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PERTURBATIONS AND BIFURCATIONS OF A THREE DIMENSIONAL FOOD CHAIN MODEL WITH HARVESTING

by

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B.Sc., Simon Fraser University, 1982

B.A.Sc., University of British Columbia, 1985

A THESIS SUBMITTED IN PARTIAL FULFILLMENT OF

THE REQUIREMENTS FOR THE DEGREE OF

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of

Mathematics

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ABSTRACT

The effect of small perturbations on the equilibria of an intermediate three dimensional food chain model with constant rate prey harvesting is studied. It is assumed that the unperturbed system has at least one simple or multiple equilibrium in the first population octant. The simple equilibrium of the unperturbed system which may be hyperbolic or nonhyperbolic under the influence of small perturbations generates a hyperbolic equilibrium. For a certain value of the constant harvesting rate, the unperturbed system has a structurally unstable multiple equilibrium for which the determinant of the Jacobian matrix is zero. The multiple equilibrium may bifurcate into equilibria of the perturbed model or disappear under the influence of small perturbations. The perturbed equilibria generated by the equilibria of the unperturbed system are investigated in case studies.

DEDICATION

To my parents

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I wish to thank my senior supervisor Dr. G.N.Bojadziev for his suggestion of a pertinent problem and his guidance in the writing of this thesis.

I also wish to thank the staff members of the Department of Mathematics and Statistics for their help; especially Mrs. Kathy Hammes and Mrs. Sylvia Holmes for arranging my teaching assistantship, and to the Departmental Graduate Studies Committee and the Senate Committee on Scholarships, Awards and Bursaries for awarding me Graduate Research Scholarship.

TABLE OF CONTENTS

INTRODUCTION

The study of the existence and stability properties of the equilibria for a system of autonomous ordinary differential equations modelling the interaction between several populations is a subject of considerable interest in the ecological literature.

Bojadziev and Gerogiannakis [2] have analysed the behaviour of the unperturbed food chain model with constant rate prey harvesting H,

$$\begin{aligned} x' &= xf(x) - yg(x) - H, \\ y' &= -ay + byg(x) - zh(y), \\ z' &= -cz + rzh(y) \end{aligned} \tag{1}$$

in R^3, which models a predator-predator-prey interaction. Here x,y, and z are the population sizes, and the functions f(x), g(x), and h(y) are subjected to certain constraint. Using [2] as a base, we analysed the behaviour of the model (1) under the influence of small perturbations. Hence the model to be considered is

$$\begin{aligned} x' &= xf(x) - yg(x) - H + \varepsilon F_1(x,y,z), \\ y' &= -ay + byg(x) - zh(y) + \varepsilon F_2(x,y,z), \\ z' &= -cz + rzh(y) + \varepsilon F_3(x,y,z), \end{aligned} \tag{2}$$

where ε is a small positive parameter.

The inclusion of the perturbation terms with factor ε makes the model (1), which is actually an approximation of a real situation, closer to reality since these terms represent small unknown errors or uncertainties.

The main objective of this thesis is to study the effect of perturbations on the nature of the equilibria for the model (1).

In Chapter 1 of this thesis we review some research papers on mathematical models in population ecology which provide a background for our study and introduce the basic assumptions about the model (2).

In Chapter 2 we give conditions for the existence of simple equilibria of the unperturbed model (1) and study their nature and stability. Further we find a condition for the existence of multiple equilibria of the model (1).

In Chapter 3 we study the nature and stability of the equilibria of the perturbed model (2) corresponding to the simple equilibria of the unperturbed model (1).

In Chapter 4 we study the effect of perturbation on the multiple equilibrium of the unperturbed model (1). The multiple equilibrium of (1) will either bifurcate into perturbed equilibria of

(2) or disappear under the influence of small perturbations.

The perturbed equilibria generated by the equilibria of (1) are investigated in case studies.

CHAPTER 1

PRELIMINARIES

In this chapter we summarize in brief some important results on unperturbed models with harvesting and perturbed models without and with harvesting, which provide the basis for this thesis. Also we introduce the basic assumptions about the model (2).

1.1 UNPERTURBED MODELS WITH HARVESTING

Brauer and Sanchez [6] studied the effect of constant rate of harvesting on the growth of two coexisting species. Brauer and Soudack [7,8] analysed the global behaviour of a predator-prey system under constant rate prey harvesting H

$$x' = xf(x,y) - H, \qquad y' = yg(x,y). \tag{1.1}$$

They also studied the predator-prey system (1.1) with stocking.

Yodzis [15] investigated the effect of harvesting, H_1 and H_2, on competitive populations modeled by

$$x' = X(x,y) - H_1, \qquad y' = Y(x,y) - H_2. \tag{1.2}$$

Freedman and Waltman [12] introduced the three species food chain model (1) without harvesting, i.e. H = 0. Bojadziev and Gerogiannakis [2] extended the work of Freedman and Waltman by adding a constant rate prey harvesting term in the first equation (see (1)). They analysed the behaviour of the three species in the vicinity of the simple equilibria and discussed the effect of harvesting on the species' coexistence.

1.2 PERTURBED MODELS WITHOUT HARVESTING

Freedman and Waltman [11] studied a perturbed predator-prey Lotka-Volterra system of the form

$$\begin{aligned} x' &= x(a-by) - \varepsilon f_1(x,y), \\ y' &= y(-y+cx) - \varepsilon f_2(x,y) \end{aligned} \tag{1.3}$$

and established a theorem for the existence of a stable limit cycle of (1.3). G. Bojadziev and M. Bojadziev [1] investigated the existence of the equilibria of (1.3) from the point of view of control and structural stability.

Freedman [10], generalizing (1.3), studied the two dimensional perturbed Kolmogorov model

$$\begin{aligned} x' &= xf_1(x,y,\varepsilon), \\ y' &= yf_2(x,y,\varepsilon). \end{aligned} \tag{1.4}$$

He investigated the nature and stability of perturbed equilibria of (1.4) and found some criteria for the existence of a limit cycle.

Bojadziev and Sattar [4,5] extended the work of Freedman [10]. They considered the general perturbed Kolmogorov model in three dimensional space

$$x_i' = x_i f_i(x_1, x_2, x_3, \varepsilon), \quad i = 1,2,3. \tag{1.5}$$

They analysed the nature and stability of simple unperturbed equilibria and their relationship with the equilibria of the perturbed system. Further they investigated how the multiple equilibrium of the unperturbed model (1.5) ($\varepsilon=0$) bifurcates into perturbed equilibria of (1.5).

1.3 PERTURBED MODELS WITH HARVESTING

Bojadziev and Kim [3] examined the two dimensional perturbed Lotka-Volterra competition model with harvesting

$$\begin{aligned} x' &= x(a_1 - \frac{a_1}{b_1} x - c_1 y) - H + \varepsilon f_1(x,y), \\ y' &= y(a_2 - b_2 x - \frac{a_2}{c_2} y) + \varepsilon f_2(x,y). \end{aligned} \tag{1.6}$$

They investigated the nature and stability property of, both, simple and double equilibria of the unperturbed model (1.6) ($\varepsilon=0$). Also they discussed the qualitative behaviour of the perturbed model (1.6) using concepts from structural stability and bifurcations.

1.4 THE MODEL AND ITS BASIC ASSUMPTIONS

Consider the three dimensional perturbed food chain model with constant rate prey harvesting (2), where x is the number of lowest trophic level species or prey, y is the number of middle trophic level species or first predator, and z is the number of highest trophic level species or second predator. The parameters a, b, c and r are positive constant, and $H > 0$ is the constant prey rate of harvesting, $\varepsilon > 0$ is a small parameter and $F_1(x,y,z)$, $F_2(x,y,z)$ and $F_3(x,y,z)$ are analytic functions in their arguments. The function f(x) is the specific growth rate of the prey, g(x) and h(y) are the response functions of the first and second predator respectively.

For these functions, as in [12] we assume

$$f(0) = s > 0, \quad f_x(x) \leq 0, \quad \text{for } x \geq 0, \tag{1.7}$$

$$g(0) = 0 \quad , \quad g_x(x) > 0, \quad \text{for } x \geq 0, \tag{1.8}$$

$$h(0) = 0 \quad , \quad h_y(y) > 0, \quad \text{for } y \geq 0, \tag{1.9}$$

where the lower subscript denotes differentiation with respect to the corresponding argument. For a model with natural carrying capacity we also assume that

$$\exists K > 0 \ni f(K) = 0. \tag{1.10}$$

The model (2) without perturbations and harvesting, i.e. $\varepsilon = 0$ and $H = 0$, has been studied by Freedman and Waltman [12] under the assumptions (1.7) - (1.10). For $\varepsilon = 0$ and $H \neq 0$, with (1.7) - (1.10) the same model (2) has been investigated by Bojadziev and Geroglannakis [2]. For, $\varepsilon \neq 0$ and $H = 0$, (2) is a particular case of the three dimensional perturbed Kolmogorov model studied by Bojadziev and Sattar [4,5].

CHAPTER 2

EQUILIBRIA OF THE THREE DIMENSIONAL UNPERTURBED FOOD CHAIN MODEL WITH CONSTANT RATE PREY HARVESTING

In this chapter first we study the existence of a simple equilibria of (1) and investigate its nature and stability. Further we give a condition for the existence of a multiple equilibrium which involves explicitly a critical value of the constant rate prey harvesting H. Also two examples are presented to illustrate the existence of critical harvesting value.

2.1 EXISTENCE OF SIMPLE EQUILIBRIA

The equilibrium positions of the unperturbed system (1) are solutions of (1) with $x' = y' = z' = 0$. Assume that (1) has at least one equilibrium point $E_o(x_o, y_o, z_o)$ (unperturbed equilibrium) in the interior of the first octant. This means that the system

$$\begin{aligned} & xf(x) - yg(x) - H = 0, \\ & -ay + byg(x) - zh(y) = 0, \\ & -cz + rzh(y) \qquad = 0 \end{aligned} \tag{2.1}$$

has at least one solution (x_o, y_o, z_o) satisfying (2.1), where $x_o > 0$, $y_o > 0$ and $z_o > 0$.

According to [2], the system (2.1) has at least one solution (x_o, y_o, z_o) if $\frac{c}{r} \in$ Range $h(y)$ which guarantees that the third equation of (2.1) has a unique solution y_o such that $h(y_o) = \frac{c}{r}$ and if

$$y_o \in \text{Range } \frac{xf(x) - H}{g(x)}, \quad x > 0, \quad xf(x) - H > 0$$

which guarantees that from the first equation of (2.1) we can find x_o in term of y_o (there may be more than one such x_o) satisfying $x_of(x_o) - y_og(x_o) - H = 0$. Then from the second equation of (2.1) we get

$$z_o = \frac{by_o g(x_o) - ay_o}{h(y_o)},$$

which is positive provided that

$$bg(x_o) - a > 0.$$

2.2 NATURE AND STABILITY OF A SIMPLE EQUILIBRIUM

In order to study locally the nature and stability property of the equilibrium position, we need to compute the Jacobian matrix of (1) (see [2(4.10)]). Let J^o be the Jacobian matrix of (1) calculated at the equilibrium $E_o(x_o, y_o, z_o)$. We obtain

$$J^o(x_o, y_o, z_o) = \begin{bmatrix} x_o f_x(x_o) + f(x_o) - y_o g_x(x_o) & -g(x_o) & 0 \\ by_o g_x(x_o) & -a + bg(x_o) - z_o h_y(y_o) & -h(y_o) \\ 0 & rz_o h_y(y_o) & 0 \end{bmatrix}. \quad (2.2)$$

For the determinant of J^o we get

$$\det J^o(x_o, y_o, z_o) = cz_o h_y(y_o)(x_o f_x(x_o) + f(x_o) - y_o g_x(x_o)). \quad (2.3)$$

We assume that

$$\det J^{o}(x_o, y_o, z_o) \neq 0 \quad \text{(noncritical case).} \tag{2.4}$$

This assumption ensures that $E_o(x_o, y_o, z_o)$ is a simple equilibrium of (1) and there is no other equilibium state in the neighbourhood of $E_o(x_o, y_o, z_o)$.

The characteristic equation for the Jacobian matrix (2.2) is

$$-\det |J^{o} - \lambda I| = \lambda^3 + a_1 \lambda^2 + a_2 \lambda + a_3 = 0, \tag{2.5}$$

where I is the unit matrix of size 3 x 3 and

$$a_1 = -x_o f_x(x_o) + f(x_o) - y_o g_x(x_o) - a + bg(x_o) - z_o h_y(y_o),$$

$$a_2 = (x_o f_x(x_o) + f(x_o) - y_o g_x(x_o))(-a + bg(x_o) - z_o h_y(y_o)) + by_o g(x_o) g_x(x_o) + cz_o h_y(y_o), \tag{2.6}$$

$$a_3 = -\det J^{o} = -cz_o h_y(y_o)(x_o f_x(x_o) + f(x_o) - y_o g_x(x_o)).$$

It is well known that the stability property of the equilibrium point $E_o(x_o, y_o, z_o)$ is determined by the signs of the real parts of the eigenvalues of the Jacobian matrix (2.2), i.e. the roots of (2.5).

From (2.4) and the third equation (2.6) it follows that $a_3 \neq 0$, hence the characteristic equation (2.5) has no zero root. The roots of the characteristic equation (2.5) can be distinct or repeated. According to Hirsch and Smale [13], an equilibrium of a system of autonomous ordinary differential equations is called hyperbolic if its characteristic equation has no roots with zero real parts, i.e. no zero roots or no purely imaginary roots; otherwise, the equilibrium is nonhyperbolic. Chow and Hale [9] stated that a hyperbolic equilibrium is structurally stable. The noncritical case (2.4) allows the existence of both, a hyperbolic equilibrium (if (2.5) has only non zero real roots or a non zero real root and a pair of complex roots with non zero real part) or a nonhyperbolic equilibrium (if (2.5) has a pair of purely imaginary roots).

Reyn [14] gave a detailed classification of the nature and stability of the equilibrium points of a three dimensional linear differential system. Bojadziev and Sattar [4] presented classification of the nature and stability of the simple equilibria of the three dimensional unperturbed Kolmogorov model (1.5) with $\varepsilon = 0$. The results obtained by Reyn [14] and Bojadziev and Sattar [4] are used in this paper.

2.3 EXISTENCE OF A MULTIPLE EQUILIBRIUM

Let $E(\bar{x},\bar{y},\bar{z})$ be a multiple equilibrium of the unperturbed model (1). Then the Jacobian matrix $J(x,y,z)$ calculated at the multiple equilibrium $E(\bar{x},\bar{y},\bar{z})$ is given by (2.2), where x_o, y_o and z_o are substituted by $\bar{x}$, $\bar{y}$ and $\bar{z}$, but its determinant is equal to zero, that is

$$\det J(\bar{x},\bar{y},\bar{z}) = 0 \quad \text{(critical case)}. \tag{2.7}$$

Similarly to (2.3) we have

$$\det J(\bar{x},\bar{y},\bar{z}) = c\bar{z}h_y(\bar{y})(\bar{x}f_x(\bar{x}) + f(\bar{x}) - \bar{y}g_x(\bar{x})) = 0. \tag{2.8}$$

Since $c\bar{z}h_y(\bar{y}) \neq 0$, (2.8) implies that

$$\bar{x}f_x(\bar{x}) + f(\bar{x}) - \bar{y}g_x(\bar{x}) = 0. \tag{2.9}$$

Equation (2.9) ensures that model (1) has a multiple equilibrium.

The characteristic equation of the Jacobian matrix (2.2) calculated at $E(\bar{x},\bar{y},\bar{z})$ is given by

$$\lambda^3 + p_1\lambda^2 + p_2\lambda = 0, \tag{2.10}$$

where

$$\begin{aligned} p_1 &= a - bg(\bar{x}) + \bar{z}h_y(\bar{y}), \\ p_2 &= b\bar{y}g(\bar{x})g_x(\bar{x}) + c\bar{z}h_y(\bar{y}). \end{aligned} \tag{2.11}$$

Consider (2.11). Since $p_1 = 0$ when $h(\bar{y})$ is linear and satisfying the assumption (1.9) (see [12]), then using (1.8) and (1.9) we see that

$$b\bar{y}g(\bar{x})g_x(\bar{x}) > 0 \quad \text{and} \quad c\bar{z}h_y(\bar{y}) > 0,$$

hence

$$\bar{p}_2 = b\bar{y}g(\bar{x})g_x(\bar{x}) + c\bar{z}h_y(\bar{y}) > 0. \tag{2.12}$$

The characteristic equation (2.10) has roots

$$\lambda_1 = 0 \quad \text{and} \quad \lambda_{2,3} = \frac{-p_1 \pm \sqrt{p_1^2 - 4p_2}}{2}. \tag{2.13}$$

The root $\lambda_1 = 0$ of (2.10) can not be double or triple since $p_2 > 0$ (2.12). Hence the 3 x 3 Jacobian matrix of system (1) calculated at the multiple equilibrium can only have rank 2. Since (2.10) has a zero root, the multiple equilibrium $E(\bar{x},\bar{y},\bar{z})$ is nonhyperbolic — structurally unstable.

We call the value of H, for which the model (1) has a multiple equilibrium, critical harvesting value, and denote it by H_c. The critical value H_c satisfies the first equation (2.1), hence

$$H_c = \bar{x}f(\bar{x}) - \bar{y}g(\bar{x}). \tag{2.14}$$

From (2.14) and (2.9) we obtain

$$H_c = \bar{y}(\bar{x}g_x(\bar{x}) - g(\bar{x})) - \bar{x}^2 f_x(\bar{x}). \tag{2.15}$$

Equation (2.15) is the condition for existence of a multiple equilibrium of (1) which involves explicitly the critical value of constant rate prey harvesting.

2.4 EXAMPLES ILLUSTRATING THE EXISTENCE OF A CRITICAL HARVESTING VALUE

We consider two food chain models which illustrate the existence of critical value of constant rate prey harvesting when (1) has a multiple equilibrium.

Example 1

Assume that the prey has a natural carrying capacity k and the functions g(x), h(x) yield the Lotka-Volterra dynamics. More specifically, we consider the model

$$\begin{aligned} x' &= x(1 - \frac{x}{k}) - yx - H, \\ y' &= -ay + byx - zy, \\ z' &= -cz + rzy. \end{aligned} \tag{2.16}$$

The equilibria of (2.16) are solutions of the system

$$x(1 - \frac{x}{k}) - yx - H = 0,$$
$$-ay + byx - zy = 0, \qquad (2.17)$$
$$-cz + rzy = 0.$$

We seek a multiple equilibrium $E(\bar{x},\bar{y},\bar{z})$. It should satisfy conditions (2.9) and (2.15). The calculations give a multiple equilibrium

$$E(\frac{k(1 - \frac{c}{r})}{2}, \frac{c}{r}, -a + \frac{bk(1 - \frac{c}{r})}{2}),$$

and a critical harvesting value

$$H_c = \frac{k(1 - \frac{c}{r})^2}{4}.$$

Example 2

In this example we modify the model of Example 1 by introducting a Holling-type predation of the second predator on the first predator. Specifically, we consider the model

$$x' = x(1 - \frac{x}{k}) - yx - H,$$
$$y' = -ay + byx - \frac{a_1yz}{1+b_1y}, \qquad (2.18)$$
$$z' = -cz + \frac{ra_1yz}{1+b_1y}.$$

Here we obtain a multiple equilibrium

$$E\left(\frac{k(1 - \frac{c}{a_1 - cb_1}}{2}, \quad \frac{c}{ra_1 - cb_1}, \quad (-a + \frac{bk(1 - \frac{c}{ra_1 - cb_1})}{2})(\frac{r}{ra_1 - cb_1}) \right),$$

and the critical harvesting value is

$$H_c = \frac{k(1 - \frac{c}{ra_1 - cb_1})^2}{4} .$$

CHAPTER 3

PERTURBATIONS OF A SIMPLE EQUILIBRIUM OF THE THREE DIMENSIONAL FOOD CHAIN MODEL WITH HARVESTING

In this chapter we study the effect of perturbation on the equilibria of the unperturbed food chain model (1) with constant rate prey harvesting in the noncritical case. We show the existence of a perturbed equilibrium of system (2) and investigate its nature and stability property. Also three examples are presented.

3.1 EXISTENCE OF A PERTURBED EQUILIBRIUM

Consider the noncritical case (2.4) of the three dimensional unperturbed food chain model with constant rate prey harvesting (1) under perturbations. The equilibrium positions of the perturbed model (2) are solutions of the system (2) with $x' = y' = z' = 0$, that is

$$\begin{aligned} &xf(x) - yg(x) - H + \varepsilon F_1(x,y,z) = 0, \\ &-ay + byg(x) - zh(y) + \varepsilon F_2(x,y,z) = 0, \\ &-cz + rzh(y) \qquad + \varepsilon F_3(x,y,z) = 0. \end{aligned} \tag{3.1}$$

Since (2.4) holds, according to the implicit function theorem the system (3.1) has a unique solution $x^*(\varepsilon)$, $y^*(\varepsilon)$ and $z^*(\varepsilon)$ in the neighbourhood of x_o, y_o and z_o, such that $x^*(0) = x_o$, $y^*(0) = y_o$, and $z^*(0) = z_o$. Hence the perturbed system (2) has a unique perturbed equilibrium $E^*(x^*(\varepsilon), y^*(\varepsilon), z^*(\varepsilon))$. This is equivalent to the statement that the determinant of the Jacobian matrix of (2) calculated at $E^*(x^*(\varepsilon), y^*(\varepsilon), z^*(\varepsilon))$ is not zero, that is

$$\det J(x^*(\varepsilon), y^*(\varepsilon), z^*(\varepsilon)) \neq 0. \tag{3.2}$$

To find a solution of (3.1), we seek $x^*(\varepsilon)$, $y^*(\varepsilon)$ and $z^*(\varepsilon)$ in terms of power series of ε in the neighbourhood of x_o, y_o and z_o in the form

$$x^*(\varepsilon) = x_o + \varepsilon x_1 + \varepsilon^2 x_2 + \ldots\ldots,$$

$$y^*(\varepsilon) = y_o + \varepsilon y_1 + \varepsilon^2 y_2 + \ldots\ldots, \qquad (3.3)$$

$$z^*(\varepsilon) = z_o + \varepsilon z_1 + \varepsilon^2 z_2 + \ldots\ldots,$$

where x_i, y_i and z_i, $i = 1,2,3,\ldots\ldots$, are to be determined. In general, it is enough to find only x_1, y_1 and z_1, since ε is a small parameter. Substituting (3.3) up to the order of ε into (3.1) gives

$$(\dot{x}_o + \varepsilon \dot{x}_1)f(x_o + \varepsilon x_1) - (y_o + \varepsilon y_1)g(x_o + \varepsilon x_1) - H$$

$$+ \varepsilon F_1(x_o + \varepsilon x_1,\ y_o + \varepsilon y_1,\ z_o + \varepsilon z_1) = 0,$$

$$-a(y_o + \varepsilon y_1) + b(y_o + \varepsilon y_1)g(x_o + \varepsilon x_1) - (z_o + \varepsilon z_1)h(y_o + \varepsilon y_1) \qquad (3.4)$$

$$+ \varepsilon F_2(x_o + \varepsilon x_1,\ y_o + \varepsilon y_1,\ z_o + \varepsilon z_1) = 0,$$

$$-c(z_o + \varepsilon z_1) + r(z_o + \varepsilon z_1)h(y_o + \varepsilon y_1)$$

$$+ \varepsilon F_3(x_o + \varepsilon x_1,\ y_o + \varepsilon y_1,\ z_o + \varepsilon z_1) = 0.$$

Expanding these equations in Taylor series, taking into consideration that x_o, y_o and z_o satisfy (2.1), dividing by ε , and equalizing the coefficients of ε to zero gives the following linear system of equations for x_1, y_1 and z_1

$$
\left.
\begin{aligned}
&(x_o f_x(x_o) + f(x_o) - y_o g_x(x_o))x_1 - g(x_o)y_1 = -F_1(x_o,y_o,z_o), \\
&by_o g_x(x_o)x_1 + (-a+bg(x_o) - z_o h_y(y_o))y_1 - h(y_o)z_1 = -F_2(x_o,y_o,z_o) \\
&rz_o h_y(y_o)y_1 = -F_3(x_o,y_o,z_o).
\end{aligned}
\right\} \quad (3.5)
$$

The system of equations (3.5) can be solved for x_1, y_1 and z_1 by using Cramer's rule

$$
x_1 = \frac{\begin{vmatrix} -F_1(x_o,y_o,z_o) & -g(x_o) & 0 \\ -F_2(x_o,y_o,z_o) & -a+bg(x_o)-z_o h_y(y_o) & -h(y_o) \\ -F_3(x_o,y_o,z_o) & rz_o h_y(y_o) & 0 \end{vmatrix}}{\det J^o},
$$

$$
y_1 = \frac{\begin{vmatrix} x_o f(x_o)+f(x_o)-y_o g_x(x_o) & -F_1(x_o,y_o,z_o) & 0 \\ by_o g_x(x_o) & -F_2(x_o,y_o,z_o) & -h(y_o) \\ 0 & -F_3(x_o,y_o,z_o) & 0 \end{vmatrix}}{\det J^o}, \quad (3.6)
$$

$$z_1 = \frac{\begin{vmatrix} x_o f_x(x_o)+f(x_o)-y_o g_x(x_o) & -g(x_o) & -F_1(x_o,y_o,z_o) \\ by_o g_x(x_o) & -a+bg(x_o)-z_o h_y(y_o) & -F_2(x_o,y_o,z_o) \\ 0 & rz_o h_y(y_o) & -F_3(x_o,y_o,z_o) \end{vmatrix}}{\det J^o},$$

where $\det J^o$ is given by (2.3).

Simplifying (3.6) we obtain

$$x_1 = -\frac{F_1(x_o,y_o,z_o)(cz_o h_y(y_o)+g(x_o)h(y_o)F_3(x_o,y_o,z_o))}{cz_o h_y(y_o)(x_o f_x(x_o)+f(x_o)-y_o g_x(x_o))},$$

$$y_1 = -\frac{F_3(x_o,y_o,z_o)}{rz_o h_y(y_o)}, \tag{3.7}$$

$$z_1 = -\frac{1}{h(y_o)}(by_o g_x(x_o)x_1+(-a+bg(x_o)-z_o h_y(y_o))y_1+F_2(x_o,y_o,z_o)).$$

Substituting (3.7) into (3.3) and neglecting the terms of order $O(\varepsilon^2)$ gives

$$x^*(\varepsilon) = x_o + \varepsilon x_1,$$
$$y^*(\varepsilon) = y_o + \varepsilon y_1, \tag{3.8}$$
$$z^*(\varepsilon) = z_o + \varepsilon z_1.$$

Hence (3.8) represents approximately the coordinates of the perturbed equilibrium $E^*(x^*(\varepsilon),y^*(\varepsilon),z^*(\varepsilon))$ generated by the unperturbed equilibrium $E_o(x_o,y_o,z_o)$.

3.2 NATURE AND STABILITY OF THE PERTURBED EQUILIBRIUM

To study locally the nature and stability of the perturbed equilibrium , we use the Jacobian matrix $J(x,y,z)$ of the system (2). The Jacobian matrix calculated at $E^*(x^*(\varepsilon),y^*(\varepsilon),z^*(\varepsilon))$ is given by

$$J(x^*(\varepsilon),\ y^*(\varepsilon),\ z^*(\varepsilon)) = (J_{ik}), \tag{3.9}$$

where J_{ik} are the elements of the 3 x 3 Jacobian matrix (3.9).

Here we have

$$J_{11} = x^*(\varepsilon)f_x(x^*(\varepsilon))+f(x^*(\varepsilon)-y^*(\varepsilon)g_x(x^*(\varepsilon))+\varepsilon F_{1x}(x^*(\varepsilon),y^*(\varepsilon),z^*(\varepsilon)),$$

$$J_{12} = -g(x^*(\varepsilon))+\varepsilon F_{1y}(x^*(\varepsilon),y^*(\varepsilon),z^*(\varepsilon)),$$

$$J_{13} = \varepsilon F_{1z}(x^*(\varepsilon),y^*(\varepsilon),z^*(\varepsilon)),$$

$$J_{21} = by^*(\varepsilon)g_x(x^*(\varepsilon))+ \varepsilon F_{2x}(x^*(\varepsilon),y^*(\varepsilon),z^*(\varepsilon)),$$

$$J_{22} = -a+bg(x^*(\varepsilon))-z^*(\varepsilon)h_y(y^*(\varepsilon))+ \varepsilon F_{2y}(x^*(\varepsilon),y^*(\varepsilon),z^*(\varepsilon)),$$

$$J_{23} = -h(y^{*}(\varepsilon))+\varepsilon F_{2z}(x^{*}(\varepsilon),y^{*}(\varepsilon),z^{*}(\varepsilon)),$$

$$J_{31} = \varepsilon F_{3x}(x^{*}(\varepsilon),y^{*}(\varepsilon),z^{*}(\varepsilon)),$$

$$J_{32} = rz^{*}(\varepsilon)h_{y}(y^{*}(\varepsilon))+\varepsilon F_{3y}(x^{*}(\varepsilon),y^{*}(\varepsilon),z^{*}(\varepsilon)),$$

$$J_{33} = -c+rh(y^{*}(\varepsilon))+\varepsilon F_{3z}(x^{*}(\varepsilon),y^{*}(\varepsilon),z^{*}(\varepsilon)).$$

By substituting (3.8) into (3.9) and expanding in Taylor series, we obtain the following matrix up to the order of ε

$$J(x^{*}(\varepsilon),y^{*}(\varepsilon),z^{*}(\varepsilon)) = J^{0}(x_{o},y_{o},z_{o}) +\varepsilon J^{1}(x_{o},y_{o},z_{o}), \tag{3.10}$$

where J^{0} is given by (2.2) and $J^{1}(x_{o},y_{o},z_{o})$ is the 3 x 3 matrix

$$J^{1}(x_{o},y_{o},z_{o}) = (J^{1}{}_{ik}), \tag{3.11}$$

where

$$J^{1}{}_{11} = x_{o}x_{1}f_{xx}(x_{o})+2x_{1}f_{x}(x_{o})-y_{o}x_{1}g_{xx}(x_{o})-y_{1}g_{x}(x_{o})$$

$$+F_{1x}(x_{o},y_{o},z_{o}),$$

$$J^{1}{}_{12} = -x_{1}g_{x}(x_{o})+F_{1y}(x_{o},y_{o},z_{o}),$$

$$J^{1}{}_{13} = F_{1z}(x_{o},y_{o},z_{o}),$$

$$J^1_{21} = by_o x_1 g_{xx}(x_o) + by_1 g_x(x_o) + F_{2x}(x_o, y_o, z_o),$$

$$J^1_{22} = bx_1 g_x(x_o) - z_o y_1 h_{yy}(y_o) - z_1 h_y(y_o) + F_{2y}(x_o, y_o, z_o),$$

$$J^1_{23} = -y_1 h_y(y_o) + F_{2z}(x_o, y_o, z_o),$$

$$J^1_{31} = F_{3x}(x_o, y_o, z_o),$$

$$J^1_{32} = rz_o y_1 h_{yy}(y_o) + rz_1 h_y(y_o) + F_{3y}(x_o, y_o, z_o),$$

$$J^1_{33} = ry_1 h_y(y_o) + F_{3z}(x_o, y_o, z_o),$$

and x_1, y_1 and z_1 are given by (3.7).

The characteristic equation of (3.10) up to the order ε is

$$\lambda^3 + (a_1 + \varepsilon b_1)\lambda^2 + (a_2 + \varepsilon b_2)\lambda + a_3 + \varepsilon b_2 = 0, \tag{3.12}$$

where a_1, a_2 and a_3 are given by (2.6) and

$$b_1 = -\sum_{i=1}^{3} J^1_{ii},$$

$$b_2 = \sum_{i=1}^{3}\sum_{k=1}^{3}\sum_{l=1}^{3}\left(\tfrac{1}{2}J^o_{ii}(J^1_{kk}+J^1_{ll}) - J^o_{ik}J^1_{ki}\right),\ i \neq k \neq l,$$

$$b_3 = -\begin{vmatrix} J^o_{11} & J^o_{12} & J^o_{13} \\ J^o_{21} & J^o_{22} & J^o_{23} \\ J^1_{31} & J^1_{32} & J^1_{33} \end{vmatrix} - \begin{vmatrix} J^o_{11} & J^o_{12} & J^o_{13} \\ J^1_{21} & J^1_{22} & J^1_{23} \\ J^o_{31} & J^o_{32} & J^o_{33} \end{vmatrix} - \begin{vmatrix} J^1_{11} & J^1_{12} & J^1_{13} \\ J^o_{21} & J^o_{22} & J^o_{23} \\ J^o_{31} & J^o_{32} & J^o_{33} \end{vmatrix}. \quad (3.13)$$

Here J^o_{ik} and J^1_{ik} are elements of the Jacobian matrices $J^o(x_o,y_o,z_o)$ and $J^1(x_o,y_o,z_o)$ respectively.

For $\varepsilon = 0$ the characteristic equation (3.12) reduces to the characteristic equation (2.5) of the Jacobian matrix (2.2) of the unperturbed system (1). The condition (3.2) ensures that the characteristic equation (3.12) does not have any zero root, or the Jacobian matrix (3.10) does not have a zero eigenvalue (noncritical case). The nature and stability of the perturbed equilibrium $E^*(x^*(\varepsilon), y^*(\varepsilon), z^*(\varepsilon))$ can be determined by the signs of the real parts of the eigenvalues of the Jacobian matrix evaluated at $x = x^*(\varepsilon)$, $y = y^*(\varepsilon)$ and $z = z^*(\varepsilon)$. Bojadziev and Sattar [4] gave a detailed classification of the equilibria of the perturbed three dimensional Kolmogorov model (1.5). We will use their results in the next section.

3.3 EXAMPLES OF PERTURBED SIMPLE FOOD CHAIN MODELS WITH HARVESTING

To illustrate the theory discussed in this chapter, we consider three particular cases of the perturbed food chain model with harvesting (2). Two of the cases concern the hyperbolic equilibrium of the unperturbed system (1) and the third case concerns the nonhyperbolic equilibrium of (1).

Example 1

The model

$$x' = x - \frac{1}{2}yx - \frac{1}{2} + \varepsilon x,$$

$$y' = -y + 3yx - yz + \varepsilon(y-z), \qquad (3.14)$$

$$z' = -2z + 2yz + \varepsilon y,$$

is a particular case of (2) with

$$f(x) = 1; \quad g(x) = \frac{1}{2}x, \quad h(y) = y,$$

$$a = 1, \qquad b = 6, \qquad c = 2, \qquad r = 2,$$

$$F_1(x,y,z) = x, \quad F_2(x,y,z) = y-z, \quad F_3(x,y,z) = y.$$

It describes a predator-predator-prey interaction under the influence of small perturbations; x is the lowest trophic level species or prey, y is the middle trophic level species or first predator, and z is the highest trophic level species or second predator. The perturbation terms in (3.14), that is the terms with factor $\varepsilon \ll 1$ indicate additional weaker types of interaction between the species. In the first equation the perturbation term means a slight increase of the growth rate of x due to internal cooperation (εx). In the second equation the perturbation term means both, a slight increase of the growth rate of y due to internal cooperation (εy) and a slight decrease of the growth rate due to increased activities ($-\varepsilon z$) of the second predator z. In the third equation there is a slight increase of the growth rate of z due to the additional prey on y.

The unperturbed equilibrium of (3.14) with $\varepsilon = 0$ is $E_o(1,1,2)$ and the corresponding perturbed equilibrium up to the order of ε is $E(1 - \frac{9}{4}\varepsilon, 1 - \frac{1}{4}\varepsilon, 2 - \frac{23}{4}\varepsilon)$. The Jacobian matrix (2.2) calculated at $E_o(1,1,2)$ is

$$J^o(1,1,2) = \begin{bmatrix} \frac{1}{2} & -\frac{1}{2} & 0 \\ 6 & 0 & -1 \\ 0 & 4 & 0 \end{bmatrix} \qquad (3.15)$$

with $\det J^o(1,1,2) = 2 \neq 0$. The characteristic equation of (3.15) is

$$\lambda^3 - \frac{1}{2}\lambda^2 + 7\lambda - 2 = 0, \tag{3.16}$$

which is a particular case of (3.6) with

$$a_1 = -\frac{1}{2}, \quad a_2 = 7, \quad a_3 = -2.$$

We find that equation (3.16) has a root $\lambda_1 > 0$ and two roots with Re $\lambda_{2,3} \neq 0$. Hence $E_o(1,1,2)$ is a hyperbolic equilibrium. From [4] it follows that E_o is an unstable spiral. By using Hirsch and Smale [13] or Bojadziev and Sattar [4] we conclude that in the neighbourhood of the simple hyperbolic equilibrium $E_o(1,1,2)$ of the unperturbed system (3.14) ($\varepsilon = 0$), which is an unstable spiral, there exists a unique equilibrium $E(1 - \frac{9}{4}\varepsilon, 1 - \frac{\varepsilon}{4}, 2 - \frac{23}{4}\varepsilon)$ of the perturbed system (3.14) which is also hyperbolic and unstable spiral.

Example 2

Consider the system

$$x' = 4x - yx - 1 + \varepsilon(2x-y),$$

$$y' = -\frac{5}{3}y + 8yx - yz + \varepsilon(y-3z), \tag{3.17}$$

$$z' = -\frac{1}{3}z + \frac{1}{3}yz + \varepsilon z,$$

which models a predator-predator-prey interactions similar to that described by (3.14). The unperturbed equilibrium of (3.17) with $\varepsilon = 0$ is $E_o(\frac{1}{3}, 1, 1)$.

The Jacobian matrix (2.2) calculated at $E_o(\frac{1}{3}, 1, 1)$ is

$$J^o(\tfrac{1}{3},1,1) = \begin{bmatrix} 3 & -\frac{1}{3} & 0 \\ 8 & 0 & -1 \\ 0 & \frac{1}{3} & 0 \end{bmatrix} \qquad (3.18)$$

with $\det J^o(\frac{1}{3}, 1, 1) = 1 \neq 0$, hence E_o is a simple equilibrium.

The characteristic equation of (3.18) is

$$\lambda^3 - 3\lambda^2 + 3\lambda - 1 = 0. \qquad (3.19)$$

Equation (3.19) has a triple root $\lambda = 1$. According to [4] the unperturbed equilibrium $E_o(\frac{1}{3}, 1, 1)$ is an unstable star.

The perturbed equilibrium of the system (3.17) up to the order ε is $E(\frac{1}{3} - \frac{2}{9}\varepsilon, 1 - 3\varepsilon, 1 + \frac{2}{9}\varepsilon)$. The Jacobian matrix (3.21) calculated at this perturbed equilibrium up to the order ε is

$$J(\tfrac{1}{3} - \tfrac{2}{9}\varepsilon, 1 - 3\varepsilon, 1 + \tfrac{2}{9}\varepsilon) = \begin{bmatrix} 3+\varepsilon & -\frac{1}{3} + \frac{4}{3}\varepsilon & 0 \\ 8+8\varepsilon & \frac{8}{3}\varepsilon & -(1+4\varepsilon) \\ 0 & \frac{1}{3} + \frac{1}{3}\varepsilon & \frac{4}{3}\varepsilon \end{bmatrix}. \qquad (3.20)$$

The characteristic equation of (3.20) up to the order ε is

$$\lambda^3 - (3+5\varepsilon)\lambda^2 + (3+27\varepsilon)\lambda - (1+\frac{80}{9}\varepsilon) = 0, \qquad (3.21)$$

which is a particular case of (3.12) with

$$a_1 = -3, \quad a_2 = 3, \quad a_3 = -1,$$

$$b_1 = -5, \quad b_2 = 27, \quad b_3 = -\frac{80}{9}.$$

We find that equation (3.21) has three roots $1 + T_1(\varepsilon)$, $1 + T_2(\varepsilon)$ and $1 + T_3(\varepsilon)$ where $T_i(0) = 0$, $i = 1,2,3$. Therefore the perturbed equilibrium $E(\frac{1}{3} - \frac{2}{9}\varepsilon, 1 - 3\varepsilon, 1 + \frac{2}{9}\varepsilon)$ is an unstable spiral. Hence, an unstable star of the unperturbed system (3.17) with $\varepsilon = 0$ under small perturbations becomes an unstable spiral.

<u>Example 3</u>

For the model

$$x' = 2x - yx - \frac{1}{2} + \varepsilon x,$$

$$y' = -y + 3yx - y^2x + \varepsilon(y-z), \qquad (3.21)$$

$$z' = -z + y^2z + \varepsilon y,$$

the unperturbed equilibrium is $E_o(\frac{1}{2}, 1, \frac{1}{2})$. The Jacobian matrix (2.2) calculated at $E_o(\frac{1}{2}, 1, \frac{1}{2})$ is

$$J^o(\frac{1}{2}, 1, \frac{1}{2}) = \begin{bmatrix} 1 & -\frac{1}{2} & 0 \\ 3 & -\frac{1}{2} & -1 \\ 0 & 1 & 0 \end{bmatrix} \quad (3.22)$$

with det $J^o(\frac{1}{2}, 1, \frac{1}{2}) = 1 \neq 0$, hence E_o is a simple equilibrium. The characteristic equation of (3.22) is

$$\lambda^3 - \frac{1}{2}\lambda^2 + 2\lambda - 1 = 0. \quad (3.23)$$

The roots of (3.23) are $\lambda_1 = \frac{1}{2}$ and $\lambda_{2,3} = \pm\sqrt{2}i$. Therefore the simple unperturbed equilibrium $E_o(\frac{1}{2}, 1, \frac{1}{2})$ is nonhyperbolic. It is a divergent vortex focus. (see [4]).

The perturbed equilibrium of the system (3.21) up to the order ε is $E(\frac{1}{2}-\varepsilon, 1-\varepsilon, \frac{1}{2}+2\varepsilon)$. The Jacobian matrix for (3.21) calculated at this perturbed equilibrium up to the order ε is

$$J(\frac{1}{2}-\varepsilon, 1-\varepsilon, \frac{1}{2}+2\varepsilon) = \begin{bmatrix} 1 & -\frac{1}{2}+\varepsilon & 0 \\ 3-3\varepsilon & -\frac{1}{2}+6\varepsilon & -1+\varepsilon \\ 0 & 1+5\varepsilon & -2\varepsilon \end{bmatrix}. \quad (3.24)$$

Its determinant is det $J = 1 + 2\varepsilon \neq 0$, hence E is a simple equilibrium. The characteristic equation of (3.24) up to the order ε is

$$\lambda^3 - (\tfrac{1}{2}+4\varepsilon)\lambda^2 + (2+\tfrac{9}{2}\varepsilon)\lambda - (1+2\varepsilon) = 0. \qquad (3.25)$$

According to Bojadziev and Sattar [4], the roots of the characteristic equation (3.25) are $\frac{1}{2} + T_1(\varepsilon)$ and $T_2(\varepsilon) \pm i(\sqrt{2}+T_3(\varepsilon))$ where $T_i(0) = 0$, $i = 1,2,3$ and $T_2(\varepsilon) > 0$. Therefore $E(\frac{1}{2} - \varepsilon,\ 1 - \varepsilon,\ \frac{1}{2} + 2\varepsilon)$ is an unstable spiral. Hence, a divergent vortex focus (nonhyperbolic) of the unperturbed system (3.21) with $\varepsilon = 0$ under small perturbations becomes an unstable spiral (hyperbolic).

CHAPTER 4

BIFURCATIONS OF A MULTIPLE EQUILIBRIUM OF THE THREE DIMENSIONAL FOOD CHAIN MODEL WITH HARVESTING

In this chapter we study the effect of perturbations on the multiple equilibrium of the food chain model (1) with harvesting and derive criteria for the existence of perturbed equilibria of the system (2). We show how the multiple equilibrium of the unperturbed system bifurcates into simple equilibria of (2) and study their stability property.

4.1 BIFURCATIONS OF A MULTIPLE EQUILIBRIUM

Consider the critical case (2.7) of the three dimensional unperturbed food chain model with constant rate prey harvesting (1). Under the influence of small perturbations, the multiple equilibrium of (1) will either bifurcate into simple equilibria of (2) or disappear without bifurcating. The equilibrium positions of the perturbed model (2) are solutions of system (3.1). Let $E(\bar{x},\bar{y},\bar{z})$ be a multiple equilibrium of the unperturbed model (1) as in section (2.3) and $E(\hat{x}(\varepsilon), \hat{y}(\varepsilon), \hat{z}(\varepsilon))$ be a perturbed equilibrium of the model (2). It is assumed that $E(\bar{x},\bar{y},\bar{z})$ is not an equilibrium of (3.1), that is

$$F_i(\bar{x}, \bar{y}; \bar{z}) \neq 0, \quad i = 1,2,3. \tag{4.1}$$

Since the system (3.1) is subjected to the condition (2.7), we can not use the classical implicit function theorem to find a unique solution $\hat{x}(\varepsilon)$, $\hat{y}(\varepsilon)$ and $\hat{z}(\varepsilon)$ of (3.1) in the neighbourhood of the solution $\bar{x},\bar{y}$ and $\bar{z}$ of the system (2.1) such that $\hat{x}(0) = \bar{x}$, $\hat{y}(0) = \bar{y}$ and $\hat{z}(0) = \bar{z}$. Using the fact that for $\varepsilon = 0$ the system (3.1) reduces to (2.1), we seek the solution of (3.1) in the form

$$\hat{x}(\varepsilon) = \bar{x} + \varepsilon m_1 + \varepsilon^2 m_2 + \ldots\ldots,$$

$$\hat{y}(\varepsilon) = \bar{y} + \varepsilon n_1 + \varepsilon^2 n_2 + \ldots\ldots, \qquad (4.2)$$

$$\hat{z}(\varepsilon) = \bar{z} + \varepsilon w_1 + \varepsilon^2 w_2 + \ldots\ldots,$$

where m_i, n_i and w_i, $i = 1,2,\ldots\ldots$ are constants to be determined. Here we find only m_1, n_1 and w_1, which is enough for our study.

Substituting (4.2) into (3.1) up to the order of ε gives

$$(\bar{x}+\varepsilon m_1)f(\bar{x}+\varepsilon m_1)-(\bar{y}+\varepsilon n_1)g(\bar{x}+\varepsilon m_1)-H+\varepsilon F_1(\bar{x}+\varepsilon m_1,\bar{y}+\varepsilon n_1,\bar{z}+\varepsilon w_1)=0,$$

$$-a(\bar{y}+\varepsilon n_1)+b(\bar{y}+\varepsilon n_1)g(\bar{x}+\varepsilon m_1)-(\bar{z}+\varepsilon w_1)h(\bar{y}+\varepsilon n_1) + \varepsilon F_2(\bar{x}+\varepsilon m_1,\bar{y}+\varepsilon n_1,\bar{z}+\varepsilon w_1)=0, \qquad (4.3)$$

$$-c+(\bar{z}+\varepsilon w_1)+r(\bar{z}+\varepsilon w_1)h(\bar{y}+\varepsilon n_1) + \varepsilon F_3(\bar{x}+\varepsilon m_1,\bar{y}+\varepsilon n_1,\bar{z}+\varepsilon w_1)=0.$$

Expanding (4.3) in Taylor series and neglecting terms of order $O(\varepsilon^2)$ gives the bifurcation system

$$-n_1 g(\bar{x})+F_1(\bar{x},\bar{y},\bar{z})+\varepsilon(\tfrac{1}{2}\bar{x}m_1^2 f_{xx}(\bar{x})+m_1^2 f_x(\bar{x})-\tfrac{1}{2}\bar{y}m_1^2 g_{xx}(\bar{x})-m_1 n_1 g_x(\bar{x})$$

$$+m_1 F_{1x}(\bar{x},\bar{y},\bar{z})+n_1 F_{1y}(\bar{x},\bar{y},\bar{z})+w_1 F_{1z}(\bar{x},\bar{y},\bar{z}))= 0,$$

$$-an_1+b\bar{y}m_1g_x(\bar{x})+bg(\bar{x})n_1-\bar{z}h_y(\bar{y})n_1-w_1h(\bar{y})+F_2(\bar{x},\bar{y},\bar{z})+\varepsilon(\tfrac{1}{2}b\bar{y}m_1{}^2g_{xx}(\bar{x})$$

$$+bm_1n_1g_x(\bar{x})-\tfrac{1}{2}\bar{z}n_1{}^2h_{yy}(\bar{y})+m_1F_{2x}(\bar{x},\bar{y},\bar{z})+n_2F_{2y}(\bar{x},\bar{y},\bar{z})+w_1F_{2z}(\bar{x},\bar{y},\bar{z}))=0, \qquad (4.4)$$

$$r\bar{z}h_y(\bar{y})n_1+F_3(\bar{x},\bar{y},\bar{z})+\varepsilon(\tfrac{1}{2}r\bar{z}n_1{}^2h_{yy}(\bar{y})+rn_1w_1h_y(\bar{y})+m_1F_{3x}(\bar{x},\bar{y},\bar{z})$$

$$+n_1F_{3y}(\bar{x},\bar{y},\bar{z})+w_1F_{3z}(\bar{x},\bar{y},\bar{z}))=0,$$

where the letter subscript indicates differentiation with respect to the corresponding argument.

The solution of (4.4) depends on whether or not the term

$$D = F_1(\bar{x},\bar{y},\bar{z}) + \frac{g(\bar{x})F_3(\bar{x},\bar{y},\bar{z})}{r\bar{z}h_y(\bar{y})} \qquad (4.5)$$

is zero or different from zero.

Case (i). D = 0.

From the first and third equation (4.4) we obtain n_1 in the form

$$n_1 = \frac{F_1(\bar{x},\bar{y},\bar{z})}{g(\bar{x})} + O(\varepsilon) = -\frac{F_3(\bar{x},\bar{y},\bar{z})}{r\bar{z}h_y(\bar{y})} + O(\varepsilon). \qquad (4.6)$$

Eliminating m_1 and n_1 from (4.4) with $D = 0$ and dividing by ε gives for w_1 the quadratic equation

$$s w_1^2 + t w_1 + u = 0, \tag{4.7}$$

where

$$s=\left(\tfrac{1}{2}\bar{x}f_{xx}(\bar{x})+f_x(\bar{x})-\tfrac{1}{2}\bar{y}g_{xx}(\bar{x})\right)\left(\frac{h(\bar{y})}{b\bar{y}g_x(\bar{x})}\right)^2,$$

$$t=\frac{g(\bar{x})\left(h(\bar{y})F_{3x}(\bar{x},\bar{y},\bar{z})+F_{3z}(\bar{x},\bar{y},\bar{z})b\bar{y}g_x(\bar{x})\right)}{rb\bar{y}\bar{z}g_x(\bar{x})h_y(\bar{y})}-\frac{g(\bar{x})F_3(\bar{x},\bar{y},\bar{z})}{r\bar{z}^2h_y(\bar{y})}+F_{1z}(\bar{x},\bar{y},\bar{z})$$

$$-\frac{2s}{h(\bar{y})}\left(\frac{F_3(\bar{x},\bar{y},\bar{z})p_1}{r\bar{z}h_y(\bar{y})}+F_2(\bar{x},\bar{y},\bar{z})\right)+\left(F_{1x}(\bar{x},\bar{y},\bar{z})+\frac{F_3(\bar{x},\bar{y},\bar{z})}{r\bar{z}h_y(\bar{y})}\right)\frac{h(\bar{y})}{b\bar{y}g_x(\bar{x})},$$

$$u=\frac{1}{2}\,\frac{g(\bar{x})}{h_y(\bar{y})}\left(\frac{F_3(\bar{x},\bar{y},\bar{z})}{r\bar{z}h_y(\bar{y})}\right)^2h_{yy}(\bar{y})-\frac{g(\bar{x})}{rb\bar{y}\bar{z}g_x(\bar{x})h_y(\bar{y})}\left(\frac{F_3(\bar{x},\bar{y},\bar{z})}{r\bar{z}h_y(\bar{y})}\,p_1\right. \tag{4.8}$$

$$\left.+F_2(\bar{x},\bar{y},\bar{z})\right)F_{3x}(\bar{x},\bar{y},\bar{z})-\frac{g(\bar{x})F_3(\bar{x},\bar{y},\bar{z})F_{3y}(\bar{x},\bar{y},\bar{z})}{(r\bar{z}h_y(\bar{y}))^2}+\frac{s}{(h_y(\bar{y}))^2}$$

$$\left(\frac{F_3(\bar{x},\bar{y},\bar{z})p_1}{r\bar{z}h_y(\bar{y})}+F_2(\bar{x},\bar{y},\bar{z})\right)^2-\frac{1}{b\bar{y}g_x(\bar{x})}\left(\frac{F_{1x}(\bar{x},\bar{y},\bar{z})+F_3(\bar{x},\bar{y},\bar{z})g_x(\bar{x})}{r\bar{z}h_y(\bar{y})}\right)$$

$$\left(\frac{F_3(\bar{x},\bar{y},\bar{z})p_1}{r\bar{z}h_y(\bar{y})}+F_3(\bar{x},\bar{y},\bar{z})\right)-\frac{F_3(\bar{x},\bar{y},\bar{z})}{r\bar{z}h_y(\bar{y})}F_{1y}(\bar{x},\bar{y},\bar{z}),$$

and p_1 is given by (2.11).

The equation (4.7) has two real roots

$$w_{1k} = \frac{-t + (-1)^k \sqrt{t^2-4su}}{2s}, \quad k = 1,2, \tag{4.9}$$

provided that $s \neq 0$ and $t^2 - 4su > 0$.

Substituting n_1 and w_{1k} from (4.6) and (4.9) into the second equation (4.4) and neglecting $O(\varepsilon)$ terms gives

$$m_{1k} = \frac{-t + (-1)^k \sqrt{t^2-4su}}{2s} \left(\frac{h(\bar{y})}{b\bar{y}g_x(\bar{x})}\right) + \frac{1}{b\bar{y}g_x(\bar{x})}\left(\frac{F_3(\bar{x},\bar{y},\bar{z})}{r\bar{z}h_y(\bar{y})}(-a+bg(\bar{x})-\bar{z}h_y(\bar{y}))-F_2(\bar{x},\bar{y},\bar{z})\right). \tag{4.10}$$

Then substituting (4.6), (4.9) and (4.10) into (4.2) and neglecting the terms of order $O(\varepsilon^2)$ we obtain

$$\begin{aligned} \hat{x}_k(\varepsilon) &= \bar{x} + \varepsilon m_{1k}, \\ \hat{y}_k(\varepsilon) &= \bar{y} + \varepsilon n_1, \\ \hat{z}_k(\varepsilon) &= \bar{z} + \varepsilon w_{1k}, \quad k = 1,2. \end{aligned} \tag{4.11}$$

Hence $E(\bar{x},\bar{y},\bar{z})$ bifurcates into two equilibria $E_k(\hat{x}_k,\hat{y}_k,\hat{z}_k)$, $k = 1,2$. The cases $s = 0$ or $t^2 - 4su = 0$ in (4.7) will require consideration of higher order terms than εm_1, εn_1 and εw_1 in (4.4). If $s \neq 0$ but $t^2 - 4su < 0$, then w_{1k} is not real, hence the multiple equilibrium $E(\bar{x},\bar{y},\bar{z})$ disappears under the influence of small perturbations.

Case (ii). $D \neq 0$, where D is given by (4.5).

Eliminating m_1 and n_1 from (4.4) and neglecting $O(\varepsilon^2)$ terms we obtain

$$\varepsilon(sw_1^{\,2} + tw_1 + u) + D = 0, \tag{4.12}$$

where s, t and u are given by (4.8) and D by (4.5). The equation (4.12) has two real roots

$$w_{1k} = -\frac{t}{2s} + (-1)^k(-\frac{D}{s})\varepsilon^{-1/2} + O(\varepsilon^{1/2}),\ k = 1,2. \tag{4.13}$$

provided that $sD < 0$.

From the first equation (4.4) we get

$$n_1 = \frac{F_1(\bar{x},\bar{y},\bar{z})}{g(\bar{x})} + O(\varepsilon). \tag{4.14}$$

Substituting w_{1k} and n_1 from (4.13) and (4.14) into the second equation (4.4) and keeping only the largest term (with factor $\varepsilon^{-1/2}$) we find

$$m_{1k} = (-1)^k \frac{h(\bar{y})}{b\bar{y}g_x(\bar{x})}\left(-\frac{D}{s}\right)^{1/2} \varepsilon^{-1/2}, \quad k = 1,2. \qquad (4.15)$$

Substituting m_{1k}, n_1 and w_{1k} into (4.2) we obtain the following approximate expressions for the coordinates of the perturbed equilibria $E_k(\hat{x}_k, \hat{y}_k, \hat{z}_k)$ up to the order $\varepsilon^{1/2}$.

$$\hat{x}_k = \bar{x} + (-1)^k \frac{h(\bar{y})}{b\bar{y}g_x(\bar{x})}\left(-\frac{D}{s}\right)^{1/2} \varepsilon^{1/2},$$

$$\hat{y}_k = \bar{y}, \qquad (4.16)$$

$$\hat{z}_k = \bar{z} + (-1)^k \left(-\frac{D}{s}\right)^{1/2} \varepsilon^{1/2}, \quad k = 1,2.$$

The case $s = 0$ in (4.12) will require consideration of higher order than εm_1, εn_1 and εw_1 in (4.4). If $s \neq 0$ but $sD > 0$ the multiple equilibrium $E(\bar{x},\bar{y},\bar{z})$ disappears under the influence of small perturbations.

For both cases, $D = 0$ and $D \neq 0$, $E_k(\hat{x}_k, \hat{y}_k, \hat{z}_k)$, $k = 1,2$, are simple perturbed equilibria if

$$\det J(\hat{x}_k(\varepsilon),\ \hat{y}_k(\varepsilon),\ \hat{z}_k(\varepsilon)) \neq 0, \qquad (4.17)$$

where $J(x,y,z)$ is the Jacobian matrix of the system (3.1).

4.2 NATURE AND STABILITY OF THE PERTURBED EQUILIBRIA

To study locally the nature and stability of the perturbed equilibria for both cases when D = 0 and D ≠ o, we need to use the Jacobian matrix (3.9) where $x^*(\varepsilon)$, $y^*(\varepsilon)$, $z^*(\varepsilon)$ are replaced by $\hat{x}(\varepsilon)$, $\hat{y}(\varepsilon)$ and $\hat{z}(\varepsilon)$.

For case (i) when D = 0 the Jacobian matrix calculated at the equilibria $E_k(\hat{x}(\varepsilon), \hat{y}(\varepsilon), \hat{z}(\varepsilon))$, k = 1,2, up to the order of ε is written in the form

$$J(\hat{x}_k(\varepsilon),\hat{y}_k(\varepsilon),\hat{z}_k(\varepsilon)) = \bar{J}^o(\bar{x},\bar{y},\bar{z}) + \varepsilon \bar{J}^1(\bar{x},\bar{y},\bar{z}), \quad k = 1,2, \qquad (4.18)$$

where

$$\bar{J}^o(\bar{x},\bar{y},\bar{z}) = (\bar{J}^o_{ik}) = \begin{bmatrix} 0 & -g(\bar{x}) & 0 \\ b\bar{y}g_x(\bar{x}) & -a+bg(\bar{x})-\bar{z}h_y(\bar{y}) & -h(\bar{y}) \\ 0 & r\bar{z}h_y(\bar{y}) & 0 \end{bmatrix}, \qquad (4.19)$$

$$\bar{J}^1(\bar{x},\bar{y},\bar{z}) = (\bar{J}^1_{ik}), \qquad (4.20)$$

and $\bar{J}^1_{ik}$ are the elements of (4.20) given by

$$\bar{J}^1_{11} = \bar{x}m_{1k}f_{xx}(\bar{x}) + 2m_{1k}f_x(\bar{x}) - \bar{y}m_{1k}g_{xx}(\bar{x}) - n_{1k}g_x(\bar{x}) + F_{1x}(\bar{x},\bar{y},\bar{z}),$$

$$\bar{J}^1_{12} = -m_{1k}g_x(\bar{x}) + F_{1y}(\bar{x},\bar{y},\bar{z}),$$

$$\bar{J}^1_{13} = F_{1z}(\bar{x},\bar{y},\bar{z}),$$

$$\bar{J}^1_{21} = b\bar{y}n_{1k}g_x(\bar{x}) + bn_{1k}g_x(\bar{x}) + F_{2x}(\bar{x},\bar{y},\bar{z}),$$

$$\bar{J}^1_{22} = bm_{1k}g_x(\bar{x}) - \bar{z}n_{1k}h_{yy}(\bar{y}) - w_{1k}h_y(\bar{y}) + F_{2y}(\bar{x},\bar{y},\bar{z}),$$

$$\bar{J}^1_{23} = -n_{1k}h_y(\bar{y}) + F_{2z}(\bar{x},\bar{y},\bar{z}),$$

$$\bar{J}^1_{31} = F_{3x}(\bar{x},\bar{y},\bar{z}),$$

$$\bar{J}^1_{32} = r\bar{z}n_{1k}h_{yy}(\bar{y}) + rw_{1k}h_y(\bar{y}) + F_{3y}(\bar{x},\bar{y},\bar{z}),$$

$$\bar{J}^1_{33} = rn_{1k}h_y(\bar{y}) + F_{3z}(\bar{x},\bar{y},\bar{z}),$$

and n_{1k}, w_{1k} and m_{1k} are given by (4.6), (4.9) and (4.10) respectively.

For case (ii) when $D \neq 0$ the Jacobian matrix calculated at the equilibria $E_k(\hat{x}(\varepsilon), \hat{y}(\varepsilon), \hat{z}(\varepsilon))$, $k = 1,2$ up to the order of ε is written in the form

$$J(\hat{x}_k(\varepsilon), \hat{y}_k(\varepsilon), \hat{z}_k(\varepsilon)) = \bar{J}^o(\bar{x},\bar{y},\bar{z}) + \varepsilon^{1/2}\bar{J}^{1/2}(\bar{x},\bar{y},\bar{z}) + \varepsilon\hat{J}^1(\bar{x},\bar{y},\bar{z}), \quad k = 1,2, \tag{4.21}$$

where $\bar{J}^{o}(\bar{x},\bar{y},\bar{z})$ is given by (4.19), $\bar{J}^{1/2}(\bar{x},\bar{y},\bar{z})$ and $\hat{J}^{1}(\bar{x},\bar{y},\bar{z})$ are 3 x 3 matrices such that

$$\bar{J}^{1/2}(\bar{x},\bar{y},\bar{z}) = (\bar{J}_{ik})$$

$$= \begin{bmatrix} d\bar{x}f_{xx}(\bar{x})+\bar{z}df_{x}(\bar{x})-d\bar{y}g_{xx}(\bar{x}) & -dg_{x}(\bar{x}) & 0 \\ bd\bar{y}g_{x}(\bar{x}) & bdg_{x}(\bar{x})-eh_{y}(\bar{y}) & 0 \\ 0 & reh_{y}(\bar{y}) & 0 \end{bmatrix}, \qquad (4.22)$$

and

$$\hat{J}^{1}(\bar{x},\bar{y},\bar{z}) = (\hat{J}^{1}_{ik}), \qquad (4.23)$$

where $\hat{J}^{1}_{ik}$ are given by

$$\hat{J}^{1}_{11} = \tfrac{1}{2}\bar{x}d^{2}f_{xx}(\bar{x}) + \tfrac{1}{2}d^{2}f_{xx}(\bar{x}) - \tfrac{1}{2}\bar{y}d^{2}g_{xx}(\bar{x}) + F_{1x}(\bar{x},\bar{y},\bar{z}),$$

$$\hat{J}^{1}_{12} = -\tfrac{1}{2}d^{2}g_{xx}(\bar{x}) + F_{1y}(\bar{x},\bar{y},\bar{z}),$$

$$\hat{J}^{1}_{13} = F_{1z}(\bar{x},\bar{y},\bar{z}),$$

$$\hat{J}^{1}_{21} = \tfrac{1}{2}b\bar{y}d^{2}g_{xx}(\bar{x}) + F_{2x}(\bar{x},\bar{y},\bar{z}),$$

$$\hat{J}^{1}_{22} = \tfrac{1}{2}bd^{2}g_{xx}(\bar{x}) + F_{2y}(\bar{x},\bar{y},\bar{z}),$$

$$\hat{J}^1_{23} = F_{2z}(\bar{x},\bar{y},\bar{z}),$$

$$\hat{J}^1_{31} = F_{3x}(\bar{x},\bar{y},\bar{z}),$$

$$\hat{J}^1_{32} = F_{3y}(\bar{x},\bar{y},\bar{z}),$$

$$\hat{J}^1_{33} = F_{3z}(\bar{x},\bar{y},\bar{z}),$$

where

$$d = (-1)^k \frac{h(\bar{y})}{b\bar{y}g_x(\bar{x})} (-\frac{D}{s})^{1/2} ,$$

and (4.24)

$$e = (-1)^k(-\frac{D}{s})^{1/2}, \quad k = 1,2.$$

We consider only case (i), that is when D = 0. The characteristic equation of the Jacobian matrix (4.18) up to the order ε is given by

$$\lambda^3 + (p_1+\varepsilon q_1)\lambda^2 + (p_2+\varepsilon q_2)\lambda + \varepsilon q_3 = 0, \tag{4.25}$$

where p_1 and p_2 are given by (2.11), and

$$q_1 = -\sum_{i=1}^{3} \bar{J}^1_{ii},$$

$$q_2 = \sum_{i=1}^{3}\sum_{k=1}^{3}\sum_{l=1}^{3} \left(\frac{1}{2}\bar{J}^o_{ii}(\bar{J}^1_{kk}+\bar{J}^1_{ll}) - \bar{J}^o_{ik}\bar{J}^o_{ki}\right), \quad i \neq k \neq l, \tag{4.26}$$

$$q_3 = -\begin{vmatrix} \bar{J}^o_{11} & \bar{J}^o_{12} & \bar{J}^o_{13} \\ \bar{J}^o_{21} & \bar{J}^o_{22} & \bar{J}^o_{23} \\ \bar{J}^1_{31} & \bar{J}^1_{32} & \bar{J}^1_{33} \end{vmatrix} - \begin{vmatrix} \bar{J}^o_{11} & \bar{J}^o_{12} & \bar{J}^o_{13} \\ \bar{J}^1_{21} & \bar{J}^1_{22} & \bar{J}^1_{23} \\ \bar{J}^o_{31} & \bar{J}^o_{32} & \bar{J}^o_{33} \end{vmatrix} - \begin{vmatrix} \bar{J}^1_{11} & \bar{J}^1_{12} & \bar{J}^1_{13} \\ \bar{J}^o_{21} & \bar{J}^o_{22} & \bar{J}^o_{23} \\ \bar{J}^o_{31} & \bar{J}^o_{32} & \bar{J}^o_{33} \end{vmatrix},$$

where $\bar{J}^o_{ik}$ and $\bar{J}^1_{ik}$ are elements of the Jacobian matrices $\bar{J}^o(\bar{x},\bar{y},\bar{z})$ and $\bar{J}^1(\bar{x},\bar{y},\bar{z})$, respectively.

For $\varepsilon = 0$ the characteristic equation (4.25) reduces to equation (2.10) of the critical case of the unperturbed system (1). The determinant (4.18) can be presented in the form

$$\det J(\hat{x}_k(\varepsilon), \hat{y}_k(\varepsilon), \hat{z}_k(\varepsilon)) = -\varepsilon q_3 + O(\varepsilon^2), \quad k = 1,2. \tag{4.27}$$

We assume that $q_3 \neq 0$, hence (4.20) is satisfied.

The assumption that $q_3 \neq 0$ guarantees the existence of a simple perturbed equilibrium of the model (2).

The local stability analysis of the perturbed equilibria requires the investigation of the signs of the roots of the equation

(4.25). Bojadziev and Sattar [5] gave a detailed classification of the nature and stability of the perturbed equilibria of the Kolmogorov model (1.5) in the critical case when the unperturbed Kolmogorov model has a multiple equilibrium. We will use the results presented in [5] in the next section of this chapter.

4.3 EXAMPLES OF PERTURBED SIMPLE FOOD CHAIN WITH HARVESTING

In order to illustrate the general theory discussed in this chapter, we present three examples for the case (i) when D = 0.

Example 4

The model

$$x' = x(2-\tfrac{1}{2}x) - yx - \tfrac{1}{2} + \varepsilon(x-2y),$$

$$y' = -\tfrac{1}{2}y + yx - zy^2 + \varepsilon(y-4z), \qquad (4.28)$$

$$z' = -z + y^2 z + \varepsilon(2z),$$

is a perturbed predator-predator-prey model with constant rate prey harvesting $H = \frac{1}{2}$ and prey carrying capacity $k = 4$. It is a particular case of (2) with

$$f(x) = 2 - \frac{1}{2}x, \qquad g(x) = x, \qquad h(y) = y^2,$$

$$a = -\frac{1}{2}, \qquad b = 1, \qquad c = 1, \qquad r = 1,$$

$$F_1 = x - 2y, \qquad F_2 = y - 4z \qquad F_3 = 2z.$$

It is clear that for the unperturbed system of (4.28), $\varepsilon = 0$, we have a situation where z eats y, and y eats x. The perturbation terms in (4.28) with factor $\varepsilon << 1$ change slightly the unperturbed system in the following way. In the first equation the perturbation term means both, a slight increase of the growth rate of x due to internal cooperation (εx) and a slight decrease of the growth rate due to increase activities ($-2\varepsilon y$) of the first predator y. In the second equation the perturbation term means both, a slight increase of the growth rate of y due to internal cooperation (εy) and a slight decrease of the growth rate due to increase activities ($-4\varepsilon z$) of the second predator z. Finally in the third equation there is a slight increase of the growth rate of z due to internal cooperation term ($\varepsilon 2z$).

The unperturbed model (4.28), $\varepsilon = 0$, has an equilibrium $E_c(1, 1, \frac{1}{2})$. The corresponding Jacobian matrix, calculated at $E_c(1, 1, \frac{1}{2})$ is

$$J(1,1,\tfrac{1}{2}) = \begin{bmatrix} 0 & -1 & 0 \\ 1 & -\frac{1}{2} & -1 \\ 0 & 1 & 0 \end{bmatrix}. \tag{4.29}$$

From (4.29) we see that det $J(1, 1, \frac{1}{2}) = 0$, hence E_c is a multiple equilibrium. We check also that condition (2.9) is satisfied. The characteristic equation of (4.29) is

$$\lambda^3 + \frac{1}{2}\lambda^2 + 2\lambda = 0. \qquad (4.30)$$

It has roots

$$\lambda_1 = 0, \qquad \lambda_{2,3} = \frac{1}{4}(-1 \pm i\sqrt{31}). \qquad (4.31)$$

For the perturbed model (4.28), condition (4.1) holds, that is, the perturbation terms in (4.28) do not vanish at $E_c(1, 1, \frac{1}{2})$. Note that the expression D given by (4.5) is zero, hence case (i) applies.

The perturbed equilibria of (4.28) up to the order ε are found to be $E_1(1-\varepsilon, 1-\varepsilon, \frac{1}{2} - \frac{3}{2}\varepsilon)$ and $E_2(1+5\varepsilon, 1-\varepsilon, \frac{1}{2} + \frac{9}{2}\varepsilon)$.

Consider first $E_1(1-\varepsilon, 1-\varepsilon, \frac{1}{2} - \frac{3}{2}\varepsilon)$. The Jacobian matrix (4.18) calculated at E_1 up to the order ε is

$$J(1-\varepsilon, 1-\varepsilon, \frac{1}{2} - \frac{3}{2}\varepsilon) = \begin{bmatrix} 3\varepsilon & -(1+\varepsilon) & 0 \\ 1-\varepsilon & -\frac{1}{2}+4\varepsilon & -(1+2\varepsilon) \\ 0 & 1-4\varepsilon & 0 \end{bmatrix}. \qquad (4.31)$$

Its characteristic equation up to the order ε is

$$\lambda^3 + (\tfrac{1}{2} - 7\varepsilon)\lambda^2 + (2 - \tfrac{7}{2}\varepsilon)\lambda - 3\varepsilon = 0, \qquad (4.32)$$

which is a particular case of (4.25) with

$$p_1 = \tfrac{1}{2}, \qquad p_2 = 2,$$

$$q_1 = -7, \qquad q_2 = -\tfrac{7}{2}, \qquad q_3 = -3.$$

Equation (4.32) has one positive eigenvalue λ_1 and two complex eigenvalues $\lambda_{2,3}$ with negative real part (see Bojadziev and Sattar [5]). Hence E_1 is a saddle spiral with stable plane focus.

Now consider $E_2(1+5\varepsilon , 1-\varepsilon , \frac{1}{2} + \frac{9}{2}\varepsilon)$. The Jacobian matrix (4.18) calculated at E_2 up to the order ε is

$$J(1+5\varepsilon , 1-\varepsilon , \tfrac{1}{2} + \tfrac{9}{2}\varepsilon) = \begin{bmatrix} -3\varepsilon & -(1+7\varepsilon) & 0 \\ 1-\varepsilon & -(\frac{1}{2}+2\varepsilon) & -(1+2\varepsilon) \\ 0 & 1+8\varepsilon & 0 \end{bmatrix}. \qquad (4.33)$$

Its characteristic equation up to the order ε is

$$\lambda^3 + (\tfrac{1}{2} + 5\varepsilon)\lambda^2 + (2 + \tfrac{35}{2}\varepsilon)\lambda + 3\varepsilon = 0, \qquad (4.34)$$

which is a particular case of (4.25) with

$$p_1 = \frac{1}{2}, \qquad p_2 = 2,$$

$$q_1 = 5, \qquad q_2 = \frac{35}{2}, \qquad q_3 = 3.$$

Equation (4.34) has one negative eigenvalue λ_1 and two complex eigenvalues $\lambda_{2,3}$ with negative real part (see [5]). Hence E_2 is an asymptotically stable pointed spiral.

Example 5

Consider the system with constant rate harvesting $H = \frac{1}{4}$

$$x' = x(1-\frac{1}{4}x) - \frac{1}{2}yx - \frac{1}{4} + \frac{1}{4}\varepsilon x,$$

$$y' = -y + 3yx - yz \qquad + \varepsilon y, \tag{4.35}$$

$$z' = -2z + 2yz \qquad + \varepsilon(z-4y).$$

Here

$$f(x) = (1-\frac{1}{4}x), \quad g(x) = \frac{1}{2}x, \quad h(y) = y,$$

$$a = 1, \qquad b = 6, \qquad c = 2, \qquad r = 2,$$

$$F_1 = \frac{1}{4}x, \qquad F_2 = y, \qquad F_3 = z-4y.$$

The system (4.35) describes a predator-predator-prey interactions similar to that of (4.28).

For the unperturbed model (4.35), $\varepsilon = 0$, condition (2.9) is satisfied and there exists a multiple equilibrium $E_c(1 , 1 , 2)$. The Jacobian matrix of the unperturbed system calculated at $E_c(1 , 1 , 2)$ is given by

$$J(1,1,2) = \begin{bmatrix} 0 & -\frac{1}{2} & 0 \\ 3 & 0 & -1 \\ 0 & 4 & 0 \end{bmatrix} \tag{4.36}$$

and its characteristic equation is

$$\lambda^3 + \frac{11}{2}\lambda = 0. \tag{4.37}$$

Hence the eigenvalues of the Jacobian matrix are

$$\lambda_1 = 0, \qquad \lambda_{2,3} = \pm i\sqrt{\frac{11}{2}} .$$

For the perturbed model (4.35) condition (4.1) holds, that is the perturbation terms in (4.35) do not vanish at $E_c(1 , 1 , 2)$. The expression D given by (4.5) is zero at $E_c(1 , 1 , 2)$, hence case (i) applies.

The perturbed equilibria of (4.35) up to the order ε are found to be

$E_1(1+(1-\frac{\sqrt{3}}{3})\varepsilon\ ,\ 1+\frac{1}{2}\varepsilon\ ,\ 2+(4-\sqrt{3})\varepsilon)$ and $E_2(1+(1+\frac{\sqrt{3}}{3})\varepsilon\ ,\ 1+\frac{1}{2}\varepsilon\ ,\ 2+(4+\sqrt{3})\varepsilon)$.

For $E_1(1+(1-\frac{\sqrt{3}}{3})\varepsilon\ ,\ 1+\frac{1}{2}\varepsilon\ ,\ 2+(4-\sqrt{3})\varepsilon)$, the Jacobian matrix (4.18) calculated at this equilibrium up to the order ε is

$$J(1+(1-\frac{\sqrt{3}}{3})\varepsilon, 1+\frac{1}{2}\varepsilon, 2+(4-\sqrt{3})\varepsilon) = \begin{bmatrix} -\frac{1}{2}(1-\frac{\sqrt{3}}{3})\varepsilon & -\frac{1}{2}(1+(1-\frac{\sqrt{3}}{3})\varepsilon) & 0 \\ 3+\frac{3}{2}\varepsilon & 0 & -(1+\frac{1}{2}\varepsilon) \\ 0 & 4+2(2-\sqrt{3})\varepsilon & 2\varepsilon \end{bmatrix}. \qquad (4.38)$$

Its characteristic equation up to the order ε is

$$\lambda^3+(\frac{3}{2}+\frac{\sqrt{3}}{6})\varepsilon\lambda^2+(\frac{11}{2}+(\frac{33}{4}-\frac{5}{2}\sqrt{3})\varepsilon)\lambda-(1+\frac{2\sqrt{3}}{3})\varepsilon = 0, \qquad (4.39)$$

which is a particular case of (4.25) with

$$p_1 = 0, \qquad p_2 = \frac{11}{2},$$

$$q_1 = \frac{3}{2}+\frac{\sqrt{3}}{6}, \qquad q_2 = \frac{33}{4}-\frac{5}{2}\sqrt{3}, \qquad q_3 = -(1+\frac{2\sqrt{3}}{3}).$$

Using [5], we find that the roots of the characteristic equation (4.39) are $T_1(\varepsilon) > 0$ and $T_2(\varepsilon) \pm i(\sqrt{\frac{11}{2}}+T_3(\varepsilon))$ where $T_i(0) = 0$, $i = 1,2,3$ and $T_2(\varepsilon) < 0$. Therefore $E_3(1+(1-\frac{\sqrt{3}}{3})\varepsilon\ ,\ 1+\frac{1}{2}\varepsilon\ ,\ 2+(4-\sqrt{3})\varepsilon)$ is a saddle spiral with stable plane focus.

For $E_2(1+(1+\frac{\sqrt{3}}{3})\varepsilon,\ 1+\frac{1}{2}\varepsilon,\ 2+(4+\ 3)\varepsilon)$, the Jacobian matrix (4.18) calculated at this equilibrium up to the order ε is

$$J(1+(1+\frac{3}{3})\ ,1+\frac{1}{2}\ ,2+(4+\ 3)\ )=\begin{bmatrix} -\frac{1}{2}(1+\frac{3}{3})\varepsilon & -\frac{1}{2}(1+(1+\frac{3}{3})\varepsilon) & 0 \\ 3+\frac{1}{2}\varepsilon & 0 & -(1+\frac{1}{2}\varepsilon) \\ 0 & 4+2(2+\sqrt{3})\varepsilon & 2\varepsilon \end{bmatrix}. \quad (4.40)$$

Its characteristic equation up to the order of ε is

$$\lambda^3+(\frac{3}{2}-\frac{\sqrt{3}}{6}\varepsilon)\lambda^2+(\frac{11}{2}+(\frac{33}{4}+\frac{5}{2}\sqrt{3})\varepsilon)\lambda+(\frac{2\sqrt{3}}{3}-1)\varepsilon = 0, \quad (4.41)$$

which is a particular case of (4.25) with

$$p_1 = 0, \qquad p_2 = \frac{11}{2},$$

$$q_1 = \frac{3}{2}-\frac{\sqrt{3}}{6}, \qquad q_2 = \frac{33}{4}+\frac{5}{2}\sqrt{3}, \qquad q_3 = \frac{2\sqrt{3}}{3}-1.$$

Using 5 , we find that the roots of the characteristic equation (4.41) are $T_1(\varepsilon) < 0$, $T_2(\varepsilon) \pm i(\sqrt{\frac{11}{2}}+T_3(\varepsilon))$, where $T_i(0) = 0$, $i = 1,2,3$ and $T_2(\varepsilon) < 0$. Hence $E_2(1+(1+\frac{3}{3})\varepsilon,\ 1+\frac{1}{2}\varepsilon,\ 2+(4+\sqrt{3})\varepsilon)$ is an asymptotically stable spiral.

Example 6

Consider the model with constant rate prey harvesting $H = \frac{1}{4}$, prey's carrying capacity $k = 4$ and a Holling-type predation of the second predator on the first predator:

$$x' = x(1-\frac{x}{4}) - yx - \frac{1}{4} + \varepsilon(x-\frac{7}{2}y),$$

$$y' = -y + 3yx - \frac{3yz}{1+y} + \varepsilon(3y-2z), \qquad (4.42)$$

$$z' = -z + \frac{3yz}{1+y} + \varepsilon z,$$

which describes a predator-predator-prey interactions similar to that of (4.28).

For the unperturbed model (4.42), $\varepsilon = 0$, condition (2.9) is satisfied and there exists a multiple equilibrium $E_c(1, \frac{1}{2}, 1)$. The Jacobian matrix of the unperturbed system calculated at $E_c(1, \frac{1}{2}, 1)$ is given by

$$J(1, \frac{1}{2}, 1) = \begin{bmatrix} 0 & -1 & 0 \\ \frac{3}{2} & \frac{2}{3} & -1 \\ 0 & \frac{4}{3} & 0 \end{bmatrix}. \qquad (4.43)$$

Its characteristic equation is

$$\lambda^3 - \frac{2}{3}\lambda^2 + \frac{17}{6}\lambda = 0. \tag{4.44}$$

Equation (4.44) has roots $\lambda_1 = 0$ and $\lambda_{2,3} = \frac{1}{3} \pm i\frac{\sqrt{98}}{6}$.

For the perturbed system (4.42) condition (4.1) holds since the perturbation terms in (4.42) do not vanish at $E_c(1, \frac{1}{2}, 1)$. The expression D given by (4.5) is zero at $E_c(1, \frac{1}{2}, 1)$, hence case (i) applies.

The perturbed equilibria of (4.42) up to the order ε are found to be

$E_1(1+(\frac{7}{2}+\frac{\sqrt{85}}{2})\varepsilon, \frac{1}{2}-\frac{3}{4}\varepsilon, 1+(\frac{17}{4}+\frac{3}{4}\sqrt{85})\varepsilon)$ and $E_2(1+(\frac{7}{2}-\frac{\sqrt{85}}{2})\varepsilon, \frac{1}{2}-\frac{3}{4}\varepsilon, 1+(\frac{17}{4}-\frac{3}{4}\sqrt{85})\varepsilon)$.

In the calculation which follows, the numbers $\frac{7}{2}+\frac{\sqrt{85}}{2}$, $\frac{17}{4}+\frac{3}{4}\sqrt{85}$, $\frac{7}{2}-\frac{\sqrt{85}}{2}$ and $\frac{17}{4}-\frac{3}{4}\sqrt{85}$, are substituted correspondingly by 8.13, 11.2, -1.11, and -2.68.

For $E_1(1+8.13\varepsilon, \frac{1}{2}-\frac{3}{4}\varepsilon, 1+11.2\varepsilon)$, the Jacobian matrix (4.18) calculated at this equilibrium up to the order ε is

$$J(1+8.13\varepsilon, \frac{1}{2}-\frac{3}{4}\varepsilon, 1+11.2\varepsilon) = \begin{bmatrix} -2.31\varepsilon & -(1+12.63\varepsilon) & 0 \\ \frac{3}{2}-3.38\varepsilon & \frac{2}{3}+12.46\varepsilon & -(1+\varepsilon) \\ 0 & \frac{4}{3}+14.93\varepsilon & 0 \end{bmatrix}. \tag{4.45}$$

Its characteristic equation up to the order ε is

$$\lambda^3 - (\tfrac{2}{3} + 10.15\varepsilon)\lambda^2 + (\tfrac{17}{6} + 30.29\varepsilon)\lambda + 3.08\varepsilon = 0, \qquad (4.46)$$

which is a particular case of (4.25) with

$$p_1 = \frac{2}{3}, \qquad p_2 = \frac{17}{6},$$

$$q_1 = -10.15, \qquad q_2 = 30.29, \qquad q_3 = 3.08.$$

According to Bojadziev and Sattar [5] the roots of the characteristic equation (4.46) are $T_1(\varepsilon)$ and $\frac{1}{3} + T_2(\varepsilon) \pm i(\frac{\sqrt{98}}{6} + T_3(\varepsilon))$ where $T_i(0) = 0$, $i = 1,2,3$ and $T_1'(\varepsilon) < 0$. Therefore $E_1(1+8.13\varepsilon, \frac{1}{2} - \frac{3}{4}\varepsilon, 1+11.2\varepsilon)$ is a saddle spiral with unstable plane focus.

For $E_2(1-1.11\varepsilon, \frac{1}{2} - \frac{3}{4}\varepsilon, 1-2.68\varepsilon)$, the Jacobian matrix (4.18) calculated at this equilibrium up to the order ε is

$$J(1-1.11\varepsilon, \tfrac{1}{2} - \tfrac{3}{4}\varepsilon, 1-2.68\varepsilon) = \begin{bmatrix} 2.03\varepsilon & -(1+2.39\varepsilon) & 0 \\ \frac{3}{2} - 3.38\varepsilon & \frac{2}{3} + 1.91\varepsilon & -(1+\varepsilon) \\ 0 & \frac{4}{3} - 2.24\varepsilon & 0 \end{bmatrix}. \qquad (4.47)$$

Its characteristic equation up to the order ε is

$$\lambda^3 - (\tfrac{2}{3} + 3.94\varepsilon)\lambda^2 + (\tfrac{17}{6} + 0.65\varepsilon)\lambda - 2.71\varepsilon = 0, \qquad (4.48)$$

which is a particular case of (4.25) with

$$p_1 = -\frac{2}{3}, \qquad p_2 = \frac{17}{6},$$

$$q_1 = -3.94, \quad q_2 = 0.65, \quad q_3 = -2.71.$$

Again from [5] it follows that the roots of the characteristic equation (4.48) are $T_1(\varepsilon)$ and $\frac{1}{3} + T_2(\varepsilon) \pm i(\frac{\sqrt{98}}{6} + T_3(\varepsilon))$ where $T_i(0) = 0$, $i = 1,2,3$ and $T_1(\varepsilon) > 0$. Then $E_2(1-1.11\varepsilon, \frac{1}{2} - \frac{3}{4}\varepsilon, 1-2.68\varepsilon)$ is an unstable pointed spiral.

CONCLUSION

We have studied the three dimensional unperturbed food chain model (1) with harvesting H in the noncritical case (simple equilibria) and the critical case (multiple equilibrium). The condition for the existence of a noncritical case is that the determinant of the Jacobian matrix of (1) calculated at the equilibrium is not zero while for the critical case the determinant of the Jacobian matrix calculated at the equilibrium is zero. The condition (2.15) for the existence of a multiple equilibrium involves explicity the harvesting rate H which demonstrates the significance of the presence of H in the model.

We have seen that in the noncritical case the equilibrium position of (1) can be hyperbolic or nonhyperbolic. However, in the critical case, the equilibrium position (multiple) is nonhyperbolic. We have investigated the effect of perturbations on the simple equilibrium of the model (1) and studied the nature and stability of the perturbed equilibrium. A simple equilibrium, hyperbolic or nonhyperbolic, can generate under small perturbations a hyperbolic equilibrium. Further we have studied the bifurcation of a multiple equilibrium of (1) into simple perturbed equilibria of (2).

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