investigate the supply-and-demand problem: that is: What are the direct and indirect requirements of raw material goods and services to produce a unit of finished product from some sector of the economy? The interdependence among the different sectors of the given system was described by a set of linear equations where the specific structural characteristics were reflected in the numerical magnitudes of the coefficients of these equations. Given a demand vector, he was able to solve the equations for the output of each industry.

Hannon [3] applied economic input-output analyses to ecological energy systems in a effort to define the structure of these systems. He concluded that it is possible, given the condition of linearity on the distribution of production energy flows, to determine the total energy flows which directly and indirectly connect an ecosystem component to the remainder of the ecosystem. If carbon flows (or any element) are proportional to the direct energy flows, then a component's direct and indirect connections to the rest of the ecosystem can be expressed in terms of carbon flows.

With additional information on the relationship between production and respiration energy for each component and on the sensitivity of the distribution of a component's output, the system equations can be perturbed to determine the system response. The system effects of air or water pollution or of small exports could be estimated.

Finn [2] introduced several measures of ecosystem structure and function by the application of economic input-output analysis to ecosystem compartment models. He defined total system through flow (TST) as the sum of all compartmental through flows. Average path length of the $i^{\underline{th}}$ inflow (APL_i) is defined as the average number of compartments through which the $i^{\underline{th}}$ inflow passes. Average path length for an average inflow ($\overline{APL}$) is the mean of APL weighted according to size of the inflows. TST can be partitioned into a portion due to cycled flow (TST_c) and a portion due to flow straight through the system (TST_S). The portion of $\overline{APL}$ due to cycled flow divided by the portion due to straight throughflow is the cycling index (CI). Comparisons of cycling indices between different ecosystems under various environmental stresses could help answer questions about stability and structural differences between systems. The other measures, TST , APL_i , $\overline{APL}$, could be used to study a single ecosystem under various stresses, or to study models with the same number of compartments. The deterministic methodologies of Hannon and Finn were designed to analyze empirical flows. They made no assumptions about the type of flow kinetics in a system.

Patten [9] defined the environ concept and developed an input-output environ analysis for linear compartmental systems, restricted to the stationary case. His motivation was to partition compartment storages, as well as flows, according to their input origins and output destinations.

Hippe [4] studied some linear input-output models with variable input vectors and he gave examples using step and periodic inputs.

In the following sections, generalizations of the concept of environ analysis to linear and nonlinear input-output systems with and without time delay are given. In addition, some old theorems are corrected and new ones are proved (Theorems 2.2.2-2.2.4). The question raised by *Patten-Hippe* about the existence of the coefficient matrix $A'(t)$ in the reversed system

$$(2.1.1) \qquad \dot{X}(t) = -A'(t)\ X(t) - Y(t)$$

is answered.

2.2. Basic Definitions and Notations

A compartment system is a system which is composed of a finite number of macroscopic subsystems (compartments) each of which is homogeneous and interacts with the other compartments by exchanging biomass, energy, chemical materials, etc. The system is said to be *closed* if there are no exchanges with the environment, otherwise it is an *open* system.

Compartmental analysis has three main levels of applications.

(i) The development of a mathematical model for any biological or ecological system (c.f. Chapter 3);

(ii) The development of the analytic theory of such a system (c.f. Chapter 3);

(iii) The determination of what data should be collected and methods of applying different inputs to get desired responses from the system (c.f. Chapter 4).

The box in Figure (2.1) represents the $i^{\underline{th}}$ compartment in a compartmental system. The symbol f_{i0} is the inflow from environment to the $i^{\underline{th}}$ compartment. f_{0i} is the loss to environment from the $i^{\underline{th}}$ compartment. f_{ji} is the intercompartmental flow from i to j .

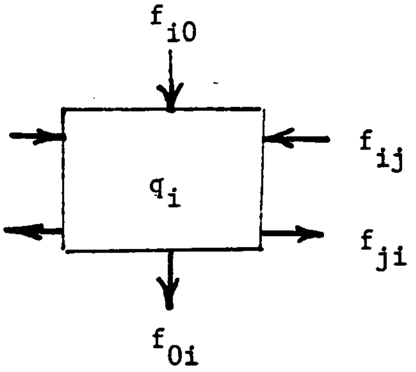


Figure 2.1
Diagramatic Representation of a Compartment

Regularity Assumptions

(i) f_{ij} $(i, j = 0, 1, \ldots, n)$, $i \neq j$ are nonnegative.

(ii) $$f_{ii} = -\left[f_{0i} + \sum_{\substack{j=1 \\ j\neq i}}^{n} f_{ji}\right] ;$$

(iii) $f_{i0} \neq 0$ or $f_{0i} \neq 0$ or both for at least one compartment (i.e., the system is open);

(iv) The model is connected (i.e., no compartment or a group of compartments is isolated from the others).

The above regularity assumptions lead to the following:

(i) The flow matrix, F , is diagonally dominant $(|f_{ii}| \geq \sum_{\substack{j=1 \\ j\neq i}}^{n} f_{ji})$;

(ii) The matrix F^{-1} exists because of the connectedness and diagonal dominance assumptions.

2.3. Environ Analysis

Environ analysis is concerned with partitioning compartment storages and flows into components associated with particular system outputs and inputs. Output environ analysis addresses the question "What will one unit of initial storage and a unit of input flow cause in the ecosystem?" Input environ analysis focusses upon the question "What partitions of inputs and initial storages and the corresponding flows add up to one unit of output flow?" Each component in the system has both an input and output environ. The set of input environs of all components forms a partition of the system storages and flows. Another partition of the same system can be formed by the set of output environs. Environ models can be classified into several types as shown in Table (2.1).

Continuous Dynamic Models

The dynamics of a compartmental model as given in Figure 2.2.

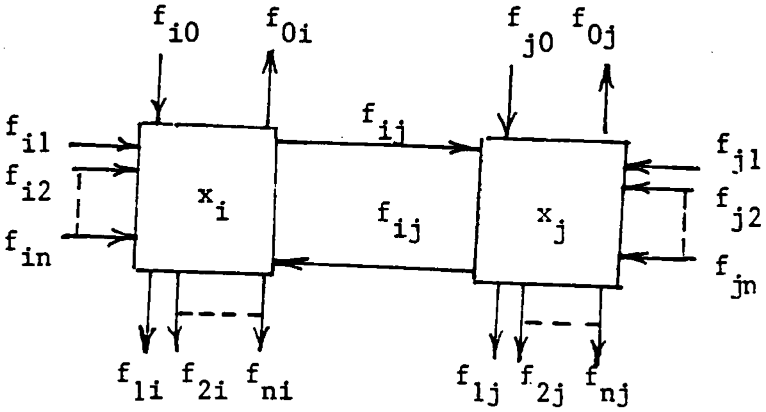
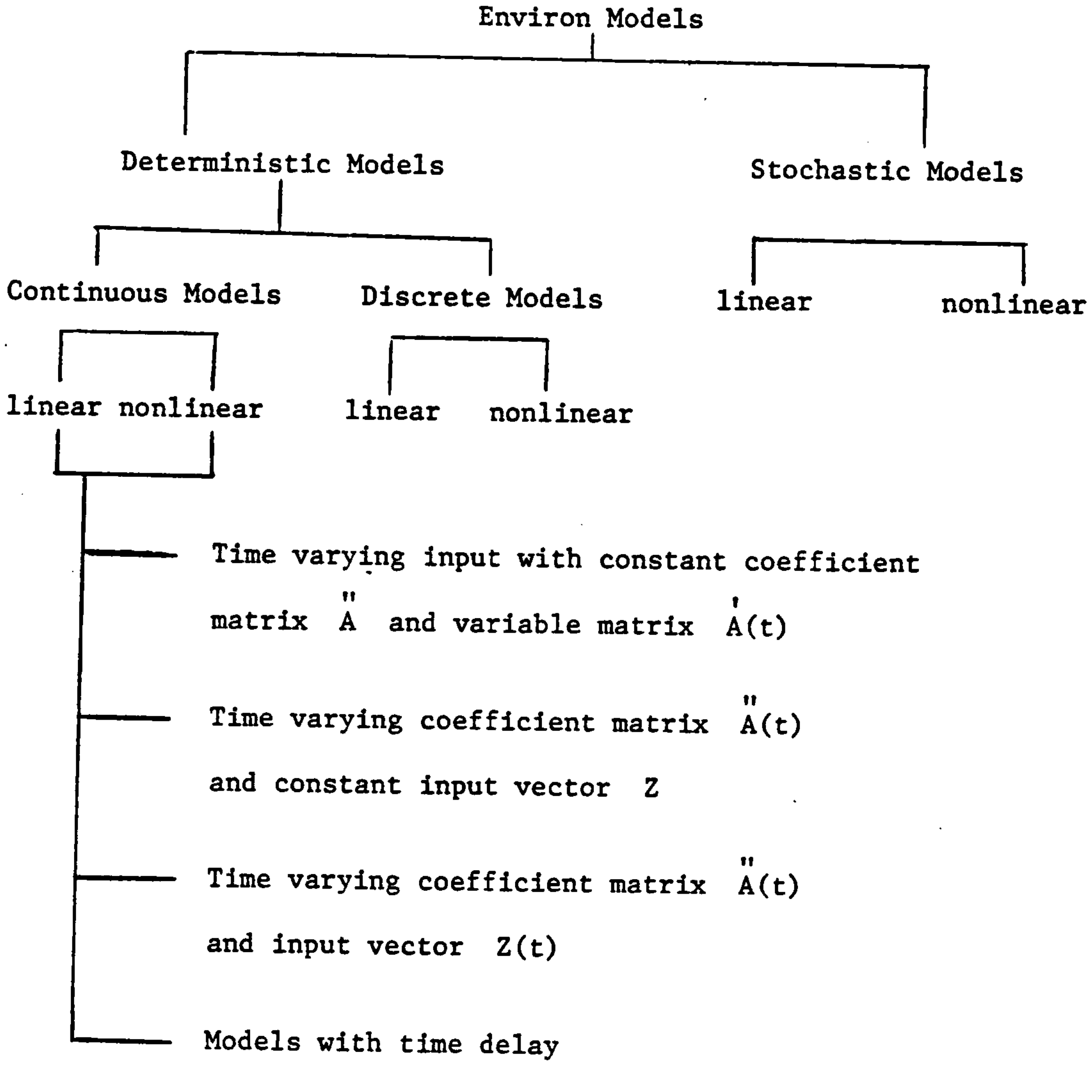


Figure 2.2

Schematic diagram of a general compartmental model

Table 2.1

CLASSIFICATION OF ENVIRON MODELS



can be described by a system of differential equations when a continuous model seems appropriate or a system of difference equations when a discrete model is useful. The continuous model can be formulated as

$$(2.3.1) \qquad \dot{x}_i(t) = [f_{i0}(t) + \sum_{\substack{j=1 \\ j \neq i}}^{n} f_{ij}(t)] - [f_{0i}(t) + \sum_{\substack{j=1 \\ j \neq i}}^{m} f_{ji}(t)]$$

$$(i = 1, 2, \ldots, n)$$

(i.e., the rate of change of the storage in the i component equals the difference between the total input and total output flows at any instant of time). For a discrete model, we have

$$(2.3.2) \qquad x_i(t + 1) - x_i(t) = [f_{i0}(t) + \sum_{\substack{j=1 \\ j \neq i}}^{n} f_{ij}(t)]$$

$$- [f_{0i}(t) + \sum_{\substack{j=1 \\ j \neq i}}^{n} f_{ji}(t)]$$

$$(i = 1, 2, \ldots, n) \; .$$

As we proved in the first chapter, the asymptotic behavior of the solutions of (2.3.2) is similar to that of the solutions of (2.3.1) in the linear and nonlinear cases in certain instances so here only the system of differential equations is considered. In equation (2.3.1)

$\dot{x}_i(t)$ is the rate of change of substances in i .

$f_{ij}(t)$ is the time dependent nonnegative flow from j to i (mass/time) .

$f_{i0}(t)$ is the environmental input to i (mass/time) ;

$f_{0i}(t)$ is the environmental output from i (mass/time);

and

n is the total number of compartments in the system.

Alternative Representations of Continuous Environ Models

Continuous environ models can be represented either in terms of the input flow (Equation 2.3.3) or the output flow (Equation 2.3.4) into and from the various compartments

$$\dot{x}_i(t) = f_{i0}(t) + \sum_{j=1}^{n} f_{ij}(t) \tag{2.3.3}$$

$$\dot{x}_i(t) = -f_{0i}(t) - \sum_{j=1}^{n} f_{ji}(t) \ . \tag{2.3.4}$$

The diagonal elements $f_{ii}(t)$ in (2.3.3) and (2.3.4) are given by

$$f_{ii}(t) = - \sum_{\substack{j=0 \\ j\neq i}}^{n} f_{ji}(t) \tag{2.3.5}$$

and

$$f_{ii}(t) = - \sum_{\substack{j=0 \\ j\neq i}}^{n} f_{ij}(t) \tag{2.3.6}$$

respectively. The matrix forms of equations (2.3.3) and (2.3.4) are

$$\dot{X}(t) = \ddot{F}(t).1 + z(t) \tag{2.3.7}$$

and

$$(2.3.8) \qquad \dot{X}(t) = -\overset{\prime}{F}(t).1 - y(t)$$

respectively, where

$$\dot{X}(t) = (x_1(t), \dots, x_n(t))^T ,$$

$$z(t) = (f_{10}(t), \dots, f_{n0}(t))^T ,$$

$$y(t) = (f_{01}(t), \dots, f_{0n}(t))^T ,$$

$$1 = (1, \dots, 1)^T$$

and the flow matrices, $\overset{\prime\prime}{F}(t)$ and $\overset{\prime}{F}(t)$ are given by

$$\overset{\prime\prime}{F}(t) = (f_{ij}(t)) \ , \quad f_{ii}(t) = -\sum_{\substack{j=0 \\ j\neq i}}^{n} f_{ji}(t)$$

and

$$\overset{\prime}{F}(t) = (f_{ij}(t)) \ , \quad f_{ii}(t) = -\sum_{\substack{j=0 \\ j\neq i}}^{n} f_{ij}(t) \ .$$

Lemma 2.3.1. At steady state, the flow matrices are related by $\overset{\prime\prime}{F}(t) = (\overset{\prime}{F})^T$.

Proof. At steady state, $\dot{X}(t) = 0$, the output and input flow equations are given by

$$(2.3.9) \qquad [f_{i0} + f_{ii} + \sum_{\substack{j=1 \\ j\neq i}}^{n} f_{ij}] = 0 = -[f_{0i} + f_{ii} + \sum_{\substack{j=1 \\ j\neq i}}^{n} f_{ji}] \ .$$

Thus,

$$(2.3.10)\qquad f_{ii} = -\sum_{\substack{j=0\\ j\neq i}}^{n} f_{ij} = -\sum_{\substack{j=0\\ j\neq i}}^{n} f_{ji}$$

and the result follows from the definitions of $\overset{''}{F}$ and $\overset{'}{F}$. The normal parameterization is achieved by making each flow a function of its donor compartment, $f_{ij} = \overset{''}{a}_{ij}\, x_j$:

$$(2.3.12)\qquad \dot{x}_i = z_i + \sum_{\substack{j=1\\ j\neq i}}^{n} \overset{''}{a}_{ij}\, x_j - \sum_{\substack{j=0\\ j\neq i}}^{n} \overset{''}{a}_{ji}\, x_i$$

$$= z_i + \sum_{j=1}^{n} \overset{''}{a}_{ij}\, x_j \, , \quad i = 1,\ldots, n \, ,$$

or in matrix notation

$$(2.3.13)\qquad \dot{X} = \overset{''}{A}\, X + Z \, .$$

An alternative linear parameterization is obtained by representing each flow as a function of its recipient compartment, $f_{ij} = \overset{'}{a}_{ij}\, x_i$:

$$(2.3.14)\qquad \dot{x}_i = \sum_{\substack{j=0\\ j\neq i}}^{n} \overset{'}{a}_{ij}\, x_i - \sum_{\substack{j=1\\ j\neq i}}^{n} \overset{'}{a}_{ji}\, x_j - y_i$$

$$= - \sum_{j=1}^{n} \overset{'}{a}_{ji}\, x_i - y_i \, , \quad i = 1,\ldots, n \, ,$$

or in matrix notation

(2.3.15) $$\dot{X} = -\overset{\prime}{A}^{T} X - y \ .$$

In the following lemma, the relations between the two matrices $\overset{\prime\prime}{A}(t)$ and $\overset{\prime\prime}{F}(t)$ or $\overset{\prime}{A}(t)$ and $\overset{\prime}{F}(t)$ are given and proved.

Lemma 2.3.2. In Equations (2.3.13) and (2.3.15), the matrices $\overset{\prime\prime}{A}(t)$ and $\overset{\prime}{A}(t)$ are given by

(2.3.16) $$\overset{\prime\prime}{A}(t) = \overset{\prime\prime}{F}(t) \ [D_{X(t)}]^{-1}$$

and

(2.3.17) $$[\overset{\prime}{A}(t)]^{T} = \overset{\prime}{F}(t)[D_{X(t)}]^{-1}$$

where

(2.3.18) $$D_{X(t)} = \mathrm{diag}(x_1(t),\ldots, x_n(t)) \ .$$

Proof. Comparison of Equations (2.3.7) and (2.3.13) yields

(2.3.19) $$\overset{\prime\prime}{F}(t)(1 \ \ldots \ 1)^{T} = \overset{\prime\prime}{A}(t) \ D_{X(t)}(1 \ \ldots \ 1)^{T} \ .$$

Thus,

$$\overset{\prime\prime}{F}(t) = \overset{\prime\prime}{A}(t) \ D_{X(t)} \ .$$

Similarly $\overset{\prime}{F}(t) = [\overset{\prime}{A}(t)]^{T} D_{X(t)}$.

Corollary 2.3.3. At steady state, the matrix $\overset{\prime}{A}$ is given by

$$(2.3.20) \qquad \overset{\prime}{A} = (D_{X*})^{-1} \overset{\prime\prime}{F}$$

where $X* = (x_1^*, \ldots, x_n^*)^T$ is the steady state storage vector.

In the following section, input-output environ partitions will be defined and derived for time invariant and time dependent linear systems. The results obtained there are examined by a counter example in each case.

2.4. Input-Output Environ Analysis for Linear Systems

Time-Invariant Linear Systems

In this section a linear system with constant coefficients matrices $\overset{\prime\prime}{A}$, $\overset{\prime}{A}$, a constant input vector, z , and a constant output vector, y , is considered. At steady state $(\dot{X} = 0)$, the equations (2.3.14) and (2.3.15) are reduced to

$$(2.4.1) \qquad \overset{\prime\prime}{A}\, X* + z = 0$$

and

$$(2.4.2) \qquad [\overset{\prime}{A}]^T\, X* + y = 0$$

which result in

$$(2.4.3) \qquad X* = -\overset{\prime\prime}{A}^{-1}\, z = -[\overset{\prime}{A}^{-1}]^T\, y$$

where X^* is the steady state storage vector. The matrices $-(\overset{''}{A})^{-1}$ and $-(\overset{'}{A})^T$ apportion system inputs z and outputs y into steady state storages X^* .

Before proceeding any further, some terminology associated with certain matrices important for the subsequent development will be introduced.

The <u>output environ flow matrix</u>, $\overset{''}{E}_i$, describes the output flows associated with a continuous unit input to i .

The <u>output environ storage vector</u>, $\overset{''}{e}_i$, gives the storages in different compartments associated with a continuous unit input to i .

The <u>output environ storage matrix</u>, $\overset{''}{\mathcal{E}}$, is the matrix whose columns are the output environ storage vectors.

The <u>input environ flow matrix</u>, $\overset{'}{E}_j$, the input environ storage vector, $\overset{'}{e}_j$, and the input environ storage matrix, $\overset{'}{\mathcal{E}}$, are defined in a similar way.

The element $\overset{''}{e}_{uv,i}$, of the matrix $\overset{''}{E}_i$, denotes the flow from v to u due to a unit input at i $(u, v = 1,\dots, n ; u \neq v)$.

The element, $\overset{'}{e}_{uv,j}$, of the matrix, $\overset{'}{E}_j$, denotes the flow from v to u that results in a unit output at j $(u, v = 1,\dots, n ; u \neq v)$.

$\overset{''}{e}_{uu,i} = - \sum_{\substack{k=0 \\ k\neq u}}^{n} e_{ku,i}$ is the outflow from u generated by a unit input at i (-the column sum in $\overset{''}{E}_i$) .

$\overset{'}{e}_{vv,i} = - \sum_{\substack{k=0 \\ k\neq v}}^{n} e_{vk,j}$ is the inflow to v that results in a unit output at j (-the row sum in $\overset{'}{E}_j$) .

From the above notation, it follows that at steady state

(2.4.4) $$X^* = \sum_i z_i \overset{\prime\prime}{e}_i = \sum_j y_j \overset{\prime}{e}_j \ ,$$

(2.4.5) $$\overset{\prime\prime}{F} = \sum_i z_i \overset{\prime\prime}{E}_i \ ,$$

and

(2.4.6) $$\overset{\prime}{F} = \sum_j y_i \overset{\prime}{E}_j \ .$$

The following theorem gives canonical formulations based on flows for the different environ matrices and vectors.

<u>Theorem</u> 2.4.1. The output and input environs for a deterministic model at equilibrium with time-invariant inputs and coefficient matrices are given by

(i) $$\overset{\prime\prime}{E}_i = \overset{\prime\prime}{F} D_{f^{\cdot i}} \ , \quad (i = 1, 2, \ldots, n)$$

$$\overset{\prime}{E}_j = \overset{\prime\prime}{F}{}^T D_{f^{\cdot j}} \ , \quad (i = 1, 2, \ldots, n)$$

(ii) $$\overset{\prime\prime}{\mathcal{E}} = -D_{X^*} \overset{\prime\prime}{F}{}^{-1}$$
$$\overset{\prime}{\mathcal{E}} = -D_{X^*} (\overset{\prime\prime}{F}{}^T)^{-1}$$

where

$$-(\overset{\prime\prime}{F})^{-1} = \left(f^{\cdot 1} \,\middle|\, --- \,\middle|\, f^{\cdot n} \right) = \begin{pmatrix} f^{1\cdot} \\ \hline \vdots \\ \hline f^{n\cdot} \end{pmatrix}$$

Proof: To verify (ii), consider the equations

(2.4.7) $$X^* = -\overset{\prime\prime}{A}{}^{-1}\ z = -(\overset{\prime}{A}{}^{T})^{-1}\ y$$

and

(2.4.8) $$X^* = \sum_i z_i\ \overset{\prime\prime}{e}_i = \sum_j y_j\ \overset{\prime}{e}_j\ , \quad i,\ j = 1,\ 2, \ldots,\ n$$

which are true for any input vector z (output vector y) . Thus, for the special case with

(2.4.9) $$z = (0\ \ldots\ \underset{\substack{\uparrow \\ i}}{1}\ \ldots\ 0)^T \qquad (y = (0\ \ldots\ \underset{\substack{\uparrow \\ j}}{1}\ \ldots\ 0)^T)$$

the steady state storage vector is

(2.4.10) $$X^* = -\overset{\prime\prime}{A}{}^{-1}(0\ \ldots\ \underset{\substack{\uparrow \\ i}}{1}\ \ldots\ 0)^T = \sum_k z_k\ \overset{\prime\prime}{e}_k = \overset{\prime\prime}{e}_i$$

or

((2.4.11) $$X^* = -(\overset{\prime}{A}{}^{T})^{-1}(0\ \ldots\ \underset{\substack{\uparrow \\ j}}{1}\ \ldots\ 0)^T = \sum_k y_k\ \overset{\prime}{e}_k = \overset{\prime}{e}_j\ .$$

Hence the output (input) environ vectors $\overset{\prime\prime}{e}_i$ $(\overset{\prime}{e}_j)$ are given by

(2.4.12) $$\overset{\prime\prime}{e}_i = -(\overset{\prime\prime}{F}\ D_{X^*})^{-1}(0\ \ldots\ \underset{\substack{\uparrow \\ i}}{1}\ \ldots\ 0)$$

which is the $i^{\underline{th}}$ column of $(-D_{X*}\overset{\prime\prime}{F}^{-1})$. Similarly,

(2.4.13) $\overset{\prime}{e}_i$ is the $j^{\underline{th}}$ column of $(-D_{X*}(\overset{\prime\prime}{F}^{-1})^T)$.

Thus the output and input storage matrices are

(2.4.14) $$\overset{\prime\prime}{E} = -D_{X*}\overset{\prime\prime}{F}^{-1}$$

and

(2.4.15) $$\overset{\prime}{E} = -D_{X*}(\overset{\prime\prime}{F}^{-1})^T$$

respectively.

To establish (i), an analogous procedure as employed above shows that the output and input environ flow matrices are

(2.4.16) $$\overset{\prime\prime}{E}_i = \overset{\prime\prime}{A} D_{ei} = \overset{\prime\prime}{F} D_{X*}^{-1} D_{(D_{X*} f^{\cdot i})} = \overset{\prime\prime}{F} D_{f^{\cdot i}}$$

and

(2.4.17) $$\overset{\prime}{E}_j = \overset{\prime}{A} D_{e_j} = \overset{\prime}{F} D_{X*}^{-1} D_{(D_{X*} f^{j\cdot})} = \overset{\prime\prime}{F}^T D_{f^{j\cdot}}$$

respectively.

From Theorem 2.3.4, it is clear the the environs are determined directly from the flow matrix $\overset{\prime\prime}{F}$ or from the coefficient matrices $\overset{\prime\prime}{A}$ and $\overset{\prime}{A}$. However, from the perspective of numerical accuracy the first set of identities appears more useful, especially if the elements of F'' are of the same order of magnitude.

Summary and Results

Each element of E_i'' represents the flow from the column compartment to the corresponding row compartment generated by one unit of input to compartment i. Each entry of E_i' gives the flow from column to row compartment required to generate one unit of output from compartment i. The diagonal elements of E_i'' represent total outflow from the corresponding column compartment. Therefore, the column sum of E_i'', represents differences between total outflows and outflows to compartments, denote outputs generated to the system environment per unit of input z_i. Similarly, the row sum of E_i' represents inputs to the system environment per unit of output y_i. Some other useful information [Patten and Matis 1979] such as the number of transfers between compartments, the entry and exit probabilities, the future and past residence times in the system or any specific subsystem can be obtained using the matrices A'', A', E_i'' and E_i'.

Example 2.4.1. The following example is a four compartment water budget model presented by Patten [9]. It is a static water balance model constructed for the Okefenokee Swamp watershed and decomposed into partition units by input-output environs analysis. The compartments are:

x_1^* = upland surface storage,

x_2^* = upland ground storage,

x_3^* = swamp surface storage,

and

x_4^* = swamp subsurface storage.

The inputs are:

z_1 = upland precipitation,

and

z_3 = swamp precipitation.

The outputs are:

y_i^1 = evapotranspirations, $i = 1, \ldots, 4$,
y_2^2 = deep storage,
y_3^3 = sheet and stream flow,
y_4^2 = percolation, deep seepage and lateral leakage,

and

y_4^3 = baseflow.

The intrasystem flows are:

f_{21} = infiltration and percolation,
f_{31} = channel and overland flow,
f_{12} = baseflow and interflow,
f_{32} = baseflow,
f_{42} = lateral seepage,
f_{43} = infiltration and percolation,

and

f_{34} = upwelling and water level rise.

State units are $10^9 m^3$, and input, output and internal flow units are $10^9\ m^3 y^{-1}$. Figures 2.3, 2.4, and 2.5 give a schematic diagram, output environs, and input environs, respectively, of the above example.

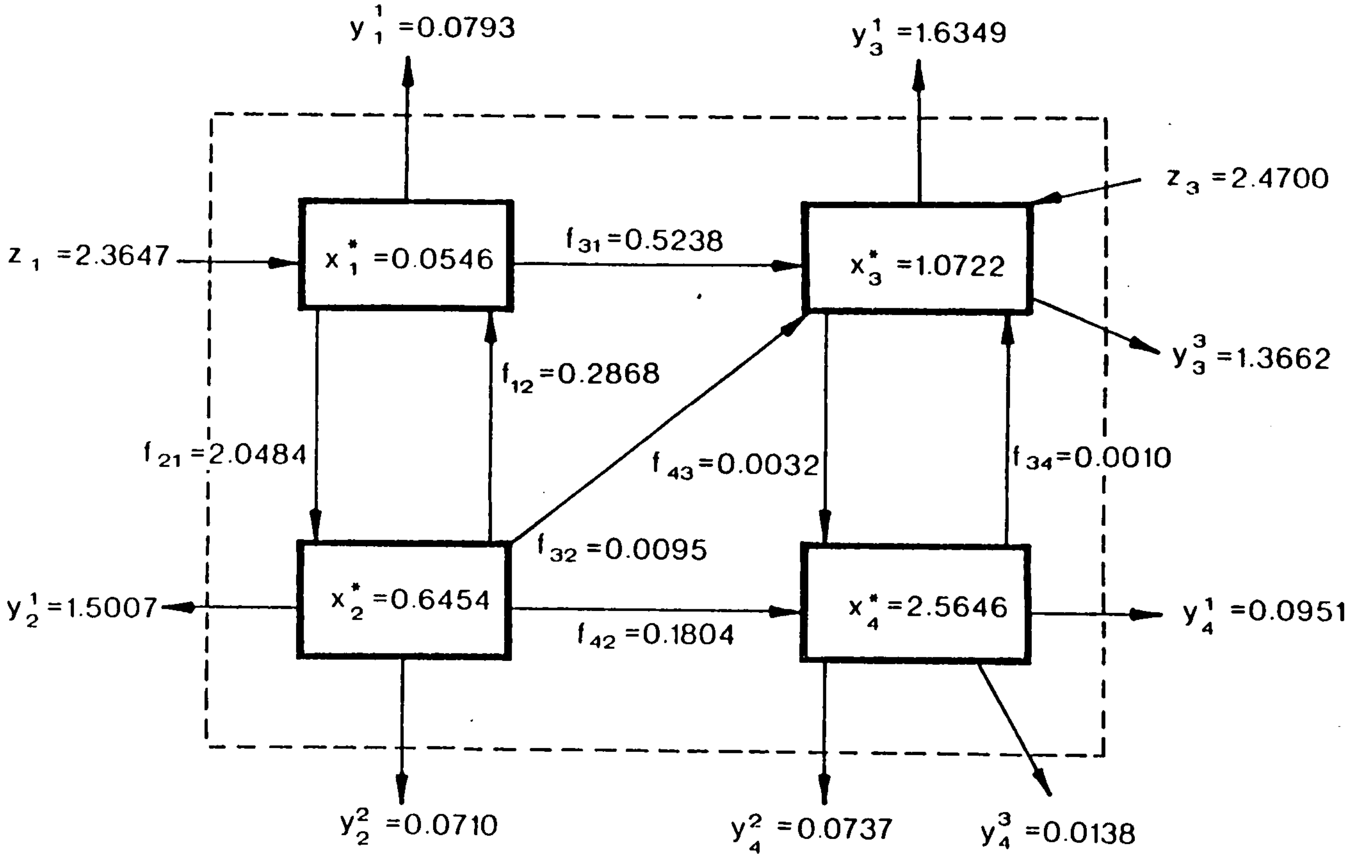


Figure 2.3

Schematic diagram for Example (2.4.1)

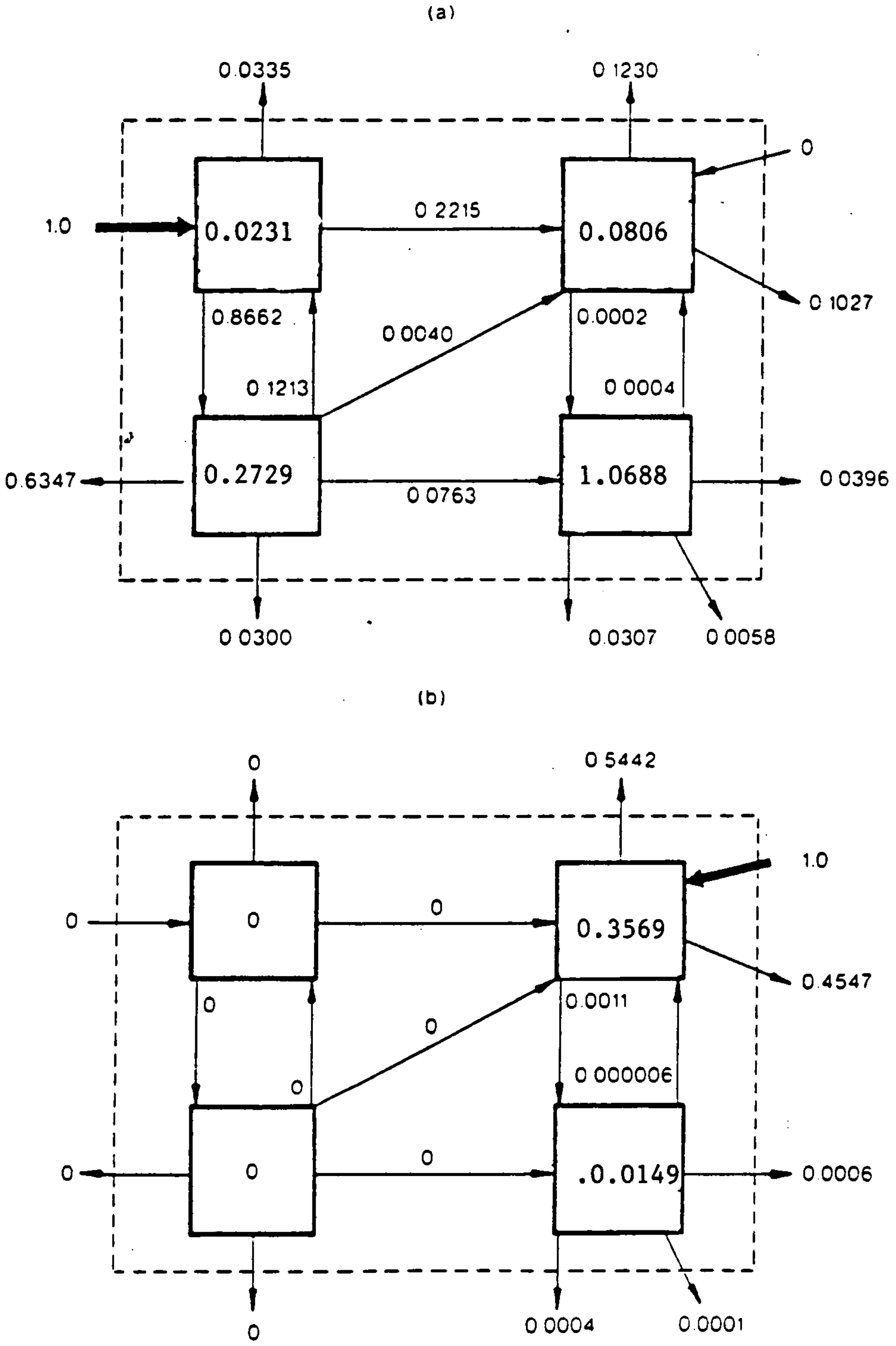


Figure 2.4 . Unit output environs for example (2.4.1) :
(a) $\ddot{E}_1$ and (b) $\ddot{E}_3$

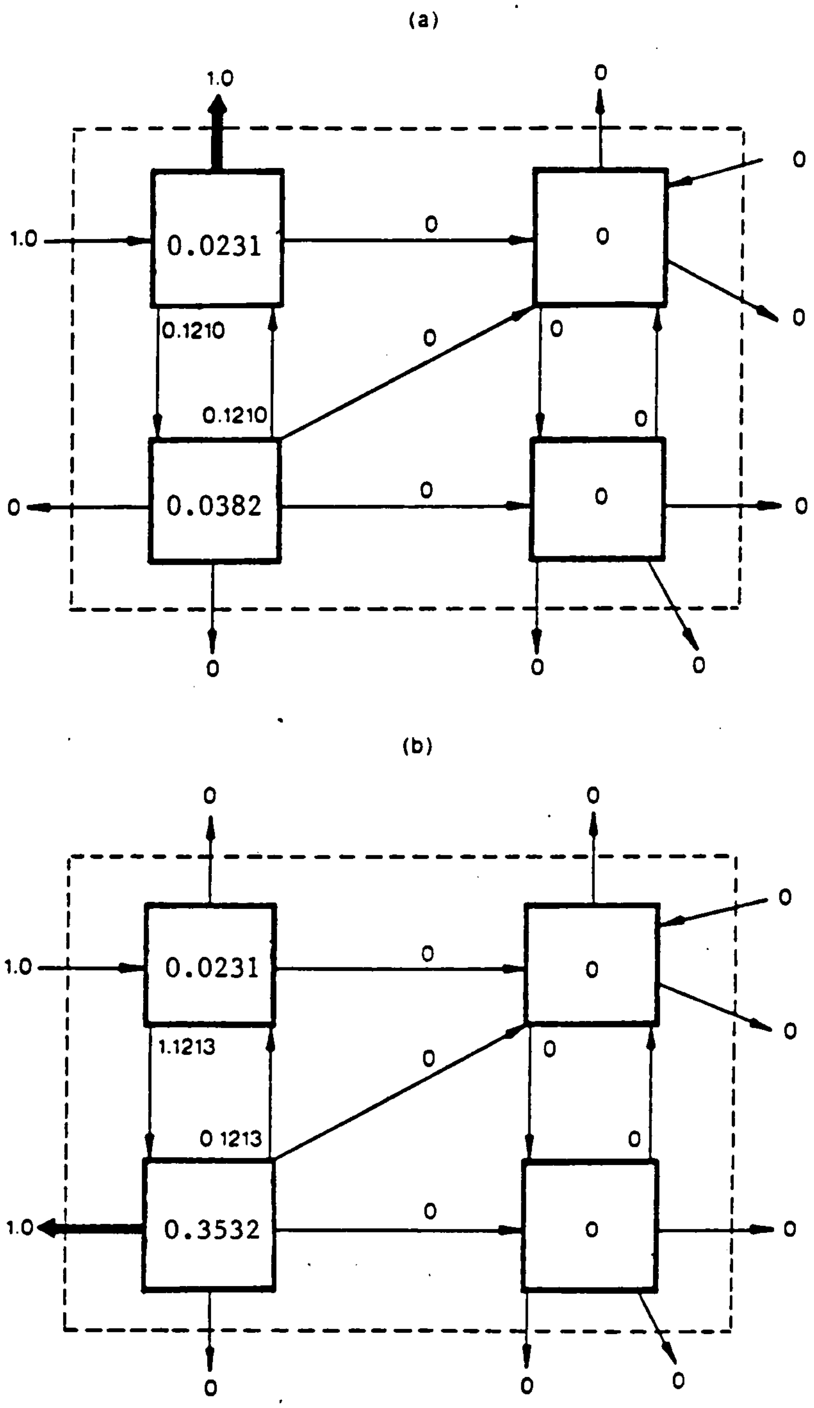


Figure 2.5 Unit input environs for example (2.4.1):

(a) $\overset{\prime}{E}_1$; (b) $\overset{\prime}{E}_2$; (c) $\overset{\prime}{E}_3$; and (d) $\overset{\prime}{E}_4$

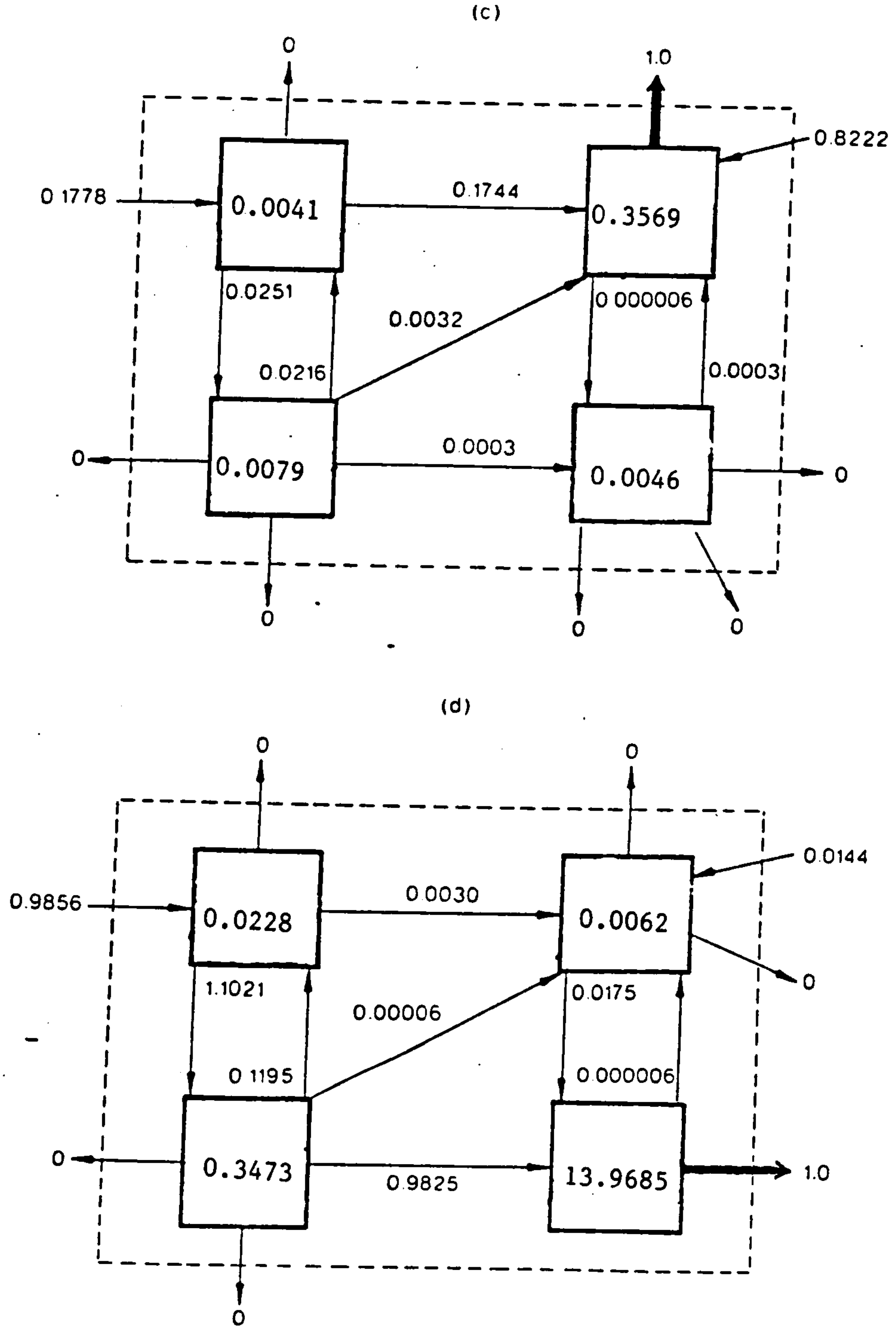


Figure 2.5. (con't)

Time Varying Linear Models

The purpose of this section is extension of the static input and output environ analysis to the case of time - varying flow structure in linear compartmental systems. The theory of environs is generalized to include two cases of time varying models. In the first case, the flow matrix $\overset{\prime\prime}{F}$ is time dependent while the coefficient matrix $\overset{\prime\prime}{A}$, is constant. In the second case (more general), both $\overset{\prime\prime}{F}$ and $\overset{\prime\prime}{A}$ are time dependent. In both cases, when defining output environs, tracing the influence of a unit input function on the ecosystem, the effect of the initial storage x_0 cannot be neglected as in the static case. This leads to the following notations

$\overset{\prime\prime}{E}{}_i^0(t)$ $(i = 1,\dots, n)$ denotes the output environ flow matrix associated with a unit of initial storage in i ;

$\overset{\prime\prime}{E}{}_i^z(t)$ $(i = 1,\dots, n)$ denotes the output environ flow matrix associated with a unit input at i ;

$\overset{\prime\prime}{e}{}_i^0(t)$ $(i = 1,\dots, n)$ denotes the output environ storage vector associated with a unit initial storage at i .

$\overset{\prime\prime}{e}{}_i^z(t)$ $(i = 1,\dots, n)$ denotes the output environ storage vector associated with a unit input at i ;

$\overset{\prime\prime}{\mathcal{E}}{}^0(t) = \left(\overset{\prime\prime}{e}{}_1^0(t) \,\middle|\, - - - - - \,\middle|\, \overset{\prime\prime}{e}{}_n^0(t) \right)$ denotes the output environ matrix due to unit initial stages ;

$\overset{\prime\prime}{\mathcal{E}}{}^z(t) = \left(\overset{\prime\prime}{e}{}_1^z(t) \,\middle|\, - - - - - \,\middle|\, \overset{\prime\prime}{e}{}_n^z(t) \right)$ is the output environ matrix due to unit inputs.

Similar definitions can be stated for the input environ storage and flow matrices $\overset{\prime}{E}{}_j^0(t)$, $\overset{\prime}{E}{}_j^y(t)$, $\overset{\prime}{e}{}_j^0(t)$, $\overset{\prime}{e}{}_j^y(t)$, $\overset{\prime}{\mathcal{E}}{}^0(t)$ and $\overset{\prime}{\mathcal{E}}{}_j^y(t)$.

From the above terminology, the environ flow matrices partition the total system flows so that

$$(2.4.18) \quad \overset{''}{F}(t) = \sum_i X_i(0)\, \overset{''}{E}{}_i^{0}(t) + \sum_i z_i(t)\, \overset{''}{E}{}_i^{z}(t) \ ,$$

$$(2.4.19) \quad [\overset{''}{F}(t)]^T = \sum_j y_j(t)\, \overset{'}{E}{}_j^{y}(t) \ ,$$

$$(2.4.20) \quad \overset{'}{F}(t) = \sum_j X_j(t)\, \overset{'}{E}{}_j^{0}(t) + \sum_j y_j(t)\, \overset{'}{E}{}_j^{y}(t) \ ,$$

and

$$(2.4.21) \quad [\overset{'}{F}(t)]^T = \sum_i z_i(t)\, \overset{''}{E}{}_j^{z}(t) \ .$$

(a) *Output Environ Analysis* (Tracing the Flows Caused by Unit Inflows and Unit Initial Storages).

Case 1: *Time Varying Linear Systems with Constant Coefficient Matrix*, $\overset{''}{A}$:

The models considered here are in the form

$$(2.4.22) \quad X(t) = \overset{''}{F}(t)\ .1 + \overset{''}{B}\ z(t) = \overset{''}{A}\ X(t) + \overset{''}{B}\ z(t)$$

$$(2.4.23) \quad Y(t) = \overset{''}{C}\ X(t) \ , \ X(t_0) = X_0$$

where $\overset{''}{B}$ is an $n \times n$ diagonal matrix with

$$(2.4.24)\quad \overset{\shortparallel}{b}_{ii} = \begin{cases} 1 & \text{when } z_i(t) \neq 0 \\ 0 & \text{when } z_i(t) = 0 , \end{cases}$$

and $\overset{\shortparallel}{C}$ is an $n \times n$ diagonal matrix with

$$(2.4.25)\quad \overset{\shortparallel}{C}_{ii} = \overset{\shortparallel}{a}_{oi} , \quad i = 1,\dots, n .$$

Hearon [1963] proves the following lemma:

Lemma 2.4.2. Given the model (2.4.22) with the regularity conditions:

(a) $f_{ji}(t) > 0$ for at least one $j \geq 0$ and for all i ;

(b) $f_{0j} > 0$ for some $j \geq 1$ (open system);

and

(c) the system is at least weakly connected (i.e. no compartment or a group of compartments is isolated from the rest of the system)

then,

(i) the eigenvalues, λ_i , of $\overset{\shortparallel}{A}$ have negative real parts (i.e. the system is stable)

(ii) the matrix T of the corresponding eigenvector is nonsingular and $T^{-1} \overset{\shortparallel}{A} T = \mathrm{Diag}(\lambda_i)$;

and

(iii) the solution of (2.4.22) is

$$(2.4.26)\quad X(t) = T\, D(e^{\lambda_i t})\, T^{-1} X(0) + T\, D\left[\frac{(1 - e^{\lambda_i t})}{-\lambda_i}\right] T^{-1} z(t)$$

$$(2.4.27)\quad Y(t) = \overset{\shortparallel}{C} X(t) .$$

The following theorem gives simple expressions for the output environ matrices (defined above) in terms of the matrices $\ddot{A}$, $\ddot{C}$, and T .

<u>Theorem</u> 2.4.3. The output environ flow and storage matrices for the system (2.4.22) are given by:

(i)
$$\ddot{\mathcal{E}}^0(t) = \left(\ddot{e}_i^0(t) \;\vdots\; \text{- - - - - - -} \;\vdots\; \ddot{e}_n^0(t) \right) = T\ D(e^{\lambda_i t})\ T^{-1} \ ;$$

$$\ddot{\mathcal{E}}^z(t) = \left(\ddot{e}_1^z(t) \;\vdots\; \text{- - - - - - -} \;\vdots\; \ddot{e}_n^z(t) \right) = T\ D\left(\frac{1 - e^{\lambda_i t}}{-\lambda_i}\right)\ T^{-1} \ ;$$

(ii)
$$\ddot{E}_i^0(t) = \ddot{A}\ D_{\ddot{e}_i^0(t)} \ ,$$

$$\ddot{Y}_i^0(t) = \ddot{C}\ \ddot{e}_i^0(t) \ .$$

and

(iii)
$$\ddot{E}_i^z(t) = \ddot{A}\ D_{\ddot{e}_i^z(t)} \ ;$$

$$\ddot{Y}_i^z(t) = \ddot{C}\ \ddot{e}_i^z(t) \ .$$

Proof. To verify (i), consider equation (2.4.26) and the definitions of $\overset{''}{e}{}_i^0(t)$ and $\overset{''}{e}{}_i^z(t)$,

(2.4.28) $X(t) = X_1(t) + X_2(t)$

where

(2.4.29) $X_1(t) = [T\ D(e^{\lambda_i t})T^{-1}]X(0) = \sum_k X_k(0)\ \overset{''}{e}{}_k^0(t)$,

and

(2.4.30) $X_2(t) = [T\ D(\frac{1 - e^{\lambda_i t}}{-\lambda_i})T^{-1}]\ Z(t) = \sum_k z_k(t)\ \overset{''}{e}{}_k^z(t)$.

Equations (2.4.29) and (2.4.30) are true for every initial vector $X(0)$ and every input vector $z(t)$. Thus, for the special case with $X(0) = (0 \ldots \underset{\overset{\uparrow}{i}}{1} \ldots 0)^T$ and $z(t) = (0 \ldots 0)^T$, the above two equations reduce to

(2.4.31) $X(t) = X_1(t) = \overset{''}{e}{}_i^0(t) = T\ D(e^{\lambda_i t})\ T^{-1}(0 \ldots \underset{\overset{\uparrow}{i}}{1} \ldots 0)^T$

which is the $i^{\underline{th}}$ column of $TD(e^{\lambda_i t})\ T^{-1}$

and

(2.4.32) $X_2(t) = 0$.

Thus, $\overset{''}{E}^0(t) = T\,D(e^{\lambda_i t})\,T^{-1}$. Similarly, with $X(0) = (0,\ldots,\,0)^T$ and $z(t) = (0 \ldots \underset{\overset{\uparrow}{i}}{1} \ldots 0)^T$

$$\overset{''}{E}^z(t) = T\,D\left(\frac{1 - e^{\lambda_i t}}{-\lambda_i}\right)\,T^{-1} .$$

For the proof of (ii), consider the following equation with $X(0) = (0 \ldots \underset{\overset{\uparrow}{i}}{1} \ldots 0)^T$ and $z(t) = (0 \ldots 0)^T$

$$(2.4.33)\quad X(t) = X_1(t) = \overset{''}{A}^{-1}\,\overset{''}{F}(t)(0 \ldots \underset{\overset{\uparrow}{i}}{1} \ldots 0)^T = \overset{''}{e}^0_i(t) .$$

Then from (2.4.18)

$$(2.4.34)\quad \overset{''}{F}(t) = \sum_K X_k(0)\,\overset{''}{E}^0_k(t) = \overset{''}{E}^0_i(t)$$

and employing (2.4.33) yields

$$\overset{''}{A}^{-1}\,\overset{''}{E}^0_i(t)\quad(1 \ldots 1)^T = \overset{''}{e}^0_i(t) = D_{\overset{''}{e}^0_i(t)}\quad(1 \ldots 1)^T$$

or

$$(2.4.35)\quad \overset{''}{E}^0_i(t) = \overset{''}{A}\,D_{\overset{''}{e}^0_i(t)}$$

and

$$(2.4.36)\quad \overset{''}{Y}^0(t) = \overset{''}{C}\,\overset{''}{e}^0_i(t) .$$

The proof of (iii) follows in a similar way but with $X(0) = (0 \ldots 0)^T$ and $z(t) = (0 \ldots \underset{\substack{\uparrow \\ i}}{1} \ldots 0)^T$. It is important to observe that if the flow matrix $\overset{''}{F}(t)$, and the input vector, $z(t)$, are time dependent in such a way that the output coefficients matrix, $\overset{''}{A}$, is constant, then this does not imply that the input coefficients matrix, $\overset{'}{A}(t)$, is also constant.

Case 2: <u>Time Varying Linear System with Time Dependent Coefficient Matrix,</u> $\overset{''}{A}(t)$.

In this situation the solution of the system (2.4.22) has the form

$$(2.4.37) \quad X(t) = \Phi(t, t_0)X(0) + \int_{t_0}^{t} \Phi(t, \tau)\, \overset{''}{B}\, Z(\tau)\, d\tau$$

$$(2.4.38) \quad Y(t) = \overset{''}{C}\, X(t)$$

where $\Phi(t, t_0)$ is the system transition matrix. The following theorem gives results similar to those obtained in Theorem 2.4.3 in the first case.

<u>Theorem</u> 2.4.4. The output environ storage and flow matrices for the system (2.4.22) with time dependent matrix $\overset{''}{A}(t)$, are given by

$$\text{(i)} \quad \overset{''}{E}{}^0(t) = \left(\begin{array}{c:c:c} \overset{''}{e}{}^0_1(t) & \text{- - - - - - - - -} & \overset{''}{e}{}^0_n(t) \end{array}\right) = \Phi(t, t_0) \ .$$

$$\overset{''}{E}{}^z(t) = \left(\begin{array}{c:c:c} \overset{''}{e}{}^z_1(t) & \text{- - - - - - - -} & \overset{''}{e}{}^z_n(t) \end{array}\right) =$$

$$\left(\begin{array}{c:c:c} \int_{t_0}^{t} \Phi(t, \tau)\, \hat{z}_1(\tau) d\tau & \text{- - -} & \int_{t_0}^{t} \Phi(t, \tau) \hat{z}_n(\tau) d\tau \end{array}\right)$$

where b_i is the $i^{\underline{th}}$ column of $\overset{''}{B}$, and $\hat{z}_i(t) = \frac{z_i(t)}{K_i}$ $(K_i > 0)$ is a normalized unit function.

$$\text{(ii)} \quad \overset{''}{E}{}_i^{0}(t) = \overset{''}{A}(t)\, D_{\overset{''}{e}{}_i^{0}(t)}$$

$$\overset{''}{Y}{}_i^{0}(t) = \overset{''}{C}\, \overset{''}{e}{}_i^{0}(t) \ ,$$

$$\text{(iii)} \quad \overset{''}{E}{}_i^{z}(t) = \overset{''}{A}(t)\, D_{\overset{''}{e}{}_i^{z}(t)}$$

and

$$\overset{''}{Y}{}_i^{z}(t) = \overset{''}{C}\, \overset{''}{e}{}_i^{z}(t) \ .$$

Proof. The proof is similar to the one given for Theorem 2.4.3 but with $T\,D(e^{\lambda_i t})T^{-1}$ replaced by $\Phi(t, t_0)$ and $T\,D(\frac{1 - e^{\lambda_i t}}{-\lambda_i})\,T^{-1}$ replaced by

$$\left(\int_{t_0}^{t} \Phi(t, \tau)\, b_1\, \hat{z}_1(\tau)\, d\tau \;\Big|\; \cdots \;\Big|\; \int_{t_0}^{t} \Phi(t, \tau)\, b_n\, \hat{z}_n(\tau)\, d\tau \right) .$$

(b) Input Environ Analysis (Tracing The Throughflow that Contribute to Specific Outflows From the Different Compartments)

The Output Environ Matrices defined in (a) allow tracing the effect of a unit initial storage in compartment i and the influence of a normalized time varying inflow from the environment via compartment i. As a dual concept, Input Environ Analysis was introduced to trace flows that contribute to a specific outflow from compartment i to the environment, or alternatively, to find that portion of flow that leaves the system via compartment i.

The static, time invariant linear case has been solved [*Leontief* 1966, *Hannon* 1973, *Finn* 1977 or *Matis and Patten* 1981]. In this section, *two* methods for the dynamic linear case are presented and examined by some examples.

Method I develops Input Environ Analysis in a manner similar to the Output Environ Analysis but for the complementary system

$$(2.4.37)' \quad \overset{\prime\prime}{X} = -\overset{\prime}{A}^{T}(t)\ X(t) - \overset{\prime}{B}\ Y(t)$$

$$Z(t) = \overset{\prime}{C}\ X(t)\ .$$

Method II develops Input Environ Analysis using a modified production matrix $P(t)$ similar to the one introduced by *Finn* (1977).

Method 1: Input environ storage and flow matrices can be obtained from the results of the following theorem.

Theorem 2.4.5. The Input Environ Matrices associated with (2.4.37) where $\overset{\prime}{A}^{T}(t)$, $\overset{\prime}{B}$ and $\overset{\prime}{C}$ have definitions similar to those of $\overset{\prime\prime}{A}(t)$, $\overset{\prime\prime}{B}$, $\overset{\prime\prime}{C}$ given in Theorems 2.4.3 and 2.4.4, and whose solution is

$$(2.4.38)' \quad X(t) = \Phi(t,\ t^{\circ})\ X^{\circ} + \int_{t}^{t^{\circ}} \Phi(t,\ \tau)\ \overset{\prime}{B}\ \overset{\prime}{\hat{Y}}(\tau)\ d\tau$$

where

$\Phi(t,\ \tau)$ is the system transition matrix,

X° is the *final* state at $t = t^{\circ}$ and $t \leq t^{\circ}$, are given by

(i) the input environ storage matrices $\overset{\prime}{E}^{\circ}(t)$ and $\overset{\prime}{E}^{y}(t)$ that partition final storage and normalized outputs respectively

$$(2.4.39)\quad \overset{\prime}{E}^{\circ}(t) = \left(\overset{\prime}{e}{}_1^{\circ}(t) \,\vdots\, \text{- - - - -} \,\vdots\, \overset{\prime}{e}{}_n^{\circ}(t) \right) = \Phi(t, t^{\circ}) \ ;$$

$$(2.4.40)\quad \overset{\prime}{E}^{y}(t) = \left(\overset{\prime}{e}{}_1^{y}(t) \,\vdots\, \text{- - - - - -} \,\vdots\, \overset{\prime}{e}{}_n^{y}(t) \right) =$$

$$= \left(\int_{t^0}^{t} \Phi(t, \tau)\overset{\prime}{b}_1 \ \hat{y}_1(\tau) \ d\tau \ \vdots \ \cdots \ \vdots \int_{t^0}^{t} \Phi(t, \tau) \ \overset{\prime}{b}_n \ \hat{y}_n(\tau) \ d\tau \right)$$

where $\overset{\prime}{b}_j$ is the $j^{\underline{th}}$ column of the matrix $\overset{\prime}{B}$ and $\hat{y}_j(t)$ is the normalized unit output vector such that $y_j(t) = k_j \ \hat{y}_j(t)$ $(k_j > 0)$;

(ii) the input environ flow matrices $\overset{\prime}{E}{}_j^{0}(t)$ and $z_j^{0}(t)$ that give the flow partitions which add up to a unit final storage at j

$$(2.4.41)\quad \overset{\prime}{E}{}_j^{0}(t) = \overset{\prime}{A}{}^{T}(t) \ D_{\overset{\prime}{e}{}_j^{0}(t)}$$

$$(2.4.42)\quad \overset{\prime}{z}{}_j^{0}(t) = \overset{\prime}{C} \ \overset{\prime}{e}{}_j^{0}(t)$$

and

(iii) the input environ flow matrices $\overset{\prime}{E}{}_j^{y}(t)$ and $z_j^{y}(t)$ that give the flow partitions which add up to a unit outflow function at j

$$(2.4.43)\quad \overset{\prime}{E}{}_j^{y}(t) = \overset{\prime}{A}{}^{T}(t) \ D_{\overset{\prime}{e}{}_j^{y}(t)}$$

$$(2.4.44) \quad \overset{\prime}{z}{}^{y}_{j}(t) = \overset{\prime}{C}\,\overset{\prime}{e}{}^{y}_{j}(t) \quad .$$

The proof of this theorem is similar to the one given for Theorem 2.4.4 but with the matrices $\overset{\prime\prime}{A}(t)$, $\overset{\prime\prime}{B}$, and $\overset{\prime\prime}{C}$ replaced by $\overset{\prime}{A}{}^{T}(t)$, $\overset{\prime}{B}$, and $\overset{\prime}{C}$ and with the input vector $z(t)$ replaced by the output vector $y(t)$.

<u>Method</u> II: Input Environ Storage and Flow Matrices Using the Production Matrix $P(t)$.

In this method, the basis for the computation of flows contributing to a unit outflow function is the concept of throughflow $T_j(t)$ of compartment j . This throughflow is either the sum of inflows $T_j(\sum \text{in})$ or the sum of outflows $T_j(\sum \text{out})$. In steady state conditions, the sum of all inflows into a compartment equals the sum of all outflows from it. In the dynamic case, the throughflows are defined as follows:

$$(2.4.45) \quad T_j(\sum \text{in}) \triangleq -\dot{x}_j^{-}(t) + z_j(t) + \sum_{i=1}^{n} f_{ji}(t) \quad (j = 1,\ldots, n)$$

or

$$(2.4.46) \quad T_j(\sum \text{out}) \triangleq \dot{x}_j^{+}(t) + y_j(t) + \sum_{k=1}^{n} f_{kj}(t) \quad (j = 1,\ldots, n)$$

where

$$\dot{x}_j^{-}(t) = \min\{\dot{x}_j(t), 0\}$$

and

$$\dot{x}_j^+(t) = \max\{\dot{x}_j(t), 0\} .$$

Equations (2.4.45) and (2.4.46) imply that decaying storage $(\dot{x}_j < 0)$ is treated as inflow and increasing storage $(\dot{x}_j > 0)$ as outflow. Hippe [1981] modified equations (2.4.45) and (2.4.46) and hence the productive matrix $P(t)$ without convincing reasons. In his input environ analysis, Hippe dropped $\dot{x}_j^+(t)$ from (2.4.46) and constructed a modified production matrix accordingly. Here input environ analysis in the general case, considering both $\dot{x}_j^-$ and $\dot{x}_j^+$, are presented.

The production matrix in this case is of the order $(5n \times 5n)$ and has the form

$$(2.4.47) \qquad P(t) = \begin{array}{c|c|c|c|c|c|}
 & z_1 \ldots z_n & -\dot{x}_1^- \ldots -\dot{x}_n^- & T_1 \ldots T_n & Y_1 \ldots Y_n & \dot{x}_1^+ \ldots \dot{x}_n^+ \\ \hline
\begin{matrix} z_1 \\ \vdots \\ z_n \end{matrix} & 0_{n\times n} & 0_{n\times n} & 0_{n\times n} & 0_{n\times n} & 0_{n\times n} \\ \hline
\begin{matrix} -\dot{x}_1^- \\ \vdots \\ -\dot{x}_n^- \end{matrix} & 0_{n\times n} & 0_{n\times n} & 0_{n\times n} & 0_{n\times n} & 0_{n\times n} \\ \hline
\begin{matrix} T_1 \\ \vdots \\ T_n \end{matrix} & \begin{matrix} z_1 & & \\ & \ddots & \\ & & z_n \end{matrix} & \begin{matrix} -\dot{x}_1^- & & \\ & \ddots & \\ & & -\dot{x}_n^- \end{matrix} & \begin{matrix} 0 & f_{ij}(t) & \\ & \ddots & (j>i) \\ f_{ji}(t) & & \\ (j>i) & & 0 \end{matrix} & 0_{n\times n} & 0_{n\times n} \\ \hline
\begin{matrix} y_1 \\ \vdots \\ y_n \end{matrix} & 0_{n\times n} & 0_{n\times n} & \begin{matrix} y_1 & & \\ & \ddots & \\ & & y_n \end{matrix} & 0_{n\times n} & 0_{n\times n} \\ \hline
\begin{matrix} \dot{x}_n^+ \\ \vdots \\ \dot{x}_n^+ \end{matrix} & 0_{n\times n} & 0_{n\times n} & \begin{matrix} \dot{x}_1^+ & & \\ & \ddots & \\ & & \dot{x}_n^+ \end{matrix} & 0_{n\times n} & 0_{n\times n} \\ \hline
\end{array}$$

Let the flow $f_{k_j}(t)$ from compartment j to k be expressed as a fraction of $T_k(\sum \text{in})$:

$$(2.4.48)\quad f_{kj} = \overset{\prime}{q}_{kj}(t)\ T_k(\sum \text{in}) \quad .$$

Substituting (2.4.45) and (2.4.48) into

$$(2.4.49)\quad [\dot{x}_j^{+}(t) + y_j(t)] - [z_j(t) - \dot{x}_j^{-}(t)] =$$

$$= \sum_{i=1}^{n} f_{ji}(t) - \sum_{k=1}^{n} f_{kj}(t)$$

gives

$$(2.4.50)\quad T_j(\sum \text{in}) = \sum_{k=1}^{n} \overset{\prime}{q}_{kj}(t)\ T_k(\sum \text{in}) + y_j(t) + \dot{x}_j^{+}(t) \quad .$$

Equation (2.4.50) can be solved for $T_j(\sum \text{in})$ by the corresponding matrix equation

$$(2.4.51)\quad T(\sum \text{in}) = (I - \overset{\prime}{Q}(t))^{-1}\ [\dot{x}^{+}(t) + y(t)] \ ,$$

where $T(\sum \text{in})$ is an $n \times 1$ vector of throughflows, I is an $n \times n$ identity matrix, $\overset{\prime}{Q}(t)$ is the $n \times n$ matrix $[\overset{\prime}{q}_{ij}(t)]$, $\dot{x}^{+}(t)$ is the $n \times 1$ vector $[\dot{x}_i^{+}(t)]$, and $y(t)$ is the $n \times 1$ vector $[f_{0i}(t)]$. The matrix $\overset{\prime}{N}(t) = [I - \overset{\prime}{Q}(t)]^{-1} = [\overset{\prime}{n}_{ij}(t)]$ defines the flow structure of the system in the sense of <u>Hannon</u> [1973] . Equation (2.4.51) gives the partition of inflows, $T(\sum \text{in})$, and time derivative of storages $\dot{x}^+(t)$ in terms of the output vector $y(t)$. To derive similar equations that partition the input vector $z(t)$ and the time derivative of storages $\dot{x}^-(t)$, we proceed as follows.

Step 1: Divide every nonzero element in each row of $P(t)$ by the corresponding row sum to get the normalized matrix

$$(2.4.52)\quad Q(t) = \left[\begin{array}{c|c|c} 0 & 0 & 0 \\ \hline Q_{21}(t) & Q'(t) & 0 \\ \hline 0 & Q_{32}(t) & 0 \end{array}\right]$$

Step 2: Define the $(5n \times 5n)$ structure matrix, $N(t)$, by

$$(2.4.53)\quad N(t) = [I - Q(t)]^{-1} = \begin{bmatrix} I_{2n\times 2n} & 0 & 0 \\ N_{21}(t) & \overset{\prime}{N}(t) & 0 \\ N_{31}(t) & N_{32}(t) & I_{2n\times 2n} \end{bmatrix}$$

where $\overset{\prime}{N}(t)$ and $\overset{\prime}{Q}(t)$ are as defined before,

$$(2.4.54)\quad \overset{\prime}{N}(t) = [I - \overset{\prime}{Q}(t)]^{-1} ,$$

$$(2.4.55)\quad N_{21}(t) = \overset{\prime}{N}(t)\ Q_{21}(t) ,$$

$$(2.4.56)\quad N_{31}(t) = Q_{31}(t)\ N_{21}(t) ;$$

and

$$(2.4.57) \quad N_{32}(t) = Q_{32}(t)\, \overset{\prime}{N}(t) \ .$$

Step 3: The partitions of inflow, time derivative of storages and compartmental throughflows in terms of the output vector $y(t)$ are given by

$$(2.4.58) \quad [z^T(t) - (\dot{x}^-)^T(t) \mid T^T(t) \mid Y^T(t)(\dot{x}^+)^T(t)]$$

$$= [y^T(t)\ \dot{x}^{+T}(t)][N_{31}(t) \mid N_{32}(t) \mid I] \ .$$

Step 4: Form the $(n \times n)$ diagonal matrices $D_{n_i}(t)$, $i = 1, 2, \ldots, n$ out of the first n rows of $N_{32}(t)$ and calculate

$$(2.4.59) \quad {}^{i}P(t) = D_{n_i}(t) \quad Q'(t) \ , \quad i = 1, 2, \ldots, n \ .$$

The elements $p^i_{jk}(t)$ of ${}^{i}P(t)$ give the intercompartmental flow contributing to one unit of outflow function $y_i(t)$ assuming that $\dot{X}^+(t^0) = 0$. It is worth noting that different inputs and different initial conditions will cause different flow patterns and therefore different sets of input environ can be determined. As the time behavior of an ecosystem due to arbitrary input functions $z_i(t)$ can be quite complex, dynamic input environ analysis may become a tedious task unless numerical techniques are used.

2.5. Examples on Input-Output Environ Analysis For Time Varying Linear Systems

Example 2.5.1: Stepwise Input Functions [Hippe 1982] (See Figures 2.6-2.20).

Stepwise input functions can be used to approximate changing environmental conditions or abrupt changes of inflow. Hippe considered in his paper the following flow model

$$(2.5.1) \qquad X(t) = \overset{''}{A}\, X(t) + \overset{''}{B}\, z(t)$$

$$Y(t) = \overset{''}{C}\, X(t)$$

with

$$\overset{''}{A} = \begin{bmatrix} -\frac{5}{3} & \frac{2}{3} \\ \frac{4}{3} & -\frac{7}{3} \end{bmatrix} , \quad \overset{''}{B} = \begin{bmatrix} 1 & 0 \\ 0 & 1 \end{bmatrix} , \text{ and}$$

$$\overset{''}{C} = \begin{bmatrix} \frac{1}{3} & 0 \\ 0 & \frac{5}{3} \end{bmatrix} .$$

Starting from the steady state flows and storage, the inputs z_1 and z_2 as shown in Figure (2.7) are changed from $z^T = [3 \quad 3]$ to $z^T = [\frac{1}{3} \quad \frac{10}{3}]$ at some time t_0 which is arbitrarily set to $t_0 = 0$, the resulting output and input partitions are as follows:

(i) Initial Steady State

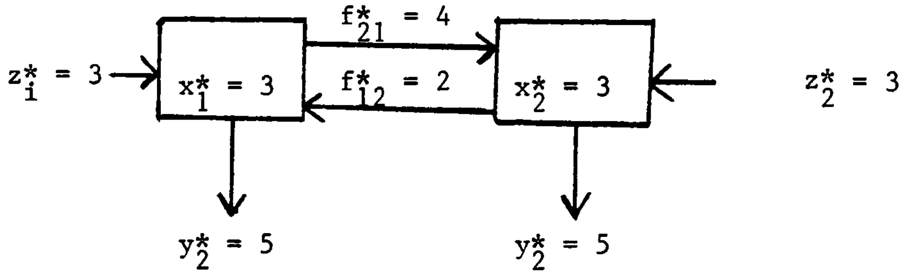


Figure 2.6

Diagrametic representation of the initial storage and flows of Example 2.5.1

(ii) Input Functions

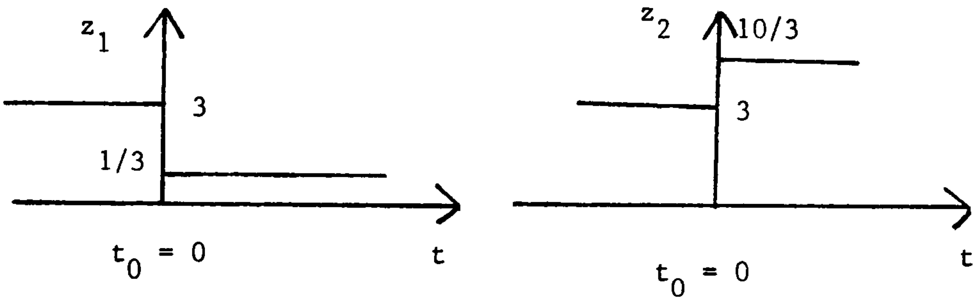


Figure 2.7

Time varying inputs for Example 2.5.1

(iii) Output Environ Partitions Due to Unit Initial Storage and Zero Inputs

$$X_0^T = [1 \quad 0]$$
$$z^T = [0 \quad 0]$$

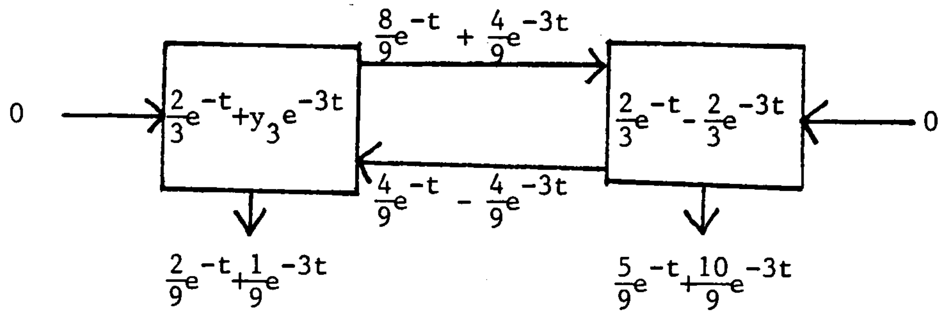


Figure 2.8

Output partitions for Example 2.5.1 due to a unit initial storage at the first compartment

$$X_0^T = [0 \; 1]$$
$$z^T = [0 \; 0]$$

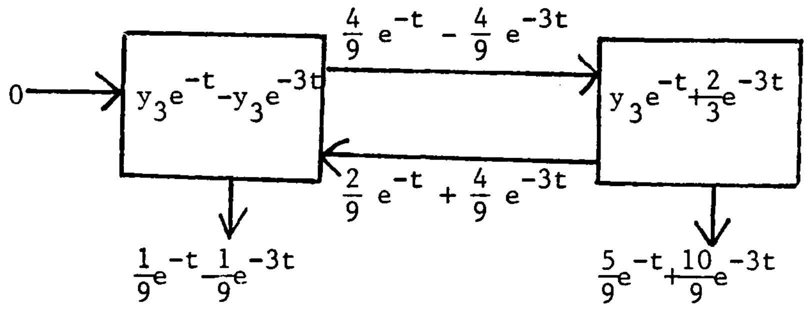


Figure 2.9

Output partitions for Example 2.5.1 due to a unit initial storage at the second compartment

(iv) Output Environ Partitions Due to Unit Inputs and Zero Initial Storage.

$$X_0^T = [0 \; 0]$$

$$z^T(t) = [1(t) \quad 0]$$

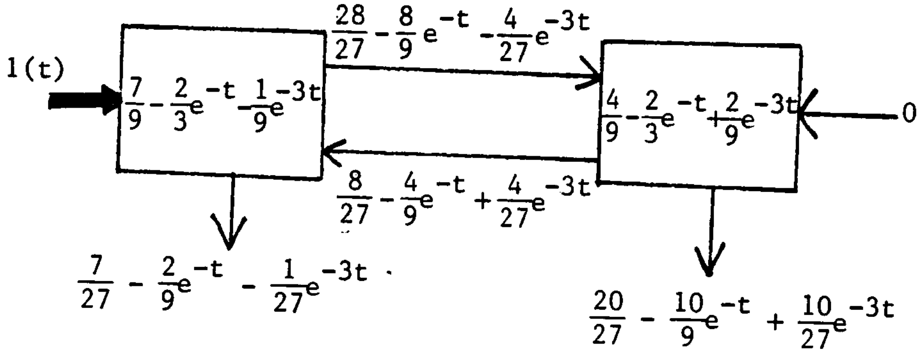


Figure 2.10

Output partitions for Example 2.5.1 due to a unit input function at the first compartment.

$$X_0^T = [0 \; 0]$$

$$z^T(t) = [0 \quad 1(t)]$$

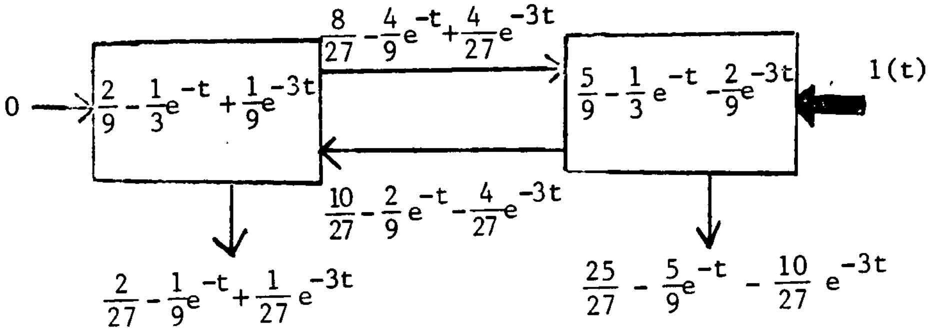


Figure 2.11

Output partitions for example 2.5.1 due to a unit input function at the second compartment

(v) Input Environ Partitions (Figures 2.12-2.13)

$Y(t)^T = [1(t) \quad 0]$

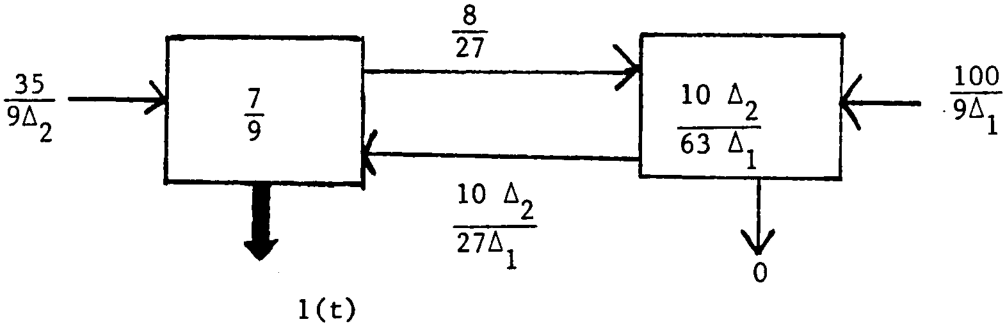


Figure 2.12

Input partitions for Example 2.5.1 contributing in a unit output from the first compartment

$Y(z)^T = [0 \quad 1(t)]$

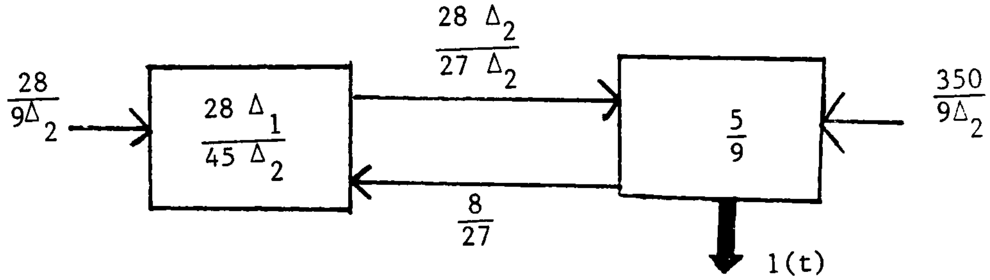


Figure 2.13

Input partitions for Example 2.5.1 contributing in a unit output from the second compartment.

where

$$\Delta_1 = 15 + 25e^{-t} + 5e^{-3t}$$

$$\Delta_2 = 42 + 35e^{-t} - 14e^{-3t} \quad .$$

Example 2.5.2: Two Compartmental System with Time Varying Matrix, $\overset{''}{A}(t)$, and a Periodic Input Function $z(t)$.

Consider the system shown in Figure 2.14

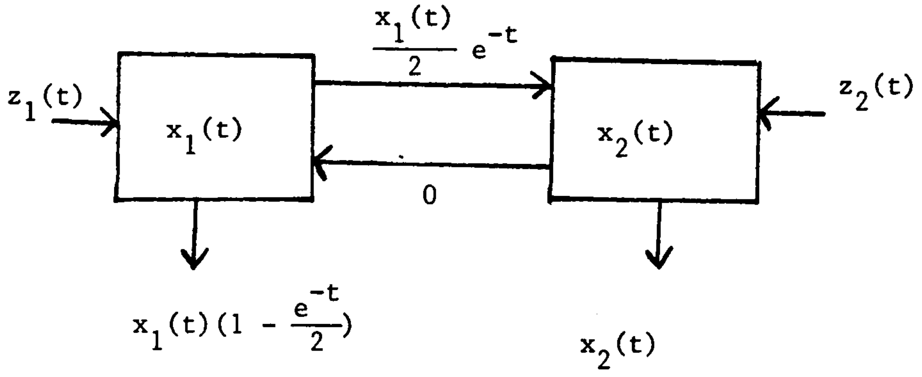


Figure 2.14

Two compartmental system with time varying coefficient matrix and a periodic input function

which governed by the following differential equation

$$\dot{X}(t) = \overset{''}{A}(t)X(t) + \overset{''}{B}\ z(t)$$

$$Y(t) = \overset{''}{C}\ X(t) \qquad , \quad X^T(0) = [1 \quad 1]$$

where,

$$A = \begin{bmatrix} -1 & 0 \\ \frac{e^{-t}}{2} & -1 \end{bmatrix}, \quad \overset{''}{B} = \begin{bmatrix} 1 & 0 \\ 0 & 1 \end{bmatrix}, \quad z^T(t) = [\sin t \quad 1(t)]$$

and

$$\overset{''}{C} = \begin{bmatrix} 1 - \frac{e^{-t}}{2} & 0 \\ 0 & 1 \end{bmatrix} .$$

(i) <u>Output Environ Partitions Due to Unit Initial Storages and Zero Inputs</u> (Figures 2.15-2.16)

$$X_0^T = [1 \quad 0]$$

$$z^T = [0 \quad 0]$$

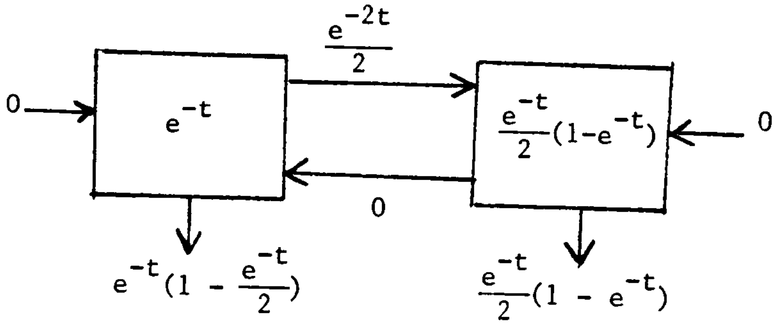


Figure 2.15

Output partitions for Example 2.5.2 due to a unit initial storage at the first compartment

$X_0^T = [0 \quad 1]$

$z^T(t) = [0 \quad 0]$

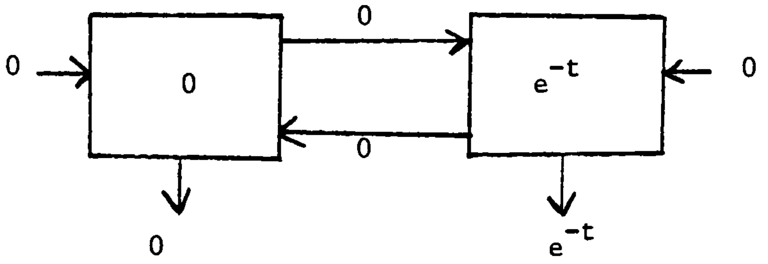


Figure 2.16

Output partitions for Example 2.5.2 due to a unit initial storage at the second compartment

(ii) <u>Output Environ Partitions Due to Unit Input Functions and Zero Initial Storages</u>:

$X_0^T = [0 \quad 0]$

$z^T(t) = [1 \sin t \quad 0]$

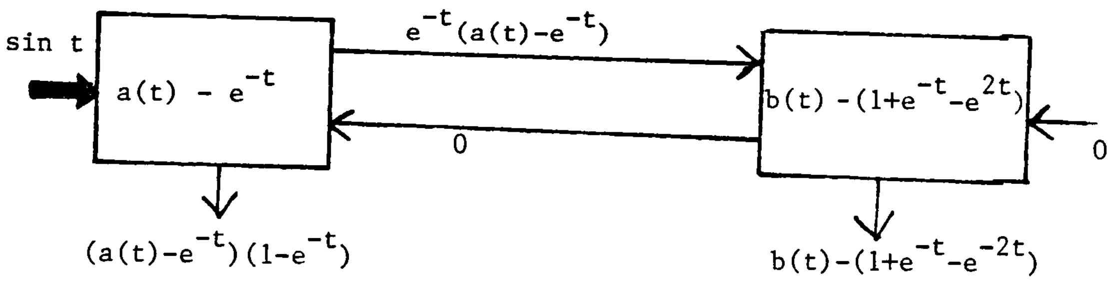


Figure 2.17

Output partitions for Example 2.5.2 due to a unit input function at the first compartment.

$X_0^T = [0 \quad 0]$

$z^T(t) = [0 \quad 1(t)]$

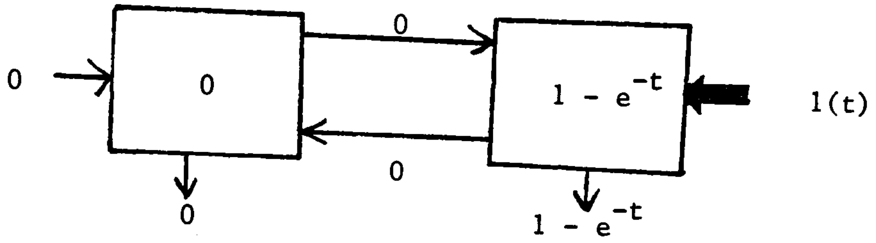


Figure 2.18

Output partitions for Example 2.5.3 due to a unit input function at the second compartment

(iii) <u>Input Environ Partitions</u> (Figures 2.19-2.20)

$X^T(t^0) = [0 \quad 0]$

$y^T(t) = [y_1(t) \quad 0]$

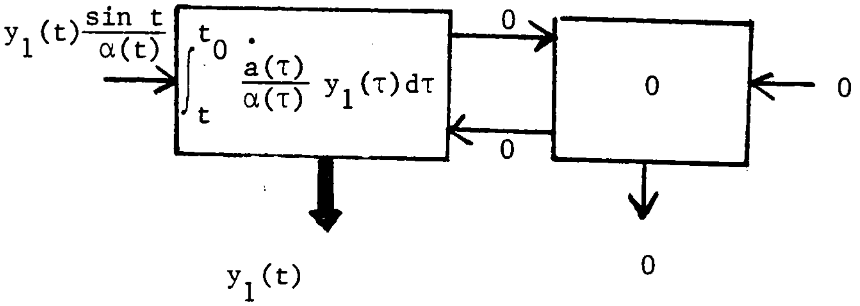


Figure 2.19

Input partition contributing in an output function from the first compartment

$X^T(t^0) = [0 \quad 0]$

$y^T(t) = [0 \quad y_2(t)]$

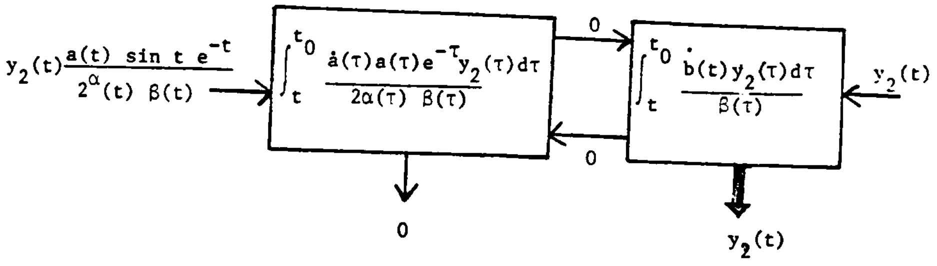


Figure 2.20

Input partitions contributing in an output function from the second compartment.

where $\alpha(t) = (\sin t - \dot{a}(t))$;

$$\beta(t) = (1(t) - \dot{b}(t) + \frac{a(t)}{2} e^{-t}) ;$$

$$y_1(t) = a(t)\ (1 - e^{-t}) + \frac{e^{-2t}}{2} ;$$

and

$$y_2(t) = b(t) + \frac{1}{2} e^{-t}(e^{-t} - 1) .$$

2.6. Environ Analysis for Nonlinear Time Varying Systems of Differential Equations

Since the assumptions of linearity are not completely justified in a real system under global conditions, it is desirable to develop a nonlinear environ analysis for either general or specific classes of non-linear systems. Linear systems theory is still a powerful tool to investigate most classes of nonlinear systems as long as the system is operating near an equilibrium and its dynamic inputs do not drive the system too far from this equilibrium. In this section a different approach is investigated for a class of nonlinear systems governed by equations in the form

$$(2.6.1) \qquad \dot{X}(t) = \overset{''}{A}\, X(t) + \Phi_1(X(t)) + \overset{''}{B}\, z(t)$$

$$y(t) = \overset{''}{C}\, X(t) \ , \quad x(t_0) = X_0$$

or

$$(2.6.2) \qquad \dot{X}(t) = \overset{''}{A}\, X(t) + \Phi(X(t), t) \quad ,$$

where $\overset{''}{A}$ and the nonlinear function $\Phi(X(t), t)$, where $\Phi(X(t), t) = [\Phi_1(X(t)) + \overset{''}{B}\, z(t))]$, satisfy the following:

1) there exist $\alpha > 0$ and $k > 0$ such that

$$||W(t)\, W^{-1}(\tau)|| \leq k \exp[-\alpha(t - \tau)] \quad \text{for all} \quad t \geq \tau \geq 0 \ ;$$

2) $\lim\limits_{t\to\infty} \int_0^t W(t)\, W^{-1}(\tau) d\tau$ exists as a matrix with finite elements.

where $W(t)$ is the fundamental matrix of solutions of the homogeneous equation

$$\dot{X}(t) = \overset{''}{A}\, X(t) \ .$$

3) for sufficiently small $||X||$, $\lim\limits_{t\to\infty} \phi(X(t), t)$ exists and is finite.

4) for sufficiently small β , $||\Phi(0, t)|| \leq \beta$ for $t \geq 0$;

5) for $\varepsilon > 0$, there exist $\delta > 0$ and $T \geq 0$ such that

$$||\Phi(X_1, t) - \Phi(X_2, t)|| \leq \varepsilon||X_1 - X_2|| \quad \text{for} \quad ||X_i|| \leq \delta, \ (i = 1, 2).$$

For the above system with the stated conditions satisfied, the solution exists, is bounded, and converges as $t \to \infty$. This solution satisfies

$$(2.6.3) \qquad X(t) = W(t)\, X_0 + \int_0^t W(t)\, W^{-1}(\tau)\, \Phi(X(\tau), \tau)\, d\tau$$

$$= W(t)\, X_0 + \int_0^t W(t)\, W^{-1}(\tau)\Phi_1(X(\tau))\, d\tau$$

$$+ \int_0^t W(t)\, W^{-1}(\tau)\, \overset{''}{B}\, z(\tau)\, d\tau .$$

The following theorem gives the output environ partitioning matrices for a class of nonlinear models described by (2.6.2).

<u>Theorem</u> 2.6.1. The output environ matrices for (2.6.2) are given by:

(i) the output environ storage matrices, $\overset{''}{E}{}^0(t)$ and $\overset{''}{E}{}^z(t)$ that partition unit initial storages and unit input functions respectively

$$(2.6.4) \qquad \overset{''}{E}{}^0(t) = \left[\overset{''}{e}{}^0_1(t) \,\middle|\, - - \,\middle|\, \overset{''}{e}{}^0_n(t) \right] =$$

$$W(t) + \left[\int_0^t V(t, \tau)\ \Phi_1(\overset{''}{e}{}^0_1(\tau))d\tau \,\middle|\, - - \,\middle|\, \int_0^t \ V(t, \tau)\Phi_1(\overset{''}{e}{}^0_n(\tau))d\tau \right]$$

$$(2.6.5) \quad \ddot{E}^{z}(t) = \left[\ddot{e}^{z}_{1}(t) \,\vdots\, ------ \,\vdots\, \ddot{e}^{z}_{n}(t)\right]$$

$$= \left[\int_{0}^{t} V(t, \tau)\ \Phi_{1}(\ddot{e}^{z}_{1}(\tau))d\tau \,\vdots\, ---- \,\vdots\, \int_{0}^{t} V(t, \tau)\Phi_{1}(\ddot{e}^{z}_{n}(\tau))d\tau\right]$$

$$+ \left[\int_{0}^{t} V(t, \tau)\ b_{1}\ z_{1}(\tau)d\tau \,\vdots\, ---- \,\vdots\, \int_{0}^{t} V(t, \tau)\ b_{n}\ z_{n}(\tau)d\tau\right]$$

where $V(t, \tau) = W(t)\ W^{-1}(\tau)$.

(ii) The output environ flow matrices $\ddot{E}^{0}_{i}(t)$ and $\ddot{Y}^{0}_{i}(t)$ that partition the unit initial storages

$$(2.6.6) \quad \ddot{E}^{0}_{i}(t) = \ddot{A}\ D_{\ddot{e}^{0}_{i}(t)} + D_{\Phi_{1}(\ddot{e}^{0}_{i}(t))} \ ;$$

$$(2.6.7) \quad \ddot{Y}^{0}_{i}(t) = \ddot{C}\ \ddot{e}^{0}_{i}(t) \ .$$

(iii) The output environ flow matrices $\ddot{E}^{z}_{i}(t)$ and $\ddot{Y}^{z}_{i}(t)$ that partition unit input functions

$$(2.6.8)\qquad \overset{''}{E}{}^{z}_{i}(t) = \overset{''}{A}\, D_{\overset{''}{e}{}^{z}_{i}(t)} + D_{\Phi(\overset{''}{e}{}^{z}_{i}(t))} \; ;$$

$$(2.6.9)\qquad \overset{''}{Y}{}^{z}_{i}(t) = \overset{''}{C}\, \overset{''}{e}{}^{z}_{i}(t) \; .$$

The proof of this theorem follows directly from the definition of output environ matrices and from (2.6.3).

The results of Theorem 2.6.1 will be applied on a three dimensional aquatic ecosystem consisting of a phytoplankton population, $P(t)$, a zooplankton population, $Z(t)$, and a nutrient, $N(t)$. The volume of water is assumed to be constant. Thus, the inflow rate of water is equal to the outflow rate. The phytoplankton and zooplankton populations are assumed to be measurable by their nitrogen concentration. The principle of conservation of nitrogen for each component can be seen in Figure 2.21.

$$(2.6.10)\qquad \dot{X} = \begin{bmatrix} \dot{N} \\ \dot{P} \\ \dot{Z} \end{bmatrix} = \begin{bmatrix} -1 & D_1 & D_2 \\ 0 & -(1+D_1) & 0 \\ 0 & 0 & -(1+D_2) \end{bmatrix} \begin{bmatrix} N \\ P \\ Z \end{bmatrix} +$$

$$\begin{bmatrix} -\dfrac{a\,P\,N}{A+N} \\ \dfrac{a\,P\,N}{A+N} - \dfrac{b\,Z\,P}{B+P} \\ \dfrac{b\,Z\,P}{B+P} \end{bmatrix} + \begin{bmatrix} 1 & 0 & 0 \\ 0 & 1 & 0 \\ 0 & 0 & 1 \end{bmatrix} \begin{bmatrix} w_1 \\ w_2 \\ w_3 \end{bmatrix} \; .$$

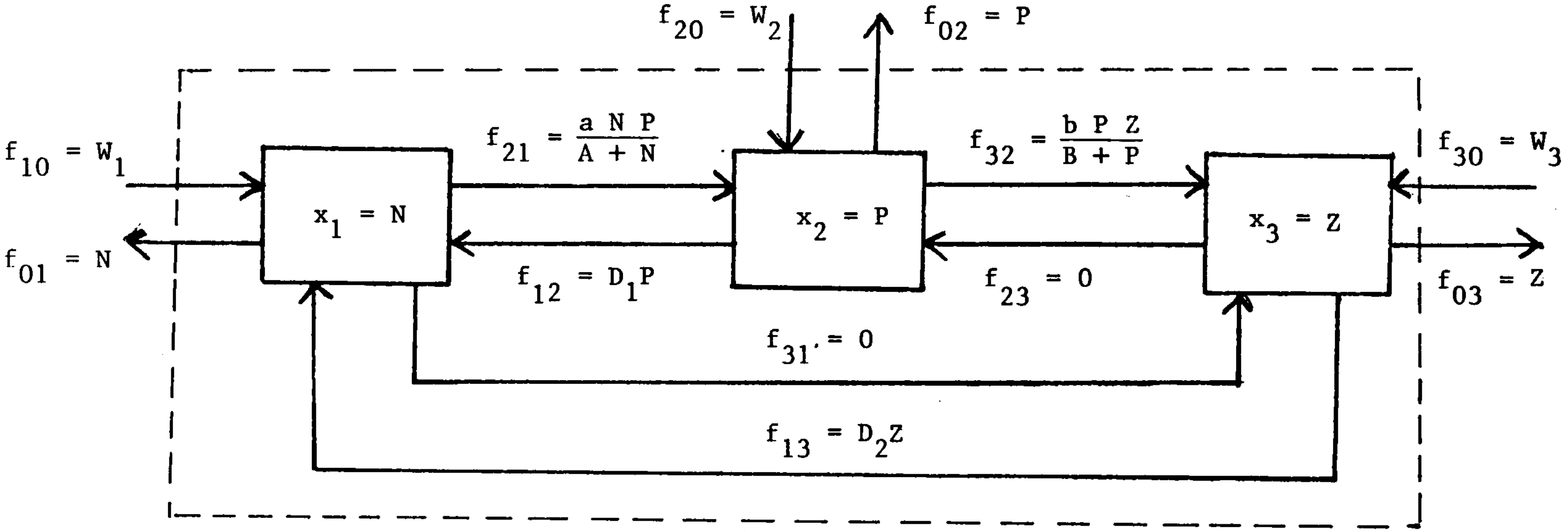


Figure 2.21

Two Trophic nonconservative Aquatic Systems

$$(2.6.11) \quad Y(t) = \begin{bmatrix} 1 & 0 & 0 \\ 0 & 1 & 0 \\ 0 & 0 & 1 \end{bmatrix} \begin{bmatrix} N \\ P \\ z \end{bmatrix}$$

with transition matrix

$$(2.6.12) \quad V(t - \tau) = e^{-(t-\tau)} \begin{bmatrix} 1 & 1-e^{-D_1(t-\tau)} & 1-e^{-D_2(t-\tau)} \\ 0 & e^{-D_1(t-\tau)} & 0 \\ 0 & 0 & e^{-D_2(t-\tau)} \end{bmatrix} .$$

Before starting to apply the results of Theorem 2.6.1, we should make sure that system (2.6.10) satisfies the conditions required by the theorem.

First, it is easy to prove that the eigenvalues of $\ddot{A}$ have negative real parts $(\lambda_1 = -1 \ , \ \lambda_2 = -(1 + D_1) \ , \ \lambda_3 = -(1 + D_2))$. Next, it is clear that the nonlinear function $\Phi(X(t), t)$ is bounded at the origin. The differentiability of $\Phi(X(t), t)$ implies Condition (5). It is a direct consequence of the definition of $V(t, \tau)$ that that $||V(t - \tau)|| < K e^{-(t--\tau)}$, with $\alpha = 1$, $K \geq 3$ and hence Condition (1) holds. It is also true that the matrix norm $\int_0^t ||V(t - \tau)|| d\tau$ is bounded for all $t \geq 0$. This follows from the definition of the matrix norm. Similarly Conditions (3) and (4) are satisfied and Theorem (1.2.4) is now applicable. Hence, it follows that the asymptotic limit of the solution of (2.6.10) is $\xi^T = (\xi_1 \xi_2 \xi_3)$ which satisfies the nonlinear equations

$$(2.6.13)\quad \begin{bmatrix} \xi_1 \\ \xi_2 \\ \xi_3 \end{bmatrix} = \begin{bmatrix} 1 & \frac{D_1}{1 + D_1} & \frac{D_2}{1 + D_2} \\ 0 & \frac{1}{1 + D_2} & 0 \\ 0 & 0 & \frac{1}{1 + D_1} \end{bmatrix} \begin{bmatrix} w_1 - \frac{a\ \xi_1\ \xi_2}{A + \xi_1} \\ w_2 + \xi_2\left(\frac{a\ \xi_1}{A+\xi_1} - \frac{b\ \xi_2}{B+\xi_2}\right) \\ w_3 + \frac{b\ \xi_2\ \xi_3}{B + \xi_2} \end{bmatrix}$$

Theorem 2.6.1 gives the output environ vectors and matrices in the form of integral equations.

The output environ <u>storage</u> <u>vectors</u> due to unit initial storages and zero input functions are

$$(2.6.14)\quad e_1^{\prime\prime 0}(t) = \begin{bmatrix} e_{11}^0(t) \\ e_{21}^0(t) \\ e_{31}^0(t) \end{bmatrix} = e^{-t} \begin{bmatrix} 1 \\ 0 \\ 0 \end{bmatrix} + \left[\int_0^t V(t - \tau)\ \Phi(e_1^{\prime\prime 0}(\tau))d\tau\right] ;$$

for $X_0^T = [1 \quad 0 \quad 0]$ and $z(t) = [0 \quad 0 \quad 0]$

$$(2.6.15)\quad e_2^{\prime\prime 0}(t) = \begin{bmatrix} e_{12}^0(t) \\ e_{22}^0(t) \\ e_{32}^0(t) \end{bmatrix} = e^{-t} \begin{bmatrix} 1 - e^{-D_1 t} \\ e^{-D_1 t} \\ 0 \end{bmatrix}$$

$$+ \left[\int_0^t V(t - \tau)\ \Phi(e_2^{\prime\prime 0}(\tau))d\tau\right]$$

for $X_0^T = [0 \quad 1 \quad 0]$, $z(t) = [0 \quad 0 \quad 0]$ and

$$\overset{''}{e}{}_3^0(t) = \begin{bmatrix} e_{13}^0(t) \\ e_{23}^0(t) \\ e_{33}^0(t) \end{bmatrix} = e^{-t} \begin{bmatrix} 1 - e^{-D_2 t} \\ 0 \\ e^{-D_2 t} \end{bmatrix} +$$

$$+ [\int_0^t V(t - \tau) \ \Phi(\overset{''}{e}{}_3^0(\tau) \ d\tau]$$

for $X_0^T = [0 \quad 0 \quad 1]$, $z(t) = [0 \quad 0 \quad 0]$.

The output environ flow matrices due to unit initial storages are

(2.6.17) $$\overset{''}{E}{}_i^0(t) = \overset{''}{A} \ D_{\overset{''}{e}{}_i^0(t)} + D_{\Phi(\overset{''}{e}{}_i^0(t))} \quad , \quad i = 1,\ 2,\ 3 \ ,$$

and

(2.6.18) $$\overset{''}{Y}{}_i^0(t) = \overset{''}{C} \ \overset{''}{e}{}_i^0(t) \ .$$

The output environ storage vectors due to unit input functions $\hat{z}(t)$ are

(2.6.19) $$\overset{''}{e}{}_1^z = \begin{bmatrix} 1 - e^{-t} \\ 0 \\ 1 \end{bmatrix} + [\int_0^t V(t - \tau) \ \Phi(\overset{''}{e}{}_1^z(\tau)) \ d\tau]$$

for $z^T(t) = [1 \quad 0 \quad 0]$, $x_0^T = [0 \quad 0 \quad 0]$;

$$(2.6.20) \quad \overset{''}{e}{}^z_2(t) = \begin{bmatrix} (1 - e^{-t}) - \frac{1}{1 + D_1}(1 - e^{-t(1+D_1)}) \\ \frac{1}{1 + D_1}(1 - e^{-t(1+D_1)}) \\ 0 \end{bmatrix}$$

$$+ [\int_0^t V(t - \tau)\ \Phi(\overset{''}{e}{}^z_2(\tau))d\tau]$$

for $z^T(t) = [0 \quad 1 \quad 0]$, $x_0^T = [0 \quad 0 \quad 0]$;

and

$$(2.6.21) \quad \overset{''}{e}{}^z_3(t) = \begin{bmatrix} (1 - e^{-t}) - \frac{1}{1 + D_2}(1 - e^{-t(1+D_2)}) \\ 0 \\ \frac{1}{1 + D_2}(1 - e^{-t(1+D_2)}) \end{bmatrix} +$$

$$+ [\int_0^t V(t - \tau)\ \Phi(\overset{''}{e}{}^z_3(\tau))d\tau]$$

for $z^T(t) = [0 \quad 0 \quad 1]$, $x_0^T = [0 \quad 0 \quad 0]$.

The output environ flow matrices due to unit input functions are

$$(2.6.22) \quad \overset{''}{E}{}^z_i(t) = \overset{''}{A}\ D_{\overset{''}{e}{}^z_i(t)} + D_{\Phi(\overset{''}{e}{}^z_i(t))}$$

$$(2.6.23) \quad \overset{''}{Y}{}^z_i(t) = \overset{''}{C}\ \overset{''}{e}{}^z_i(t) \ .$$

Asymptotic Behavior of Output Environs:

As a consequence of Theorem (1.2.4), the asymptotic output environ vectors due to unit initial storages satisfy the following equations

$$(2.6.24)\quad e_i^{''0}(\infty) = \begin{bmatrix} e_{1i}^{*0} \\ e_{2i}^{*0} \\ e_{3i}^{*0} \end{bmatrix} = \begin{bmatrix} 1 & \frac{D_1}{1 + D_1} & \frac{D_2}{1 + D_2} \\ 0 & \frac{1}{1 + D_1} & 0 \\ 0 & 0 & \frac{1}{1 + D_2} \end{bmatrix} \cdot \begin{bmatrix} -\frac{a\, e_{1i}^{*0}\, e_{2i}^{*0}}{A + e_{1i}^{*0}} \\ e_{2i}^{*0} \left(\frac{a\, e_{1i}^{*0}}{A + e_{1i}^{*0}} - \frac{b\, e_{2i}^{*0}}{B + e_{2i}^{*0}}\right) \\ \frac{b\, e_{2i}^{*0}\, e_{3i}^{*0}}{B + e_{2i}^{*0}} \end{bmatrix} \quad (i = 1,\ 2,\ 3).$$

Similarly, the asymptotic output environ vector due to unit inputs satisfy the following equations:

$$(2.6.25)\quad e_i^{''z}(\infty) = \begin{bmatrix} e_{1i}^{*z} \\ e_{2i}^{*z} \\ e_{3i}^{*z} \end{bmatrix} = \begin{bmatrix} 1 & \frac{D_1}{1 + D_1} & \frac{D_2}{1 + D_2} \\ 0 & \frac{1}{1 + D_1} & 0 \\ 0 & 0 & \frac{1}{1 + D_2} \end{bmatrix} \cdot$$

$$\cdot \begin{bmatrix} -\dfrac{a\, e^{*z}_{1i}\, e^{*z}_{2i}}{A + e^{*z}_{1i}} \\ e^{*z}_{2i}\left(\dfrac{a\, e^{*z}_{1i}}{A + e^{*z}_{1i}} - \dfrac{b\, e^{*z}_{3i}}{B + e^{*z}_{2i}}\right) \\ b\, \dfrac{e^{*z}_{2i}\, e^{*z}_{3i}}{B + e^{*z}_{2i}} \end{bmatrix} + \begin{bmatrix} e_i \end{bmatrix} \qquad (i = 1, 2, 3)$$

where $e_i^T = [0 \cdots \overset{i}{\overset{\downarrow}{1}} \cdots\cdot 0]$.

Employing (2.6.23) and (2.6.24), the rest of the asymptotic output environ matrices can be formulated as follows:

(2.6.26) $\overset{\prime\prime}{E}{}^{0}_{i}(\infty) = A\, D_{\overset{\prime\prime}{e}{}^{0}_{i}(\infty)} + D_{\phi(\overset{\prime\prime}{e}{}^{0}_{i}(\infty))}$; $i = 1, 2, 3$.

(2.6.27) $\overset{\prime\prime}{Y}{}^{0}_{i}(\infty) = \overset{\prime\prime}{C}\, \overset{\prime\prime}{e}{}^{0}_{i}(\infty)$;

(2.6.28) $\overset{\prime\prime}{E}{}^{z}_{i}(\infty) = \overset{\prime\prime}{A}\, D_{\overset{\prime\prime}{e}{}^{z}_{i}(\infty)} + D_{\phi(\overset{\prime\prime}{e}{}^{z}_{i}(\infty))}$;

and

(2.6.29) $\overset{\prime\prime}{Y}{}^{z}_{i}(\infty) = \overset{\prime\prime}{C}\, \overset{\prime\prime}{e}{}^{z}_{i}(\infty)$.

Next, estimates for the deviations of the environ vectors $\overset{\prime\prime}{e}{}^{0}_{i}(t)$ and $\overset{\prime\prime}{e}{}^{z}_{i}(t)$ from their asymptotic values $\overset{\prime\prime}{e}{}^{0}_{i}(\infty)$ and $\overset{\prime\prime}{e}{}^{z}_{i}(\infty)$ respectively are obtained in terms of the norm of the nonlinear functions $||\Phi(\overset{\prime\prime}{e}{}^{0}_{i}(\infty))||$

and $\|\Phi(e_i^{''z}(\infty))\|$. From the identities,

$$\|W(t)\| = 3e^{-t} \;;\quad \|e_i^{''0}(0)\| = 1 \;;\quad \|V(t - \tau)\| = 3e^{-(t-\tau)}$$

and the Lipschitz condition

$$\|\Phi(e_i^{''0}(\tau)) - \Phi(e_i^{''0}(\infty))\| \leq \varepsilon_i \|e_i^{''0}(\tau) - e_i^{''0}(\infty)\|$$

and from the facts that

$$\left\|\int_0^t Y(t - \tau)d\tau - V(\tau)\right\| = 3e^{-3t} \;,$$

it follows that

$$(2.6.30) \quad \|e_i^{''0}(t) - e_i^{''0}(\infty)\| \leq 3e^{-(1-3\varepsilon_i)t} \;.$$

Similar estimates can be derived for the deviation of $e_i^{''z}(t)$ from $e_i^{''z}(\infty)$. From

$$(2.6.31) \quad [e_i^{''z}(t) - e_i^{''z}(\infty)] = \int_0^t [V(t - \tau)d\tau - V(\infty)]\; \Phi(e_i^{''z}(\infty)) +$$

$$+ \int_0^t V(t - \tau)\; [\Phi(e_i^{''z}(\tau)) - \Phi(e_i^{''z}(\infty))]$$

$$+ \left[\int_0^t V(t - \tau)d\tau - V(\infty)\right] z(\infty) +$$

$$+ \int_0^t V(t - \tau)[z(\tau) - z(\infty)]d\tau$$

we find

$$(2.6.32)\quad \| e_i^{\prime\prime z}(t) - e_i^{\prime\prime z}(\infty) \| \le 3 \| \Phi(e_i^{\prime\prime z}(\infty)) + z(\infty) \| \, e^{-(1-3\varepsilon_i)t} \; .$$

Nonlinear Input Environ Analysis

The production matrix for the above model is

$$(2.6.33)\quad P(t) = \left[\begin{array}{c|c|c} 0 & 0 & 0 \\ \hline P_{21}(t) & P_{22}(t) & 0 \\ \hline 0 & P_{32}(t) & 0 \end{array}\right]$$

where

$$P_{21}(t) = \left[\begin{array}{ccc|ccc} w_1 & 0 & 0 & \dot{N}(t) & 0 & 0 \\ 0 & w_2 & 0 & 0 & \dot{P}(t) & 0 \\ 0 & 0 & w_3 & 0 & 0 & \dot{z}(t) \end{array}\right] ;$$

$$P_{22}(t) = \begin{bmatrix} 0 & D_1 P(t) & D_2 z(t) \\ \dfrac{aN(t)P(t)}{A + N(t)} & 0 & 0 \\ 0 & \dfrac{b\,P(t)z(t)}{B + P(t)} & 0 \end{bmatrix} ;$$

and

$$P_{32}(t) = \begin{bmatrix} N(t) & 0 & 0 \\ 0 & P(t) & 0 \\ 0 & 0 & z(t) \end{bmatrix} .$$

The flow structure matrix is $\overset{\prime}{N}(t) = (I - \overset{\prime}{Q}(t))^{-1}$ where $\overset{\prime}{Q}(t)$ has the same definition as in (2.4.50):

$$(2.6.34)\quad \dot{Q}(t) = \begin{bmatrix} 0 & \dfrac{D_1P}{\Delta_1} & \dfrac{D_2Z}{\Delta_2} \\ \dfrac{\dfrac{a\ NP}{A + N}}{\Delta_2} & 0 & 0 \\ 0 & \dfrac{\dfrac{b\ PZ}{B + P}}{\Delta_2} & 0 \end{bmatrix}$$

where

$$\Delta_1 = w_1 + D_1P + D_2Z - \dot{N} ;$$

$$\Delta_2 = w_2 + \frac{a\ NP}{A + N} - \dot{P} ;$$

and

$$\Delta_3 = w_3 + \frac{b\ Pz}{B + P} - \dot{Z} .$$

Thus,

$$(I - \dot{Q}(t)) = \begin{bmatrix} 1 & \dfrac{-D_1\ P}{N(1+\dfrac{aP}{A+N})} & \dfrac{-D_2Z}{N(1 + \dfrac{aP}{A + N})} \\ \dfrac{-aN}{(A+N)(1+D_1+ \dfrac{bZ}{B + P})} & 1 & 0 \\ 0 & \dfrac{-bP}{(B+P)(1+D_2)} & 1 \end{bmatrix}$$

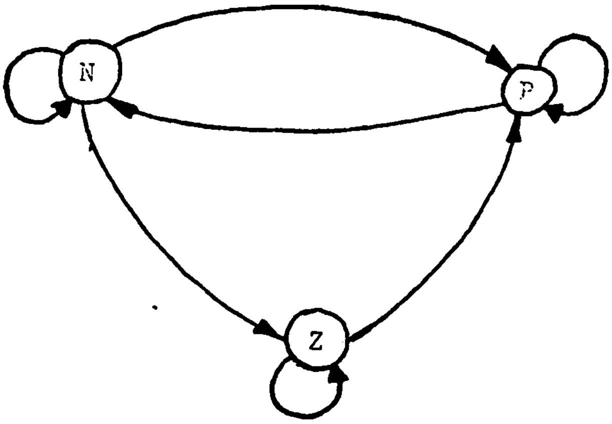
The matrix $(I - \overset{\prime}{Q}(t))$ is nonsingular for $X(t)$ sufficiently small. To see this, it suffices to show that

(i) $(I - \overset{\prime}{Q}(t))$ is connected;

and

(ii) $(I - \overset{\prime}{Q}(t))$ is diagonally dominant.

For (i), it is clear that $(I - \overset{\prime}{Q}(t))$ is connected from the matrix flow diagram



For (ii), in the third row, for diagonal dominance

$$\left|\frac{-b\ P(t)}{(B + P(t))(1 + D_2)}\right| < 1$$

or

$$P(t) \leq \frac{B(1 + D_2)}{b - (1 + D_2)} = \theta_2$$

Now, assuming that $N(t) < \theta_1$ for all $t \in [0, T]$, then from the first and second rows

$$(2.6.34) \quad D_1\ P(t) + D_2\ Z(t) < N(t) + \frac{a\ \theta_2\ N(t)}{A + N(t)}$$

and

$$(2.6.35) \quad \frac{a\ N(t)}{A + N(t)} < (1 + D_1) + \frac{b}{B} z(t) \ .$$

Thus, from (2.6.34) and (2.6.35)

$$(2.6.36) \quad z(t) < \frac{\theta_1 + (1 + D_1)\ \theta_2}{(D_2 - b/B\ \theta_2)}$$

where

$$D_2 > \frac{b}{B} \theta_2 \quad \text{if} \quad \theta_2 < \frac{B\ D_2}{b} \ .$$

Hence, for diagonal dominance

$$N(t) < \theta_1 \ ; \quad P(t) \leq \theta_2 = \min\{\frac{B\ D_2}{b} \ , \ B\frac{(1 + D_2)}{b - (1 + D_2)}\} \quad ;$$

and

$$z(t) < \frac{\theta_1 + (1 + D_1)\ \theta_2}{(D_2 - \frac{b}{B}\ \theta_2)} \quad \text{for all} \quad t \in [0, T] \ ,$$

and from (i) and (ii), $(I - \dot{Q}(t))^{-1}$ exists. As in linear models, the partitions of inflow, time derivatives of storages, and compartmental throughflow in terms of the output vector $Y(t)$ are given by

$$(2.6.37) \quad [z^T(t) - \dot{x}^T(t) \ \vdots \ T^T(t) \ \vdots \ Y^T(t)]$$

$$= Y^T(t)[N_3(t) \ \vdots \ \dot{N}(t) \ \vdots \ I]$$

where

$$\overset{\prime}{N}(t) = (I - \overset{\prime}{Q}(t))^{-1}$$

$$N_{31}(t) = Q_{21}(t)\ \overset{\prime}{N}(t)\ .$$

From the analysis in sections 2.4, 2.5, and 2.6, we can conclude that linear and nonlinear output and input environ partitions have, in general, similar formulations. Besides the regularity assumption in the linear case, the function $\Phi(X(t))$ in the nonlinear models has to satisfy some continuity, differentiability, boundedness, etc. conditions for the environ vectors to exist and to converge for large values of t. Although the computation of the linear output environ is straightforward and simple, it is quite tedious and needs some numerical techniques in the nonlinear case. Another essential difference between the two cases is that the linear output environ matrices are independent of the magnitude of the initial values or the input functions, but the nonlinear output environ matrices are dependent on the nonlinear part, $\Phi(X)$, and cannot be scaled to different initial values or different inputs. As for input environ analysis, especially using the production matrix method, the basic equations are the same except in the nonlinear case we have to specify a neighborhood $\mathcal{D}$ of $X = 0$ such that $(I - \overset{\prime}{Q}(t))^{-1}$ exists for all $X \in \mathcal{D}$.

2.7. Environ Analysis for Systems of Differential Equations With Time Delay

2.7.1 Introduction

In the mathematical formulation of ecological models, the simplest approach is to assume that the future behavior of the system depends only upon the present state and not at all upon its past history, and furthermore, that the influence of the present state is instantaneous. This assumption leads to a system of ordinary differential equations. In modern modelling theory the physical processes are sometimes controllable. Control processes often involve nonnegligible time delays between any particular incident in the behavior of the quantities being controlled, and the result of the operation of the controlling system brought about by this incident. Moreover, for some ecological systems the hereditary effects have a considerable importance during the evolution of the process. A formulation by a system of ordinary differential equations is not possible to describe processes of this kind; but, they can be described by a system of delay-differential equations. The significance of these equations lies in their ability to describe processes with after effect.

In this section an attempt to present in a connected fashion the theory of environs and ordinary delay-differential equations is made. The first part of this section, (2.7.2), is a systematic introduction to the type of delay models considered. In the second part, (2.7.3), input-output environ partitions are derived for a simple delayed system.

2.7.2. Adjoint Linear Delay-Differential Equations: [12]

In this section we shall investigate a simple version of the linear integro-difference-differential equations of the form

$$(2.7.1) \qquad \dot{X}(t) + \lambda \sum_{\nu=0}^{m} A_\nu(t)\, X(t - h_\nu) + \mu \int_{t_0}^{t} K(\tau, t)\, X(\tau)\, d\tau = Z(t) ,$$

where λ and μ are two arbitrary real parameters, and

$$(2.7.2) \qquad 0 = h_0 < h_1 < h_2 < \ldots < h_m .$$

We assume that

(i) the matrices $A_\nu(t)$, $\nu = 0, 1, \ldots, m$, are continuous for $t \geq t_0$;

(ii) the kernel $K(\tau, t)$ is continuous in τ for $\tau \in I[t_0, t]$ and in t for $t \geq t_0$;

(iii) the vector function $Z(t)$ is continuous for $t \geq t_0$.

Let $\Phi(t) \in C(I[\alpha, t_0], G)$, G being any compact set in E^n and $\alpha = t_0 - h_m$. It is known that [12] for the system (2.7.1), the solution $X(t, t_0, \phi, Z)$ corresponding to the initial function $\phi(t)$ has the form

$$(2.7.3) \qquad X(t, t_0, \phi, Z) = \int_{\alpha}^{t_0} M(\sigma, t)\phi(\sigma)\, d\sigma + \int_{t_0}^{t} N(\sigma, t) Z(\sigma)\, d\sigma$$

where the kernel matrices $M(\sigma, t)$ and $N(\sigma, t)$ of the first and second kind satisfy the adjoint equations

$$(2.7.4) \quad \frac{\partial M(\sigma, t)}{\partial t} + \lambda \sum_{\nu=0}^{m} A_\nu(t) M(\sigma, t - h_\nu) + + \mu \int_{t_0}^{t} K(\tau, t) M(\sigma, \tau) d\tau = 0$$

with initial conditions

$$(2.7.5) \quad M(\sigma, t) = \delta(t - \sigma)I \quad \text{for} \quad t \in I[\alpha, t_0], \quad \sigma \in I[\alpha, t_0]$$

and

$$(2.7.6) \quad \frac{\partial N(\sigma, t)}{\partial t} + \lambda \sum_{\nu=0}^{m} A_\nu(t) N(\sigma, t - h_\nu) + + \mu \int_{\sigma}^{t} K(\tau, t) N(\sigma, \tau) d\tau = 0$$

with initial conditions

$$(2.7.7) \quad N(\sigma, t) = \begin{cases} 0 & \text{for} \quad t < \sigma \\ I & \text{for} \quad t = \sigma \end{cases}$$

or equivalently the Volterra integral equations

$$(2.7.8) \quad M(\sigma, t) = F(\sigma) + \int_{t_0}^{t} G(\tau, t) M(\sigma, \tau) d\tau$$

$$\text{for} \quad t > t_0 , \ \sigma \in I[\alpha, t_0] ,$$

and

$$(2.7.9) \quad N(\sigma, t) = I + \int_{\alpha}^{t} G(\tau, t)\, N(\sigma, \tau) d\sigma$$

$$\text{for} \quad t > \sigma \ , \ \sigma \geq t_0$$

where the matrices $F(\sigma)$ and $G(\tau, t)$ are defined by

$$(2.7.10) \quad F(\sigma) = \sum_{\nu=0}^{m} A_{\nu}(\sigma, h_{\nu})[e(\sigma - t_0 + h_{\nu}) - e(\sigma - t_0)]$$

and

$$(2.7.11) \quad G(\tau, t) = \int_{\tau}^{t} K_1(\tau, s) ds + \sum_{\nu=0}^{m} A_{\nu}(\tau + h_{\nu})\ e(t - h_{\nu} - \tau)$$

where

$$(2.7.12) \quad e(t) = \begin{cases} 0 & \text{for} \quad t < 0 \\ 1 & \text{for} \quad t > 0 \ ; \end{cases}$$

$$(2.7.13) \quad K_1(\tau, t) = \int_{\tau}^{t} K(\sigma, s) ds \ ;$$

and

$$(2.7.14) \quad \delta(t) = \begin{cases} 0 & \text{for} \quad t \neq 0 \\ +\infty & \text{for} \quad t = 0 \quad . \end{cases}$$

The matrices M and N are uniquely determined.

2.7.3. Environ Analysis For Delayed Systems of Differential Equations

As a generalization to the input-output environ analysis, a simple system of differential equations with a single time delay is presented and studied in detail. Consider the equation

$$\dot{X}(t) + \lambda A_0(t) X(t) + \lambda A_1(t) X(t - t_0) = Z(t) \tag{2.7.15}$$

with initial function $\phi(t)$ defined for $t \in I[0, t_0]$. The solution of this system is in the form

$$X(t, t_0, \phi, Z) = \int_0^{t_0} M(\sigma, t)\phi(\sigma)\, d\sigma + \int_{t_0}^{t} N(\sigma, t)\, Z(\sigma)\, d\sigma \tag{2.7.16}$$

where

$$M(\sigma, t) = F(\sigma) + \int_{t_0}^{t} G(\tau, t) M(\sigma, \tau)\, d\tau \text{ for } t > t_0, \sigma \in [0, t_0], \tag{2.7.17}$$

$$N(\sigma, t) = I + \int_{\sigma}^{t} G(\tau, t)\, N(\sigma, \tau)\, d\tau \tag{2.7.18}$$

where

$$F(\sigma) = A_0(\sigma + t_0)(e(\sigma) - e(\sigma - t_0)) , \tag{2.7.19}$$

and

$$G(\tau, t) = A_0(\tau)e(t - \tau) + A_1(\tau + h_0)e(t - t_0 - \tau) . \tag{2.7.20}$$

Output Environ Analysis

The output environ matrices for the above system are given by the following theorem.

Theorem 2.7.1. The output environ flow and storage matrices for the system (2.7.15) are

(i) the output environ storage matrices, $\ddot{\mathcal{E}}^0(t)$ and $\ddot{\mathcal{E}}^z(t)$ that partition unit initial storages and unit input functions respectively

$$(2.7.21) \quad \ddot{\mathcal{E}}^0(t) = \left(\ddot{e}_1^0(t) \,\vdots\, \text{-------} \,\vdots\, \ddot{e}_n^0(t) \right) = \int_0^{t_0} M(\sigma, t)\, d\sigma \,,$$

$$(2.7.22) \quad \ddot{\mathcal{E}}^z(t) = \left(\ddot{e}_1^z(t) \,\vdots\, \text{-------} \,\vdots\, \ddot{e}_n^z(t) \right)$$

$$= \left[\int_{t_0}^{t} \eta_i(\sigma, t)\, \hat{z}_1(\sigma)\, d\sigma \,\vdots\, \vdots \int_{t_0}^{t} \eta_n(\sigma, t) \hat{z}_n(\sigma) d\sigma \right]$$

where $\eta_i(\sigma, t)$ is the $i^{\underline{th}}$ column of $N(\sigma, t)$;

(ii) the output environ flow matrices $\ddot{E}_i^0(t)$ and $\ddot{E}_i^0(t - t_0)$ that partition unit initial storages

$$(2.7.23) \quad \ddot{E}_i^0(t) = A_0(t)\, D_{\ddot{e}_i^0(t)} \,, \quad \text{for} \quad t > t_0 \,,\ \sigma \in I[\alpha, t_0] \,,$$

and

$$(2.7.24) \quad \ddot{E}_i^0(t - t_0) = A_1(t)\, D_{\ddot{e}_i^0(t-t_0)} \quad \text{for} \quad \sigma \geq t_0 \,,\ t > \sigma \,;$$

$$+ A_0(t)\, D_{\ddot{e}_i^0(t)}$$

(iii) the output environ flow matrices $\overset{\prime\prime}{E}{}^z_i(t)$ that partition unit input functions

(2.7.25) $$\overset{\prime\prime}{E}{}^z_i = A_0(t)\, D_{\overset{\prime\prime}{e}{}^z_i(t)} \quad , \text{ for } t > t_0 \; , \; \sigma \in I[\alpha, t_0]$$

(2.7.26) $$= A_1(t)\, D_{\overset{\prime\prime}{e}{}^z_i(t - t_0)} \quad \text{for } \sigma \geq t_0 \; , \; t > \sigma \; .$$
$$+ A_0(t)\, D_{\overset{\prime\prime}{e}{}^z_i(t)}$$

Input Environ Analysis

In this case the system production matrix, $P(t)$, is modified to include the effect of the delayed flows.

Consider again the system (2.7.15) or equivalently

(2.7.27) $$\dot{X}(t) = F_0(t).1 + F_1(t - t_0).1 + z(t)$$

where $1 = [1 \ldots 1 \ldots 1]^T$.

For the above system, define the throughflow through the compartment j as follows:

(2.7.28) $$T_j(t) = \sum_{\substack{k=1 \\ k \neq j}}^{n} [f_{(0)jk}(t) + f_{(1)jk}(t - t_0)] + z_j(t) - \dot{x}_j^-(t)$$

or

(2.7.29) $$T_j(t) = \sum_{\substack{k=1 \\ k \neq j}}^{n} [f_{(0)kj}(t) + f_{(1)kj}(t - t_0)] + y_j(t) + \dot{x}_j^+(t)$$

From this definition, the modified production matrix, the partitions of inflows, time derivatives of storages and compartmental throughflows in terms of the output vector y(t) will be similar to (2.4.47) and (2.4.48) except in this case

$$f_{ij} = f_{(0)ij}(t) + f_{(1)ij}(t - t_0) \ . \tag{2.7.30}$$

2.8. Conclusions

Environ Analysis (input-output analysis) is introduced in ecology to provide information about input origins, output destinations of both flows and storages within the system, the number of intercompartmental transfers among different components and the expectations and variances for the residence time components as well as for total time in the system. It differs from previous flow analysis methods in providing storage partitions in addition to the usual flow partitions accomplishing both by more straightforward formulations and computation procedures using partitioning matrices and vectors.

As shown in sections 2.5, 2.6, and 2.7, static input-output-environ analysis for time-invariant linear intercompartmental systems can be extended to the cases of time varying coefficient matrix and input functions, specific classes of nonlinear systems and to models described by systems of differential equations with constant time delay.

Though linear systems theory is a powerful tool to investigate most classes of systems as long as the system is operating near an equilibrium point, a new method based on the results of Theorem 1.2.4 was introduced to analyze nonlinear systems. The output and input matrices in this case and in the case of time delay are given in the form of simple integral equations.

CHAPTER III

SOME NONLINEAR DYNAMIC MODELS OF EUTROPHICATION

3.1. Introduction

Biological production in any body of water plays an important role in determining the quality of that body of water. Increase in biological production due to increased nutrient content has been seen to have a profound impact on the overall condition of the natural water [10] . Eutrophication is the term used to describe this process by which an increase in biological production occurs. Fundamentally, it is described as an increase in the nutrient supply from soil and lake processes and from human activities in the drainage basin; this results in an increase in biological production. The sector which is most directly affected by this increase in nutrient content and therefore experiencing the most profound fluctuations is the phytoplankton population. The majority of the studies in this field have been done only within the past twenty years and many have been concerned with the lake eutrophication [9] . Some of the lakes extensively studied in the United States are the Laurencian Great Lakes with the most attention being given to Lake Michigan and Lake Erie.

The quality of natural waters can be markedly influenced by the growth and distribution of phytoplankton. Utilizing radiant energy, these microscopic plants assimilate inorganic chemicals and convert them to cell material which, in turn, is consumed by the various animal species in the next trophic levels. Thus, the existence of phytoplankton is essential to all aquatic life. On the other hand, the quality of a body of water can be adversely affected if the population of phytoplankton becomes so large as to interfere with either water use or the higher forms of aquatic life. In particular, high concentrations of algal biomass cause large diurnal variations in dissolved oxygen which can be fatal to fish life. Phytoplankton can also cause taste and odor problems in water supplies and, in addition, contribute to filter clogging in water treatment plants.

In this chapter two phytoplankton population models in natural waters are presented. These models are constructed on the basis of the principle of conservation of mass. The primary purpose of this work is to introduce some models of phytoplankton population dynamics as a step towards the more important goal of controlling this phenomenon.

In the first model, dynamics of the nitrogen cycle in a lake are analyzed and conditions for persistence and noncyclic behavior are given. In the second model, dynamics of both the nitrogen and phosphorus cycles are combined and similar persistence results are proved.

3.2. Review of Previous Grazing Formulation

The interaction between the phytoplankton population and the next trophic level, the herbivorous zooplankton, is a complex process. In the literature, three types of grazing representations prevail . The earliest formulation for the grazing function (Lotka 1925, Volterra 1928), the mass action product, considered the grazing rate G , as directly proportional to the product of the concentration of nutrient in phytoplankton and zooplankton.

$$(3.2.1) \qquad G(P, Z) = kPZ$$

where k is a proportionality constant. However, this formulation has a serious disadvantage, as pointed out by Smith (1952) and Minorsky (1962). Equation (3.2.1) appears inadequate under conditions of abundant food supply where the grazing rate should become proportional only to the zooplankton population, Z . When phytoplankton is superabundant, zooplankton will feed at a maximum rate per unit zooplankton biomass, and further increase in phytoplankton supply will not be reflected in increased grazing rates.

Modifications of (3.2.1) have been suggested (Ivlev 1961, Gallopin 1971a,b) of the form

$$(3.2.2) \qquad G = E\ Z(1 - e^{-LP}) \quad \text{(Ivlev);}$$

$$(3.2.3) \qquad G = E\ Z(1 - e^{-\alpha\ P/Z}) \quad \text{(Gallopin).}$$

where E and α are constants. A third formula for grazing is a Michaelis-Menten-Monod (M^3) type which has been widely used, e.g., see Di Toro et al (1971), Steele (1974), and Walsh (1975)

$$(3.2.4) \qquad G = E\ \frac{ZP}{R + P}$$

where E and R are constants. Equations (3.2.2)-(3.2.4) permit grazing rate to become proportional to zooplankton population as phytoplankton becomes abundant. However, formulation (3.2.4) has conceptual shortcomings. First, as pointed out by D.L. DeAngelis (1975) situations can occur in which consumer population density, Z , increases but G will not increase proportionally as a result of natural interference between consumers. Second, from the stability analysis of equilibrium points associated with (3.2.4), (T.G. Hallam 1977, 1978) the equilibrium value of the phytoplankton population is independent of the total nutrient in the system which does not reflect the eutrophication phenomenon.

Therefore, a modification of equation (3.2.4) is suggested to overcome the above two shortcomings:

$$(3.2.5) \qquad G = \frac{E\ P\ Z}{R + P + bZ}$$

where E and R are parameters of the model measured in units of time^{-1} , concentrations of nutrients respectively and b is the dimensionless normalizing constant $(0 \leq b)$.

3.3. A Modified Mathematical Model for Nitrogen in a Two Trophic Level Aquatic System

The aquatic model studied here is a two trophic level system consisting of a resource component, nitrogen; a plant component, phytoplankton; and a herbivore component, zooplankton. The nitrogen in the system is assumed to be conservative and is fundamental in the sense that a modification of the total amount of nutrient can have significant effect upon the balance of the system.

The principle of conservation of nutrient (nitrogen) for each element in Figure (3.1) gives

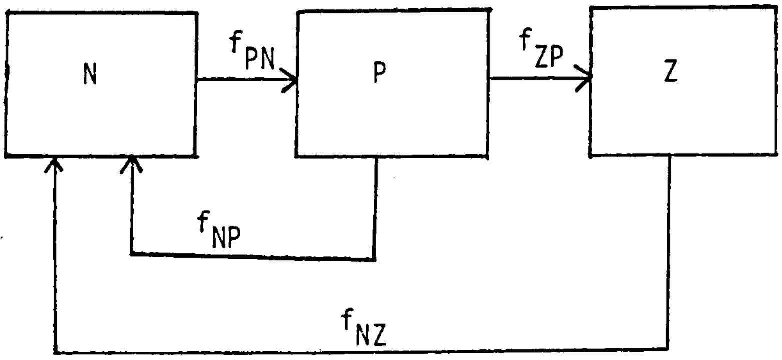


Figure 3.1

Two trophic conservative aquatic model.

(3.3.1)
$$\dot{P} = P[\frac{Vm\ N}{K+N} - B - \frac{E\ Z}{R + P + bZ}]$$

$$\dot{Z} = Z[\frac{\theta\ E\ P}{R + P + bZ} - D]$$

$$\dot{N} = -\frac{Vm\ P\ N}{K+N} + BP + DZ + E(1 - \theta)\ \frac{P\ Z}{R + P + bZ}\ ,$$

$$0 < \theta \leq 1$$

and

(3.3.2) $P + Z + N = M =$ constant

where

N = concentration of nitrogen in the pool (μgm N/ℓ)

P = concentration of phytoplankton nitrogen (μgm N/ℓ)

Z = concentration of zooplankton nitrogen (μgm N/ℓ)

B = death (or washout) rate of phytoplankton (hr^{-1})

D = death (or washout) rate of zooplankton (hr^{-1})

$\frac{Vm\ N}{K + N}$ is the growth rate of phytoplankton (uptake of nutrient by phytoplankton;

Vm is the maximum uptake rate (hr^{-1}) of nutrient by phytoplankton;

K is the concentration of nutrient that supports one half of the maximum uptake rate.

$\frac{\theta\ E\ P}{R + P + bZ}$ is the growth rate of zooplankton;

θ is the zooplankton conversion efficiency;

E, R, and b are as given in (3.2.5) .

Since all the physical quantities are non-negative, take the following hypotheses:

(1) The variables P, Z, and N are nonnegative.

(2) All values of the system parameters are positive.

Assumptions.

In this model, we consider an idealized aquatic system, (i.e. water temperature, light intensity at the surface and photo-period are constants). Therefore, all system parameters are also constants. Some properties of the solutions of (3.3.1):

1. There exists a unique solution $X(t)$ satisfying $X(t_0) = X_0$ for each $X_0 \in \mathcal{D} = \{(P, Z, N); P, Z, N \geq 0\}$. [Picard-Lindelof theorem (Hall 1969)] .

2. The solution of (3.3.1) is nonnegative. (It is necessary and sufficient to prove that $\dot{N}|_{N=0} \geq 0$, $\dot{P}|_{P=0}$ and $\dot{Z}|_{Z=0} \geq 0$ where (P_0, Z_0, N_0) is the initial point).

Critical points of (3.3.1)

The above system has the form

$$\dot{P} = P[v_m \psi_1(N) - B - E Z \phi_1(P, Z)] \tag{3.3.3}$$

$$\dot{Z} = Z[\theta EP \phi_1(P, Z) - D]$$

$$\dot{N} = -V_m P \psi_1(N) + BP + DZ + E(1 - \theta) PZ \phi_1(P, Z)$$

with

$$\psi_1(N) = \frac{N}{K + N} \quad , \text{ and} \tag{3.3.4}$$

$$\phi_1(P, Z) = \frac{1}{R + P + bZ} \ .$$

The substitution of (3.3.2) into (3.3.1) yields

$$\dot{P} = P[V_m \psi_1(M - P - Z) - B - E Z \phi_1(P, Z)] \ , \text{ and}$$

(3.3.5)

$$\dot{Z} = Z[\theta E P \phi_1(P, Z) - D]$$

which is a two-dimensional system in the variables P and Z .

The point $(P, Z) = (0, 0)$ is always an equilibrium point of (3.3.5).

If the equation

$$(3.3.6) \qquad V_m \psi_1(M - P) - B = 0$$

has a positive solution P_2^* , that is, if

$$(3.3.7) \qquad M > \frac{BK}{V_m - B} > 0 \text{, where it is assumed that } V_m > B \text{ ,}$$

then the point $(P, Z) = (P_2^*, 0)$ becomes an equilibrium point, where

$$(3.3.8) \qquad P_2^* = M - \frac{BK}{V_m - B} \quad .$$

If we have the solution (P_3^*, z_3^*) of the equation

$$(3.3.9) \qquad \theta E F \phi_1(P_3^*, Z_3^*) - D = 0$$

$$(3.3.10) \quad V_m \psi_1(M - P_3^* - Z_3^*) - B Z_3^* \phi_1(P_3^*, Z_3^*) = 0$$

in the domain $\mathcal{D}$, that is if

$$0 < P_3^* < M \text{ , } 0 < Z_3^* < M$$

then the point (P_3^*, Z_3^*) is an equilibrium point.

<u>The Equilibrium Point</u> (P_3^*, Z_3^*)

For simplicity we assume $\theta = 1$. Then the system is reduced to

(3.3.11a) $\dot{P} = P[\frac{V_m N}{K + N} - B - \frac{E Z}{R + P + bZ}]$

(3.3.11b) $\dot{Z} = Z[\frac{E P}{R + P + bZ} - D]$

(3.3.11c) $\dot{N} = - \frac{N P V_m}{K + N} + BP + DZ$.

At equilibrium, and with $PZ N \neq 0$, equation (3.3.11b) gives

(3.3.12) $P = \frac{DR}{E - D} + \frac{D bZ}{E - D} = P^* + K_1 Z$

where P^* is the equilibrium value for $b = 0$, $K_1 = \frac{Db}{E - D}$.

From equation (3.3.9) and the first equation in the system, we have

(3.3.13) $\alpha N^2 + \beta(M)N + \gamma(M) = 0$

where

(3.3.14) $\alpha = E[(E - D) - b(V_m - B)] =$ constant.

(3.3.15) $\beta(M) = (V_m - B)(E - D + bD)(R + P^*) - \alpha(M - P^*) +$

$+ Ek[(E - D) + bB]$

(3.3.16) $\gamma(M) = -Bk[(E - D) + bD](R + P^*) - Ek[(E - D) + bB](M - P^*) < 0$.

Case 1. $0 \leq b < \frac{E - D}{V_m - B}$ which implies that $\alpha > 0$ and

(3.3.17) $(\beta^2 - 4\alpha\gamma) > 0$ (special case $b = 0$) .

Thus the positive solution of (3.3.13) is

(3.3.18) $$N_3^*(M) = - \frac{\beta(M) + \sqrt{\beta^2(M) - 4\alpha\gamma(M)}}{2\ \alpha} .$$

Case 2. $b > \frac{E - D}{V_m - B}$ which implies that $\alpha < 0$.

In this case we have two positive solutions for $N(M)$ but one of them is in $\mathcal{D}$ (i.e. $0 < N < M$) and the other is $> M$.

(3.3.19) $$0 < N_3^*(M) = - \frac{\beta(M) + \sqrt{\beta^2(M) - 4\alpha\gamma(M)}}{2\alpha} < M .$$

From cases (1) and (2), the interior equilibrium point is $(P^* + K_1\ Z_3^*,\ Z_3^*)$ where

(3.3.20) $$Z_3^* = \frac{(M - P^* - N_3^*)(E - D)}{(E - D) + Db} \qquad (= M - P_3^* - N^* \ ,\ b = 0).$$

Thus, from (i), (ii), and (iii), we obtain the following three cases for the distribution of the equilibrium points. The system takes one of these cases according to the values of the parameters.

[Case i]: (0, 0)

[Case ii]: (0, 0) , $(P_2^*, 0)$

[Case iii]: (0, 0) , $(P_2^*, 0)$, (P_3^*, Z_3^*) .

Stability Analysis of the Equilibrium Points

Here the stability analysis of the nonlinear system (3.3.11) is performed by perturbation analysis about the equilibrium points, i.e., linearizing the system about these points and examining the characteristic equations.

(i) Linearized form of equation (3.3.11) about the point (0, 0) becomes

$$(3.3.21)\qquad \begin{bmatrix} \dot{\Delta P} \\ \dot{\Delta Z} \end{bmatrix} = \left.\frac{\partial F}{\partial X}\right|_{(0,\ 0)} \begin{bmatrix} \Delta P \\ \Delta Z \end{bmatrix}$$

where

$$(3.3.22)\qquad \begin{bmatrix} F_1 \\ F_2 \end{bmatrix} = \begin{bmatrix} P(V_m\ \psi_1(M - P - Z) - B - E\ Z\ \phi_1(P,\ Z)) \\ Z(\theta E\ P\ \phi_1(P;\ Z) - D) \end{bmatrix}$$

and

$$(3.3.23)\qquad \left.\frac{\partial F}{\partial X}\right|_{(0,\ 0)} = \begin{bmatrix} (V_m - B) - \frac{K}{K + M} & 0 \\ 0 & -D \end{bmatrix} .$$

The characteristic equation and its roots of the above equations are given by

$$(3.3.24)\qquad (\lambda + D)\ [(V_m - B - \frac{K}{K + M}) - \lambda] = 0 .$$

(3.3.25) $\lambda_1 = V_m - B - \frac{K}{K + M}$, and

(3.3.26) $\lambda_2 = -D < 0$.

Thus, the point (0, 0) is stable (node if

(3.3.27) $M < \frac{B\ k}{V_m - B}$.

and the equilibrium point $(P_2^*, 0)$ exists if $M > \frac{B\ k}{V_m - B}$.

(3.3.27) demonstrates that if the (Michaelis-Menten) uptake rate of the phytoplankton component evaluated at the maximum total available nutrient, M , is less than the loss rate of nutrient, B , of the phytoplankton component, then the phytoplankton population is eliminated.

(ii) Linearized equations about the point $(P_2^*, 0)$ become

(3.3.28) $$\begin{bmatrix} \dot{\Delta P} \\ \dot{\Delta z} \end{bmatrix} = \frac{\partial F}{\partial X}\bigg|_{(P_2^*,\ 0)} \begin{bmatrix} \Delta P \\ \Delta Z \end{bmatrix}$$

with characteristic equations

$$\left[\frac{\theta\ EP_2^*}{R + P_2^*} - D - \lambda\right] \left[\frac{V_m(M - P_2^*)}{K + M - P_2^*} - B + \frac{P_2^*\ V_m\ K}{(K + M - P_2^*)^2} + \lambda\right] = 0$$

and characteristic roots

(3.3.29) $$\lambda_1 = -\frac{P_2^*\ V_m\ K}{(K + M - P_2^*)^2} + B - \frac{V_m(M - P_2^*)}{K + M - P_2^*}$$

and

(3.3.30) $$\lambda_2 = \frac{\theta\ E\ P_2^*}{R + P_2^*} - D .$$

But,

$$(3.3.31)\quad P^*_2 = M - \frac{BK}{V_m - B} \text{ implies that } B = V_m \frac{M - P^*_2}{K + M - P^*_2} .$$

Thus,

$$(3.3.32)\quad \lambda_1 = - \frac{P^*_2 V_m K}{(K + M - P^*_2)^2} < 0$$

Hence, if

$$(3.3.33)\quad M < \frac{RD}{E - D} + \frac{BK}{V_m - B} , \; (P^*_2, 0) \text{ is stable (node)}$$

and if

$$(3.3.34)\quad M > \frac{RD}{\theta E - D} + \frac{BK}{V_m - B} , (P^*_2, 0) \text{ is unstable (saddle point)}$$

and we have the equilibrium point (iii).

Inequality (3.3.33) indicates that the total amount of nutrient present is not sufficient for the requirements of the system and hence, the ecosystem cannot be maintained. (The right side of (3.3.34) can be roughly interpreted as net population loss of nutrient by the phytoplankton and zooplankton components.

(iii) Linearized equations about the point (P^*_3, Z^*_3) becomes

$$(3.3.35)\quad \begin{bmatrix} \dot{\Delta P} \\ \dot{\Delta z} \end{bmatrix} = \left. \frac{\partial F}{\partial X} \right|_{(P^*_3 \, , \, Z^*_3)} \begin{bmatrix} \Delta P \\ \Delta Z \end{bmatrix}$$

with characteristic equation

$$(3.3.36)\quad \left[\lambda + \frac{Eb\ Z_3^* \ P_3^*}{(R + P_3^* + b\ Z_3^*)^2}\right] \left[\lambda + \left(\frac{V_m\ KP}{(K + M - RZ_3^*)^2} - \frac{E\ P_3^*\ Z_3^*}{(R + P_3^* + bZ_3^*)^2}\right)\right] +$$

$$+ \frac{E\ P_3^* Z_3^* (R + bZ_3^*)}{(R + P_3^* + bZ_3^*)^2} \left[\frac{V_m\ K}{(K + M - P_3^* - Z_3^*)^2} + \frac{E(R + P_3^*)}{(R + P_3^* + bZ_3^*)^2}\right] = 0 \ .$$

In the form

$$(3.3.37)\quad \lambda^2 - q(P_3^*,\ Z_3^*)\lambda + \ell(P_3^*,\ Z_3^*) = 0\ ,$$

where

$$(3.3.38)\quad \ell(P_3^*,\ Z_3^*) =$$

$$\lambda_1\lambda_2 = \frac{E\ P_3^*\ Z_3^*}{(R + P_3^* + bZ_3^*)}\left(\frac{K\ V_m}{(K + M - P_3^* - Z_3^*)^2} + \frac{E\ R}{(R + P_3^* + bZ_3^*)^2}\right) > 0\ ,$$

that is, λ_1, λ_2 have real parts of the same sign, and

$$(3.3.39)\quad q(N_3^*) = \lambda_1 + \lambda_2 = -\left[\frac{E\ P_3^*\ Z_3^*}{(R + P_3^* + bZ_3^*)^2}\ (b - 1) + \frac{V_m\ KP_3^*}{(K + N_3^*)^2}\right] .$$

From equation (3.3.39) it is clear that there is a critical value, b^*, for the parameter b such that $q(N_3^*) < 0$ for $b > b^*$ and for all $0 < P_3^*$, Z_3^*, $N_3^* < M$. On the other hand if $0 \leq b \leq b^*$ the sign of $q(N_3^*)$ depends on the total nutrient level, that is $q(N_3^*) > 0$ if $M > M^*$ and $q(N_3^*) < 0$ if $M < M^*$ where M^* is the bifurcation level of the total nutrient. Thus, the following two cases are considered.

Case 1: $b^* < b$.

In this case $(\lambda_1 + \lambda_2) = q(N) < 0$ which implies that the two eigenvalues have negative real parts. Thus, the equilibrium point (P_3^*, Z_3^*) can be either a spiral or a node. The flow associated with system (3.3.11) (with $b > b^*$) cannot contain a limit cycle. This may be demonstrated by employing Dulac's modification of Bendixon's non-existence criterion (Sansome and Conti, 1964, p. 176). Utilizing the closure condition (3.3.2), we write (3.3.11) as

$$\frac{dP}{dt} = F_1(P, Z) = P\left[\frac{V_m(M - P - Z)}{(K + M - P - Z)} - B - \frac{E\ Z}{R + P + bZ}\right]$$

$$\frac{dZ}{dt} = F_2(P, Z) = z\left[\frac{E\ P}{R + P + bZ} - D\right] .$$

Defining h by

$$h(P, Z) = \frac{1}{PZ} , P > 0 , Z > 0 ,$$

we find that $\operatorname{div}(hF_1, hF_2) = -\frac{V_m K}{Z(K + M - P - Z)^2} - \frac{E(b - 1)}{(R + P + bZ)^2} < 0$.

Dulac's result establishes that there are no limit cycles in the quadrant $P > 0$, $Z > 0$.

Case 2: $b^* > b \geq 0$.

From (3.3.39) and (3.3.11) $q(N_3^*)$ can be rewritten as

$$(3.3.43)\quad q(N_3^*) = (V_n - B - \frac{K\ V_m}{(K + N)}(1 + \frac{P_3^*}{K + N_3^*}) - $$

$$- \frac{E\ Z_3^*}{(R + P_3^* + bZ_3^*)^2}(R + b(P_3^* + Z_3^*))$$

and for M^3 model with $b = 0$

$$(3.3.44) \quad q(N_3^*) = (V_m - B) - \frac{K\ V_m}{(K + N_3^*)} (1 + \frac{P_3^*}{K + N_3^*}) - \frac{E\ R\ Z_3^*}{(R + P_3^*)^2} \ .$$

Since q is an increasing function of N_3^*, in view of (3.3.19), q is also an increasing function of M. Since $b < b^*$, it follows that

$$(3.3.45) \quad q(\infty) = (V_m - B) + \frac{E\ R\ P_*}{R(1 + K_1) + P_*(1 - b)} > 0 \ .$$

Furthermore,

$$(3.3.46) \quad q(\alpha) = - \frac{K\ V_m}{(K + \alpha)} (1 + \frac{P_3^*}{K + \alpha}) + \frac{E\ Z_3^*(R + P_3^* + Z_3^*)}{(R + P_3^* + b\ Z_3^*)} < 0$$

where

$$(3.3.47) \quad \alpha = \frac{K\ B}{V_m - B} > 0 \ .$$

Consequently, the equation $q(N_3^*) = 0$ has a unique positive solution N_c given by

$$(3.3.48) \quad c_1\ N_c^4 + c_2\ N_c^3 + c_3\ N_c^2 + c_4 N_c + c_5 = 0$$

where

$$(3.3.49) \quad c_1 = -E(1 - b)(V_m - B)(D + K_1(V_m - B))P_* \ ;$$

(3.3.50) $c_2 = E(1 - b)\ V_m\ K\ DP_* \ ;$

(3.3.51) $$c_3 = (1 - b)EP_*\ V_m^2\ K^2\ K_1 + K\ V_m[(R + P_*)(D + K(V_m - B))$$

$$+ (K_1 + B)P_*(V_m - B)]^2$$

(3.3.52) $$c_4 = 2KV_m[(R + P_*)(D + K_1(V_m - B)) + (K_1 + B)P_*(V_m - B)]$$

$$[(R + P_*)V_M\ K\ K_1 - (K_1 + B)P_*\ V_mK]$$

and

(3.3.53) $$c_5 = K\ V_m[(R + P_m)\ V_m\ KK_1 - (K_1 + b)\ P_*\ V_m\ K]^2\ .$$

The solution N_c , and hence M^*, are found numerically. The values of the critical levels, M^* , of the total nutrient for different values of b are given in Table (3.1) and Figure (3.2) .

Note that for M^3 model with $b = 0$, $c_4 = c_5 = 0$, and hence (3.3.48) is reduced to

(3.3.54) $$c_1\ N_c^2 + c_2\ N_c + c_3 = 0\ .$$

Thus, we see that

(a) $\mathrm{Re}(\lambda_j) < 0$ if $M^* > M > \dfrac{RD}{(E - D)} + \dfrac{BK}{(V_m - B)}$

(b) $\mathrm{Re}(\lambda_j) = 0$ if $M^* = M$,

and

TABLE 3.1

THE CRITICAL VALUE OF THE TOTAL NUTRIENT M*
VERSUS THE PARAMETER b IN THE
GRAZING FUNCTION $G = \frac{E\ P\ Z}{R + P + bZ}$.

	b	N	P	Z	M*
(M^3) Model	0.00	1.3720	.8824	3.5000	5.7550
	0.01	1.4610	.9042	3.7150	6.0800
	0.02	1.5490	.9287	3.9350	6.4130
	0.03	1.6360	.9558	4.1640	6.7560
	0.04	1.7220	.9860	4.4040	7.1120
	0.05	1.8080	1.0190	4.6560	7.4840
	0.06	1.8930	1.0560	4.9240	7.8740
	0.07	1.9780	1.0970	5.2110	8.2860
	0.08	2.0620	1.1420	5.5200	8.7250
	0.09	2.1460	1.1920	5.8550	9.1940
	0.1	2.2300	1.2480	6.2210	9.6990
	0.11	2.3140	1.3110	6.6230	10.2500
	0.12	2.3980	1.3810	7.0680	10.8500
	0.13	2.4810	1.4610	7.5660	11.5100
	0.14	2.5650	1.5520	8.1260	12.2400
	0.15	2.6480	1.6560	8.7630	13.0700
	0.16	2.7320	1.7760	9.4950	14.0000
	0.17	2.8160	1.9170	10.3500	15.0800
	0.18	2.9000	2.0840	11.3500	16.3300
	0.19	2.9850	2.2850	12.5500	17.8200
	0.20	3.0700	2.5310	14.0100	19.6100
	0.21	3.1550	2.8390	15.8400	21.8300
	0.22	3.2410	2.2360	18.1900	24.6700
	0.23	3.3270	3.7680	21.3300	28.4200
	0.24	3.4140	4.5140	25.7200	33.6500
	0.25	3.5010	5.6370	32.3300	41.4700
	0.26	3.5890	7.5220	43.4100	54.5200
	0.27	3.6780	11.3300	65.8000	80.8100
	0.28	3.7670	23.1100	134.9000	161.8000
	0.289	3.8480	386.2000	2266.0000	2656.0000
	0.2895	3.8530	3091.0000	18150.0000	21240.0000
	0.28957	3.8530	160800.0000	944200.0000	1105000.0000

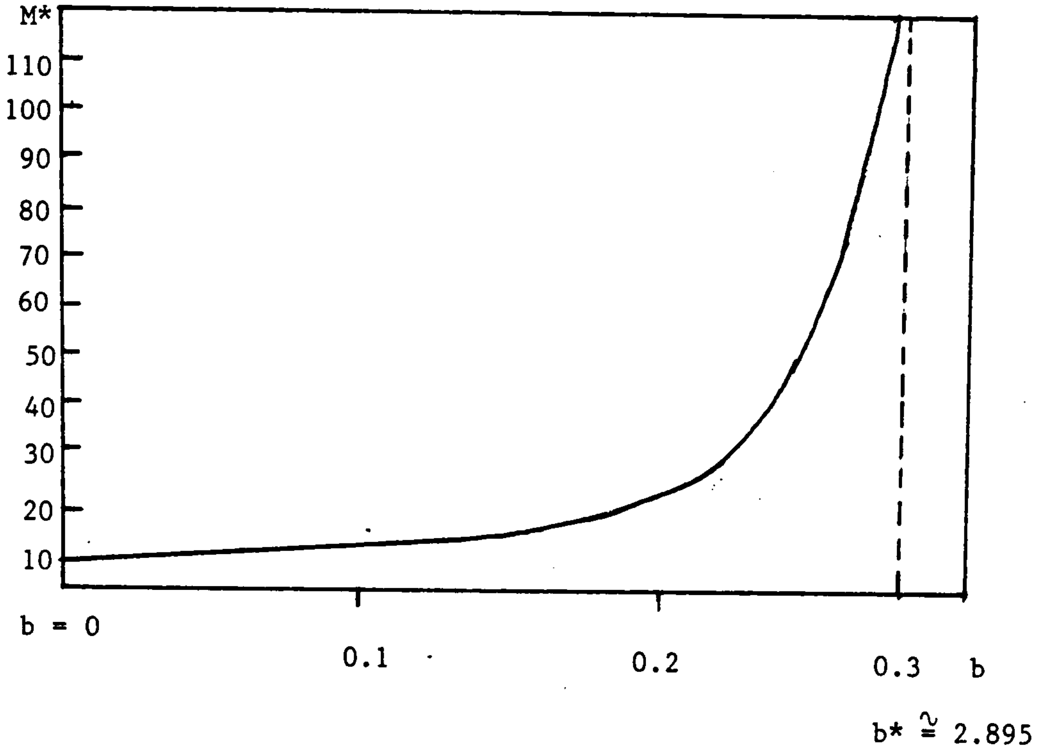


Figure 3.2

The Critical Value of the Total Nutrient versus the Parameter b in the Grazing Function

$$G = \frac{E\ P\ Z}{R + P + bZ}$$

Note: b = 0 (M^3) Model

b* ≅ 2.8957

(c) $Re(\lambda_j) > 0$ if $M^* > M$, $i = 1, 2$.

Now we can conclude that

(a) (P_3^*, Z_3^*) is asymptotically stable if

$$M^* > M > [\frac{RD}{E - D} + \frac{BK}{V_m - B}] \ ;$$

and

(b) (P_3^*, Z_3^*) is unstable if $M > M^*$.

Figures (3.3) thru (3.20) represent the solution curve of (3.3.5) for different values of b and for $M > M^*$ in each case. As M increases, the waveform of the periodic solution becomes distorted and the amplitude becomes larger. The solution becomes stable as b approaches the critical value $b^* \cong 0.2589$.

Hopf Bifurcation

Proposition 3.1. A Hopf bifurcation occurs at $M = M^*$. Moreover, there is a neighborhood N of $M = M^*$ such that any closed orbit corresponding to $M \in N$ has a period $\approx \frac{2\pi}{\lambda^*}$ and radius growing like $(|M - M^*|)^{1/2}$ (Marsden and McCracken 1976, p. 20).

Proof. When the value of M is near M^* , (3.7.37) has complex conjugate solutions λ and $\overline{\lambda}$ such that

$$(3.3.55) \quad R(\lambda)\Big|_{M=M^*} = 0 \ , \quad |Img(\lambda)\Big|_{M=M^*} = \sqrt{q^*} = \lambda^* > 0$$

where q^* denotes the value of $(\lambda_1 + \lambda_2)$ corresponding to $M = M^*$. Consider the equations

$$(3.3.56) \quad Re(\lambda) = \frac{q}{2} \ .$$

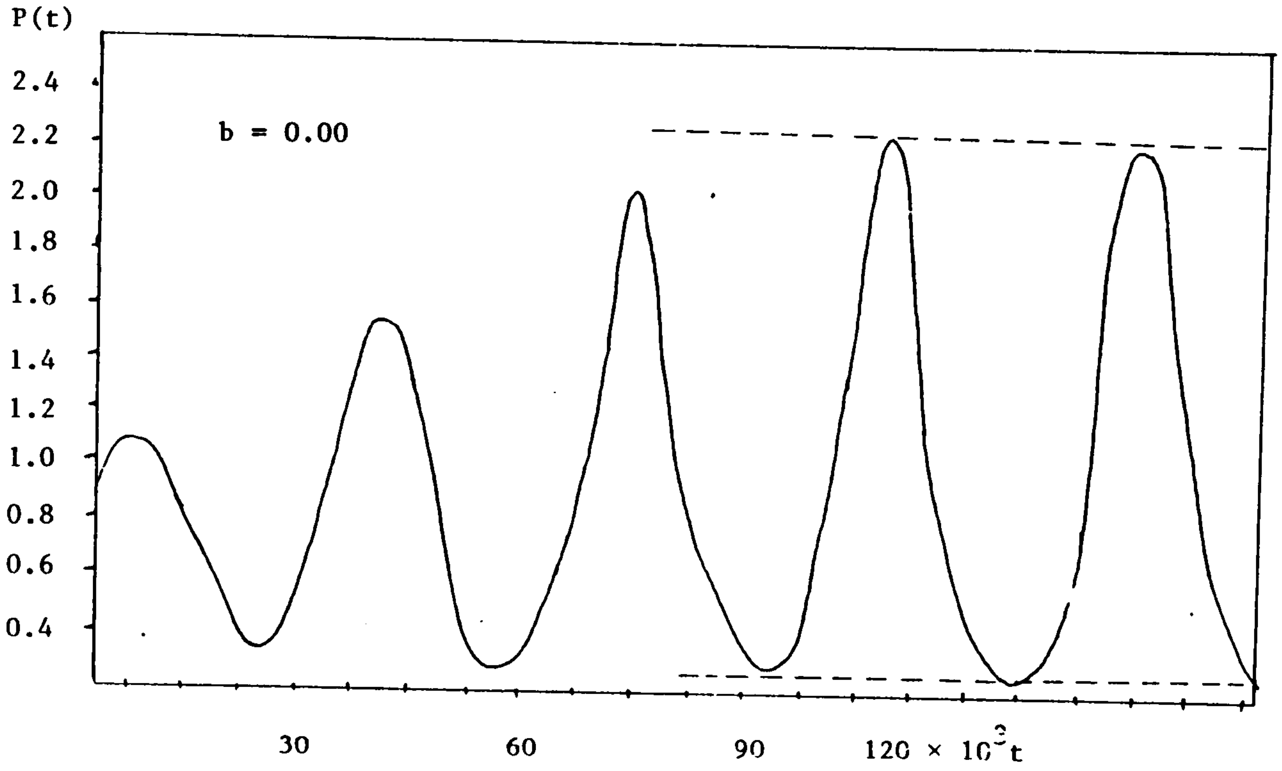


Figure 3.3 Solution curve of P(t) for M = 6.6 > M* and b = 0.00

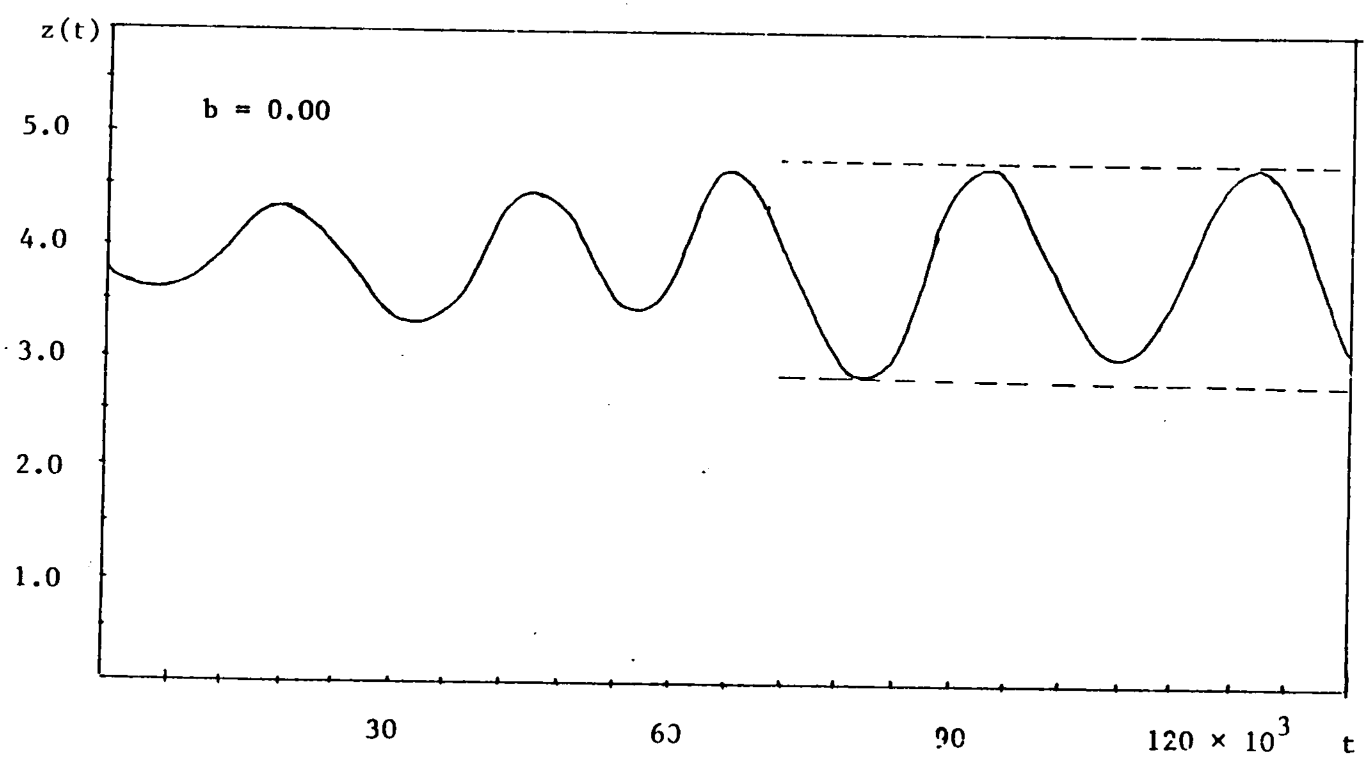


Figure 3.4 Solution curve of z(t) for $M = 6.6 > M^*$ and $b = 0.00$

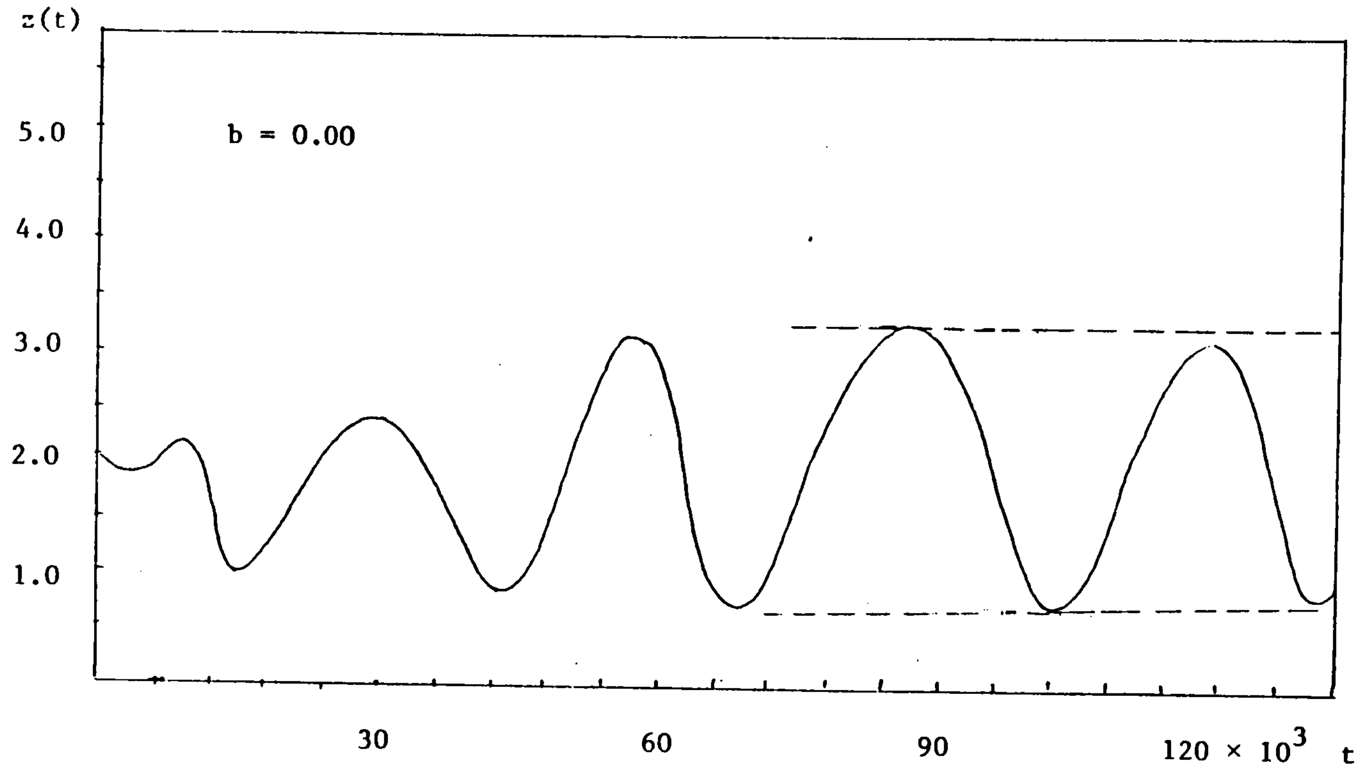


Figure 3.5 Solution curve of N(t) for M = 6.6 > M* and b = 0.00

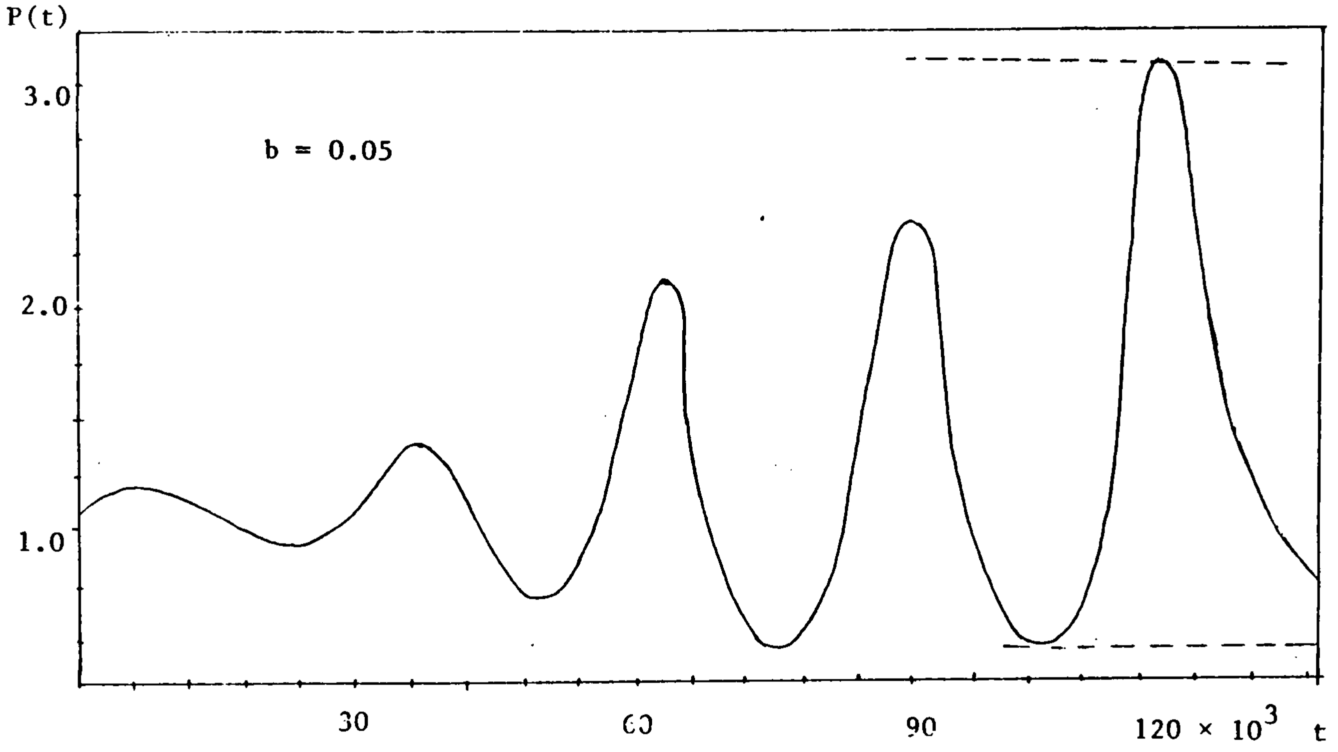


Figure 3.6 Solution curve of P(t) for M = 8.1 > M* and b = 0.05

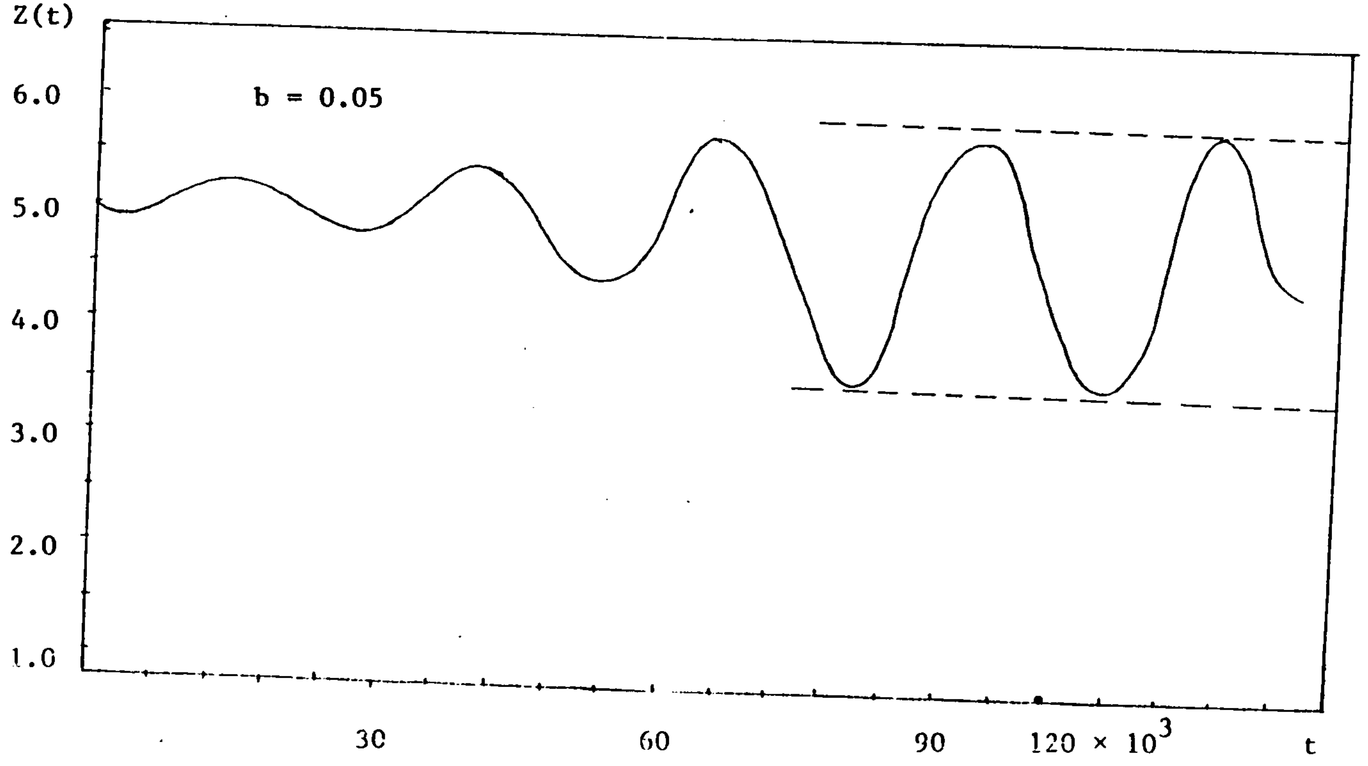


Figure 3·7, Solution curve of Z(t) for $M = 8.1 > M^*$ and $b = 0.05$

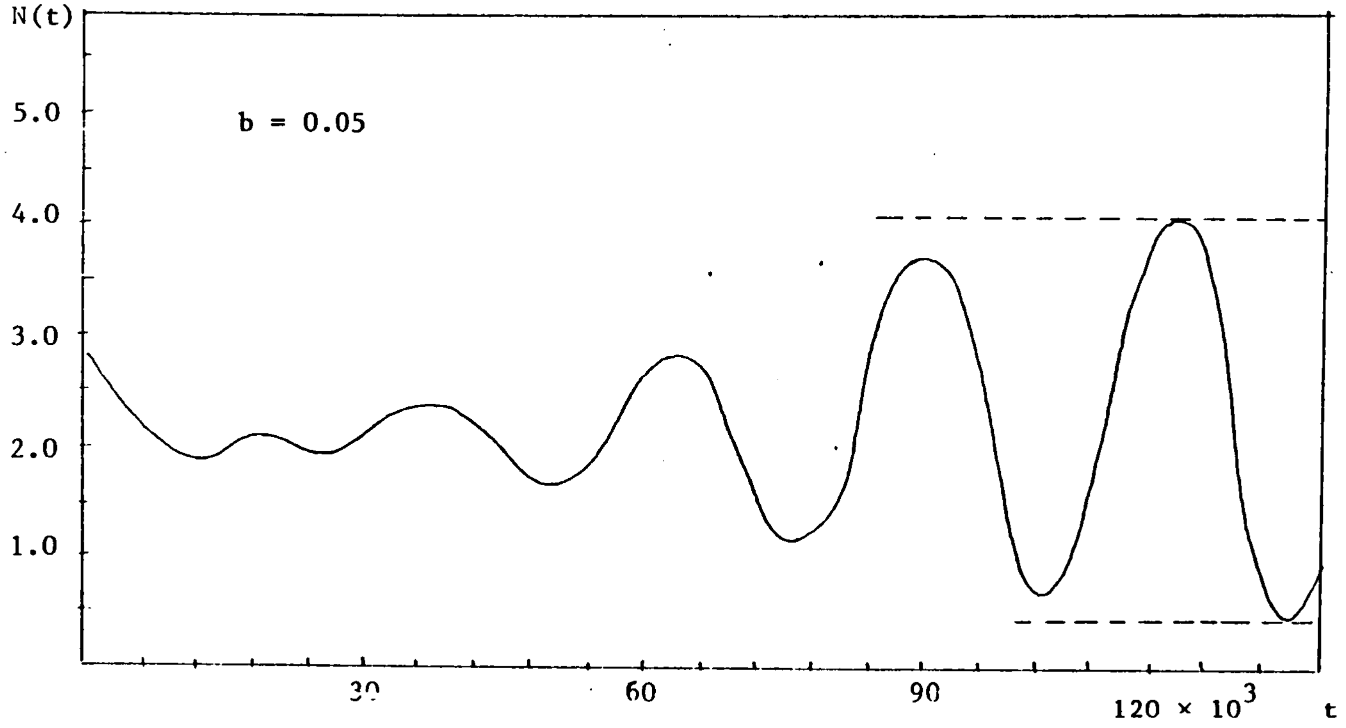


Figure 3.8, Solution curve of N(t) for $M = 8.1 > M^*$ and $b = 0.05$

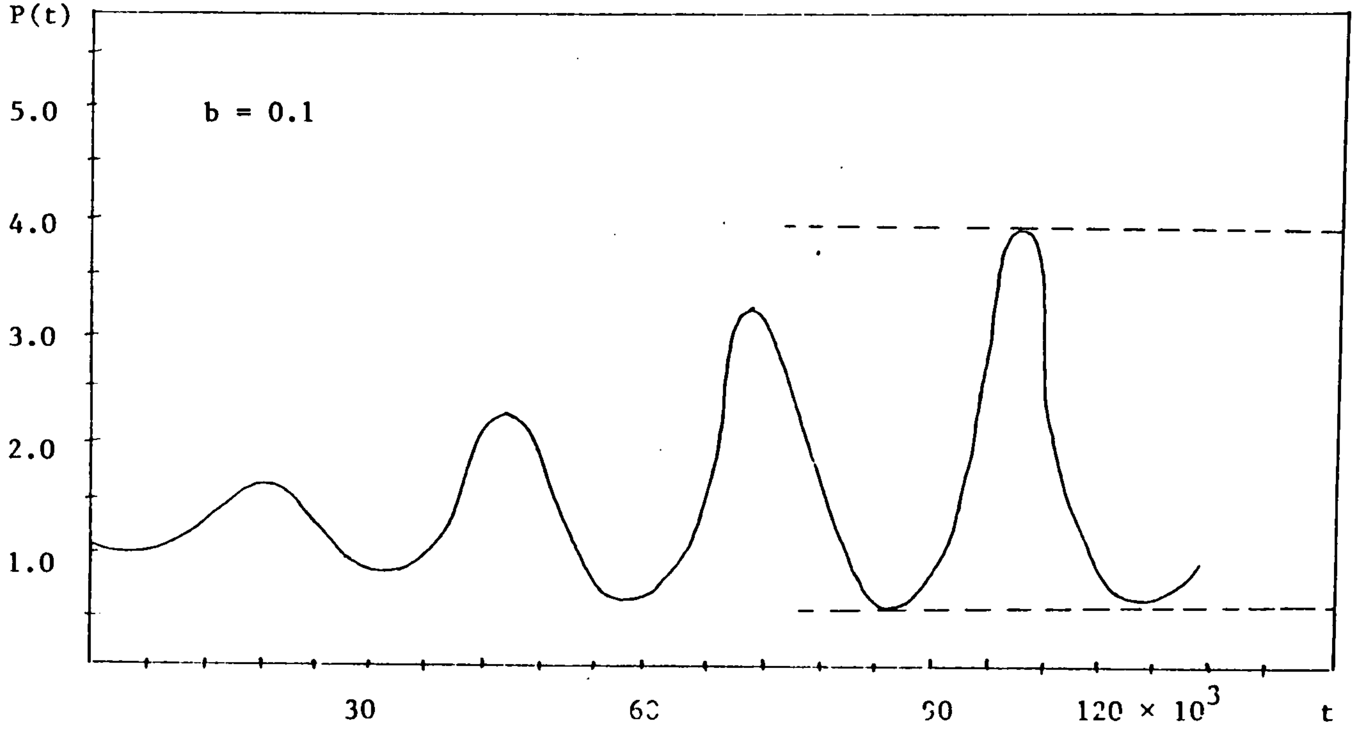


Figure 3.9 Solution curve of P(t) for M = 10.0 > M* and b = 0.1

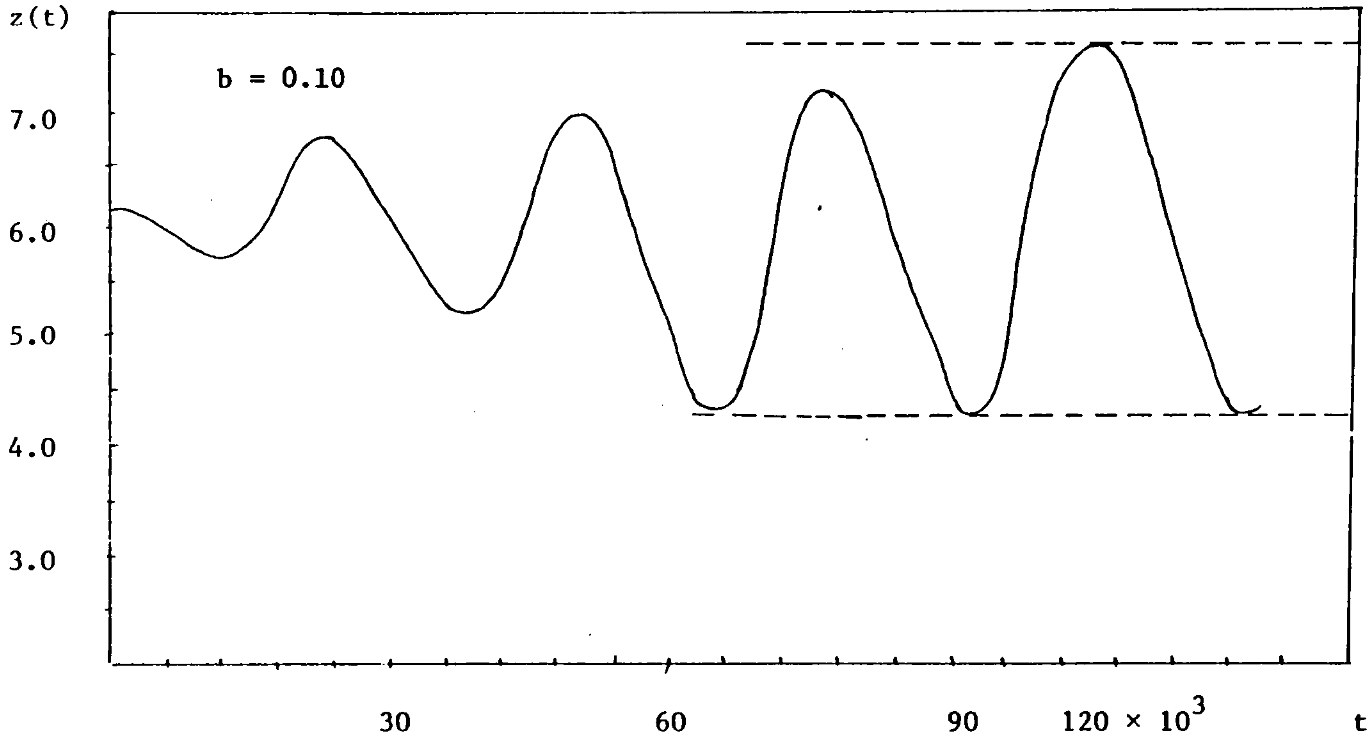


Figure 3.10 Solution curve of $z(t)$ for $M = 10.0 > M^*$ and $b = 0.1$

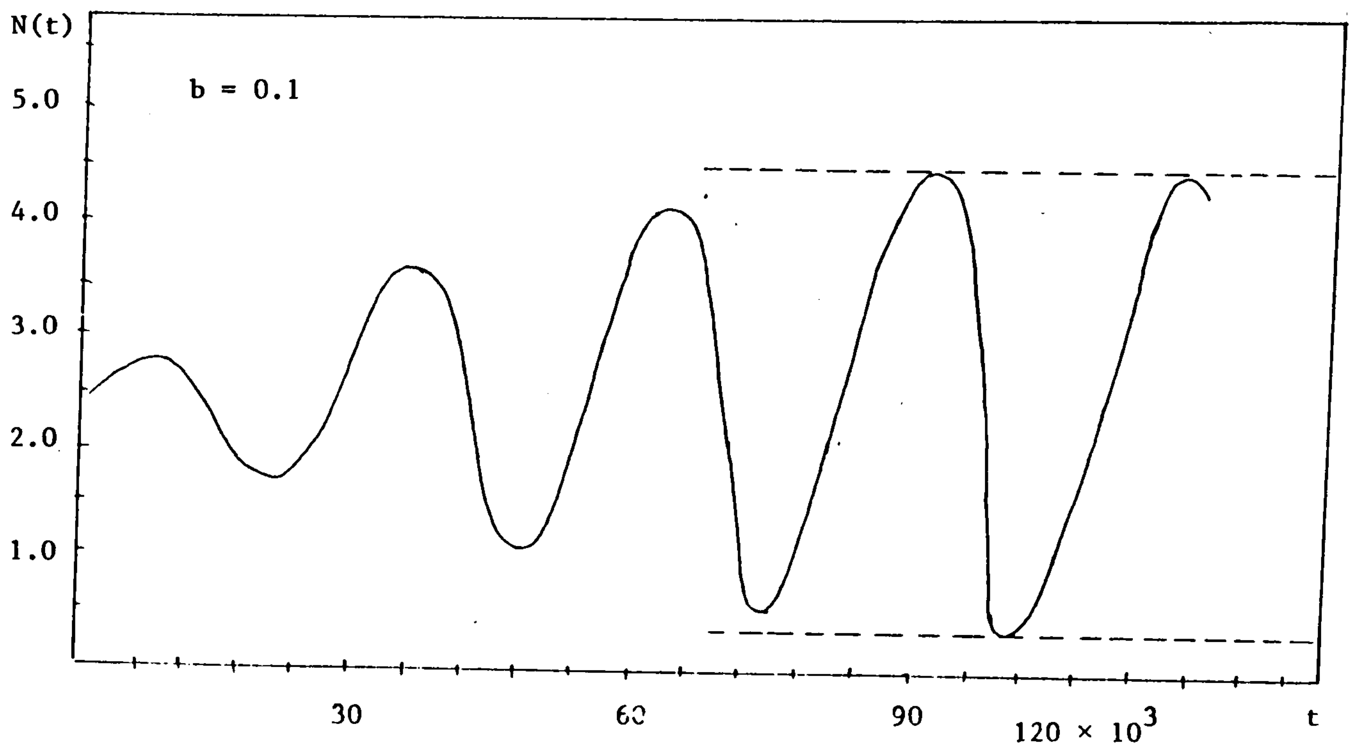


Figure 3.11 Solution curve of N(t) for $M = 10.0 > M^*$ and $b = 0.1$

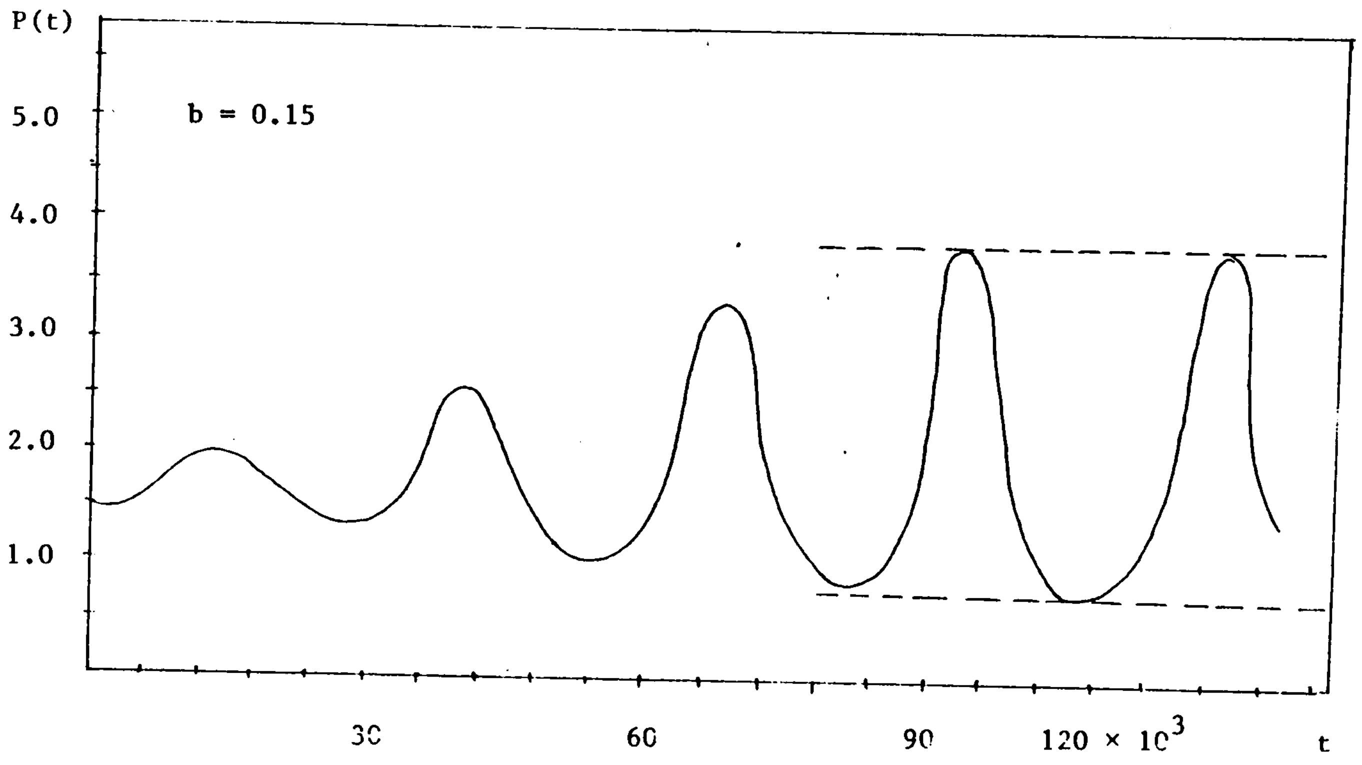


Figure 3.12 Solution curve of P(t) for M = 13.3 > M* and b = 0.15

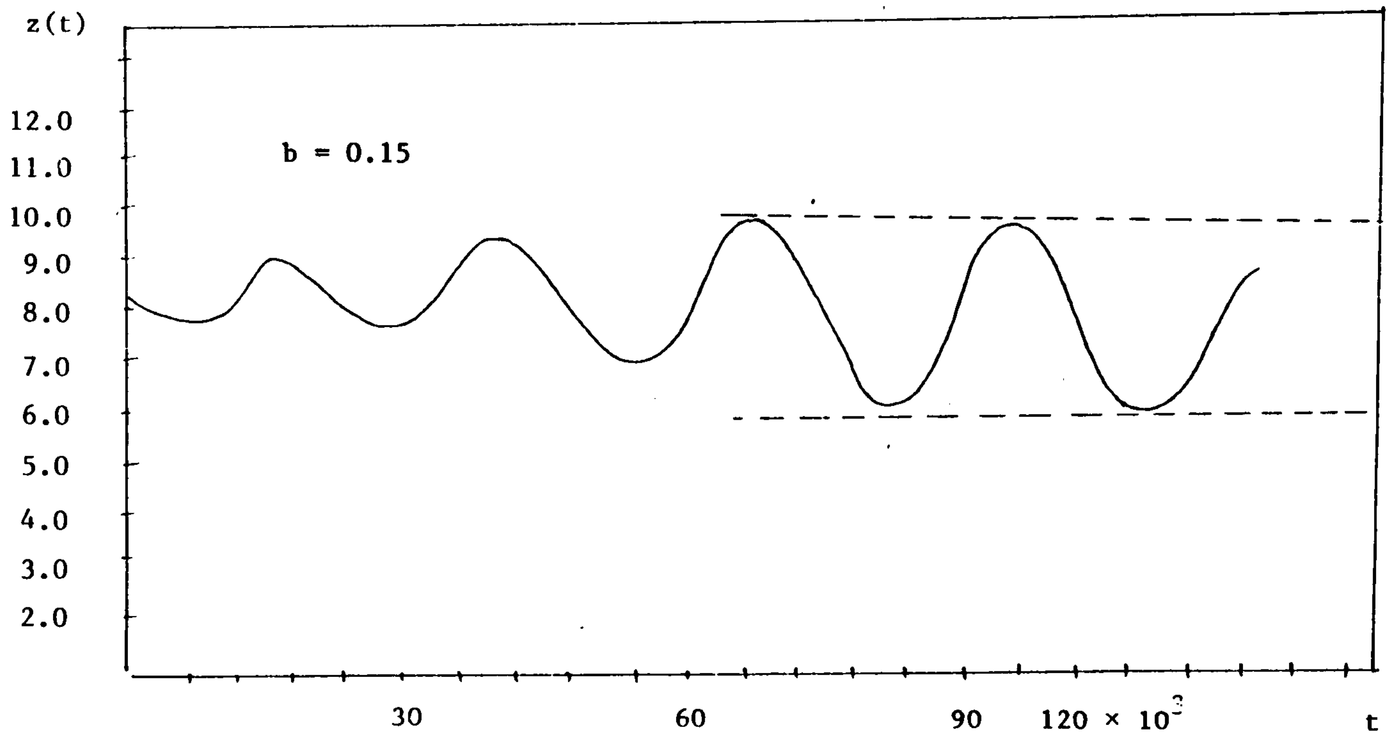


Figure 3.13 Solution curve of z(t) for $M = 13.3 > M^*$ and $b = 0.15$

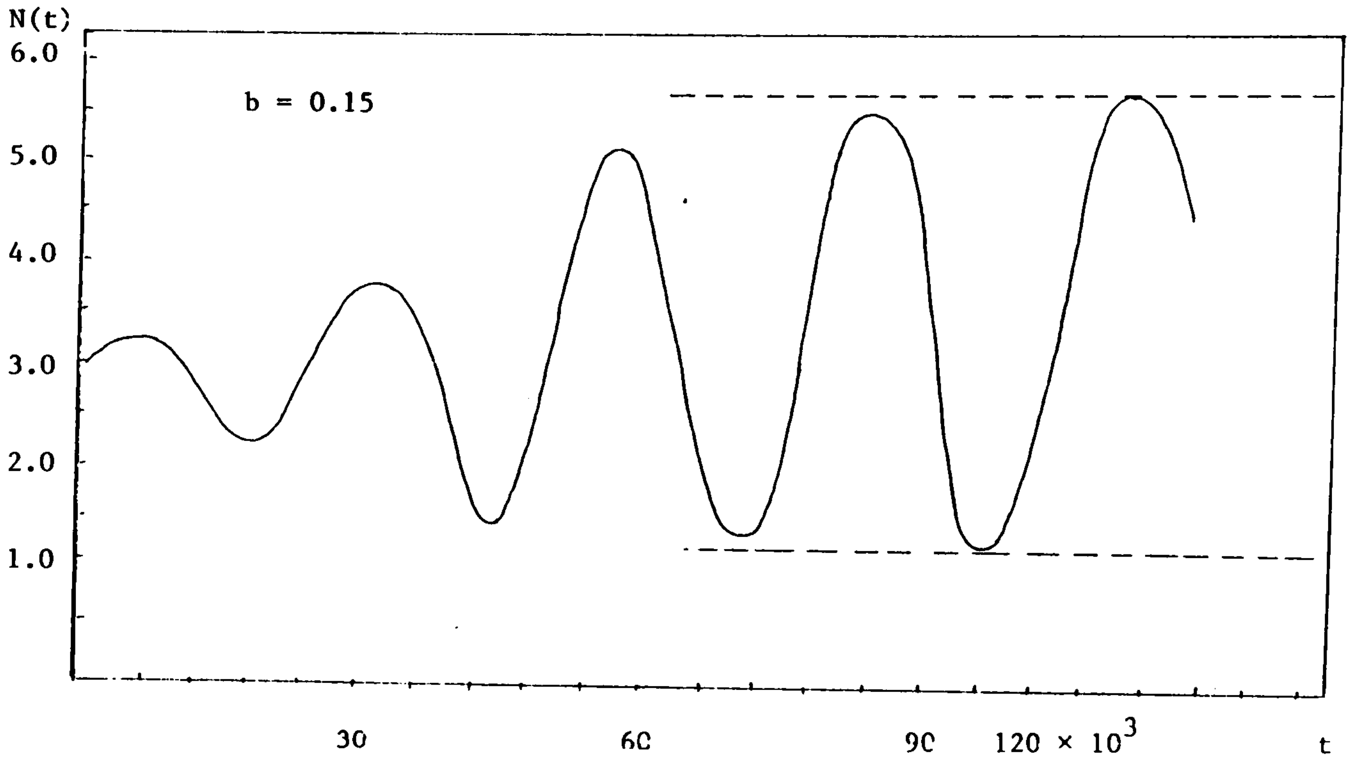


Figure 3.14 Solution curve of N(t) for $M = 13.3 > M^*$ and $b = 0.15$

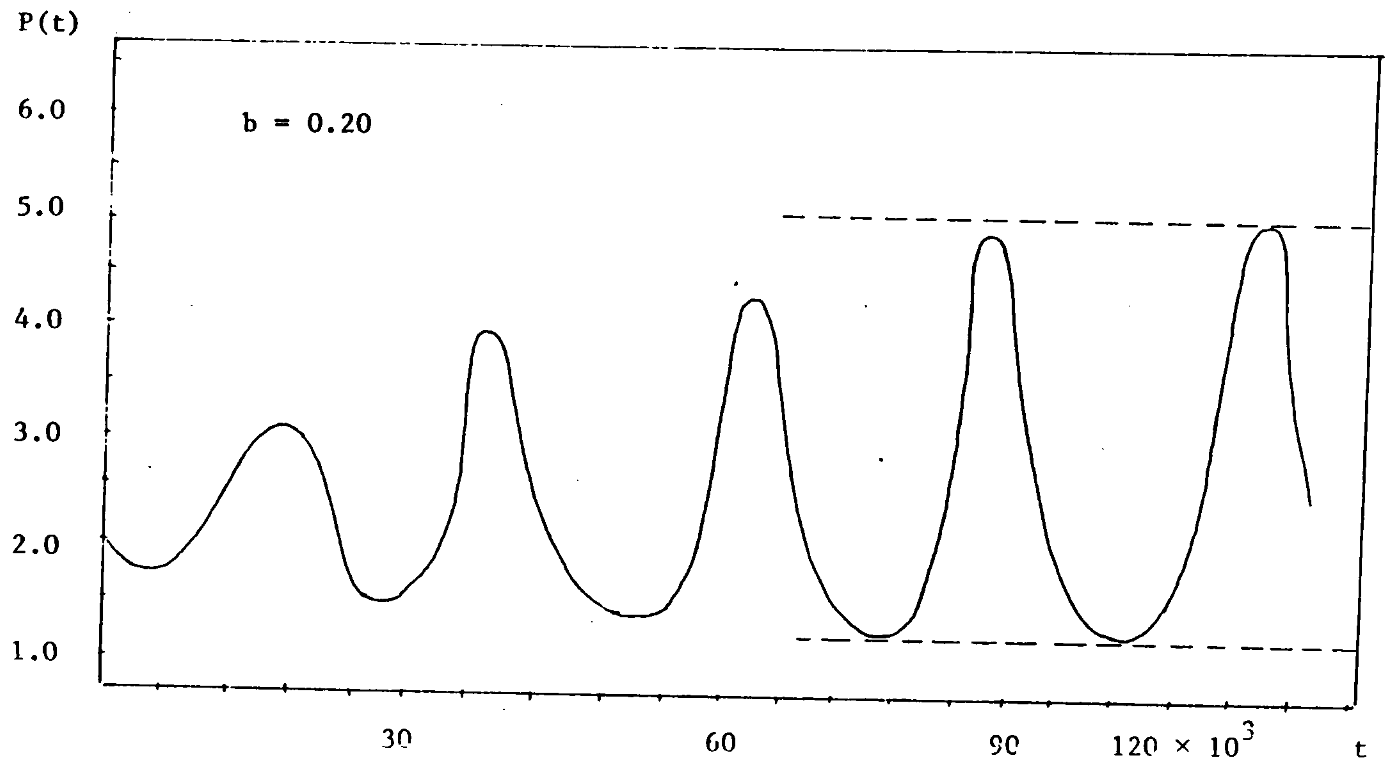


Figure 3.15 Solution curve of P(t) for M = 20.5 > M* and b = 0.2

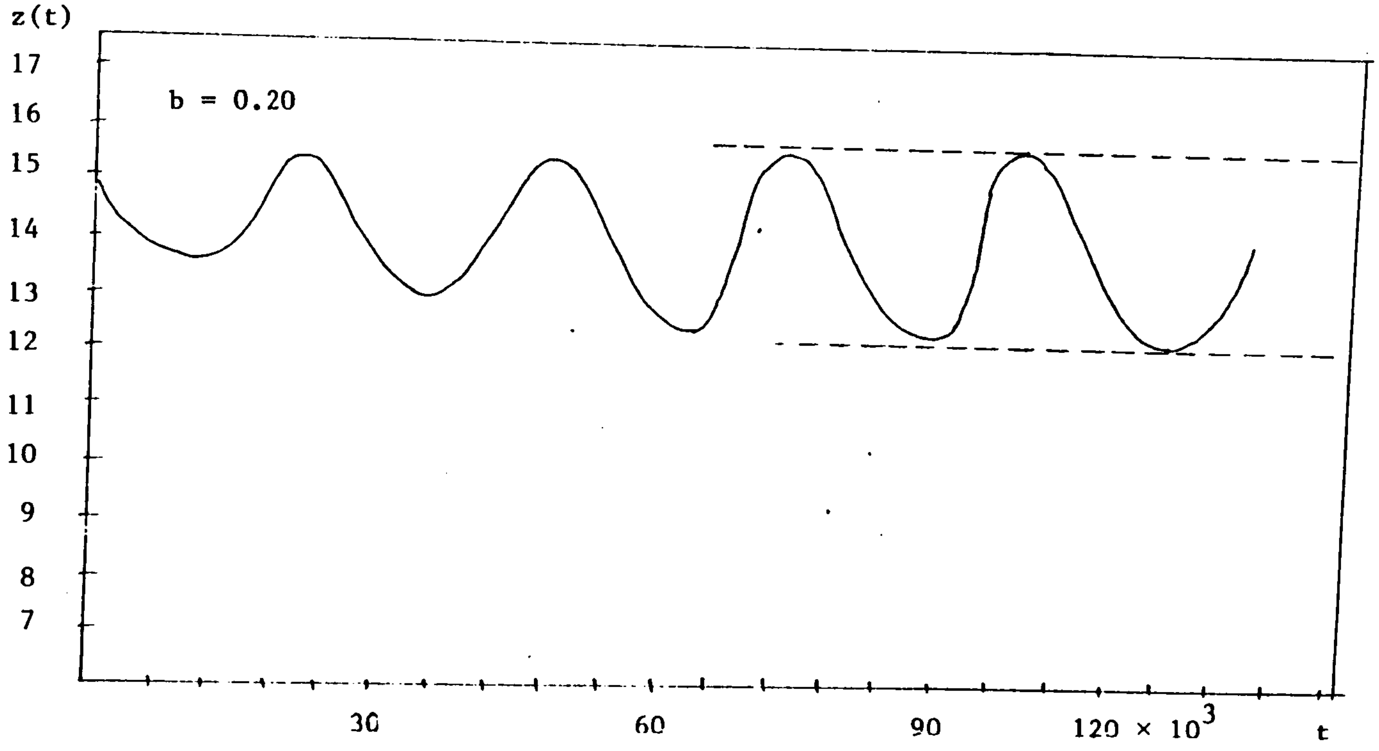


Figure 3.16 Solution curve of $z(t)$ for $M = 20.5 > M^*$ and $b = 0.2$

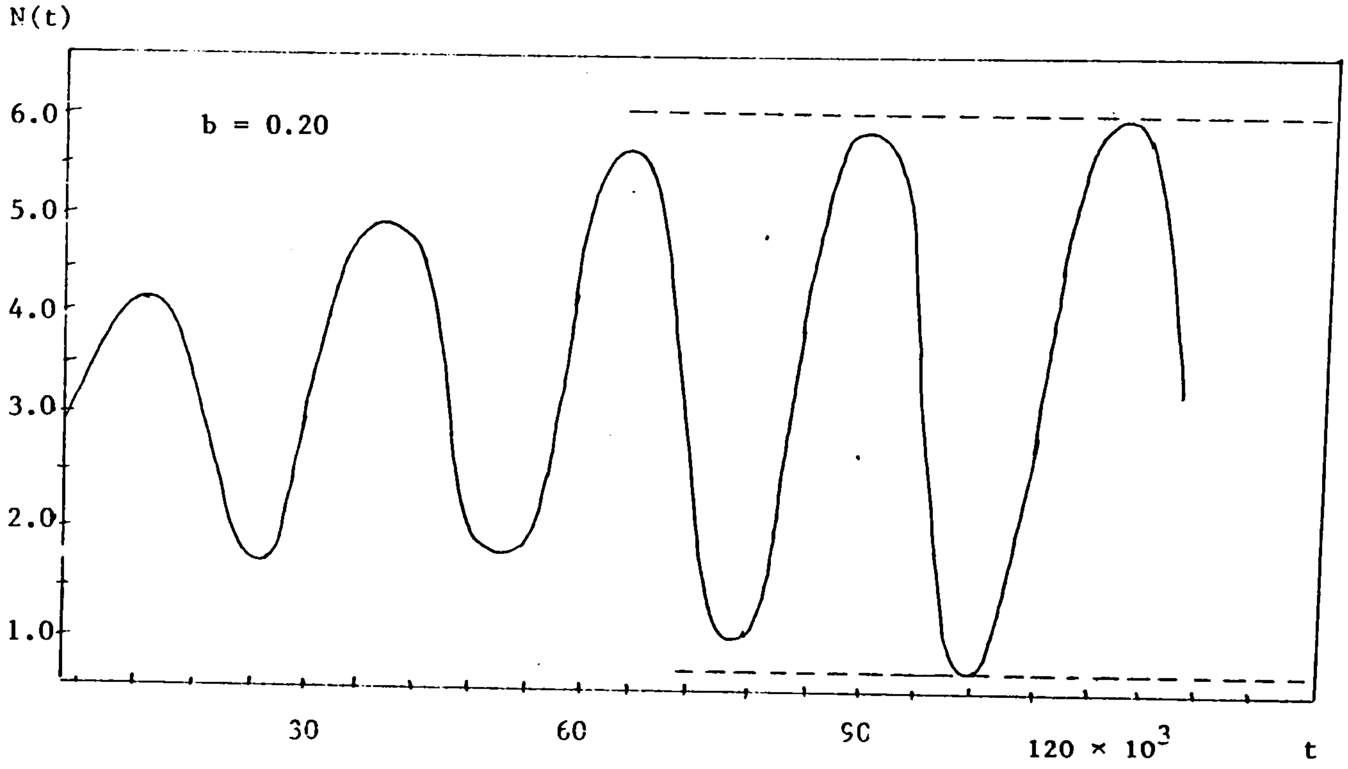


Figure 3.17 Solution curve of N(t) for M = 20.5 > M* and b = 0.2

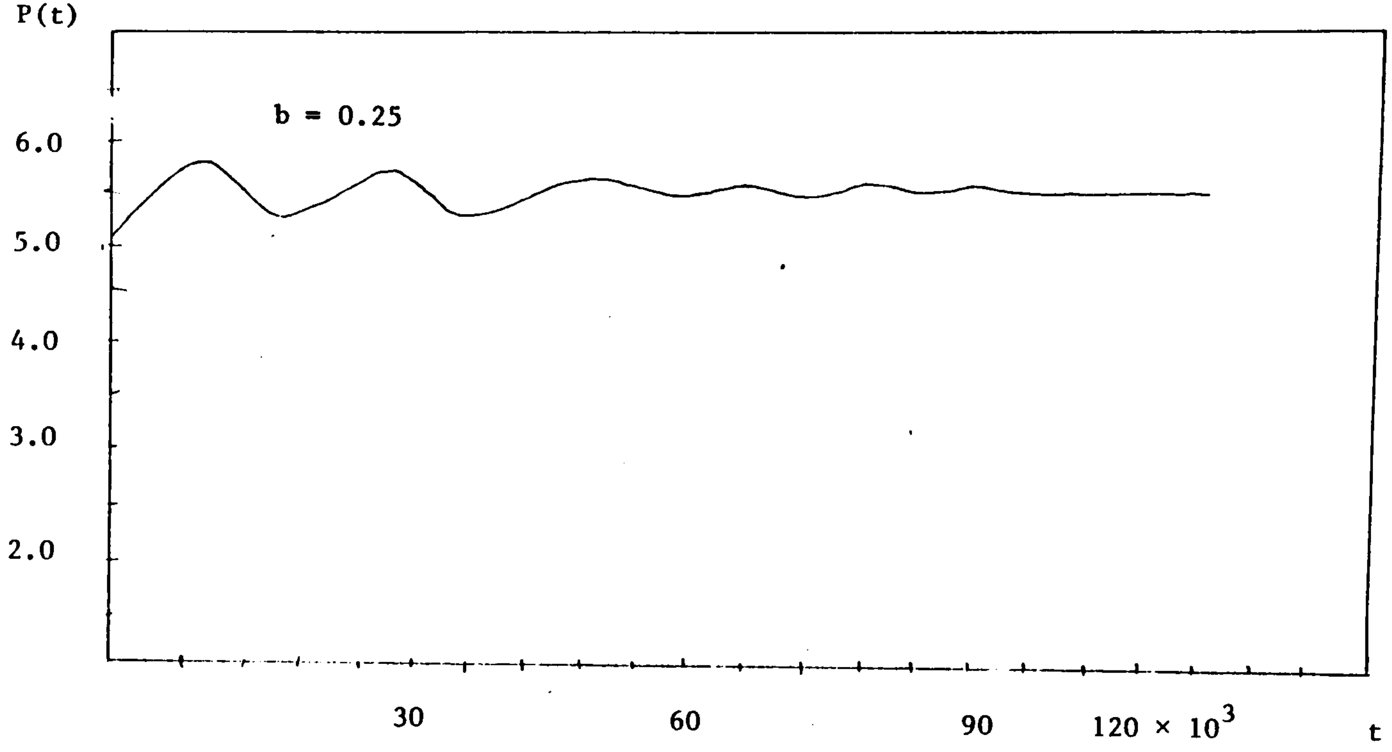


Figure 3.18 Solution curve of P(t) for $M = 42.2 > M^*$ and $b = 0.25$

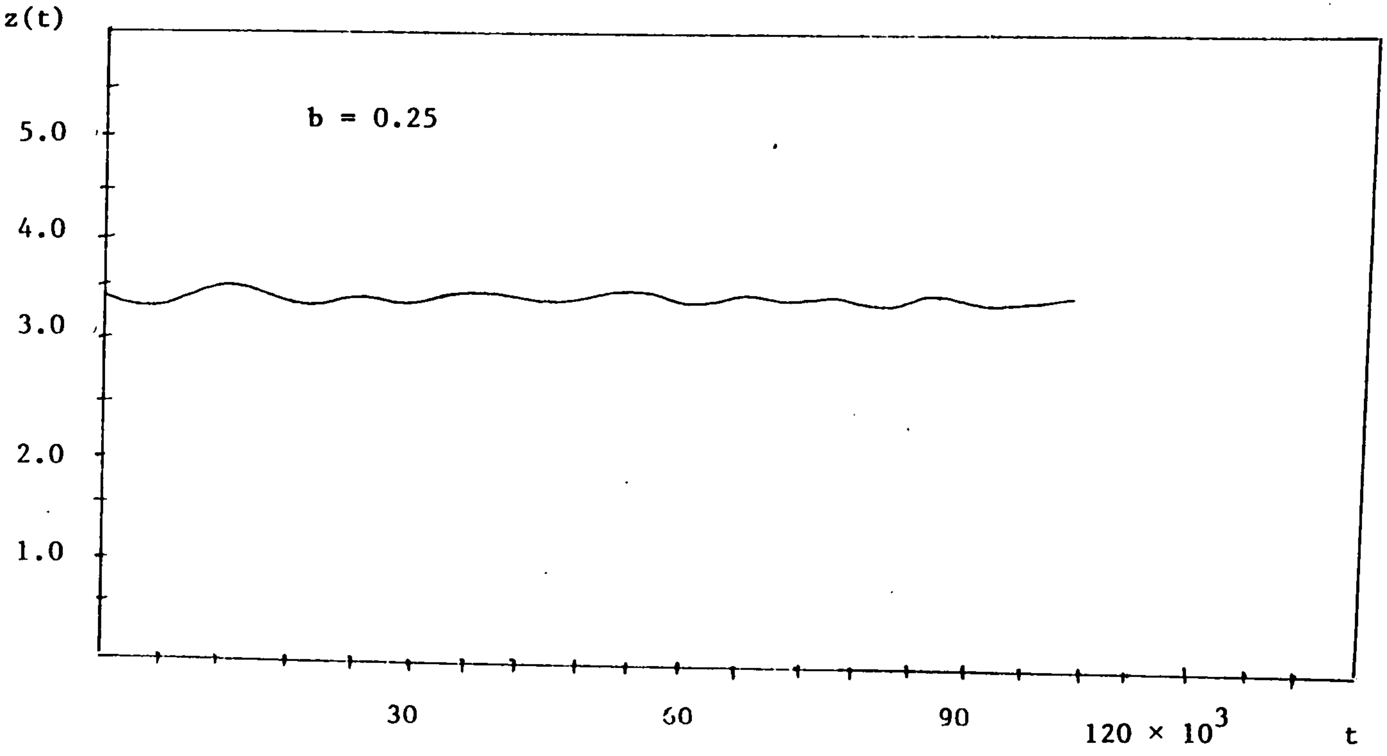


Figure 3.19. Solution curve of z(t) for M = 42.2 > M* and b = 0.25

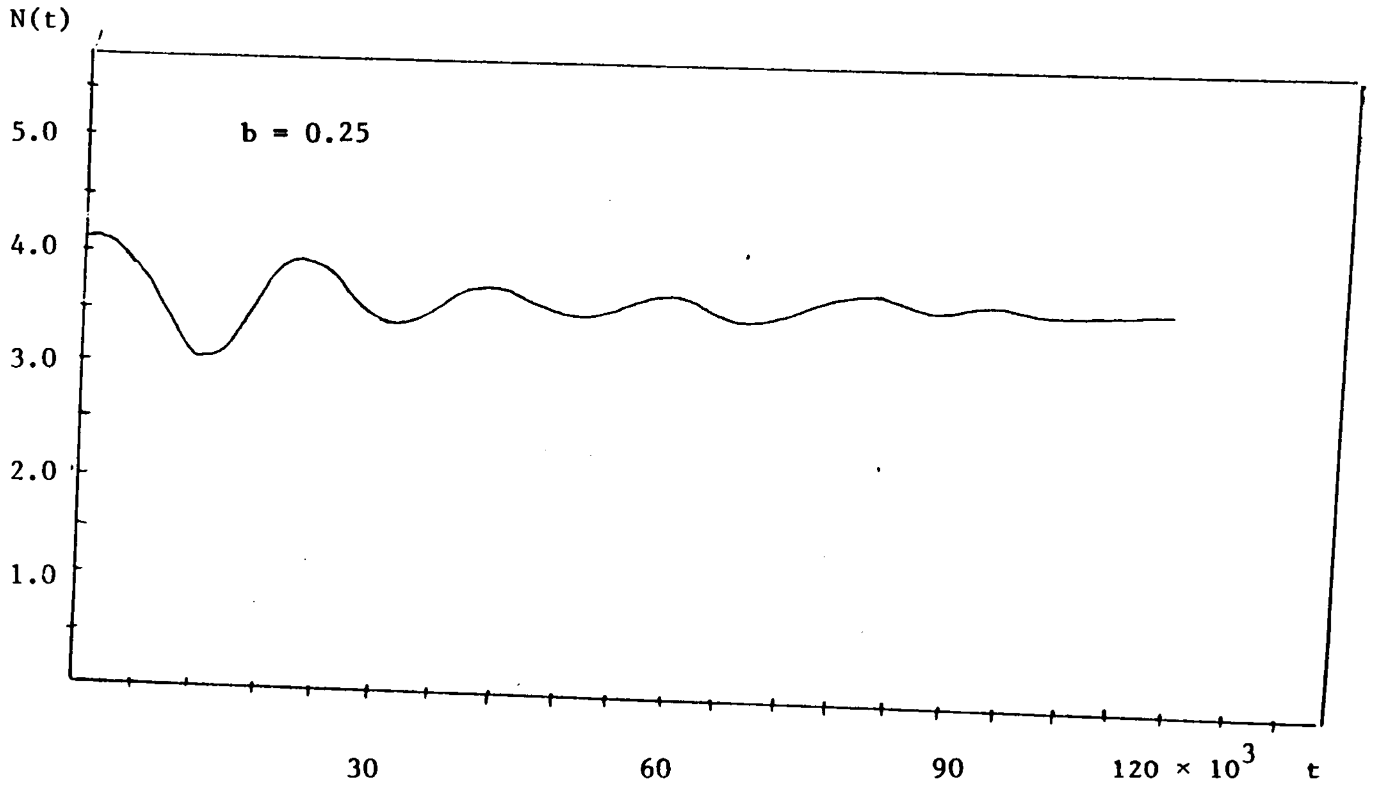


Figure 3.20 Solution curve of N(t) for $M = 42.2 > M^*$ and $b = 0.25$

Differentiating both sides with respect to M yields

$$\frac{d(\mathrm{Re}(\lambda))}{d\ M} = \frac{1}{2}\frac{\partial g}{\partial N}\left.\frac{\partial N}{\partial M}\right|_{M=M*} = \frac{V_m K P}{(K + N)^3}\left.\frac{\partial N}{\partial M}\right|_{M=M*}$$

But $\frac{\partial N}{\partial M} > 0$ (N is an increasing function of M) $\Rightarrow \frac{d\ \mathrm{Re}(\lambda)}{d\ M} > 0$. Then the eigenvalues λ_1, λ_2 cross the imaginary axis with non-zero speed, so a Hopf bifurcation occurs at $M = M*$. Consequently, there is a neighborhood N of $M = M*$ such that any closed orbit corresponding to $M \in N$ has period $\approx \frac{2\pi}{\lambda*}$ and radius growing like $(|M - M*|)^{1/2}$.

Extinction Analysis

Theorem 3.4.1 If the parameters B, V_m, and K satisfy the inequality

$$(3.3.58) \quad B > \frac{V_m M}{M + K}$$

then corresponding to the P-component of each solution of (3.1.11) there exists a constant P_0 such that

$$(3.3.59) \quad P(t) \leq P_0\, e^{-[B - \frac{V_m M}{M + K}]t} \quad .$$

In particular, there exists a ξ_P , $0 \leq \xi_P \leq \infty$, such that $P(\xi_P) = 0$.

Proof. Using $Z \geq 0$, $P \geq 0$ in the differential equation (3.3.11a) we find

$$(3.3.60) \quad \dot{P} \leq \frac{V_m P N}{K + N} - BP = P[V_m(1 - \frac{K}{N + K}) - B] \ .$$

As long as $P \neq 0$

$$(3.3.61) \quad \frac{1}{P}\frac{dP}{dt} \leq (V_m - B) - \frac{V_m K}{N + K} .$$

The nutrient component $N(t)$ satisfies $0 \leq N(t) < M$ so that

$$(3.3.62) \quad \frac{1}{P}\frac{dP}{dt} \leq (V_m - B) - \frac{V_m K}{M + K} .$$

An integration from 0 to t leads to

$$(3.3.63) \quad \ln[\frac{P(t)}{P(0)}] \leq t[V_m - B - \frac{V_m K}{M + K}] .$$

Solving for P gives the conclusion of the theorem:

$$(3.3.64) \quad P(t) \leq P(0)\, e^{-[B - \frac{V_m K}{M + K}]\, t} .$$

Table (3.2) summarizes what we have discussed so far for the model (3.3.5). In Table (3.2) , S means that the critical point is stable, and $_mU$ (m = 1, 2) means that the critical point is unstable and the number of unstable eigenvalues of the Jacobian matrix at the critical point is equal to m .

Table 3.2

PROPERTIES OF THE CRITICAL POINTS OF (3.3.5)

$$M_1 = \frac{RD}{\theta E - D} + \frac{BK}{V_m - B}$$

CONDITIONS			CRITICAL POINTS		
			(0, 0)	(P_2^*, 0)	(P_3^*, Z_3^*)
$V_m > B$ $E > D$	$b > b^*$	$0 < M < \frac{BK}{V_m - B}$	S	-	-
		$\frac{BK}{V_m - B} < M < M_1$	U	S	-
		$M_1 < M < M^*$	1^U	1^U	S
		$M^* < M$	1^U	1^U	S
	$0 \leq b \leq b^*$	$0 < M < \frac{BK}{V_m - B}$	S	-	-
		$\frac{BK}{V_m - B} < M < M_1$	1^U	S	-
		$M_1 < M < M^*$	1^U	1^U	S
		$M^* < M$	1^U	1^U	2^U

Theorem 3.4.2. If the parameters R, θ, E, and D satisfy

$$(3.3.65) \quad M \leq \frac{R}{b + 1} \left[\frac{1}{\theta E - D} - 1\right] ,$$

then corresponding to each solution of (3.3.11) there exists a ξ_Z, $0 \leq \xi_Z \leq \infty$, such that the Z component satisfies $Z(\xi_z) = 0$. If $\varepsilon > \delta$, then corresponding to the Z-component of each solution of (3.3.11), there exists a T_Z, $0 \leq T_Z < \infty$ such that $Z(T_Z) = \frac{\varepsilon - \delta}{\Delta}$ and if $T_Z < \infty$, then $Z(\xi) \leq \frac{\varepsilon - \delta}{\Delta}$ for $\xi \geq T_Z$ where

(3.3.66) $\varepsilon = \theta E - D$,

(3.3.67) $\delta = \frac{R}{(1 + b)M + R}$,

and

(3.3.68) $\Delta = \frac{\delta}{R} b$.

Proof. Using $0 \leq P$, $z \leq M$ in the differential equation (3.3.11b) we find

(3.3.69) $$\frac{dZ}{dt} \leq Z[(\theta E - D) - \frac{R}{(1 + b)M + R}] - \frac{b\ Z^2}{(1 + b)M + R}$$

comparing with

(3.3.70) $$\frac{du}{dt} = u[(\theta E - D) - \frac{R}{(1 + b)M + R}] - \frac{b\ u^2}{(1 - b)M + \gamma}$$

leads to

(3.3.71) $Z(t) \leq u(t)$ for $t \geq 0$ if $Z(0) \leq u(0)$.

Let

$$\varepsilon = \theta E - D ,$$

$$\delta = \frac{R}{(1 + b)M + R}$$

and

$$\Delta = \frac{\delta}{R} b$$

then

(3.3.72) $$\frac{du}{dt} = (\varepsilon - \delta) - \Delta u^2 .$$

Separating the variables u and t , we get

(3.3.73) $$\frac{du}{u\,\Delta[\frac{\varepsilon - \delta}{\Delta} - u]} = dt .$$

An integration from 0 to t leads to

(3.3.74) $$t = \frac{1}{\varepsilon - \delta} \ln \frac{u}{c_0[u - \frac{\varepsilon - \delta}{\Delta}]}$$

where

(3.3.75) $$c_0 = \frac{u(0)}{u(0) - \frac{\varepsilon - \delta}{\Delta}} .$$

Solving for u , it follows

(3.3.76) $$u(t) = \frac{(\varepsilon - \delta)/\Delta}{C_0\ e^{t(\varepsilon-\delta)} - 1} + (\varepsilon - \delta)/\Delta$$

$$= \frac{(\varepsilon - \delta)}{\Delta} \left[1 + \frac{1}{C_0\ e^{(\varepsilon - \delta)t} - 1}\right] .$$

(i) If $\varepsilon < \delta$, (i.e., $\theta E - D < \frac{R}{(b + 1)M + R}$) , then

$$\lim_{t\to\infty} u(t) = 0 .$$

(ii) If $\varepsilon > \delta$, (i.e. $\theta E - D > \frac{R}{(b + 1)M + R}$) , then

$$\lim_{t\to\infty} u(t) = \frac{\varepsilon - \delta}{\Delta} .$$

(iii) If $\varepsilon = \delta$ (i.e., $\theta E - D = \frac{R}{(b - 1)M + R}$) , then

$$\lim_{t\to\infty} (\lim_{\delta\to\varepsilon} u(t)) = \lim_{t\to\infty} \lim_{\delta\to\varepsilon} \frac{C_0\ t(\varepsilon - \delta)^2\ e^{t(\varepsilon - \delta)}}{\Delta[C_0\ e^{t(\varepsilon - \delta)} - 1]^2}$$

$$= \lim_{t\to\infty} \frac{C_1}{t} = 0$$

where C_1 is a positive constant. Thus

(a) The solution space structure of $\dot{u} = (\varepsilon - \delta)u - u^2$ for $\varepsilon \leq \delta$ is given in Figure (3.21):

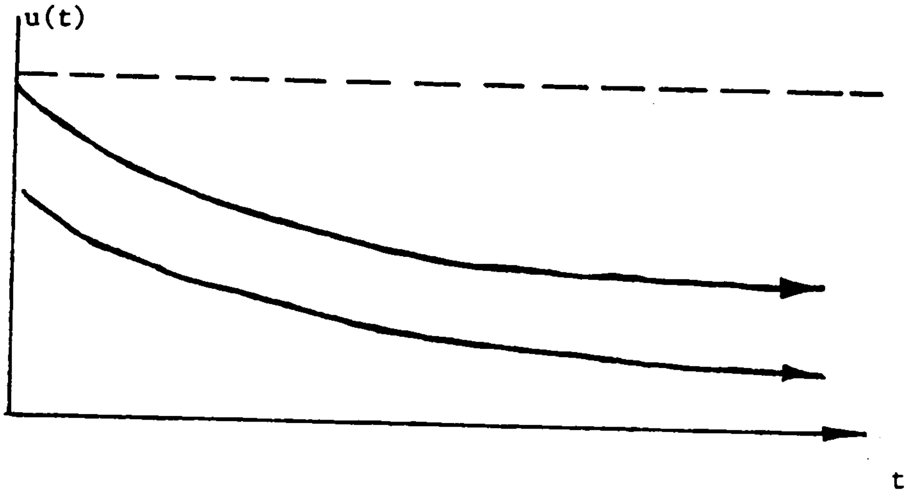


Figure (3.21)

The solution space structure for $\varepsilon \leq \delta$

(b) The solution space structure of $\dot{u} = (\varepsilon - \delta)u - \Delta u^2$ for $\varepsilon > \delta$ is given in Figure (3.22):

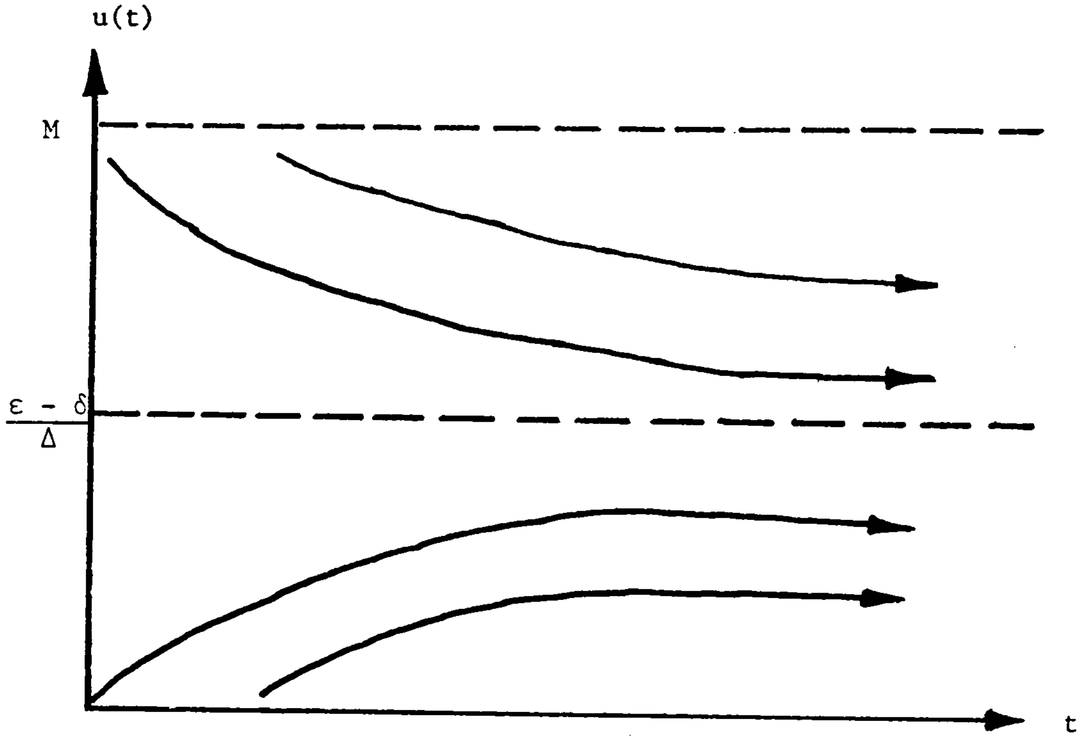


Figure (3.22)

The solution space structure for $\varepsilon > \delta$

Theorem 3.4.3. Let $\alpha \equiv \min \frac{1}{V_m} \{B, D\}$ satisfy $\alpha \geq 1$, then corresponding to any solution of (3.3.11), there exists a $\xi_0 = \xi_0(P, Z)$, $0 \leq \xi_0 \leq \infty$, such that the P and Z components of the solution satisfy $P(\xi_0) = 0$ and $Z(\xi_0) = 0$.

If $M > \frac{K}{1 - \alpha}$ then corresponding to any solution of (3.4.11c) there exists a ξ_N, $0 \leq \xi_N \leq \infty$, such that the nutrient component of the solution satisfies $N(\xi_N) = \frac{K}{1 - \alpha}$ and if $\xi_N < \infty$, $N(\xi_N) \leq N(\xi)$ for all $\xi \geq \xi_N$.

Proof. From (3.3.11c),

$$\frac{dN}{dt} = - \frac{V_n PN}{K + N} + BP + DZ + E(1 - \theta) \frac{P Z}{R + P + bZ} , \quad 0 \leq \theta \leq 1 ;$$

thus,

(3.3.77) $$\frac{dN}{dt} \geq - \frac{V_m PN}{K + N} + \alpha V_m(P + Z) = - \frac{V_m PN}{K + N} + \alpha V_m(M - N)$$

where

(3.3.78) $\alpha V_m = \min\{B, D\}$.

Using $\alpha \leq P \leq M - N$ in (3.3.77), it follows

(3.3.78) $$\frac{dN}{dt} \leq - \frac{V_m(1 - \alpha)(M - N)(N - \overline{C})}{K + N}$$

where

$$\overline{C} = \frac{K \alpha}{1 - \alpha} .$$

Case 1:

If $\alpha > 1$, then

(3.3.80) $$\frac{dN}{dt} \geq V_m K \frac{(M - N)}{K + N} \geq \frac{V_m K}{K + M} (M - N) ,$$

comparing with

(3.3.81) $$\frac{du}{dt} = \frac{V_m K}{K + M} (M - u)$$

leads to

(.3.82) $N(t) \geq u(t)$ for $t \geq 0$ if $N(0) \geq u(0)$.

Solving (3.3.81) for $u(t)$ gives

(3.3.83) $$u(t) = M - [(M - u(0)) e^{-\frac{V_m Kt}{K + M}}] .$$

Thus, the differential inequality (3.3.80) leads to

$$\lim_{t \to \infty} N(t) = M$$

which in turn implies extinction of both P and Z .

Case 2:

(3.3.81) $$\alpha \leq 1 \text{ , } M > \overline{C} = \frac{K \alpha}{1 - \alpha} .$$

In this case, the differential inequality (3.3.77) has the form

(3.3.82) $$\frac{dN}{dt} \geq - V_m(1 - \alpha) \frac{(M - N)(N - \overline{C})}{(K + N)} .$$

Comparing with

$$(3.3.83)\quad \frac{du}{dt} = - V_m(1 - \alpha) \frac{(M - u)(u - \overline{C})}{(K + M)}$$

leads to $N(t) \geq u(t)$ for $t \geq 0$ if $N(0) \geq u(0)$. Solving (3.3.83) for $u(t)$ gives

$$(3.3.84)\quad \frac{(u - M)^{K+M}}{(u - \overline{C})^{K+M}} = C_0 \, e^{-V_m(M - \overline{C})(\alpha - 1)t}$$

where

$$(3.3.85)\quad C_0 = \frac{(u(0) - M)^{K+M}}{(u(0) - \overline{C})^{K+\overline{C}}} \quad .$$

Thus, $\lim_{t \to \infty} N(t) = \overline{C} = \frac{K \alpha}{1 - \alpha}$, which leads to the last conclusion of the theorem.

Persistence Condition

The main persistence result for this model is

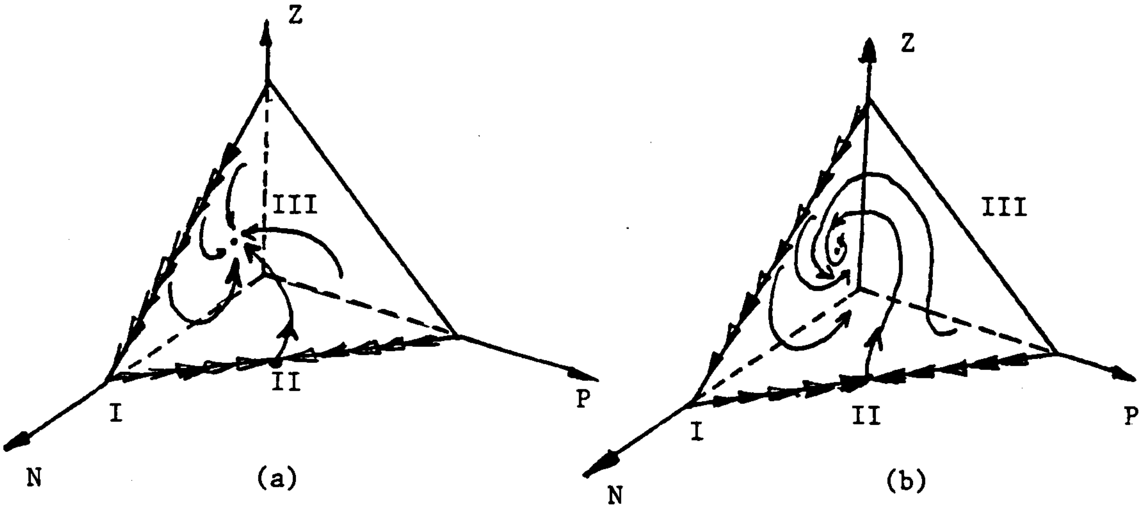
Theorem 3.4.4: The model (3.3.1) is dynamically persistence if and only if the parameters B, K, V_m, D, R, E, and θ satisfy the inequality

$$(3.4.8)\quad M > [\frac{BK}{V_m - B} + \frac{DR}{\theta E - D}]$$

Proof. The result of this theorem follows from the topological structures about the equilibrium points which lie on the boundary of the phase triangle (Δ: $P + Z + N = M$) . From the inequalities (3.3.27) and (3.3.33), it follows that the equilibrium point

I, (P, Z, N) = (0, 0, M) is a saddle point, for the nonlinear system (3.3.1), and the equilibrium point II, (P, Z, N) = (P^*_2 , 0 , M - P^*_2) is also a saddle point if (3.4.8) holds. The equilibrium point, II, is an asymptotically stable node for parameters satisfying the complementary inequality. The set of attractive separatrices for the saddles I and II lie on the boundary of Δ . From this instability and from the fact that Δ is a positive invariant set, we conclude that the trajectory through any initial vector (n(0), p(0), z(0)) in the interior of Δ must be bounded away from the boundary of Δ. Thus, system (3.3.1) with the grazing function $\frac{E\ P\ Z}{R + P + bZ}$ is dynamically persistent provided (3.4.8) holds.

Figures (3.23) and (3.24) show the equilibrium points of the above model for different values of b and M .



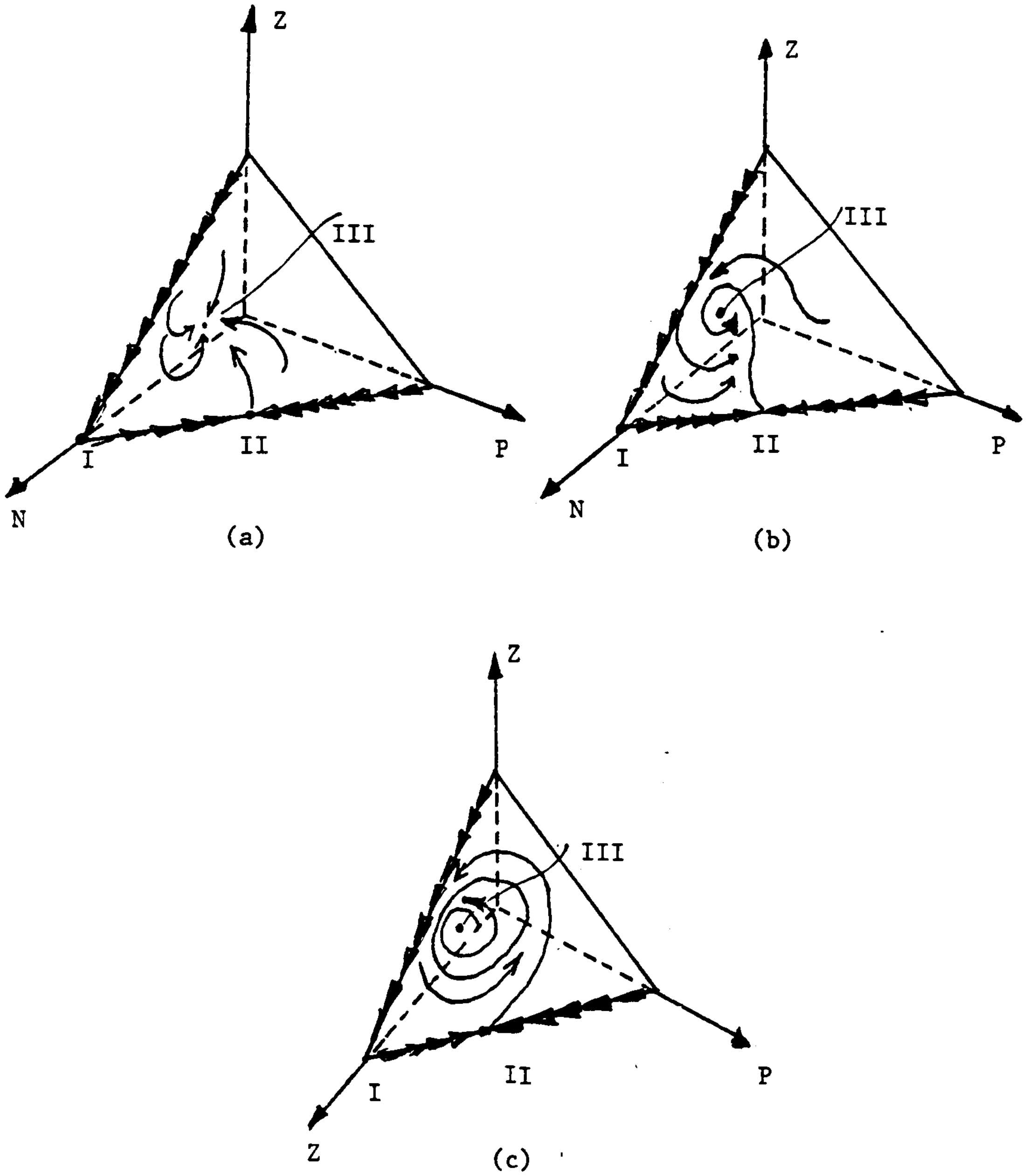
(a) (b)

Figure 3.23

Equilibrium Points of Model 3.3.1 with b > b*

a) Phase triangle diagram of the model (3.3.1) with b > b* when equilibrium points I and I are saddle points and III is an asymptotically stable node.

b) Phase triangle diagram of the model (3.3.1) with b > b* when equilibrium points I and II are saddle points and III is an asymptotically stable spiral.



(a) (b)

(c)

Figure 3.24

Equilibrium Points of Model 3.3.1 with $0 < b < b*$

a) Phase triangle diagram of the model (3.3.1) with $0 < b < b*$ when equilibrium points I and II are saddle points and III is an asymptotically stable node.

b) Phase triangle diagram of the model (3.3.1) with $0 < b < b*$ when equilibrium points I and II are saddle points and III is an asymptotically stable spiral.

c) Phase triangle diagram of the model (3.3.1) with $0 < b < b*$ when equilibrium points I and II are saddle points and III is an unstable spiral and a limit circle exists.

3.4. Two Nutrient Model Functionally Coupled Through Transformation Rate Dependencies

The main objective of the research in this section is to construct a two nutrients dynamic eutrophication model for a lake and to provide basic information for the future exploration of water quality management.

In real ecosystem, information external to a particular element cycle is commonly required to determine the rates of the transformation matter flows within the cycle. For example, experimental data [18] indicate that element cycles are functionally coupled through intercycle rate dependencies associated with nutrient uptake matter flows. Such dependencies represent purely signal flow couplings between two or more element cycles [18] . These signal flow couplings are typically directed from one nutrient storage in one element cycle (say, the phosphorus cycle) to a nutrient-uptake matter flow in another element cycle (say, the nitrogen or carbon cycles) [5] .

The Model

Nitrogen and phospuorus are considered to be the major nutrients in the lake. That is, a modification of the total amount of either one can have significant effect upon the balance of the system

An outline of their cycle is illustrated in Figure (3.25) . For the sake of simplicity nutrients are given as total nitrogen and total phosphorus.

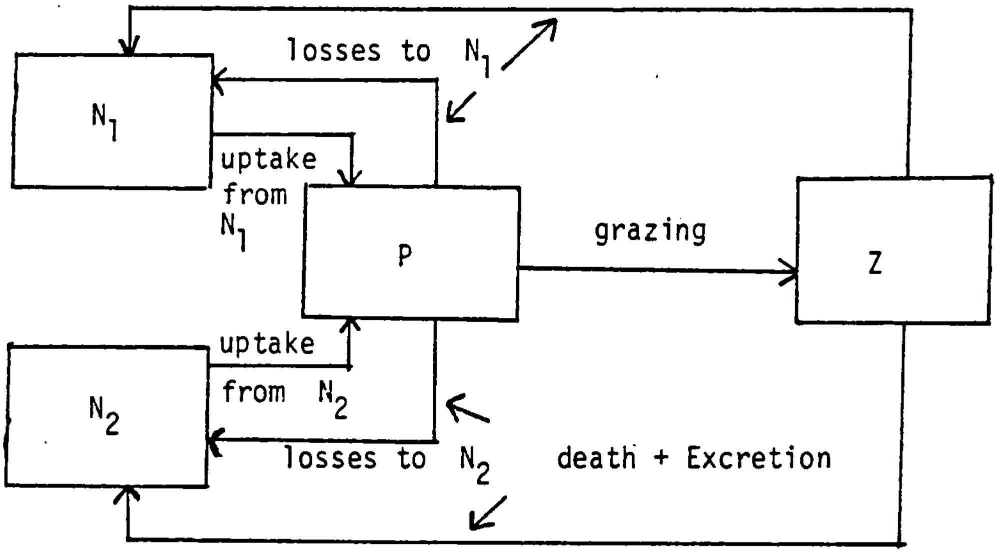


Figure 3.25

Two nutrients aquatic model

The model presented here is a simple model which illustrate how two element cycles (say, the N_1 and the N_2 cycles) in the same region of space may functionally interact in an aquatic ecosystem. This model consists of two rudimentary element-cycle models symmetrically cross-coupled by signal flow linkages directed from the nutrient storages (N_i) in one element cycle to the nutrient uptake matter flow in the other element cycle $F_{P_i N_i}$ respectively through the uptake rate coefficients (a_1, a_2) such that

(3.4.1) $a_1 = a_1(N_2)$, $a_2 = a_2(N_1)$

where $F_{P_iN_j}$ is the flow from N_j to P_i , $(i \neq j)$.

In the particular model studied in this section, the uptake rate coefficients a_1, a_2 are assumed to be in the Michaelis-Menten form

$$(3.4.2) \quad a_1(N_2) = \frac{a_1 N_2}{C_1 + N_2}$$

and

$$a_2(N_1) = \frac{a_2 N_1}{C_2 + N_1}$$

where C_1 and C_2 are parameters which regulate the degree of intercoupling between the two element cycles. For instance, $N_i >> C_j$ would imply luxury storage of element N_i relative to the uptake requirement of element N_j and N_i would be effectively uncoupled from the N_j cycle.

The structure of the resulting model of two functionally coupled rudimentary element-cycles is

$$(3.4.3) \quad \dot{P}_1 = a_1(\frac{N_2}{C_1 + N_2})(\frac{N_2}{A + N_1})P_1 - b_1P_1(\frac{Z_1}{B_1 + P_1}) - D_{P_1} P_1$$

$$\dot{Z}_1 = \frac{b_1 Z_1 P_1}{B_1 + P_1} - D_{Z_1} Z_1$$

$$\dot{N}_1 = -a_1(\frac{N_2}{C_1 + N_2})(\frac{N_1}{A_1 + N_1})P_2 - b_2 P_2(\frac{Z_2}{B_2 + P_2}) - D_{P_1} Z_1$$

$$\dot{P}_2 = a_2(\frac{N_1}{C_2 + N_1})(\frac{N_2}{A_2 + N_2}) P_2 - b_2P_2(\frac{Z_2}{B_2 + P_2}) - D_{P_2} P_2$$

$$\dot{Z}_2 = b_2 Z_2(\frac{N_1}{B_2 + P_2}) - D_{Z_2} Z_2$$

$$\dot{N}_2 = -a_2(\frac{N_1}{C_2 + C_1})(\frac{N_2}{A_2 + N_2})P_2 + D_{P_2} P_2 + D_{Z_2} Z_2$$

where $N_i(t)$, $(i = 1, 2)$ is the concentration of biologically limiting nutrients in the euphotic zone at time t .

$P_i(t)$, $(i = 1, 2)$ is the concentration of the nutrient in the phytoplankton component at time t .

$Z_i(t)$, $(i = 1, 2)$ is the concentration of the nutrient in the zooplankton component at time t ; D_p , D_{Z_i} $(i = 1, 2)$ are the death (washout) rates of phytoplankton and zooplankton respectively.

It can easily be seen that intercycle modulations do not affect strict conservation of elemental matter within each element cycle, that is

$$(3.4.4) \quad \dot{P}_i + \dot{Z}_i + \dot{N}_i = 0 \text{ implies that } P_i(t) + Z_i(t) + N_i(t) = M_i$$
$$= \text{constant}, \quad (i = 1,2)$$

Indeed, intercycle signal-flow couplings preserve the physical distinctness of noncognate element cycles while permitting the functional interaction of states and rates between such element cycles [18] .

Simplified Model

Since it is difficult to examine the qualitative nature of the system of equation (3.4.3) by means of analytical method, let us consider a simplified version of the above system, a conservative system with constant biomass stochiometry, (i.e., $\frac{P_1}{P_2} = \theta_1$ = constant, $\frac{Z_1}{Z_2} = \theta_2$ = constant, and $\frac{N_1}{N_2} = \theta_3$ = constant), and in the average, for some major nutrients we can take $\theta_1 \cong \theta_2 \cong \theta_3 \cong \theta$ [10] .

Thus, one may reduce the six-variable model discussed in the foregoing to a functionally equivalent three-variable model which exhibits identical behavior. Then, corresponding to equations (3.4.3) we have

$$
\begin{aligned}
(3.4.5) \qquad & \dot{P} = a(\frac{N}{A + N})(\frac{\theta N}{C + \theta N}) P - \frac{b\ P\ Z}{B + P} - D_P\ P \qquad , t \in R_+ = [0, \infty) \ , \\
& \dot{Z} = \frac{b\ Z\ P}{B + P} - D_Z Z \ , \quad t \in R_+ \ , \\
& \dot{N} = -a(\frac{N}{A + N})(\frac{\theta N}{C + \theta N}) P + D_P P + D_Z Z \ , \quad t \in R_+ \ ,
\end{aligned}
$$

and

$$(3.4.6) \qquad P + Z + N = M = \text{constant.}$$

It is easy to show that system (3.4.5) has a unique nonnegative solution for each nonnegative initial condition $(X_0 \in \mathcal{D} = \{(P, Z, N) \ ; \ P, Z, N \geq 0\})$.

<u>Critical Points of</u> (3.4.5)

The system (3.4.5) has the form

$$\dot{P} = P[a\ \psi_2(N) - D_P - bZ\ \phi_2(P)]$$

$$(3.4.7)\qquad \dot{Z} = Z[bP\ \phi_2(P) - D_Z]$$

$$\dot{N} = -a[P\ \psi_2(N) + D_P P + D_Z Z]$$

with

$$(3.4.8)\qquad \psi_2(N) = \frac{\theta N^2}{(A + N)(C + \theta N)}$$

and

$$(3.4.9)\qquad \phi_2(P) = \frac{1}{B + P}\ .$$

The substitution of equation (3.4.6) into (3.4.8) yields

$$(3.4.10)\qquad \dot{P} = P[a\ \psi_2(M - P - Z) - D_P - bZ\ \phi_2(P)]\ ,$$

and

$$\dot{Z} = Z\ b\ P\phi_2(P) - D_Z$$

which is a two-dimensional system in the variables P and Z .

(i) The point $(P, Z) = (0, 0)$ is always an equilibrium point of (3.4.10) .

(ii) If the equation

$$(3.4.11)\qquad a\ \psi_2(M - P) - D_P = 0$$

has a positive solution P_2^* , that is, if

$$(3.4.12) \quad M > \frac{D_P(C + \ A) + \sqrt{(D_P \ C + \theta A)^2 + 4D_P \ C \ A\theta(a - D_P)}}{2 \ (a - D_P)}$$

where it is assumed that $a > D_P$, then the point $(P , Z) = (P_2^*, 0)$ becomes an equilibrium point, where

$$(3.4.13) \quad P_2^* = M - \frac{D_P(C + \theta A) + \sqrt{D_P(C + \theta A)^2 + 4D_P \ C \ A\theta(a - D_P)}}{2 \ (a - D_P)} .$$

(iii) If we have the solution (P_3^*, Z_3^*) of the equations

$$(3.4.14) \quad b \ P_3^* \ \phi_2(P_3^*) - D_Z = 0$$

and

$$(3.4.15) \quad a \ \psi_2(M - P_3^* - Z_3^*) - D_P - b \ Z_3^* \ \phi_2(P_3^*) = 0$$

in the domain $\mathcal{D}$, that is, if

$$(3.4.16) \quad 0 < P_3^* < M , \ 0 < Z_3^* < M ,$$

then the point (P_3^*, Z_3^*) is an equilibrium point. It can be shown that the solution (P_3^*, Z_3^*) is unique if

$$(3.4.17) \quad M > \frac{D_Z \ B}{(b - D_Z)} > 0 .$$

assuming that $b > D_Z$.

Thus, from (i), (ii), and (iii), we obtain the following three cases for the distribution of the equilibrium points. The system takes one of these cases according to the value of the parameters.

Case 1: $(0, 0, M)$ for all $0 < M < M_0$

Case 2: $(0, 0, M)$, $(P_2^*, 0, M_0)$ for $M_0 < M < P_3^*$

Case 3: $(0, 0, M)$, $(P_2^*, 0, M_0)$ and $(P_3^*, Z_3^*, M - (P_3^* + Z_3^*))$ for $P_3^* < M$

where

$$(3.4.18) \quad M_0 = \frac{D_P(C + \theta A) + \sqrt{[D_P(C + \theta A)]^2 + 4D_P\ CA\theta(a - D_P)}}{2\theta(a - D_P)} > 0 \ ;$$

$$(3.4.19) \quad P_2^* = M - M_0 \ ,$$

and

$$(3.4.20) \quad P_3^* = \frac{D_Z\ B}{b - D_Z} > 0 \ .$$

Stability Analysis of the Equilibrium Points

Here the stability analysis of the non-linear system (3.4.10) is performed by perturbation about the equilibrium points, i.e., linearizing the system about these points and examining its characteristic equations.

(i) Linearized form of equations (3.4.10) about the point (0, 0) becomes

$$(3.4.20)\quad \dot{\Delta P} = [a\ \psi_2(M) - D_P]\Delta P$$

and

$$(3.4.21)\quad \dot{\Delta Z} = -D_Z\ \Delta Z\ .$$

The characteristic equation and its roots are given by

$$(3.4.22)\quad -(D_Z + \lambda)\ [\frac{a\ \theta M^2}{(A + M)(C + \theta M)} - D_P - \lambda] = 0\ ;$$

$$(3.4.23)\quad \lambda_1 = \frac{a\ \theta M^2}{(A + M)(C + \theta M)} - D_P\ ;$$

and

$$(3.4.24)\quad \lambda_2 = -D_Z < 0\ .$$

Thus, the point (0, 0) is stable (node) if $M < M_0$ and it is unstable (saddle point) and the equilibrium point $(P_2^*, 0)$ exists if $M > M_0$.

(ii) Linearized form of equations (3.4.10) about the point $(P_2^*, 0)$ becomes

$$(3.4.25)\quad \dot{\Delta P} = [a\ P_2^*\ \frac{\partial\psi_2(M - P_2^*)}{\partial P}]\ P + [a\ P_2^*\ \frac{\partial\psi_2(M - P_2^*)}{\partial\ Z} - bP_2^*\ \phi_2(P_2^*)]\Delta Z$$

and

$$(3.4.26)\quad \dot{\Delta Z} = [\frac{b\ P_2^*}{B + P_2^*} - D_Z]\ \Delta Z$$

The characteristic roots are given by

$$(3.4.27) \quad \lambda_1 = -a\, P^{*}_{2} \left.\frac{\partial\, \psi_2}{\partial\, N}\right|_{*} < 0$$

and

$$(3.4.28) \quad \lambda_2 = [\frac{b\, P^*_2}{B + P^*_2} - D_Z] < 0 \quad \text{if}$$

$$(3.4.29) \quad P^*_2 < \frac{D_Z\, B}{b - D_Z} = P^*_3 \, .$$

(iii) Linearized form of equations (3.2.10) about the point (P^*_3, Z^*_3) is

$$(3.4.30) \quad \Delta P = P^*_3[\frac{a\ \partial\psi_2(M - P^*_3 - Z^*_3)}{\partial\ P} + \frac{b\ Z^*_3}{(P^*_3 + B)^2}]\Delta P + $$

$$+ P^*_2[\frac{a\ \partial\psi_2(M - P^*_3\ Z^*_3)}{\partial\ Z} - \frac{b}{P^*_3 + B}]\ \Delta Z$$

$$(3.4.31) \quad \Delta Z = Z^*_3[\frac{b\ B}{(P^*_3 + B)^2}]\Delta P \, .$$

Thus, the characteristic equation at (P^*_3, Z^*_3) is

$$(3.4.32) \quad \lambda^2 + \alpha_1\lambda + \alpha_2 = 0$$

where

$$(3.4.33) \quad \alpha_1 = - P^*_3[a\ \frac{\partial\psi_2(M - P^*_3 - Z^*_3)}{\partial\ P} + \frac{b\ Z^*_3}{(P^*_3 + B)^2}] \, ,$$

and

$$(3.4.34)\quad \alpha_2 = Z_3^* \, P_3^*[\frac{bB}{(P_3^* + B)^2}] \cdot [a \frac{\partial\psi_2(M - P_3^* - Z_3^*)}{\gamma\, Z} - \frac{b}{P_3^* + B}]$$

and the characteristic roots are

$$(3.4.35)\quad \lambda_{1,2} = \frac{1}{2}(-\alpha_1 \pm \sqrt{\alpha_1^2 - 4\alpha_2}) \ .$$

Hence, if

$$(i)\quad [a \frac{\partial\ \psi_2(M - P_3^* - A_3^*)}{\partial\ P} + \frac{b\ Z_3^*}{(P_3^*,\ Z_3^*)^2}] < 0 \ ,$$

and

$$(ii)\quad \alpha_1^2 - 4\alpha_2 > 0 \ ,$$

$(P_3^*,\ Z_3^*)$ is stable (node) and if (i) holds and

$$(3.4.36)\quad \alpha_1^2 - 4\alpha_2 < 0 \ ,$$

$(P_3^*,\ Z_3^*)$ is stable (spiral) .

The possibility of bifurcation and limit cycles exists if

$$(3.4.37)\quad (i)\quad a \frac{\partial\psi_2(M - P_3^* - Z_3^*)}{\partial\ P} + \frac{b\ Z_3^*}{(P_3^* + B)^2} = 0 \quad \text{at} \quad M = M^* > 0$$

and

$$(3.4.38)\ (ii)\quad \frac{d}{dM}\,(a \frac{\partial\ \psi_2(M - P_3^* - Z_3^*)}{\partial\ P} + \frac{b\ Z_3^*}{(P_3^* + B)^2})\Big|_{M=M^*} > 0$$

where $M = M^*$ is the bifurcation limit. Thus, if (i) and (ii) hold, there is a neighborhood $\mathcal{N}$ of $M = M^*$ such that any closed orbit corresponding to $M \in \mathcal{N}$ has period $\approx \frac{e\pi}{\lambda^*}$ and radius growing like $(|M - M^*|)^{1/2}$, where $\lambda^* = \text{Img}\ \lambda_2$ at $M = M^*$ [Marsden and McCraken 1976, p. 20] .

Extinction Analysis

Theorem 3.2.1: If the parameters a, c, A, D_P, and θ satisfy the inequalities

$$\text{(i)} \quad C > \theta A , \qquad M < \frac{a\ K_2}{(a - D_P) - AK_1/A} - C/\theta \ ;$$

$$\text{(ii)} \quad C < \theta A , \qquad M < \frac{a\ K_1}{(a - D_P) - a\ \ K_2/C} - A \ ;$$

or

$$\text{(iii)} \quad C = \theta A , \qquad M < \frac{D_P\ A}{(a - D_P)}$$

where

$$(3.4.39) \quad K_1 = \frac{-A^2}{C/\theta - A} \ ,$$

$$(3.4.40) \quad K_2 = \frac{(C/\theta)^2}{(C/\theta - A)} \ ,$$

then corresponding to the P-component of each section of (3.4.7) there exists a constant P_0 such that

$$(3.4.41) \quad P(t) \leq P(0)\ e^{-\gamma_1 t} \ , \quad \gamma_1 > 0 \ .$$

In particular, there exists a τ_P , $0 \leq \tau_P \leq \infty$, such that $P(\tau_P) = 0$.

Proof. Using $Z \geq 0$, $P \geq 0$ in the differential equations (3.2.7) we find

$$(3.4.42) \quad \frac{dP}{dt} \leq (a - D_P)P - aP(\frac{K_1}{A + N} + \frac{K_2}{C/\theta + N}) \quad , \quad c \neq \theta A ,$$

where K_1 and K_2 are given by (3.4.39) and (3.4.40) respectively.

From the constraints (i) and inequality (3.4.42), it follows that $K_1 < 0$, $K_2 > 0$, and

$$(3.4.43) \quad \frac{dP}{dt} \leq (a - D_P)P - \frac{a\ P\ K_1}{A} - \frac{a\ P\ K_2}{C/\theta + M} \quad .$$

Integrating from 0 to t and solving for P leads to

$$(3.4.44) \quad P(t) \leq P(0)\ e^{-[\frac{a\ K_2}{M + C/\theta} - (a - D_P) - a/A(-K_1)]t} \quad .$$

Similarly, from the constraints in (ii) and inequality (3.4.42) it follows that

$$K_1 > 0 \ ; \ K_2 < 0$$

and

$$(3.4.45) \quad P(t) \leq P(0) \quad e^{-[\frac{a\ K_2}{M + C/\theta} - (a - D_P) - \theta a/C(-K_2)]t} \quad .$$

In the special case, $c = A$, inequality (3.2.42) is reduced to

$$(3.4.46)\quad \frac{dP}{dt} \leq P[a(\frac{M}{A + M}) - D_P]$$

and by integrating from 0 to t and solving for $P(t)$, it follows that

$$(3.4.47)\quad P(t) \leq P(0)\, e^{-(D_P - \frac{aM}{A + M})t} .$$

<u>Theorem</u> 3.4.2. If the parameters D_Z, B, and b satisfy the inequality

$$(3.4.48)\quad M < \frac{D_2\ B}{b - D_Z}$$

then corresponding to the P-component of each solution of (3.4.7) there exists a constant $Z(0)$ such that

$$(3.4.49)\quad Z(t) \leq Z(0)\, e^{-\gamma_2 t} \quad , \quad \gamma_2 > 0 .$$

In particular, there exists a τ_Z, $0 \leq \tau_Z < \infty$, such that $Z(\tau_Z) = 0$.

<u>Proof</u>. Using $P \geq 0$, $Z \leq M$ in the differential equation (3.4.5) we find that

$$(3.4.50)\quad \frac{dZ}{dt} \leq Z[(b - D_Z) - \frac{bB}{B + M}] .$$

Integrating from 0 to t and solving for Z leads to

$$(3.4.51) \quad Z(t) \leq Z(0)\, e^{-[\frac{bB}{B + M} - (b - D_Z)]t}$$

Theorem 3.4.3. Let $\alpha = \min\{D_P, D_Z\}$, then corresponding to any solution of (3.4.7), there exists a $\tau_0 = \tau_0(P, Z)$, $0 \leq \tau_0 \leq \infty$, such that the P and Z components of the solution $P(\tau_0) = 0$ and $Z(\tau_0) = 0$. Moreover, if

$$(3.4.52) \quad (i) \quad C > \theta A \ , \quad a \leq \alpha \ , \quad M > \bar{\theta} \ ;$$

$$(3.4.53) \quad (ii) \quad C < \theta A \ , \quad a \leq \alpha \ , \quad M > \bar{\bar{\theta}} \ ;$$

or

$$(3.4.54) \quad (iii) \quad C = \theta A \quad , \quad a \leq \alpha \ , \quad M > \frac{Aa}{A\alpha} \ ;$$

where

$$(3.4.55) \quad \bar{\theta} = -(A - \frac{a\, K_1}{(\alpha - a)\bar{\alpha}}) \ ,$$

$$(3.4.56) \quad \bar{\bar{\theta}} = -(C/a - \frac{a(-K_2)}{(\alpha - a)\bar{\bar{\alpha}}} \quad ,$$

$$(3.4.57) \quad \bar{\alpha} = 1 + \frac{a\, K_2}{(\alpha - a)(M + C/\theta)}$$

$$(3.4.58) \quad \bar{\bar{\alpha}} = 1 + \frac{a\, K_1}{(\alpha - a)(A + M)} \ .$$

K_1 and K_2 are as given in Theorem 3.2.1, then corresponding to any solution of (3.4.7) there exists a τ_N , $0 \leq \tau_N \leq \infty$, such that the nutrient component of the solution satisfies

(i) $N(\tau_N) = \overline{\theta}$, if $C > \theta A$, $a > \alpha$,

(ii) $N(\tau_N) = \overset{=}{\theta}$, if $C < \theta A$, $a > \alpha$,

or

(iii) $N(\tau_N) = \frac{A\ \alpha}{a - \alpha}$ if $C = \theta A$, $a > \alpha$.

Proof. In the differential equation,

(3.4.59) $$\frac{dN}{dt} = (D_P P + D_Z Z) - \frac{a\ N^2\ P}{(A + N)(C/\theta + N)} ,$$

let

(3.4.60) $$\alpha = \min\{D_P, D_Z\} .$$

Thus,

(3.4.61) $$\frac{dN}{dt} \geq \alpha(P + Z) - \frac{a\ P\ N^2}{(A + N)(C/\theta + N)} .$$

But, $P \leq M - N$ implies that

(3.4.62) $$\frac{dN}{dt} \geq (M - N)[(\alpha - a) + \frac{a\ K_2}{(C/\theta + N)} + \frac{a\ K_1}{(A + N)}] .$$

In case 1, $C > \theta A$ implies that $K_1 < 0$, and $K_2 > 0$, thus inequality (3.4.63) takes the form

(3.4.64) $$\frac{dN}{dt} \geq - \bar{\alpha} \, (a - \alpha) \, \frac{(M - N)}{(A + N)}(N - \bar{\theta}) \ .$$

Comparing (3.4.64) with the equation

(3.4.65) $$\frac{du}{dt} = - \bar{\alpha}(a - \alpha) \, \frac{(M - u)}{(A + u)}(u - \bar{\theta})$$

leads to $N(t) \geq u(t)$ for all t if $N(0) \geq u(0)$. Separating the variables in (3.4.65) yields

(3.4.66) $$\frac{(A + u) \quad du}{(M - u)(u - \bar{\theta})} = - \bar{\alpha}(a - \alpha)dt \ .$$

Integrating both sides from 0 to t yields

(3.4.67) $$\frac{(u - \bar{\theta})^{M}}{(u - M)^{G}} = C_0^* \, e^{-\bar{\alpha}(a - \alpha)t}$$

where

(3.4.68) $$G = - \frac{(A + M)}{(M - \bar{\theta})} \quad , \quad H = \frac{(A + \bar{\theta})}{(M - \bar{\theta})} \quad , \text{ and } \quad C_0^* = \text{constant.}$$

Thus,

$N \rightarrow M$ as $t \rightarrow \infty$ if $a > \alpha$ and
(i.e., $(P, Z) \rightarrow 0$)
$N \rightarrow \bar{\theta}$ as $t \rightarrow \infty$ if $a > \alpha$.

In case 2, $C < \theta A$ implies that $K_1 > 0$ and $K_2 < 0$ and inequality (3.4.69) takes the form

$$\frac{dN}{dt} \geq - \frac{(M - N)(a - \alpha)}{(C/\theta + N)} \ \bar{\bar{\alpha}} \ (N - \bar{\bar{\theta}}) \ ,$$

then, as in the first case, comparing with

$$(3.4.70) \quad \frac{du}{dt} = - \bar{\bar{\alpha}}(a - \alpha) \ \frac{(M - u)}{(C/a + u)} \ (u - \bar{\bar{\theta}})$$

leads to $N(t) \geq u(t)$ for all t if $N(0) \geq u(0)$.

Separating the variables and integrating from 0 to t yields

$$(3.4.71) \quad \frac{(u - \bar{\theta})^{H}}{(u - M)^{G}} = C_0^{**} \ e^{- \bar{\bar{\alpha}} \ (a - \alpha)t}$$

where

$$\bar{G} = - \frac{(C/\theta + M)}{(M - \bar{\bar{\theta}})} \quad , \quad \bar{H} = \frac{(C/\theta + \bar{\bar{\theta}})}{(M - \bar{\bar{\theta}})} \quad .$$

Thus, $N \to M$ as $t \to \infty$ if $a < \alpha$ and $N \to \bar{\bar{\theta}}$ as $t \to \infty$ if $a > \alpha$.

In case 3, with $C = \theta A$, we have the inequality

$$(3.4.72) \quad \frac{dN}{dt} \geq \alpha(M - N) - a(M - N)(1 - \frac{A(2N + A)}{(A + N)^2})$$

$$\geq (M - N)[(\alpha - a) + \frac{aA}{A + N}] =$$

$$= - \frac{(a - \alpha)(M - N)}{(A + N)} \ (N - \frac{A\alpha}{a - \alpha})$$

Similarly, as in cases 1 and 2,

$$N \to M \quad \text{as} \quad t \to \infty \quad \text{if} \quad a < \alpha$$

$$(\text{i.e.,} \quad P,\ Z \to 0)$$

and

$$N \to \frac{A\,\alpha}{a - \alpha} \quad \text{as} \quad t \to \infty \quad \text{if} \quad a > \alpha\ .$$

Persistence Condition

The main persistence result for this model is:

Theorem 3.4. . The model (3.2.7) is dynamically persistent if and only if the parameters a, b, D_P, B, C, and θ satisfy the inequality

$$(3.4.73) \quad M > \frac{D_P(C + \theta A) + [D_P^2(C + \theta A)^2 + 4D_P\ C\ A\theta(a - D_P)]^{\frac{1}{2}}}{2\theta(a - D_P)} + \frac{D_Z\ B}{b - D_Z} \quad .$$

Proof. The proof here is similar to the one given for theorem (3.4.4) but using inequalities (3.4.18) and (3.4.29). It is worth noting that the dynamic persistence condition (3.4.73) can be generally realized by the relative locations of the P_2^* and P_3^* :

$$(3.4.74) \quad P_2^* < \frac{D_Z B}{b - D_Z} = P_3^* \ .$$

3.5. Conclusions

Eutrophication in bodies of water is a critical environmental problem on both local and global scales, which is mainly due to nitrogen and phosphorus contained in the polluted inflows from surrounding urbanized, agricultural or industrial areas.

In this chapter, a nonlinear function general enough to include the effects of feeding saturation, intraspecific consumer interference and eutrophication phenomenon was used to represent the transfer of material from phytoplankton to zooplankton population. This grazing function has the form $G = \frac{E\,P\,Z}{R + P + bZ}$ where E, R, and b are parameters of the model. If $P >> R + bZ$, then phytoplankton is superabundent, i.e., an increase in phytoplankton population, P, will not increase the rate of grazing per unit zooplankton, $\frac{G}{Z}$. For this condition, $\frac{G}{Z}$ is a constant equal to E. If zooplankton population, Z, is increased while the phytoplankton is held constant, then when $bZ >> R + P$, the grazing rate, G, becomes $\frac{EP}{b}$, a linear phytoplankton dependent function. Also, the grazing rate per unit zooplankton population density varies inversely with zooplankton population density.

It was also shown that the phytoplankton population density at equilibrium increases proportionally with the total nutrient which reflects the eutrophication phenomenon and agrees with some recent experimental data.

Another interesting feature of this function is the stability of all equilibrium points of the model achieved for $b > b^*$, a critical value of the parameter b, for all values of the total nutrient, M, in the system. Thus, nutrient enrichment does not lead to a cyclic system behavioral mode.

The effects of nitrogen and phosphorus contained in the polluted inflows were combined in a simple conservative aquatic model with the assumption that the ratio of their concentrations in the system is kept constant.

The two models were subjected to equilibrium and stability analysis to ascertain their mathematical implications. These analysis led to interesting extinction and persistence results and to important suggestions to control the models to stable persistent states.

CHAPTER IV

OPTIMAL CONTROL THEORY AND ITS APPLICATIONS FOR AQUATIC MODELS

4.1 Introduction

Applications of Optimal Control Theory to ecological problems was initiated only in the late 1960's. It appears that several authors, independently of each other, began to apply optimal control theory to ecological problems at about the same time (Watt, 1968, Goh, 1969/1970; Becker, 1970; Clark, 1971). Recently Clark (1976), Conway (1977), and Wickwise (1977) have reviewed the applications of optimal control theory in resource management and in the control of epidemic.

In applying optimal control theory to ecological problems, one faces at least two difficulties. First, an adequate model of the ecosystem is required. Second, realistic models of ecosystems would have many state variables. This leads to considerable computational difficulties. For these reasons the potential usefulness of optimal control in the management of ecosystems is demonstrated here by applying it to some simple nutrient controlled aquatic model.

By applying optimal control theory to aquatic models, we tried to achieve the following goals.

(i) Discovering what, if anything, can be optimized in aquatic models (e.g. biomass, effort, energy, etc.)

(ii) Finding some nutrient control programs to manage water systems subject to accelerated eutrophication because of waste discharges.

(iii) Predicting the effects of expected future nutrient discharges.

The formulations and equations presented in Chapter III with the analytical methods employed there, demonstrated that some ecomodels can be controlled to state of persistence by addition of sufficient quantity of nutrient. As we shall see in the present chapter, this controlling nutrient can be applied to one or several components. The results achieved here for two trophic level conservative models can be extended to more generalized models of higher dimension which need not necessarily be conservative.

4.2 Outline

The outline of the optimization problems considered in this chapter is given in Table 4.1. The results of these different cases are presented and compared in the following sections. Suggestions to expand them to higher dimensions and nonconservative models are made.

4.3 Aquatic Models With One Control Variable

The models considered here are described by a nonlinear system of differential equations in the form

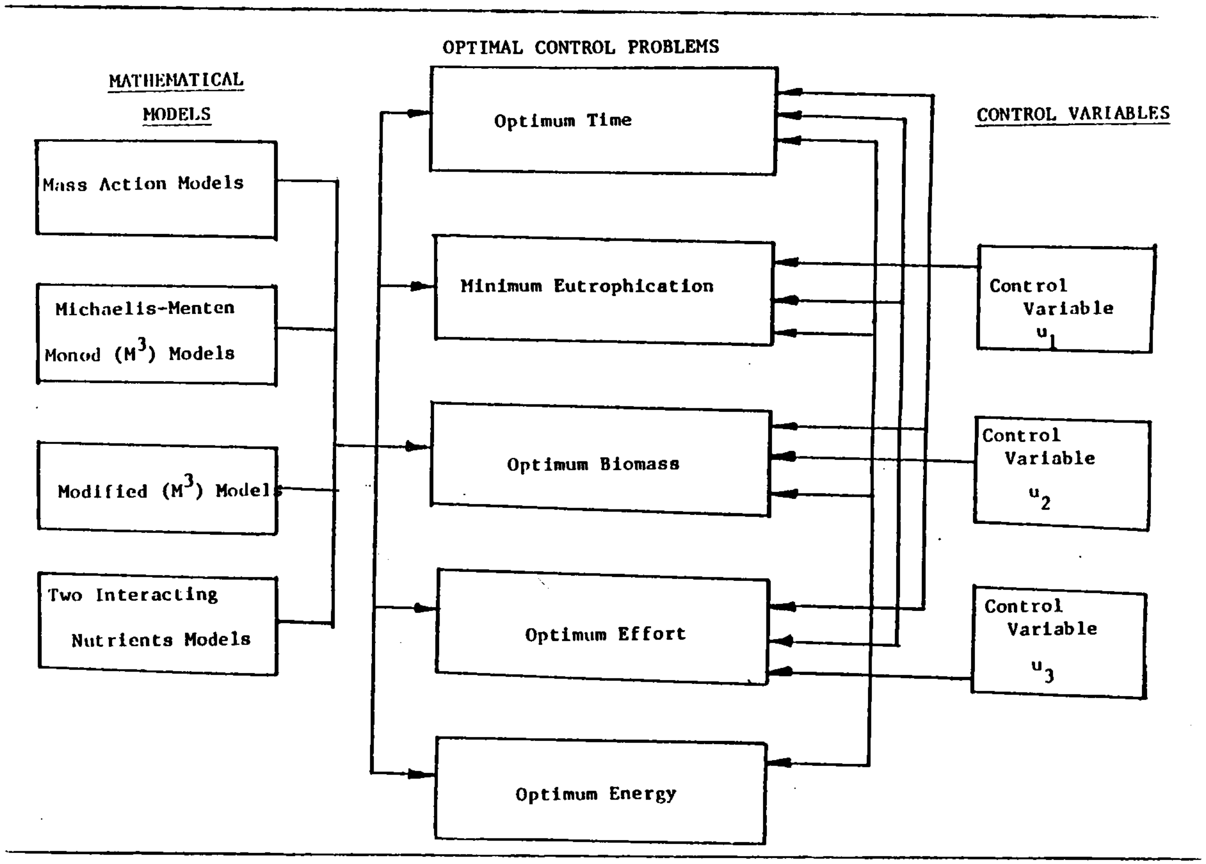
$$\dot{P}(t) = P\ \phi_i(N) - BP - Z\ \psi_i(P, Z) = F_1(P, Z, N, u)$$

(4.3.1)

$$\dot{Z}(t) = Z\ \psi_i(P, Z) - DZ = F_2(P, Z, N, u)$$

Table 4.1

VARIOUS OPTIMAL CONTROL PROBLEMS IN AQUATIC MODELS



$$\dot{N}(t) = -P\ \phi_i(N) + BP + DZ + \delta\ u(t) = F_3(P, Z, N, u), \quad i =$$

1, 2, 3, 4,

with

$$(4.3.2) \qquad P(t) + Z(t) + N(t) = P(t_0) + Z(t_0) + N(t_0) + \delta \int_{t_0}^{t} u(s)ds$$

where

$P(t_0)$, $Z(t_0)$ and $N(t_0)$ are the initial values at $t = t_0$,

$P(t)$, $Z(t)$ and $N(t)$ are as defined in Chapter 3,

B, D are death (washout) rates of phytoplankton and zooplankton respectively,

$u(t)$ is the input control variable, $u(t) \in U_t$, and

U_t is the set of all admissible controls. (piecewise continuous functions bounded by two finite constant limit).

The various formulations which have been utilized previously in (4.3.1) are:

Mass Action Model: (i = 1) (Figure 4.1)

$$(4.3.3) \quad \phi_1(N) = \frac{V_m N}{K+N} \quad ; \quad \psi_1(P, Z) = EP$$

Michaelis- Menten-Monod Model: (i = 2) (Figure 4.1)

$$(4.3.4) \quad \phi_2(N) = \frac{V_m N}{K+N} \quad ; \quad \psi_2(P, Z) = \frac{EP}{P+P}$$

Modified Michaelis - Monod Model: (i = 3) (Figure 4.1)

$$(4.3.5) \quad \phi_3(N) = \frac{V_m N}{K+N} \quad ; \quad \psi_3(P, Z) = \frac{E\ P}{R+P+bZ}$$

Two Nutrient Interacting Cycles Model: (i = 4) (Figure 4.2))

$$(4.3.6) \quad \phi_4(N) = \frac{\theta\ V_m N^2}{(K+N)(K+\theta N)} \quad ; \quad \psi_4(P, Z) = \frac{EP}{R+P}$$

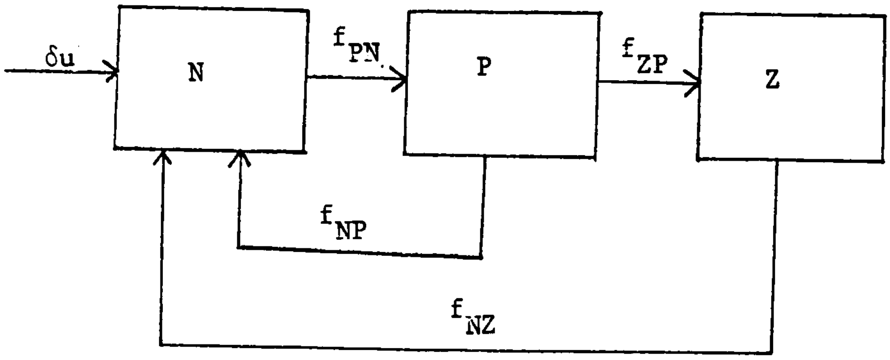


Figure 4.1

Single Nutrient Controlled Aquatic Model
(i = 1, 2, 3)

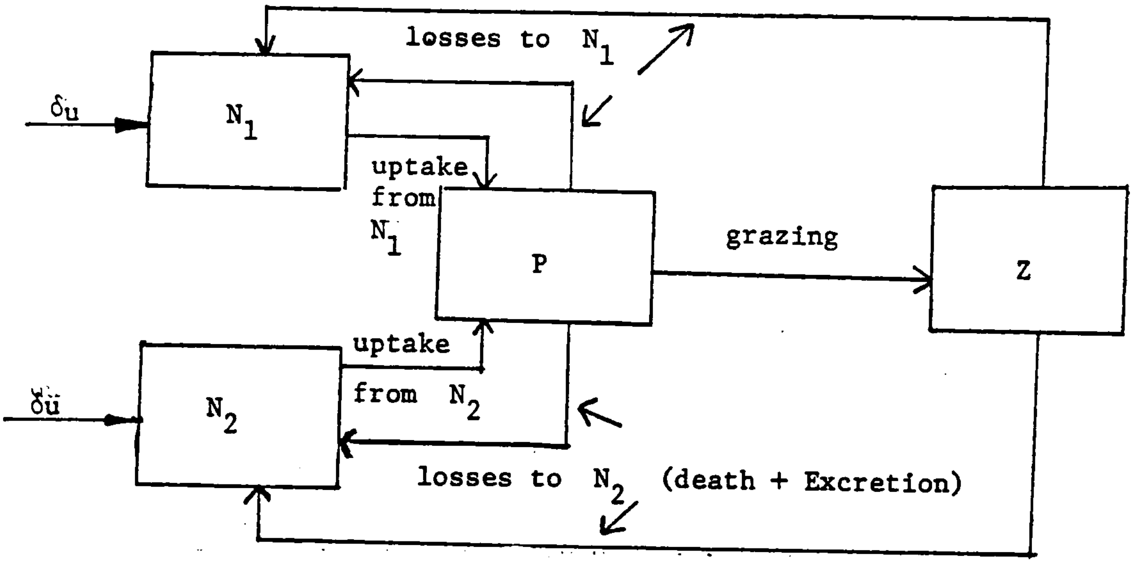


Figure 4.2

Two nutrient interchanging cycles model with one control variable (i = 4)

The contents of Tables 4.2 and 4.3 will be used in the following sections

Table 4.2

THE FUNCTIONS $\phi_i(N)$ AND $\frac{d\phi_i(N)}{dN}$ AND THEIR TIME DERIVATIVES: (i = 1, 2, 3)

$\phi_i(N) = \frac{V_m N}{K+N}$	$\phi_i'(N) = \frac{V_m K}{(K+N)^2}$
$D(\phi_i(N)) = \frac{V_m K\dot{N}}{(K+N)^2}$	$D(\phi_i'(N)) = \frac{-2V_m \dot{N}K}{(K+N)^3}$

Table 4.3

THE FUNCTIONS $\phi_4(N)$ AND $\frac{\partial\phi_4(N)}{\partial N}$, AND THEIR TIME DERIVATIVES

$\phi_4(N) = \frac{\theta V_m N^2}{(K+N)(C+\theta N)}$	$\phi_4'(N) = \frac{\theta V_m N[2KC+(C+\theta K)N]}{(K+N)^2(C+\theta N)^2}$
$D(\phi_4(N)) = \frac{\theta V_m NN[2KC+(C+\theta K)N]}{(K+N)^2(C+\theta K)^2}$	$D(\phi_4'(N)) = \frac{-2\theta V_m \dot{N}\ G(N)}{(K+N)^3(C+\theta N)^3}$

where $G(N) = \theta(C+\theta K)N^3 + 2KC(1-\theta)N^2 + 2KC(1-\theta)N + K^2C^2$

Table 4.4

THE FUNCTIONS $\psi_1(P,\ Z)$, $\frac{\partial\psi_1(P,\ Z)}{\partial P}$, AND $\frac{\partial\psi_1(P,\ Z)}{\partial Z}$, AND THEIR TIME DERIVATIVES.

$\psi_1(P,\ Z) = EP$	$\psi_{1P} = E$	$\psi_{1Z} = 0$
$D(\psi_1(P,\ Z)) = EP$	$D(\psi_{1P}) = 0$	$D(\psi_{1Z}) = 0$

Table 4.5

THE FUNCTIONS $\psi_i(P, Z)$, $\frac{\partial\psi_i(P, Z)}{\partial P}$, AND $\frac{\partial\psi_i(P, Z)}{\partial Z}$ AND THEIR TIME DERIVATIVES $(i = 2,4)$

$\psi_1(P, Z) = \frac{EP}{R+P}$	$\psi_{iP} = \frac{ER}{(R+P)^2}$	$\psi_{iZ} = 0$
$D(\psi_i(P, Z) = \frac{ER\dot{P}}{(R+P^2}$	$D(\psi_{iP}) = \frac{-2ER\dot{P}}{(R+P)^3}$	$D(\psi_{iZ}) = 0$

Table 4.6

THE FUNCTIONS $\psi_3(P, Z)$, $\frac{\partial\psi_3(P, Z)}{\partial P}$, AND $\frac{\partial\psi_3(P, Z)}{\partial Z}$, AND THEIR TIME DERIVATIVES:

$\psi_3(P, Z) = \frac{EP}{(R+P+bZ)}$	$\psi_{3P}(P, Z) = \frac{E(R+bZ)}{(R+P+bZ)^2}$	$\psi_{3Z}(P, Z) = \frac{EbP}{(R+P+bZ)^2}$
$D(\psi_3(P, Z)) = \frac{EP}{(R+P+bZ)^2} [(R+bZ)\dot{P} - b\dot{P}Z]$		
$D(\psi_3(P, Z)) = \frac{-2E}{(R+P+bZ)^3} [(R+bZ)\dot{P} - \frac{b}{2} (R+bZ-P)\dot{Z}]$		
$D(\psi_{3Z}(P, Z)) = \frac{-Eb}{(R+P+bZ)^3}[(R+bZ)\dot{P} - 2bP\dot{Z}]$		

From Tables 4.2-4.6, the time derivatives of the different functions can be rewritten in the following simple forms where the f_{ij} , are defined in an obvious way.

$$(4.3.7) \quad D(\phi_i) = f_{1i}(P, Z, N) + \delta f_{2i}(P, Z, N) u ;$$

$$(4.3.8) \quad D(\phi_i') = f_{3i}(P, Z, N) + \delta f_{4i}(P, Z, N) \dot{u} ;$$

$$(4.3.9) \quad D(\psi_i) = f_{5i}(P, Z, N)P + f_{6i}(P, Z, N) Z ;$$

$$(4.3.10) \quad D(\psi_{ip}) = f_{7i}(P, Z, N)P + f_{8i}(P, Z, N) Z ;$$

and

$$(4.3.11) \quad D(\psi_{iZ}) = f_{9i}(P, Z, N)P + f_{10i}(P, Z, N) Z ; i = 1, 2, 3, 4$$

4.4 Optimal Control Problems

For ecosystem models described by differential equations, the appropriate tool for formulating optimal policies is the continuous-time optimal control theory using the maximum principle. The standard continuous-time optimal control problem for managing an ecosystem is as follows:

Find the control program u(t) (that is, determine (i) rate of application; and (ii) periods of application) that satisfy the following:

(4.4.1) (System): $\dot{X}(t) = F(X(t), u(t))$;

(4.4.2) (Initial conditions) $X(t_0) = X_0$;

(4.4.3) (Terminal conditions) $L_s(T, X(T)) = 0$, $s = 1, 2, \ldots, k$;

(4.4.4) (Control variable constraints $U_{min} \leq u(t) \leq U_{max}$;

(4.4.5) (State variables constraints) $(P(t) + Z(t) + N(t)) - k_i \geq 0$, $i = 1, 2, 3, 4$; $N(t) \geq 0$

where k_i's are the persistence limits for the different models;

(4.4.6) (Objective) $\min_u [G(X(T), T) + \int_{t_0}^{T} f_0(X(t), u(t))dt]$.

Here G and f_0 denote scalar continuous objective functions. For example, G might be

(4.4.7) $G(X(t), T) = [(P(T) - C_1)^2 + (Z(T) - C_2)^2 + (N(T) - C_3)^2]$

which presents the deviation of the final point $(P(T), Z(T), N(T))$ from a desired target (C_1, C_2, C_3) .

Necessary Conditions For Optimality:

In the following two theorems we state without proof [8] the necessary condition for optimality.

Theorem 4.1: If $(X(\overset{*}{t}), u^*(t)$ is a normal optimal set, then there exists a costate vector $\Lambda(t)$ and constant multipliers $P_1, \ldots, P_k$ such that for $i = 1, \ldots, n$

(4.4.8) $\lambda_i(t) = -\frac{\partial H}{\partial X_i}$;

(4.4.9) $\lambda_i(T) = \frac{\partial G}{\partial X_i}(T) + \sum_{s=1}^{k} P_s \frac{\partial L_s}{\partial T} = 0$;

where H is the scalar function given by

(4.3.22) $H = \lambda_0 f_0 + \sum_{i=1}^{n} \lambda_i(t) \cdot f_i(X(t), u(t))$;

(4.4.11) $u^*(t) = U_{min}$ only if $\frac{\partial H}{\partial u} > 0$;

(4.4.12) $u^*(t) = U_{max}$ only if $\frac{\partial H}{\partial u} < 0$;

and

(4.4.13) $U_{min} < u(t) < U$ only if $\frac{\partial H}{\partial u} = 0$.

<u>Theorem 4.2</u>: If $u*(t)$ belongs to the interior of U_t (define before), necessary conditions for optimality are

(4.4.14) (i) $\frac{\partial H}{\partial u} = 0$;

(4.4.15) (ii) $(-1)^k \frac{\partial}{\partial u} [\frac{d^k}{dt^k}(\frac{\partial H}{\partial u})] > 0$ where k is the smallest positive integer for which

$$\frac{d^m(Hu)}{d\ t^m} , \quad m \geq 2$$ is an explicit function of u .

<u>Additional Necessary Conditions For Optimality</u>

Pontryagin and his co-workers have also derived other necessary conditions for optimality that will prove useful. We now state, without proof, two of these necessary conditions [14].

1. If the final time is fixed and the Hamiltonian, H , does not depend explicitly on time, then the Hamiltonian must be a constant when evaluated on an extremal trajectory; that is,

(4.4.16) $H(X^*(t)\ ,\ u^*(t),\ \Lambda^*(t)) = c\ ,\ \text{for}\ \ t \in [t_0,\ T]\ .$

2. If the final time is free, and the Hamiltonian does not explicitly depend on time, then the Hamiltonian must be identically zero when evaluated on an extremal trajectory; that is,

$$H(X^*(t),\ u^*(t),\ \Lambda^*(t)) = 0\ ,\ \text{for}\ \ t \in [t_0,\ T]\ .$$

4.4.1 Optimal Control Problems With Linear Control Variable.

The problem to be solved in this section is to find the control program for model (4.3.1) that drives the system from a given initial state to a desired target set, and such that the performance index J , given by (4.4.17)

$$(4.4.17) \qquad J = [(P(T) - C_1)^2 + (Z(T) - C_2)^2 + (N(T) - C_3)^2 + \int_0^t (\theta + \alpha|u| + \beta P + \eta Z + \gamma N)dt]$$

is minimized.

In this problem we have state variables constraints in the form

(4.4.18) $g(X(t)) \geq 0$,

where g is an ℓ-vector function of the state and possibly time, having continuous first and second partial derivatives with respect to $X(t)$. Our approach will be to transform the ℓ-inequality constraints (4.4.18) into a single equality constraint, and then to augument the performance measure with this equality constraint.

Let us define a new variable $w(t)$ by

$$(4.4.19) \quad \dot{w}(t) \triangleq [g_1(X(t))]^2 U_1 + \ldots + [g_\ell(X(t))]^2 U_\ell$$

where U_i is a unit Heavside step function defined by

$$(4.4.20) \quad U_i = \begin{cases} 0 & \text{for } g_i \geq 0 \\ 1 & \text{for } g_i < 0 \end{cases} , \text{ for } i = 1, 2, \ldots, \ell$$

Notice that $w(t) \geq 0$ for all t , and that $w(t) = 0$ only for time when all of the constraints (4.4.18) are satisfied. Now let us require that the variable $w(t)$, given by

$$(4.4.21) \quad w(t) = \int_{t_0}^{T} w(t)\, dt + w(t_0)$$

satisfies the two boundary conditions

$$(4.4.22) \quad w(t_0) = 0 = w(T) .$$

Since $w(t) \geq 0$ for all t , satisfaction of these boundary conditions implies that $w(t)$ must be zero throughout the interval $[t_0, T]$, but this occurs only if the constraints are satisfied for all t $[t_0, T]$. Thus, to minimize the functional (4.4.17) subject to the equations constraints (4.3.1)

and

$$(4.4.23) \quad w = (P + Z + N - K_i)^2 U_1 + N^2 U_2 = F_4(P, Z, N, u) \;;$$

constraints on the control variables (4.4.4), and state inequality constraints

$$(4.4.24) \quad (P(t) + Z(t) + N(t)) - K_i \geq 0 \;; \quad i = 1, 2, 3, 4 \;;$$

and

$$(4.4.25) \quad N(t) > 0 \;,$$

first the Hamiltonian is formed:

$$(4.4.26) \quad H = \lambda_0(\theta + \alpha|u| + \beta P + \eta Z + \gamma N) + \sum_{i=1}^{n} \lambda_i(t)F_i(P, Z, N, u) \,.$$

Notice that the Hamiltonian does not contain $w(t)$ explicitly. For optimal contol $u = u^*(t)$ and optimal trajectory $X^*(t)$ for all

$t \in [t_0, T]$ the λ_0, λ_1, λ_2, λ_3 and λ_4 are costate variables, not all zero, which satisfy $\lambda_0 = \text{constant} \geq 0$ and

$$(4.4.27) \qquad \dot{\lambda}_1 = \frac{-\partial H}{\partial P} = - \lambda_0 \beta - \lambda_1(\phi_i(N) - B - Z\, \psi_{iP}(P, Z)$$

$$- \lambda_2 Z\, \psi_{iP}(P, Z)$$

$$+ \lambda_3(\phi_i(N) - B)$$

$$- 2\lambda_4(P + Z + N - K_i)\, U_1 \; ;$$

$$(4.4.28) \qquad \dot{\lambda}_2 = \frac{-\partial H}{\partial N} = - \lambda_0 \eta + \lambda_1 P(Z\, \psi_{iZ}(P, Z) + \psi_i(P, Z))$$

$$- \lambda_2\, (Z\, \psi_{iZ} + \psi_i - D)$$

$$- \lambda_3\, D$$

$$- 2\, \lambda_4\, (P + Z + N - K_i)\, U_1 \; ;$$

$$(4.4.29) \qquad \dot{\lambda}_3 = \frac{-\partial H}{\partial N} = - \lambda_0 \gamma + (\lambda_3 - \lambda_1) P\, \phi'_i(N) -$$

$$2\lambda_4[(P + Z + N - K_i)U_1 + NU_2] \; ;$$

(4.4.30) $\dot{\lambda}_4 = \frac{-\partial H}{\partial W} = 0$;

and

(4.4.31) $H(X^*(t), u^*(t), \Lambda^*(t), t) \leq H(X^*(t), u(t), \Lambda^*(t), t)$

for all admissible $u(t)$. Condition (4.4.30) implies that λ_4 is a constant. The boundary conditions $X(t_0)$ are specified $[w^*(t_0) = 0 = w^*(T)]$ while the remaining boundary conditions at $t = T$ can be determined using the results in Theorem 4.1.

In the following sections some special cases of the performance index J will be considered.

1. Optimal Time Problems

In this case, $\alpha = \beta = \dot{\eta} = \gamma = 0$; $\theta = 1$. Thus (4.4.17) and (4.4.26) take the forms

(4.4.32) $$J = G(X(t)) + \int_0^T dt$$

where $G(X(t)) = (P(T) - C_1)^2 + (Z(T) - C_2)^2 + (N(T) - C_3)^2)$.

and

(4.4.33) $H = \lambda_\theta + \lambda\ F_1 + \lambda_2 F_2 + \lambda_3 F_3 + \lambda_4 F_4$

respectively.

Also, the costate variables satisfy (4.4.27) - (4.4.30) but with $\beta = \eta = \gamma = 0$.

Thus, the control program for this problem is as follows

$$(4.4.34) \qquad u^*(t) = \begin{cases} U_{max} & \text{if } H_u = \delta\, \lambda_3(t) < 0 \\ U_{min} & \text{if } H_u = \delta\, \lambda_3(t) > 0 \\ \text{Singular control} & \text{if } H_u = \delta\, \lambda_3(t) = 0 \text{ for} \\ & t \in [t_1, t_2]\ , \ t_0 \leq t_1 \leq t_2 \leq T\ . \end{cases}$$

Singular Control Analysis

If on the subinterval $[t_1, t_2]$, $t_1 \neq t_2$

$$(4.4.35) \qquad H_u = \delta\, \lambda_3(t) = 0\ ,$$

the control scheme requires a singular control. In what follows, we shall denote total differentiation with respect to time t by D or dot, and let $P = P^*(t)$, $Z = Z^*(t)$, and $N = N^*(t)$. Differentiating (4.4.35) totally.

$$(4.4.36) \qquad D(H_u) = \delta\, \lambda_3(t)$$

and employing (4.4.29) it follows that

$$(4.4.37) \qquad (\lambda_3 - \lambda_1)P\phi_i(N) - 2\lambda_4[(P+Z+N-K_i)U_1 + NU_2] = 0\ .$$

We are interested in states which satisfy

(4.4.38) $P(t) > 0 \;,\; Z(t) > 0 \;,\; N(t) > 0 \;;$

hence (4.4.37) and (4.4.38) imply

(4.4.39) $$\lambda_1(t) = -\frac{2\lambda_4}{P\phi_i'}\left[(P + Z + N - K_i)\, U_1 + NU_2\right) .$$

Similarly we get

(4.4.40) $$D^2(H_u) = 0 = -\lambda_1[P\phi'_i + PD(\phi_i)] -$$

$$\lambda_1\phi'_i P_{-2}\ \lambda_2[\delta u U_1 + NU_2]$$

where ϕ'_i and $D(\phi_i')$ are as given in Table 4.1. (p. 170). Substituting (4.4.8) and (4.4.27) into (4.4.40) yield

(4.4.41) $$\boxed{u_{s_{1i}} = \frac{\phi_{1i}(X_{s_{1i}}(t)\ \Lambda_{s_{1i}}(t))}{\textcircled{H}_{1i}(X_{s1i}(t),\ \Lambda_{s1i}(t))}}$$

$; \; i = 1, 2, 3, 4 \; .$

where

(4.4.42) $$\phi_{1i} = P\,\phi_i'(N_3)\,[\lambda_1(\phi_i(N_3) - B - Z\,\psi_{iP}(P, Z)) + \lambda_2 Z\psi_{ip}(P,Z)$$

$$+ 2\,\lambda_4(P + Z + N - K_i)U_1]$$

$$- \lambda_1 P\,[\phi_i'(N)(\phi_i(N_s) - B - Z\,\psi_i(P, Z) + f_{3i}]$$

$$- 2\lambda_4(BP + DZ - P\,\phi_i(N))U_2$$

and

(4.4.43) $$\textcircled{H}_{1i} = \delta[\lambda_1\,P\,f_{4i} + 2\,\lambda_4\,(U_1 + U_2)]$$

where $X_{s_{1i}}(t)$ and $\Lambda_{s_{1i}}(t)$ are the singular state and costate vector respectively.

Two observations concerning the optimal control scheme follow. Using Theorem 4.2, the singular control, u_s , is optimal and admissible if

$$(-1)^2\,\textcircled{H}_{1i} > 0 \quad \text{and} \quad U_{min} < \frac{\phi_{1i}}{\textcircled{H}\,1i} < U_{max} \quad \text{for all}$$

$$t \in [t_1, t_2]\ .$$

For trajectories satisfying the state variables constraints, (i.e., $U_1 = 0 = U_2$) , we have the following relations

(4.4.44) $$\lambda_3(t) = \lambda_2(t) = \lambda_1(t) = 0\ .$$

From the additional condition (4.4.17) (for free final time) we have

$$(4.4.45) \qquad \lambda_0 = 0$$

which contradicts the assumption that

$$(4.4.46) \qquad \sum_{i=0}^{n} \lambda_i^2(t) > 0 \quad \text{for all} \quad t \in [t_0, T] \; .$$

Thus, in this case, there is no singular control and the control program is a bang-bang one.

2. Entrophication Control Problem

The object of the control in this model is the management of water system quality subject to accelerated entrophication because of waste discharge. In this case, the performance index and the Hamiltonian function have the forms

$$(4.4.47) \qquad J = G(X(T)) + \beta \int_{t_0}^{T} P(t)dt$$

and

$$(4.4.48) \qquad H = \lambda_0\beta P + \lambda_1 F_1 + \lambda_2 F_2 + \lambda_3 F_3 + \lambda_4 F_4$$

respectively. The costate variables satisfy (4.4.27) - (4.4.30) but with $\beta > 0$, $\theta = \eta = \gamma = \alpha = 0$ and the control program is given by (4.4.34).

Singular Control Analysis

As in problem 1 , the singular control, $u_s(t)$, for all $t \in [t_1, t_2]$ is given by

$$(4.4.47) \quad \boxed{u_{s_{2i}}(t) = = \frac{\phi_{2i}(X_{s_{2i}}(t)\ ,\ \Lambda_{s_{2i}}(t))}{\textcircled{H}_{2i}(X_{s_{2i}}(t)\ ,\ \Lambda_{s_{2i}}(t))}}$$

except in this case $\lambda_1(t)$ is given by (4.4.27).

For trajectories satisfying the state variable constraints, we have the following relations for all $t \in [t_1, t_2]$

$$(4.4.48) \quad \lambda_3 = \lambda_1 = 0 \ , \quad \lambda_2(t) = -\frac{\lambda_0\beta}{Z(t)\psi_{iP}(P,\ Z)}\ , \quad Z > 0$$

and from the additional condition (4.4.17) with $\lambda_0\beta \neq 0$ we have

$$(4.4.49) \quad \boxed{P\ \psi_{iP}(P,\ Z) - \psi_i(P,\ Z) + D = 0}$$

which is the equation of the singular trajectory for this problem. Taking the derivative of functions defined by (4.4.49) and using (4.3.9) and (4.3.10) yield

$$(4.4.50) \quad \dot{P} = \dot{Z}\ \frac{S_{2i}(P,\ Z)}{R_{2i}(P,\ Z)} \quad \text{where}$$

$$(4.4.51) \quad S_{2i}(P,\ Z) = f_{6i} - P\ f_{8i}\ ,$$

and

(4.4.52) $R_{2i}(P, Z) = \psi_{iP} + P\, f_{7i} - f_{5i}$; $i = 1, 2, 3, 4$.

Thus, from (4.4.50) and (4.3.1)

(4.4.53) $$N(t) = K\left[\frac{V_m P(t)}{(V_m - B)P(t) + [D\,\frac{S_{2i}}{R_{2i}} - \psi_i(\frac{S_{2i}}{R_{2i}}) + 1)]z} - 1\right]$$

$$= Q_{2i}(P(t), Z(t))$$

and the singular control is given by

(4.4.54) $$\boxed{U_{S_{2i}}(t) = \frac{1}{\delta}[Z(t)(1 + \frac{S_{2i}}{R_{2i}}) + \dot{Q}_{2i}(P(t), Z(t))]}$$

Special Cases:

(i) Mass-Action Model: (i = 1)

In this model with ψ_1 , $D(\psi_i)$, ψ_{1P} and $D(\psi_{1P})$ as given in Table 4.2 (a), equation (4.4.49) implies that $D = 0$ which is not true. Thus, there is no singular control in this case.

(ii) M^3 And Two Interacting Nutrient Cycles Models: (i = 2, 4)

In these models with ψ_i , $D(\psi_i)$, ψ_{iP} and $D(\psi_{iP})$ as given in Table 4.2 (b), equation (4.4.49) implies that

(4.4.55) $$P_S = \frac{R\sqrt{D}}{E-D}(\sqrt{D} + \sqrt{E}) = \text{constant.}$$

Substituting (4.4.55) and (4.4.53) into (4.4.54) yields

$$(4.4.56)\quad u_{S_{2i}}(t) = \frac{Z_S[\psi_i(P,\ Z) - D]}{\delta}\left\{1 + \frac{KV_m\ \psi_i(P,\ Z)P}{[(V_m-B)P - \psi_i(P,\ Z)Z]^2}\right\}$$

(iii) Similar expressions can be derived for the modified M^3 model (i = 3)

3. Optimal Biomass Problem

The object in this problem is to find the control program $u(t)$ that maximizes the function J given by

$$(4.4.57)\quad J = \int_0^T (\beta P + \eta Z)dZ - G(X(T))$$

and drives the system from an observed state (P_0, Z_0, N_0) to a desired final state.

In this problem, the Hamiltonian function and the costate variables are as given in (4.4.26) - (4.4.31) with $\theta = \alpha = \gamma = 0$ and λ_0 constant ≤ 0 . The control program is given by

$$(4.4.58)\quad u^*(t) = \begin{cases} U_{max} & \text{if } H_u = \delta\ \lambda_3(t) > 0 \\ Umin & \text{if } H_u = \delta\ \lambda_3(t) < 0 \\ \text{Singular control if } & H_u = \delta\ \lambda_3(t) = 0 \\ \quad \text{for } t & [t_1,\ t_2]\ ,\ t_0 \leq t_1 < t_3 < T\ . \end{cases}$$

Singular Control Analysis:

As in problem 2 , the singular control has the general form

$$(4.4.59) \quad \boxed{\begin{array}{l} u_{S_{3i}}(t) = \dfrac{\Phi_{3i}(X_{S_{3i}}(t)\ ,\ \Lambda_{S_{3i}}(t))}{\textcircled{H}_{3i}(X_{S_{3i}}(t)\ ,\ \Lambda_{S_{3i}}(t))} \\ \qquad\qquad\qquad\qquad\qquad i = 1,\ 2,\ 3,\ 4 \end{array}}$$

where $X_{S_{3i}}(t)$ and $\Lambda_{S_{3i}}(t)$ are the singular state and costate vectors respectively. For trajectories satisfying the state variables constraints, λ_1, λ_2 and λ_3 satisfy (4.4.48) and the singular trajectory and singular control are given by

$$(4.4.60) \quad \boxed{(\beta P + \eta Z)\ \psi_{iP}(P,\ Z) - \beta(\psi_i(P,\ Z) - D) = 0}$$

and

$$(4.4.61) \quad \boxed{u_{S_{3i}} = \frac{1}{\delta}\ [Z(t)\ (1 + \frac{S_{3i}}{R_{3i}}) + Q_{3i}]}$$

respectively where

$$(4.4.62) \quad S_{3i} = \beta\ f_{6i} - \eta\ \psi_{iP}(P,\ Z) - (\beta P + \eta Z)\ f_{8i}\ ;$$

$$(4.4.63) \quad R_{3i} - \beta\ \psi_{iP}(P,\ Z) + (\beta P + \eta Z)\ f_{7i} - \beta\ f_{5i}\ ;$$

and

(4.4.64) $Q_{3i}(P(t), Z(t)) = N(t)$.

Special Case:

Mass-Action Model: $(i = 1)$

The singular trajectory is given by

(4.4.65) $Z_S(t) = - \frac{\beta}{\eta} \frac{D}{E} (> 0 \text{ if } \frac{\beta}{\eta} < 0)$.

The singular control is

(4.4.66) $u_{S_{3i}}(t) = 0$.

Notice that, there is no singular control if β and η have the same sign.

4. Optimal Effort Problem (General Case)

Minimum effort (fuel) problems may be visualized in terms of reachable states; that is, the minimum effort solution is given by the intersection of the target set $S(t)$ with the set of reachable state $R(t)$, which requires the smallest amount of consumed effort. To represent this idea geometrically we could use a state-time-consumed fuel coordinate system and determine the intersections (if any) of $S(t)$ and $R(t)$. Unfortunately, although such a geometric representation is helpful as a conceptual device, it is of limited value in actually obtaining solutions. Instead, we shall approach the minimum effort problem by starting with the necessary conditions provided by Theorem 4.1.

The performance measure and the Hamiltonian functions are given by (4.4.17) and (4.4.26) respectively with $\theta \geq 0$, $\alpha > 0$, $\beta > 0$ $(\beta < 0)$, $\eta > 0$ $(\eta < 0)$ and $\delta \geq 0$.

The minimum principle require that

$$H(X^*(t), u^*(t), \Lambda^*(t)) \leq H(X^*(t), u(t), \Lambda^*(t)) \tag{4.4.67}$$

or

$$(\lambda_0\alpha|u^*(t)| + \lambda_3^*\delta\ u^*(t)) \leq (\lambda_0\alpha|u(t)| + \lambda_3^*\delta u(t) \tag{4.4.68}$$

for all admissible $u(t)$ and for all $t \in [t_0, T]$. Using the definition of $|u(t)|$ it follows that

(4.4.69-a)

$$(\lambda_0\alpha|u(t)| + \lambda_3^*(t)\delta\ u(t)) = \begin{cases} \lambda_0\alpha(1 + \dfrac{\lambda_3^*(t)\delta)}{\lambda_0\alpha})u(t) \\ \qquad \text{for } u(t) \geq 0 . \\ \lambda_0\alpha(-1 + \dfrac{\lambda_3^*(t)\delta}{\lambda_0\alpha})u(t) \\ \qquad \text{for } u(t) \leq 0 . \end{cases}$$

(4.4.69-b)

If $\frac{\lambda_3^*(t)}{\lambda_0} \frac{\delta}{\alpha} > 1$, the minimum value of (4.4.69-a) is obtained for $U(t) = -1$ and is equal to $\lambda_0 \alpha(1 - \lambda_3^*(t) \frac{\delta}{\alpha}) < 0$.

If $\frac{\lambda_3^*(t)}{\lambda_0} \frac{\delta}{\alpha} < 1.0$, the minimum value of both (4.4.56-a) and (4.4.69-b) are zero and are attained for $U(t) = 0$.

The same reasoning is used for $\lambda_3^*(t) \frac{\delta}{\alpha} < 0$. In summary, the form of the optimal control is

$$
u^*(t) = \begin{cases} U_{max} & \text{for } \frac{\lambda_3^*(t)\delta}{\lambda_0\alpha} < -1.0 \\ 0 & \text{for } -1.0 < \frac{\lambda_3^*(t)\delta}{\lambda_0\alpha} < 1.0 \\ U_{min} & \text{for } \frac{\lambda_3^*(t)\delta}{\lambda_0\alpha} > 1.0 \\ \text{an undetermined nonnegative value if} & \frac{\lambda_3^*(t)\delta}{\lambda_0\alpha} = -1.0 \\ \text{an undetermined nonpositive value if} & \frac{\lambda_3^*(t)\delta}{\lambda_0\alpha} = 1.0 \end{cases} \quad (4.4.70
$$

Notice that where in minimum-time problems the optimal control is bang-bang (see Fig 4.3) the minimum-fuel control may be described

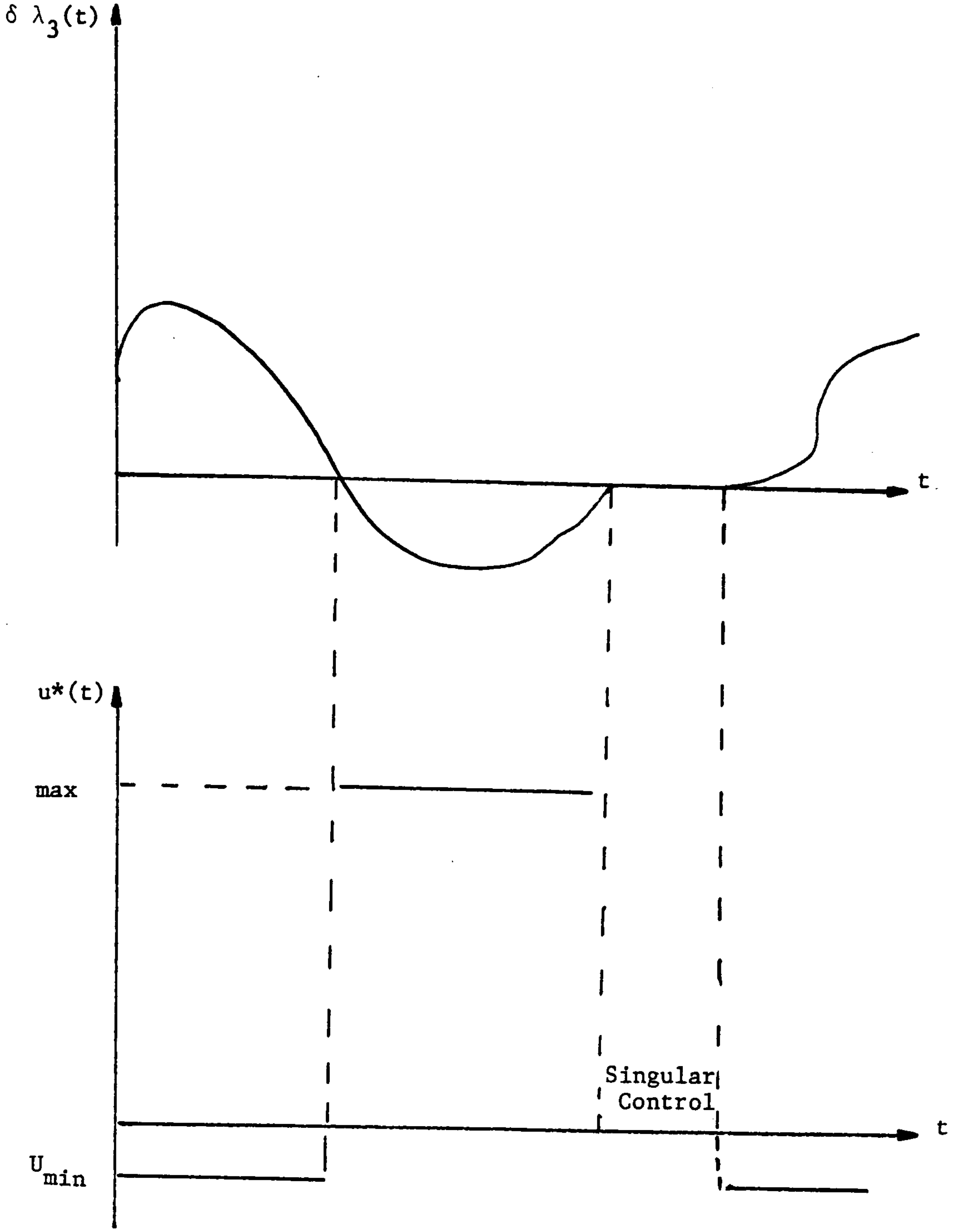


Figure 4.3

The relationship between a time-optimal control and its

coefficient in the Hamiltonian

as bang-off-bang (see Fig. 4.4) (if we assume no singular intervals).

Singular Control Analysis

If on the subinterval $[t_1, t_2] > t_1 \neq t_2$

$$\lambda_3^*(t) = \pm \frac{\lambda_0 \alpha}{\delta} , \tag{4.4.71}$$

we have singular control. Differentiate (4.4.71) totally, this yield

$$\lambda_3^*(t) = 0 . \tag{4.4.72}$$

Employing (4.4.29) we obtain

$$\lambda_0 \gamma + (\lambda_1 - \lambda_3)\dot{P}\phi_i + 2\lambda_4[(P + Z + N - K_i)U_1 + NU_2] = 0 . \tag{4.4.73}$$

Differentiating (4.4.73) totally and using (4.3.8) lead to

$$\boxed{\begin{array}{c} u_{S_{4i}}(t) = \dfrac{\phi_{4i}(X_{S_{41}}(t) , \Lambda_{S_{4i}}(t))}{\textcircled{H}_{4i}(X_{S_{4i}}(t) , \Lambda_{S_{4i}}(t))} , \\ \\ \hfill i = 1, 2, 3, 4 . \end{array}} \tag{4.4.74}$$

where

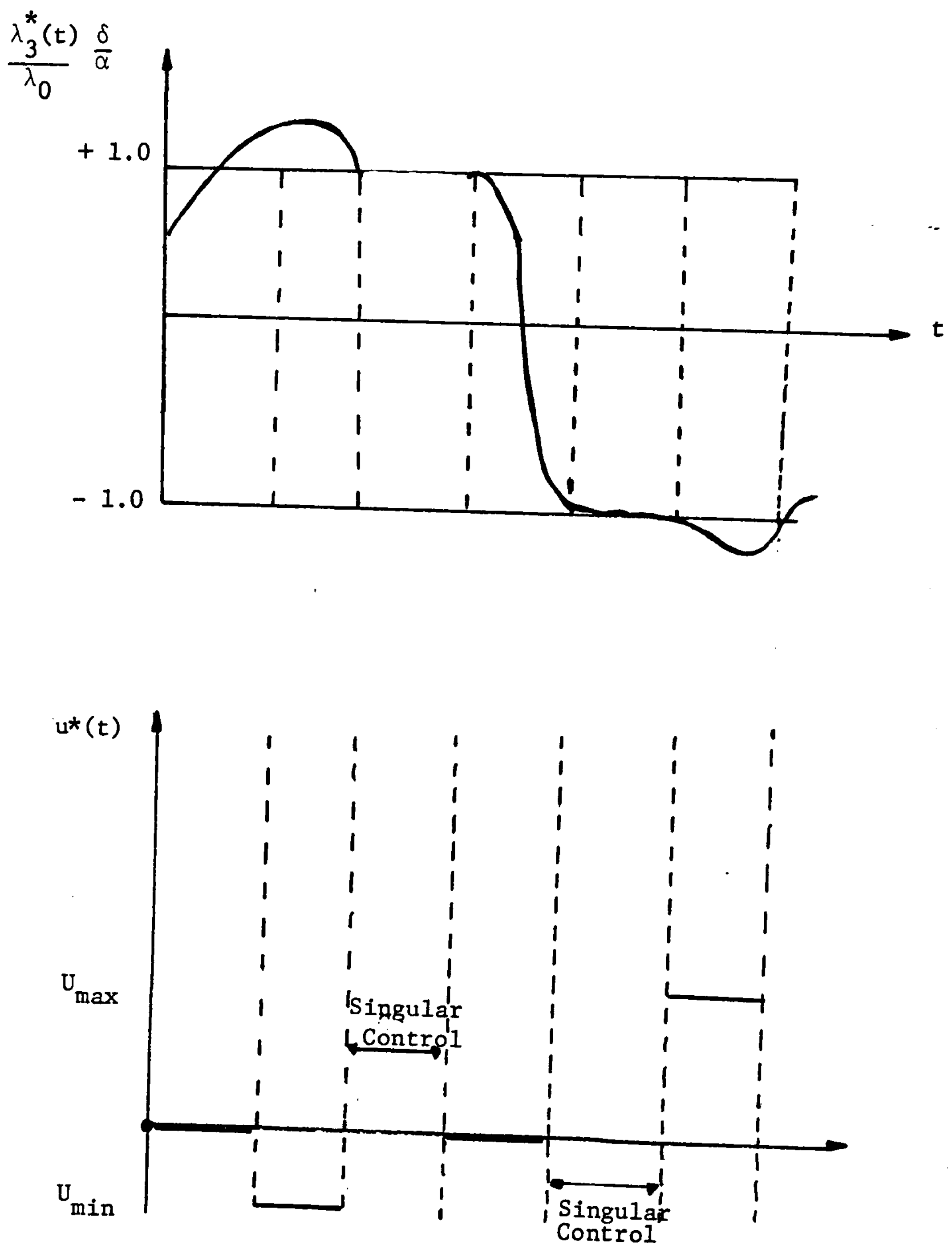


Figure 4.4. The relationship between a fuel-optimal control and the switching function $\frac{\lambda_3^*(t)\delta}{\lambda_0\alpha}$.

$$(4.4.75)\quad \phi_{4i}(X_{S_{4i}}(t)\ ,\ \Lambda_{S_{4i}}(t)) = (\lambda_3 - \lambda_1)(P\ \phi_i' + Pf_{3i})$$

$$- \lambda_1\ P\ \phi_i - 2\ \lambda_4(-P\ \phi_i + BP + DZ)U_2$$

and

$$(4.4.76)\quad Ⓗ_{4i}(X_{S_{4i}}(t)\ ,\ \Lambda_{S_{4i}}(t) = \delta[(\lambda_1 - \lambda_3)Pf_{4i} + 2\ \lambda_4(U_1 + U_2)]$$

For trajectories satisfying the state variables constraints, λ_1, and λ_3 satisfy

$$(4.4.77)\quad \lambda_1 = (\lambda_3 - \frac{\lambda_0\gamma}{P\phi_i'})\quad ,$$

$$(4.4.78)\quad \lambda_3 = \pm\ \frac{\lambda_0\alpha}{\delta}\quad .$$

Differentiating (4.4.77) totally and using (4.4.27) and (4.3.8) we have

$$(4.4.79)\quad \boxed{\begin{aligned} U_{S_{4i}}(t) = \frac{-P\ \phi_i'}{\lambda_0\gamma\delta f_{4i}}\ [\lambda_0\beta + (\lambda_1 - \lambda_3)(\phi_i - B) - \\ (\lambda_1 - \lambda_2)Z\psi_{iP} + \frac{\lambda_0\gamma}{P\phi_i}\ (\frac{\dot{P}}{P} + \frac{f_{3i}}{\phi_i})] \\ i = 1,\ 2,\ 3,\ 4. \end{aligned}}$$

5. Optimal Energy Problem

The characteristic of effort optimal problems and energy-optimal problems are similar; therefore, the following discussion will be limited to considering the same model as before with the performance index given by

$$(4.4.80) \qquad J = G(X(T)) + \int_0^T \mu\, u^2(t)dt \;,$$

with control constraints given by (4.4.4).

The Hamiltonian function for this problem is given by

$$(4.4.81) \qquad H = \lambda_0 \mu\, u^2 + \sum_{i=1}^{4} \lambda_i(t)\, F_i\, (P,\, Z,\, N, u\,)$$

where $\lambda_i(t)$ satisfy (4.4.27) - (4.4.30) for $i = 1, 2, 3, 4$ respectively.

For $U_{min} < u^*(t) < U_{max}$, (i.e. interior control), the control that minimizes H is the solution of the equation

$$(4.4.82) \qquad H_u = 2\lambda_0 \mu\, u^*(t) + \delta\, \lambda_3^*(t) = 0 \;.$$

Notice that H is quadratic in $u(t)$ and

$$(4.4.83) \qquad \frac{\partial^2 H}{\partial u^2} = 2\lambda_0\, \mu > 0 \;,$$

so

(4.4.84) $$u*(t) = \frac{-\delta\ \gamma_3^*(t)}{2\ \lambda_0\mu}$$

does globally minimize the Hamiltonian for $U_{min} < u*(t) < U_{max}$.

or, equivalently, for

(4.4.85) $$\frac{-2\ \lambda_0\mu\ U_{max}}{\delta} < \lambda_3^*(t) < \frac{-2\ \lambda_0\mu\, U_{min}}{\delta} .$$

If $\lambda_3^*(t) \geq \frac{-2\ \lambda_0\mu\ U_{min}}{\delta}$ or $\lambda_3^*(t) \leq \frac{-2\ \lambda_0\mu\ U_{max}}{\delta}$, then the control that minimizes H is

(4.4.86) $$u^*(t) = \begin{cases} U_{max} & \text{for } \lambda_3^*(t) \leq \frac{-2\ \lambda_0\mu}{\delta}\ U_{max} \\ U_{min} & \text{for } \lambda_3^*(t) \geq \frac{-2\ \lambda_0\mu}{\delta}\ U_{min} \end{cases} .$$

Putting equations (4.4.84) and (4.4.86) together, we obtain

(4.4.87) $$u*(t) = \begin{cases} U_{max} & \text{for} \quad \lambda_3^*(t) \leq \frac{-2\ \lambda_0\mu}{\delta}\ U_{max} \\ \frac{-\delta\ \lambda_3^*(t)}{2\lambda_0\mu} & \text{for} \quad \frac{-2\lambda_0\mu U_{max}}{\delta} < \lambda_3^*(t) < \\ & \qquad \frac{-2\ \lambda_0\mu\ U_{min}}{\delta} \\ U_{min} & \text{for} \quad \lambda_3^*(t) \geq \frac{-2\lambda_0\mu\ U_{min}}{\delta} \end{cases}$$

This relationship between an extremal control and an extremal costate is illustrated in Figure 4.5.

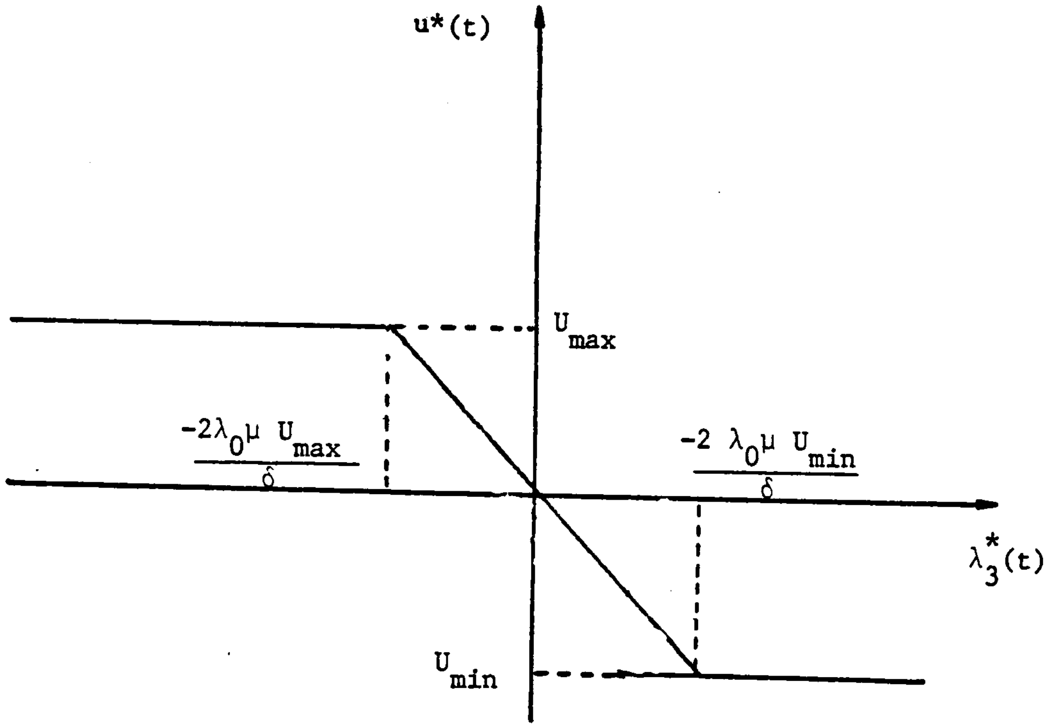


Figure 4. 5. The relationship between an extremal control and an extremal costate for problem 5.

4.5. Aquatic Models With More Than One Control Variable

In this section the different models presented before are considered again but with three different control variables applied to the three components P, Z, and N as seen in Figures (4.6 and 4.7). The analysis of the different control problems is similar to those with one control variable except for the necessary conditions of optimality

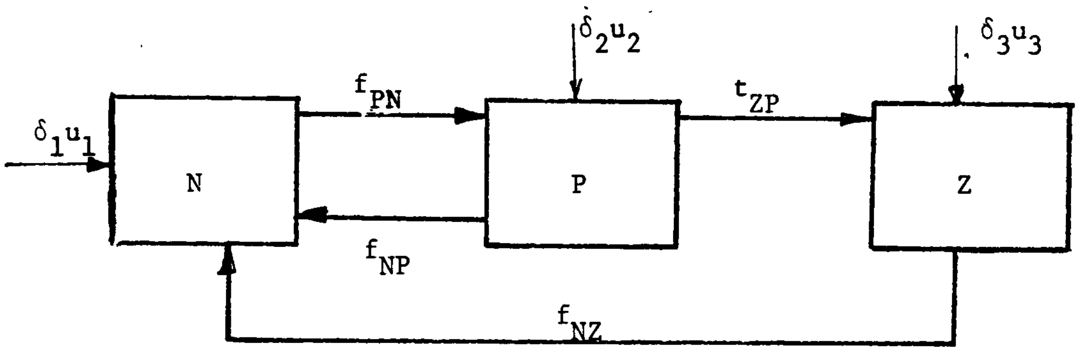


Figure (4.6)   Two trophic level conservative aquatic system with three control variables (i = 1, 2, 3)

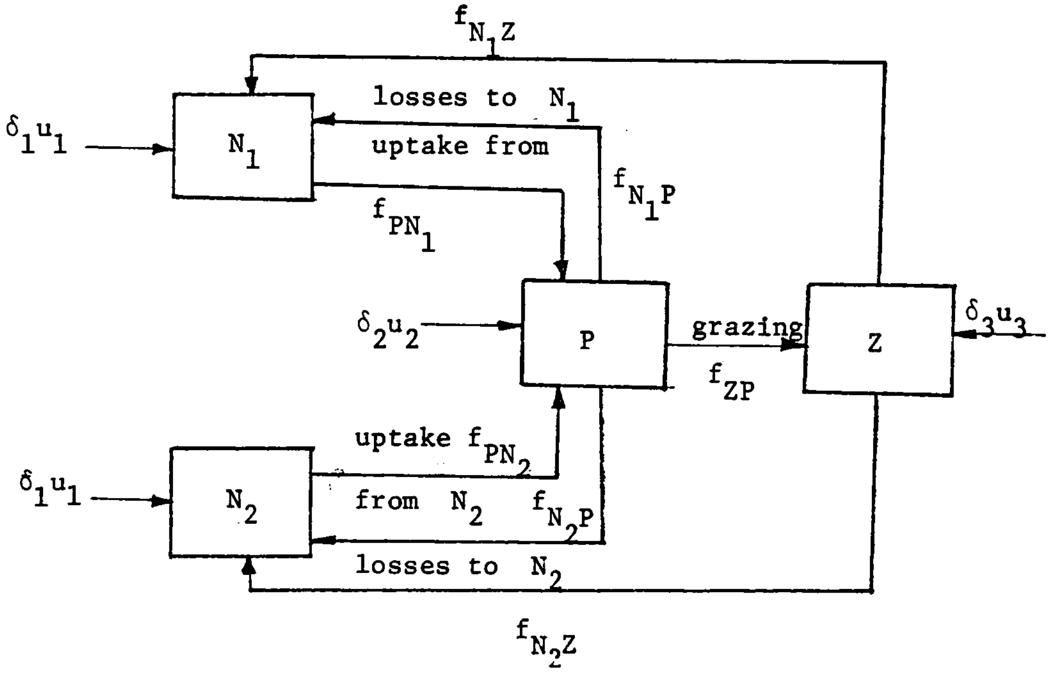


Figure 4.7. Two nutrient interacting cycles model with three control variables (i = 4).

of the singular control. The following two theorems are generalizations of Theorem 4.1 and 4.2 stated before.

Theorem 4.3: If $(X^*(t), u^*(t))$ is a normal optimal set, then there exists a costate vector $\Lambda(t)$ and constant multipliers $P_1, P_2, \ldots, P_k$ such that for $i = 1, 2, \ldots$ and $r = 1, 2, \ldots, m$

$$\lambda_1(t) = \frac{\partial H}{\partial X_i} ;$$

$$\lambda_i(T) = \frac{\partial G}{\partial X_i}(T) + \sum_{S=1}^{k} P_S \frac{\partial L_S}{\partial X_i}(T) ,$$

$$H(T) + \frac{\partial G}{\partial T} + \sum_{S=1}^{k} P_S \frac{\partial L_S}{\partial T} = 0 ;$$

$$u_r^* = U_{r_{\min}} \quad \text{only if} \quad \frac{\partial H}{\partial U_r} > 0 ;$$

$$u_r^* = U_{r_{\max}} \quad \text{only if} \quad \frac{\partial H}{\partial U_r} < 0 ;$$

$$U_{r_{\min}} < u_r^* < U_{r_{\max}} \quad \text{only if} \quad \frac{\partial H}{\partial U_r} = 0 .$$

Let V and W be subvectors of $\bar{u}$. Suppose v appears nonlinearly in $H(X, V. W, \Lambda)$ and w appears linearly in H . The next theorem describes some necessary conditions for a singular extremal to be optimal. More general conditions are discussed elsewhere (Goh, 1973).

<u>Theorem 4.4.</u>: Along a singular extremal, if $H_{ww} = 0$ and $H_{wv} = 0$, then necessary conditions for optimality are

(i) $[DH_w]_w = 0$;

(ii) if (i) is satisfied, the matrix

$$\begin{bmatrix} H_{vv} & -[DH_w]_v^T \\ -[DH_w]_v & -[D^2H_w]_w \end{bmatrix}$$

must be positive semidefinite. The nutrient controlled aquatic model here is in the form

$$\begin{aligned} \dot{P} &= P\phi_i(N) - BP = Z\psi_i(BZ) + \delta_1 u_1 &&= F_1(P, Z, N, U_1) \\ \dot{Z} &= Z\psi_i(P, Z) - DZ + \delta_2 u_2 &&= F_2(P, Z, N, U_2) \\ \dot{N} &= -P\ \phi_i(N) + BP + DZ + \delta_3 u_3 &&= F_3(P, Z, N, U_3) \\ \dot{W} &= (P + Z + N - K_i)^2\ U_1 + N^2 U_2 &&= F_4(P, Z, N) \end{aligned} \qquad (4.5.1)$$

with performance index J given by

$$J = \int_0^t [\theta + \alpha_1|u_1| + \alpha_2|u_2| + \alpha_3|u_3| + \beta P + \eta Z + \delta N]dt \ ; \qquad (4.5.2)$$

Control constraints

$$(4.5.3) \quad U_{r_{\min}} < u_r < U_{r_{\max}} \quad , \quad i = 1, 2, 3$$

and state variables constraints given by (4.4.24) and (4.4.26). The first step, as usual, is to form the Hamiltonian,

$$(4.5.4) \quad H = \lambda_0(\theta + \beta P + \eta Z + \gamma N + \sum_{r=1}^{3} \alpha_r |u_r|) + \sum_{i=1}^{4} \lambda_i(t) F_i(P, Z, N, u_1, u_2, u_3) \quad .$$

The costate equations are

$$(4.5.5) \quad \dot{\lambda}_1(t) = \frac{-\partial H}{\partial P} = -\lambda_0 \beta - \sum_{i=1}^{4} \lambda_i \frac{\partial F_i}{\partial P}$$

$$(4.5.6) \quad \dot{\lambda}_2(t) = \frac{-\partial H}{\partial Z} = -\lambda_0 \eta - \sum_{i=1}^{4} \lambda_i \frac{\partial Fi}{\partial Z}$$

$$(4.5.7) \quad \dot{\lambda}_3(t) = \frac{-\partial H}{\partial N} = -\lambda_0 \gamma - \sum_{i=1}^{4} \lambda_i \frac{\partial F_i}{\partial N}$$

$$(4.5.8) \quad \dot{\lambda}_4(t) = \frac{-\partial H}{\partial W} = 0$$

From (4.4.31), it follows that

$$(4.5.9) \quad \sum_{r=1}^{3} (\lambda_0 \alpha_r |u_r^*(t)| + \lambda_r^* \delta_r u_r^*(t)) \leq \sum_{r=1}^{3} (\lambda_0 \alpha_r |u_r(t)| + \lambda_r^* \delta_r u_r(t))$$

Using the defintion of $|u_r(t)|$, it follows that

$$(4.5.10.a)\quad \lambda_0\alpha_r|u_r(t)| + \lambda_r^*(t)\delta_r u_r(t) = \begin{cases} \lambda_0\alpha_r(1 + \frac{\lambda_r^*(t)\ \delta_r}{\lambda_0\alpha_r})u_r(t) \\ \quad \text{for } u_r(t) \geq 0 \\ \lambda_0\alpha_r(-1 + \frac{\lambda_r^*(t)\delta_r}{\lambda_0\alpha_r})u_r(t) \quad (4.5.10.b) \\ \quad \text{for } u_r(t) \leq 0\ ; \\ \quad r = 1,\ 2,\ 3\ . \end{cases}$$

As in problem 4, the optimal control program is

$$(4.5.11)\quad u_r^*(t) = \begin{cases} u_{r_{max}} & \text{for } \frac{\lambda_r^*(t)\delta_r}{\lambda_0\alpha_r} < -1.0 \\ 0 & \text{for } -1.0 < \frac{\lambda_r^*(t)\delta_r}{\lambda_0\alpha_r} < 1.0 \\ U_{r_{min}} & \text{for } \frac{\lambda_r^*(t)\delta_r}{\lambda_0\alpha_r} > 1.0 \\ \multicolumn{2}{l}{\text{an undetermined nonnegative value for}} \\ \multicolumn{2}{l}{\quad u_r^*(t) \text{ if } \frac{\lambda_r^*(t)\delta_r}{\lambda_0\alpha_r} = -1.0} \\ \multicolumn{2}{l}{\text{an undetermined nonpositive value for}} \\ \multicolumn{2}{l}{\quad u_r^*(t) \text{ if } \frac{\lambda_r^*(t)\delta_r}{\lambda_0\alpha_r} = 1.0\ ;} \\ \multicolumn{2}{l}{\quad r = 1,\ 2,\ 3\ .} \end{cases}$$

By definition the control vector u^* is singular if the matrix $\frac{{}^2H(X^*, u^*, \Lambda)}{\partial u_r \; \partial u_j}$ is singular.

In the above problem,

$$\frac{\partial H}{\partial u_r} = \lambda_0\alpha_r \begin{cases} (1 + \frac{\lambda_r\delta_r}{\lambda_0\alpha_r}) & \text{for} \quad u_r^*(t) \geq 0 \\ (1 - \frac{\gamma_r\delta_r}{\lambda_0\alpha_r}) & \text{for} \quad u_r^*(t) < 0 \end{cases}$$

Thus, $\frac{\partial^2 H}{\partial u_r} = 0$, $\frac{\partial^2 H}{\partial u_r \partial u_j} = 0$ and the matrix $\frac{\partial^2 H}{\partial u_r \partial u_j}$ (H^*, u^*, Λ) is singular.

Singular Control Analysis:

From the conditions in Theorem 4.4 the singular control is optimal if

(i) $[DH_u]_u = 0$

(ii) $-[D^2H_u]_u$ is positive semidefinite.

For (i),

$$H_{u_r} = \lambda_0\alpha_r[\text{sgn } u_r^*(t) + \frac{\delta_r\lambda_r(t)}{\lambda_0\alpha_r}] \quad ; \quad r = 1, 2, 3$$

$$D[H_{u_r}]_{u_r} = \delta_r \lambda_r(t) \quad , \quad r = 1, 2, 3 \ .$$

Thus, $[DH_{u_r}]_{u_r} = [\delta_r \lambda_r(t)]_{u_r} = 0$ because $\lambda_r(t)$ is not an explicit function of u_r , $r = 1, 2, 3$.

<u>For (ii)</u>, consider the following relations $H_{u_r} = \lambda_o \alpha_r[\text{sgn } u_r + \frac{\delta_r \lambda_r}{\lambda_0 \alpha_r}]$ which implies $D(H_{u_r}) = \delta_r \lambda_r(t)$ which in turn implies $D^2(H_{u_r}) = \delta_r \dot{\lambda}_r(t)$.

Thus, if we write $\ddot{\lambda}_r(t)$ in the form

(4.5.12) $$\ddot{\lambda}_r(t) = \phi_r(u_1, u_2, u_3) + \phi_r(X, \Lambda) \ ,$$
$$(r = 1, 2, 3)$$

then the singular control is optimal if the matrix

(4.5.13) $$\begin{bmatrix} \frac{\partial \phi_1}{\partial u_1} & \frac{\partial \phi_1}{\partial u_2} & \frac{\partial \phi_1}{\partial u_3} \\ \frac{\partial \phi_2}{\partial u_1} & \frac{\partial \phi_2}{\partial u_2} & \frac{\partial \phi_2}{\partial u_3} \\ \frac{\partial \phi_3}{\partial u_1} & \frac{\partial \phi_3}{\partial u_2} & \frac{\partial \phi_3}{\partial u_3} \end{bmatrix}$$ is positive semidefinite

where

$$\frac{\partial \Phi_1}{\partial u_1} = \delta_1[(\lambda_1 - \lambda_2)Zf_{1i} - 2\lambda_4 U_1]$$

$$\frac{\partial \phi_1}{\partial u_2} = \delta_2[(\lambda_1 - \lambda_2)(Zf_{8i} + \psi_{iP}) - 2\lambda_4 U_1]$$

$$\frac{\partial \phi_1}{\partial u_3} = \delta_3[(\lambda_3 - \lambda_1)f_{2i} - 2\ \lambda_4 U_1]$$

$$\frac{\partial \phi_2}{\partial u_1} = \delta_1(\lambda_1 - \lambda_2)(f_{5i} + Zf_{9i} - 2\lambda_4 U_1)$$

$$\frac{\partial \phi_2}{\partial u_2} = \delta_2[(\lambda_1 - \lambda_2)\psi_{iZ} + f_{6i} + Zf_{10i} - 2\lambda_4 U_1]$$

$$\frac{\partial \phi_2}{\partial u_3} = -\ 2\delta_3 \lambda_4 U_1$$

$$\frac{\partial \phi_3}{\partial u_1} = \delta_1[(\lambda_3 - \lambda_1)\ \phi_i' - 2\lambda_4 U_1]$$

$$\frac{\partial \phi_3}{\partial u_2} = -2\delta_2 \lambda_4 U_1$$

$$\frac{\partial \phi_3}{\partial u_3} = \delta_3[(\lambda_3 - \lambda_1)P\ f_{4i} - 2\lambda_4(U_1 + U_2)]$$

Remarks:

(1) A singular control can exist if one of the following situations occurs,

(i) $\lambda_1 = \pm \frac{\lambda_0\alpha_1}{\delta_1}$, $\lambda_2 \neq \frac{\lambda_0\alpha_2}{\delta_2}$, $\lambda_3 \neq \pm \frac{\lambda_0\alpha_3}{\delta_3}$

(ii) $\lambda_1 \neq \pm \frac{\lambda_0\alpha_1}{\delta_1}$, $\lambda_2 = \pm \frac{\lambda_0\alpha_2}{\delta_2}$, $\lambda_3 \neq \pm \frac{\lambda_0\alpha_3}{\delta_3}$

(iii) $\lambda_1 \neq \pm \frac{\lambda_0\alpha_1}{\delta_1}$, $\lambda_2 \neq \pm \frac{\lambda_0\alpha_2}{\delta_2}$, $\lambda_3 \neq \pm \frac{\lambda_0\alpha_3}{\delta_3}$

(iv) $\lambda_1 = \pm \frac{\lambda_0\alpha_1}{\delta_1}$, $\lambda_2 = \pm \frac{\lambda_0\alpha_2}{\delta_2}$, $\lambda_3 \neq \pm \frac{\lambda_0\alpha_3}{\delta_3}$

(v) $\lambda_1 = \pm \frac{\lambda_0\alpha_1}{\delta_1}$, $\lambda_2 \neq \pm \frac{\lambda_0\alpha_2}{\delta_2}$, $\lambda_3 = \pm \frac{\lambda_0\alpha_3}{\delta_3}$

(vi) $\lambda_1 \neq \pm \frac{\lambda_0\alpha_1}{\delta_1}$, $\lambda_2 = \pm \frac{\lambda_0\alpha_2}{\delta_2}$, $\lambda_3 = \pm \frac{\lambda_0\alpha_3}{\delta_3}$

(vii) $\lambda_1 = \pm \frac{\lambda_0\alpha_1}{\delta_1}$, $\lambda_2 = \pm \frac{\lambda_0\alpha_2}{\delta_2}$, $\lambda_3 = \pm \frac{\lambda_0\alpha_3}{\delta_3}$,

(2) The analysis in any of the first three cases is similar to the one control variable problems considered before.

(3) It is sufficient for illustration, to consider one of the last four situations in detail. (e.g. (vii))

In case vii, the costate variables satisfy

$$\lambda_1 = \pm \frac{\lambda_0\alpha_1}{\delta_1} \ , \quad \lambda_2 = \pm \frac{\lambda_0\alpha_2}{\delta_2} \ , \quad \lambda_3 = \pm \frac{\lambda_0\alpha_3}{\delta_3}$$

hence, $\dot{\lambda}_1 = \dot{\lambda}_2 = \dot{\lambda}_3 = 0$.

Similarly

$$\ddot{\lambda}_1 = 0 \ , \ \ddot{\lambda}_2 = 0 \ \text{ and } \ \ddot{\lambda}_3 = 0 \qquad t \quad [t_1, t_2]$$

and from (4.4.99) with ϕ_1, ϕ_2, and ϕ_3 as given in (4.5.12) where ϕ_1, ϕ_2, and ϕ_3 are

$$\phi_1 = (\lambda_3 - \lambda_1)f_{i1} + (\lambda_1 - \lambda_2)[Zf_{ui}(F_1 + f_{8i}\,F_2) + \psi_{iP}F_2] \ , \tag{4.5.14}$$

$$\phi_2 = (\lambda_1 - \lambda_2)[F_2\,\psi_{i2} + f_{5i}F_1 + f_{6i}F_2 + Zf_{9i}F_1 + Zf_{10i}F_2] \tag{4.5.15}$$

and

$$\phi_3 = (\lambda_3 - \lambda_1)[F_1\phi'_i + Pf_{3i}] - 2\lambda_4F_3U_2 \tag{4.5.16}$$

Now, solving the following system of equations in the three variable u_{S_1}, u_{S_2}, and u_{S_3}

$$\bar{\phi}_1 = a_{11}\,u_{S_1} + a_{12}\,u_{S_2} + a_{13}\,u_{S_3} = -\phi_1 \tag{4.5.17}$$

$$\bar{\phi}_2 = a_{21}\,u_{S_1} + a_{22}\,u_{S_2} + a_{23}\,u_{S_{33}} = -\phi_2 \tag{4.5.18}$$

(4.5.19) $$\bar{\phi}_3 = a_{31}\, u_{S_1} + a_{32}\, u_{S_2} + a_{33}\, u_{S_{33}} = -\phi_3$$

we get ,

(4.5.20) $$u_{S_1} = \frac{\begin{vmatrix} \phi_1 & a_{12} & a_{13} \\ \phi_2 & a_{22} & a_{23} \\ \phi_3 & a_{32} & a_{33} \end{vmatrix}}{\Delta}$$

(4.5.21) $$u_{S_2} = -\frac{\begin{vmatrix} a_{11} & \phi_1 & a_{13} \\ a_{21} & \phi_2 & a_{23} \\ a_{31} & \phi_3 & a_{33} \end{vmatrix}}{\Delta}$$

(4.5.22) $$u_{S_3} = \frac{\begin{vmatrix} a_4 & a_{47} & \phi_1 \\ a_{21} & a_{33} & \phi_2 \\ a_{31} & a_{32} & \phi_3 \end{vmatrix}}{\Delta}$$

(4.5.23) $$\text{where } \Delta = \begin{vmatrix} a_{11} & a_{12} & a_{13} \\ a_{21} & a_{22} & a_{23} \\ a_{31} & a_{32} & a_{33} \end{vmatrix} \quad .$$

4.6. Discussion

In this chapter, the use of optimal control theory to obtain optimal strategies for the control of aquatic models was illustrated. Several types of control variables were used. One control variable was the rate of applying nutrient to the system. The other types of control variables were the rates of change of nutrient concentrations in the phytoplankton and zooplankton populations. It has been demonstrated how optimal control theory can be applied to different models subjected to different state and control variables constraints. Though the techniques were basically the same, the characters of the solutions and the control strategies were dependent on the model and the function to be optimized in each problem. Explicit expressions were given and optimality conditions were checked for singular controls whenever they existed. Some numerical techniques were suggested to put together the optimal control parts in the right sequence.

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BIBLIOGRAPHY

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CHAPTER II

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APPENDICES

Appendix I: The Maximum Principle

An important class of optimal control problems may be formulated in the following manner. In a specified class of functions C , find a scalar control u(t) which minimize the scalar functional

$$(\text{AI.1}) \qquad J(u) = G(X(T), T) + \int_0^T f_0(x(t), u(t), t)dt$$

subject to the following condition

$$(\text{AI.2}) \qquad x = f(x, u, t) \qquad (\quad . = d/dt)$$

$$(\text{AI.3}) \qquad x(t_0) = x_0$$

$$(\text{AI.4}) \qquad L(X(T), T) = 0$$

$$(\text{AI.5}) \qquad u(t) \quad U(t)$$

The functional in (AI.1) is referred to as the performance index. In (AI.2) $x = (x_1, \ldots, x_n)$ is the state vector, and $f(x, u, t)$ is an n-component vector function. Equation (AI.4) describes the terminal manifold, a hypersurface in the (n+1)-dimensional x, t space, which represents the set of allowable terminal state (X(T), T) . The notation $u(t) \in U(t)$ indicate that admissible values of u(t) are those belonging to a specified closed set U(t) .

The problem defind by equation (AI.1)-(AI.5) for suitably restricted G , f_0, and f can, in principle, be solved by application of Pontryagin's maximum principle.

The Maximum Principle: [10]

Let a Hamiltonian function H be defined as

(AI.6) $H(X, \Lambda, u, t) = < \Lambda, f(x, u, t)> + \lambda_0 f_0$

where $< \Lambda, f(x, u, t)>$ is the inner product of Λ and $f(x, u, t)$ and $\Lambda = (\lambda_1, \ldots, \lambda_n)$ is an n vector. Then, a scalar control $u^*(t)$ which minimizes equation (AI.1), subject to the condition in equations (AI.2) - (AI.5), must necessarily yield the minimum admissible value of $H(x, \Lambda, u, t)$ for every set (X^*, Λ^*, t'), $\lambda_0 \geq 0$. Thus, the optimal control in the form $u^*(t) = u^*(X^*(t), \Lambda^*(t), t)$ is obtained from the finite equation

(AI.7) $$H^*(X^*(t), \Lambda^*(t), u^*(t), t) = \min_{u \in U(t)} H(X^*(t), \Lambda^*(t), u(t), t)$$

$$(t_0 < t \leq T)$$

The vector Λ is called the conjugate adjoint vector. The vectors $X(t)$ and $\Lambda(t)$ in (AI.7) satisfy the canonical equations

(AI.8) $$x_i = \frac{\partial H^*(X^*, \Lambda^*, u^*, t)}{\partial \lambda_i}$$

(AI.9) $$\lambda_i = - \frac{\partial H^*(X^*, \Lambda^*, u^*, t)}{\partial x_i} \qquad (i = 1, \ldots, n)$$

At the terminal time T , the tranversality condition

$$\text{(AI.10)} \quad 0 = [H^*(X^*(t), \Lambda^*(t), u^*(t), t) - \frac{\partial G(X, t)}{\partial t}]_{t=T} \; dt -$$

$$\sum [\lambda_i(t) + \frac{\partial G(x, t)}{\partial x_i}] dx_i$$

must be satisfied for every direction $(dx_1, \ldots, dx_n, dt)$ tangent to the terminal manifold [Eq. (AI.4)] at the state $(X(T), T)$. It may further be shown that

$$\text{(AI.11)} \quad \frac{dH^*}{\partial T}(X^*(t), \Lambda^*(t), u^*(t), t) = \frac{\partial H^*}{\partial t}(X^*(t), \Lambda^*(t), u^*, t)$$

$$(t_0 \leq t \leq T)$$

This implies that $H^*(X^*(t), \Lambda^*(t), U^*(t), t)$ is constant along an optimal trajectory when equation (AI.6) is not an explicit function of time.

Equations (AI.8) and (AI.9) are valid if $u^* = u^*(t)$. If $u^* = u(X, t)$, the canonical equation must be written

$$\text{(AI.12)} \quad \dot{x}_i = \frac{\partial H^*(x^*, \Lambda^*, u^*, T)}{\partial \lambda_i} - \frac{\partial H(x, \Lambda, u, t)}{\partial u} \frac{\partial u^*(x, \Lambda, t)}{\partial \lambda_i}$$

$$\text{(AI.13)} \quad \dot{\lambda}_i = - \frac{\partial H^*(X^*, \Lambda^*, u^*, t)}{\partial x_i} + \frac{\partial H(x, \Lambda, u, t)}{\partial u} \frac{\partial u^*(x, \Lambda, t)}{\partial x_i}$$

The canonical equations (AI.8) and (AI.9) form a system of 2 n simultaneous first-order, ordinary differential equation which must be solved subject to the conditions of equations (AI.3)-(AI.5), (AI.7), (AI.10) and (AI.11). The integral curves of equations (AI.8) and (AI.0) may be visualized in a (2n + 1)-dimensional Euclidean space whose points have coordinates $x_1, \ldots, x_n, \lambda_1, \ldots, \lambda_n, t$. By this means the problem of optimal control described above leads to the study of 2n-dimensional vector-differential equations with two-point boundary conditions. Each particular solution of equations (AI.8), AI.9) which satisfies the condition of equations (AI.3)-(AI.5), (AI.7), (AI.10) and (AI.11) is a candidate for the solution of the optimal control problem. If more than one candidate exists further tests may be required to identify the optimal solution. It is remarked that, in some cases, the optimal solution is not unique.

Appendix II: Computational Algorithms

The final job of putting together the different parts of the optimal control program in the right sequence has to be done numerically.

A convergent numerical solution to the equations provided, say, by the minimum principle will yield an extremal control and the corresponding state and costate trajectories. Since there is always some arbitrary initial guess involved then the iterative process will converge to a solution which is "close" (in some sense) to the initial guess.

To illustrate some of the different ideas that are being used for the evaluation of the optimal control using iterative technique, the necessary conditions provided by the minimum principle will be restated. It is assumed that when the optimal control $u^*(t)$ exists it is unique, and the extremal control are also unique. Recall that the necessary conditions were stated in the form

(1) Canonical Equation

$$\text{(AII.1)} \quad \frac{d}{dt} X^*(t) = \frac{\partial H}{\partial \lambda(t)}\Big|_* \quad \text{(state equation)}$$

$$\frac{d}{dt} \lambda^*(t) = - \frac{\partial H}{\partial X(t)}\Big|_* \quad \text{(costate equation)}$$

(2) Boundary Conditions

$X^*(t_0) = x_0$ (x_0 is the initial state)

(AII.2) $X^*(T) \in S$ (S is the target set)

$\Lambda^*(T)$ normal to S at $X^*(T)$.

Minimization of the Hamiltonian

(AII.4) $H[X^*(t); \Lambda^*(t); u^*(t)] \leq H[X^*(t); \Lambda^*(t); u(t)]$ for

$u(t) \in U(t)$ and $t \in (t_0, T]$

The general idea behind many of the iterative procedures which are available today is to satisfy a pair of necessary conditions and iterate until the third one is satisfied.

First Method:

Iterative methods utilize the necessary condition (AII.3) and solve for the optimal control $u^*(t)$ as a function of $X^*(t)$ and $\Lambda^*(t)$. If this is possible, one obtains from (AII.3) an expression of the form

(AII.4) $U^* = k[X^*(t), \Lambda^*(t)]$

Equation (AII.4) is then substituted into the cononical equations (AII.1); the control $u^*(t)$ is eliminated from the canonical equations which then reduce to the form

$$\frac{dx^*(t)}{dt} = h[X^*(t); \Lambda^*(t)]$$

(AII.5)

$$\frac{d\Lambda^*(t)}{dt} = g[X^*(t); \Lambda^*(t)]$$

Since one has used the necessary conditions (AII.1) and (AII.3), one must iterate on the boundary conditions (AII.2). One can now proceed in two ways

a) Guess an initial value for the costate. Itegrate, forward to time, the system of differential equations (AII.5), using the correct value $X^*(t_0) = X_0$ and the guessed value $\Lambda^*(t_0) = \Lambda_0$. Check whether or not, at time T , the remaining boundary conditions (AII.2) are satisfied; if not, change $\Lambda^*(t_0)$ using, say, a gradiant method or Newton's method.

b) The same as in (a), except here we guess value for the terminal state S and construct the corresponding costate $\Lambda^*(T)$ so that it is normal to S at $X^*_u(T)$, Integrate, backward is time, (AII.5).

Second Method:

In this method, we try to satisfy the canonical equation and the boundary conditions (AII.2) and to iterate until the necessary condition (AII.3) is satisfied. The basic idea is to guess a control function $u^*_0(t)$, $t \in [t_0, T]$, such that the integration of the canonical equations (AII.1) yields a solution which satisfies the boundary conditions (AII.2). One then adjusts the initial guess $u^*_0(t)$ until either the inequality (AII.3) is satisfied or until the cost functional J is minimized.

VITA

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