NETAJI SUBHAS OPEN UNIVERSITY

STUDY MATERIAL

MATHEMATICS

POST GRADUATE

PG (MT) - IX B(II)
(APPLIED MATHEMATICS)

Mathematical Models
in Ecology

PREFACE

In the auricular structure introduced by this University for students of Post- Graduate degree programme, the opportunity to pursue Post-Graduate course in Subject introduced by this University is equally available to all learners. Instead of being guided by any presumption about ability level, it would perhaps stand to reason if receptivity of a learner is judged in the course of the learning process. That would be entirely in keeping with the objectives of open education which does not believe in artificial differentiation.

Keeping this in view, study materials of the Post-Graduate level in different subjects are being prepared on the basis of a well laid-out syllabus. The course structure combines the best elements in the approved syllabi of Central and State Universities in respective subjects. It has been so designed as to be upgradable with the addition of new information as well as results of fresh thinking and analysis.

The accepted methodology of distance education has been followed in the preparation of these study materials. Co-operation in every form of experienced scholars is indispensable for a work of this kind. We, therefore, owe an enormous debt of gratitude to everyone whose tireless efforts went into the writing, editing and devising of a proper lay-out of the materials. Practically speaking, their role amounts to an involvement in invisible teaching. For, whoever makes use of these study materials would virtually derive the benefit of learning under their collective care without each being seen by the other.

The more a learner would seriously pursue these study materials the easier it will be for him or her to reach out to larger horizons of a subject. Care has also been taken to make the language lucid and presentation attractive so mat they may be rated as quality self-learning materials. If anything remains still obscure or difficult to follow, arrangements are there to come to terms with them through the counselling sessions regularly available at the network of study centres set up by the University.

Needless to add, a great deal of these efforts is still experimental-in fact, pioneering in certain areas. Naturally, there is every possibility of some lapse or deficiency here and there. However, these do admit of rectification and further improvement in due course. On the whole, therefore, these study materials are expected to evoke wider appreciation the more they receive serious attention of all concerned.

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Unit 1 ◻ Introduction

Objectives : The object of this chapter is to present the basic concepts of ecology along with the mathematical modeling of ecological system.

Structure

1.1 ◻ Ecology : Basic Concepts

Definition : Environment:

The place where a living organism lives with its surrounding form its environment. Environment consists of two parts : abiotic and biotic. Soil, water, air and different minerals form the abiotic (or physical) environment, where as the biotic environment is formed of the plants and animals. The living organisms and environment are interrelated.

Definition : Ecology

The branch of science which deals with the study of interrelationship among the living organisms in relation with the environment is known as ecology. German biologist E. Haeckel (1968) first introduced the term 'ecology', which is derived from the Greek word 'Oikos' meaning dwelling place or house and 'logy' meaning the study of.

Parts of Ecology:

The study of ecology consists of four parts : (i) individual (ii) population (iii) community (iv) ecosystem. We describe them separately.

(i) Individual : It deals with the study of growth, development, reproduction and mortality of an individual.

(ii) Population : It deals with the study of the problems of the different organisms of the same single species. It studies whether a population will grow or decline, it studies why some populations are stable over many generations while other show outbreaks and crashes, it studies the causes of extinction.

(iii) Community : It deals with populations of different species. The problems to be studied are whether populations of different species co-exist ? Do the details of feeding relationship (who eats whom) matter ?

(iv) Ecosystem : Ecosystem is the fundament unit of ecology, where both biotic and abiotic components of the environment interplay. An ecosystem consists of several factors which may be divided into two categories : abiotic and biotic.

Components of Ecosystem:

Abiotic factors :

(i) **Different organic and inorganic components** : Calcium, sulpher, magnesium, potassium, oxygen, nitrogen, carbon dioxide, water, soil, amino-acids etc.

(ii) **Physical factors** : Light, humidity, temperature, atmospheric pressure, rainfall etc.

(iii) **Soil factor** : Nature of soil, water holding capacity, percolation of water through soil etc.

(iv) **Topographic factors** : Altitude, undulating landscape, amount of light falling on a place, wind blowing through etc.

Biotic factors:

(i) **Producers** : Green plants which produce proteins, amino acids, glucose etc. by the process of photosynthesis in the presence of sun-light,

(ii) **Consumers:**

(a) **Primary consumers** : Plant eaters - minute animals in the upper level of water constitute zoo plankton e.g. paphia, protozoa. The primary consumers in the lower level of water are called bottom forms e.g. orthopods, snails, small fishes, etc. Primary consumers of land are harvivores e.g. grasshopper, rabbits, monkey, dears, cows etc.

(b) **Secondary consumers** : Carnivores feeding on primary consumers such as frogs, toads, spider etc.

(c) **Territory consumers** : The animals feeding on the secondary consumers are called territory consumers e.g. Tiger, Lion, Leopard, whale, hawk, eagle etc.

(iii) **Decomposers** : (also called microorganisms) Certain bacteria, fungi breakdown the complex compounds of dead protoplasm, absorb certain decomposed produced and release certain simple substance for further utilization by the producers.

Different Types of Ecosystems :

(i) **Aquatic Ecosystems** : A pond is an example of an aquatic ecosystem. It comprises of four components : abiotic factors, producers, consumers and decomposers,

(ii) **Terrestrial Ecosystem** : A forest is a typical example. It also comprises of four components : abiotic substances, producers, consumers and decomposers.

1.2 ❑ Ecological Systems : Mathematical Models

Much of the monograph is devoted to the formulation and analysis of mathematical models. A mathematical model is a set of assumptions about an ecological system expressed in mathematical language. Mathematical reasonings or computations may then be used to generate predictions about the system.

Definition : Dynamical Model

A dynamical model of a system is a mathematical statement of the rules governing the changes of the states or conditions of the system with time. A dynamical model may be deterministic or stochastic. A dynamical model may be discrete-time or a continuous time.

1.2.1 Deterministic Models and State variables

The simplest ecological models, called deterministic models, make assumption that if we know the present conditions of a system, we can predict its future accurately. To determine the current state or condition of the system we have to choose some quantities called state variables. The choice of state variables involve a subtle balance of biological realism and mathematical complexity.

(i) State variables for individual are age, sex, development stage, physiological variable such as weight or size. For many cases age and size (or weight) are sufficient to serve as state variables.

(ii) State variables for populations are the number of living organisms the population

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contains. A more general population is a structured population. Structured populations are of two types : (a) age-structured population which involves both the number of individuals and their ages as state variables (b) spatially-structured population which involves the number of individuals along with their positions or locations at any time.

(iii) State variables for a community (a group of populations of different species) are the number of individuals of each dynamically interacting species.

(iv) In ecosystem the species are divided into some functional groups such as primary producers, herbivores, carnivores having interaction among the groups. Workable state variables to an ecosystem is a list of the biomasses of each of the functional group.

1.2.2a   Modelling in Discrete-time

Let the variable X_t denotes the state of the system at time t. The system state at time $t + \Delta t$ denoted by $X_{t+\Delta t}$ is a function of X_t i.e.

$$X_{t+\Delta t} = F(X_t) \qquad \qquad \text{...} \qquad (2.1)$$

The functional form of F depends on the system under consideration. If the function F is explicitly independent of time t the equation (2.1) is called an autonomous difference equation. The difference equation model forecasts the state of the system at series of equally spaced times. For example, if we know the state at time t = 0, we can calculate its state at times $t = \Delta t, 2 \Delta t, 3 \Delta t ...; \Delta t$ represents a single number, say one second, one minute, one year etc. For non-autonomous systems the difference equation is of the form

$$X_{t+\Delta t} = F(X_t, t) \qquad \qquad \text{...} \qquad (2.2)$$

1.2.2.b Modelling in Continuous—time

Continuous—time models aim to predict the values of the state variables at all future time, not at integer multiples of some time increment Δt. To write down the dynamics of a system we require the rate of change of the state variable X. It can be written in the form of the non-autonomous differential equation

$$\frac{dX}{dt} = g(X,t) \qquad \qquad \text{...} \qquad (2.3)$$

For autonomous system the rate of change of the state variable that is, the function g does not depend explicitly on t. In this case the equation becomes

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$$\frac{dX}{dt} = g(X) \qquad \qquad \cdots \qquad (2.4)$$

1.2.3 Balance (or conservation) Equation

Changes in abundance, stock or concentration of any physical or biological entity occur only through the operation of an identifiable process. For example, the concentration of physically and chemically stable material in an enclosed region can only change because of the import or export across the boundaries of the region. If the system is reactive then we must add the possibility of chemical transformation. Similarly, the population of organisms in an enclosed region can only change because of reproduction, mortality, export and import of the population across the boundaries. The dynamical equation which represents the changes in mathematical language is called the conservation or balance equation.

(a) Balance Equation for Chemically Inert Substances

We consider a chemically non-reactive substance located within a region of space. Let Q_t represents the quantity of the substance within the region at any time t. Then the balance equation is given by

$$Q_{t+\Delta t} = Q_t + \text{inflow} - \text{outflow} \qquad \qquad \cdots \qquad (2.5)$$

where the terms 'inflow' and 'outflow' represent the total inflow and outflow of the material during the time interval $(t, t + \Delta t)$. The equation (2.5) is an example of discrete-time balance equation. The analogue equation for continuous time is

$$\frac{dQ(t)}{dt} = \text{inflow rate} - \text{outflow rate} \qquad \qquad \cdots \qquad (2.6)$$

(b) Balance Equation for Chemically reacting substances

In the above balance equations the stock changes because of transport into and out of the region of interest. Most ecologically interesting situations involve chemical and biological transformation within the region being modeled. For example, the balance equation for a chemically reacting system is

$$\frac{dQ(t)}{dt} = \text{inflow rate} - \text{outflow rate} + \text{formation rate} - \text{transformation rate}$$

$$\cdots \qquad (2.7)$$

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In conclusion, the deterministic models of ecological systems involves three steps :

(i) Choose the state variables appropriate to the system under consideration,

(ii) Derive the balance (or conservation) equations. The balance equations represent the model equations for the growth process of the system under consideration,

(iii) For the successful utilization of the model equations we have to make model-specific assumptions.

1.2.4 Randomness and Stochastic Models

In the deterministic models the state of a system at any future time can be predicted exactly from its present state. This assumption is of course untenable. Unpredictability or randomness enter ecological dynamics in two ways. First no environment outside the laboratory is truely predictable. For example, the average light intensity measured each day at place vary randomly. Since light provides the energy for primary production the dynamics of ecological system will be seriously affected by the variability. Similarly, the random variation of humidity, temperature and other factors for an ecosystem can not be correctly predicted by deterministic models.

A second important way in which randomness affects ecological dynamics is that similar organisms do not necessarily respond in the same way to a given environment. Genetically identical individuals with identical histories in identical environment exhibit considerable variability in the timing, amount of reproduction and mortality. Although randomness is ubiquitous and stochastic models are essential, deterministic models are appropriate starting point for many ecological systems and are prerequisite to the formulation, analysis and better understanding of stochastic models of complex systems under investigation. In this monograph we shall be concerned mainly with the deterministic dynamical models of ecological systems.

1.2.5. Summary

The chapter consists of two parts:

(i) The first part consists of a brief discussion of ecology and ecological systems,

(ii) The second part is concerned with the dynamical modeling of ecological system.

It explains the concepts of state variables, continuous-time and discrete-time models of ecological systems The difference between deterministic and stochastic models of ecological system has been explained.

Unit 2 □ Single-Species Population : Continuous-Time Models

Objectives: The object of this chapter is to present the basic biological and mathematical postulates necessary for the continuous-time models of single-species populations together with their mathematical analysis.

Structure

2.1 □ Introduction : Basic Postulates

For the development of continuous-time models of population we assume the following three biological and mathematical postulates :

(i) The postulate of Parenthood

This states that every living organism has arisen from at least one parent of like kind to itself; it is often called 'the principle of a biogenesis'. For any one who believes in the initial terrestrial origin of life, the postulate is not universally valid; but since under present condition spontaneous generation has never been observed, we can take it as true enough to use in our investigation.

(ii) The postulate of upper limit

The second postulate is that in a finite space there is an upper limit to the number of living beings that can in some way occupy or utilize the space under consideration. The living beings require supply of energy at a certain rate to maintain their stability; obviously the space can not contain more of such living beings that utilize the energy input in the space.

(iii) The postulate of continuity

In addition to the above two biological postulates, it is convenient for mathematical reasons initially to adopt the convention that the variation of a population size x behaves as if x is a continuous variable, capable of taking any value, integral, fractional between the possible upper and lower limits of the population. The convention, though strictly untrue, is harmless when we are dealing with a sufficiently large population not having definite breeding or dying seasons, in which reproduction occurs at random among all members of the appropriate age class, and death occurs according to some statistically defined pattern not varying with time. When definite breeding seasons occur, or when mortality is much greater at sometimes of the year than at others, finite difference equations are to be used.

2.2 ❑ Population Growth : General Model Equation

Let x(t) denotes the population size (or density) at any time t and according to the postulate (iii) x(t) is assumed to be differentiable every where, that is, a smooth function of time t. The general model equation of growth of a single-species population can be written as

$$\frac{dx}{dt} = f(x) \qquad \qquad (2.1)$$

where the growth rate $\frac{dx}{dt}$ depends only on the population size (or density). Such an assumption appears to be reasonable for simple organisms such as microorganisms. For more complicated organisms like animals or humans this is an over simplification as it ignores intra-species competitions for resources and other factors, including age structure (the morality rate may depend on age rather than on population size). If the function f is sufficiently smooth, we can expand it in Taylor's series,

$$f(x) = \sum_{n=0}^{\cdot} a_n x^n = a_0 + a_1 x + a_2 x^2 + a_3 x^3 + \dots \qquad \qquad (2.2)$$

The postulate (i) requires f(o) = 0 to dismiss the possibility of spontaneous generation, the production of living organisms from inanimate matter. This is equivalent to

$$\frac{dx}{dt}\Big|_{x=0} = f(o) = 0$$

so that we may assume $a_0 = 0$ and then

$$\frac{dx}{dt} = a_1 x + a_2 x^2 + a_3 x^3 + \dots$$

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$$= x(a_1 + a_2 x + a_3 x^2 + ...)$$

$$= x\, g(x) \qquad\qquad ... \qquad (2.3)$$

The quantity $\dfrac{1}{x}\dfrac{dx}{dt} = \dfrac{x'(t)}{x(t)}$ is called the per capita growth rate i.e. the rate of growth per member. It is also known as intrinsic growth rate and the polynomial $g(x)$ of (2.3) is, therefore, the intrinsic growth rate of the population. We shall now study several specific growth models and study their characteristic behaviours.

2.3 ❑ Malthus Population Model: Exponential Growth

We first look at a population in which all individuals develop independently of one another. The organisms live in an unrestricted environment, where there is no form of competition. The rate of change of populations size (or density) can be computed if the birth-rate, death-rate and migration rate are known. For a closed population system there is no migration and the population size changes due to changes in births and deaths. Let b be the per capita birth rate and d be the per capita death rate. Then the change in population during a small time-internal $(t, t + h)$ is given by

$$x(t + h) - x(t) = (b - d)\, x(t)\, h$$

or, $\dfrac{x(t+h) - x(t)}{h} = (b - d)\, x(t)\, h$

Taking the limit $h \to 0$, we have,

$$\frac{dx}{dt} = (b - d) x = rx \qquad\qquad ... \qquad (2.4)$$

where $r = (b - d)$ \qquad\qquad ... \qquad (2.5)

is the net growth (or reproduction) rate.

The equation (2.4) is the famous Malthus model equation of population growth. This is the simplest form of the general model equation (2.3) with coefficients of $g(x)$ as

$$a_1 = r, a_2 = a_3 = ... = 0 \qquad\qquad ... \qquad (2.6)$$

The equation (2.4) can be solved to give the exponential distribution

$$N(t) = N_0 e^{rt} \qquad\qquad ... \qquad (2.7)$$

where $N_0 = N(o)$, the initial population. For this reason, the population obeying the equation (2.4) is said to be undergoing exponential growth. This constitutes the

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simplest minimal model of bacterial growth or indeed growth of any reproductive population. It was first initiated by Malthus in the year 1798 in human populations in a treatise that caused sensation in the scientific community of the day. He (Malthus) claimed that, barring natural disasters, the world's population would grow exponentially and thereby eventually outgrow its resources. He concluded that mass starvation would befall huminity.

The equation (2.4), while very simple, turns up in a number of natural processes. By reversing the sign of r one obtains a model of a population in which a fraction r of the individuals is continually removed per unit time, such as by death or migration. The equation

$$\frac{dN}{dt} = -rx \qquad \qquad \dots \qquad (2.8)$$

with solution $N(t) = N_0 e^{-rt}$ $\qquad \qquad \dots \qquad (2.9)$

describes a decaying process. This equation is commonly used to describe radioactive decay.

One can define a population doubling time τ_2 (for $r > 0$) or half-life τ_1 (for $r < 0$) in the following way. For growing population, seek a time t_2 such that

$$\frac{N(\tau_2)}{N_o} = 2$$

Putting this in equation in (2.7), we obtain

$$\frac{N(\tau_2)}{N_o} = 2 = e^{ct}$$

or, $\ln 2 = r\tau_2$ or $\tau_2 = \frac{\ln 2}{r}$ $\qquad \qquad \dots \qquad (2.10)$

The doubling time τ_2 is thus inversely proportional to the reproductive constant r. In a similar way we can find the half-life of a decaying population.
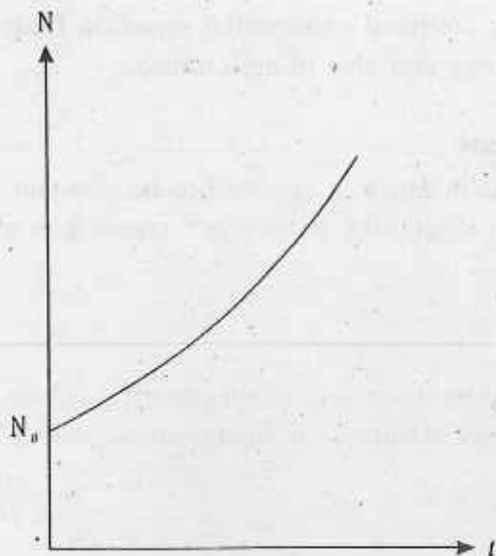
Fig. 2.3a

Fig. 2.3b

Malthus law for exponential growth · Malthus law for exponential delay

Remark:

The model (2.4) is not accurate for all time. Populations that grow exponentially at first are commonly observed in nature. However, their growth rates usually tend to decrease as population size increases. In fact, exponential growth or decay may be considered typical local behaviour. In other words, populations dynamics can usually be approximated by this simple model only for a short period of time. The assumption that the rate of growth of a population is proportional to its size (linear assumption) is unrealistic on long time scales. In the next section we shall modify this model for a realistic population growth. Note that a population that grows exponentially to infinity violates our basic postulates of finite upper limit.

Example (2.1): Confined Exponential Distribution

In order to prevent the infinitely large population size in Malthus exponential growth model we replace it by a confined exponential growth model equation as

$$\frac{dx}{dt} = r(x^* - x), \qquad x(o) = x_o$$

where x^* is the equilibrium value of x.

With initial condition $x(o) = x_o$, the solution of the equation is

$$x = x^* - (x^* - x_0) e^{-rt}$$

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which is a confined exponential function. The confined exponential equation finds wide applications in physical science, technology and also in agriculture.

Example (2.2) : Time-dependent Growth Rate

In Malthus model equation (2.4) the growth rate r is assumed to be constant. However, r may vary with time. For example, if we rake $r(t) = r_0 e^{-kt}$ where k is a positive constant, we get the equation

$$\frac{dx}{dt} = r_0 e^{-kt} x$$

which is known as Gompertz equation and is to be discussed independently later on. If we put $r(t) = [r_0 + r_m \sin(wt + \phi)]$ that is, if we assume a simple harmonic growth rate, we have the equation

$$\frac{dx}{dt} = [r_0 + r_m \sin(wt + \phi)]x.$$

This type of equation is useful for the certain types of trees whose mass vary periodically with a period of one year on the average.

2.4 ❑ Logistic Population Model

To correct prediction based on Malthus model or law (that a population grows indefinitely at an exponential rate), we consider a non-constant intrinsic growth rate g(x). The logistic model is perhaps the simplest extension of Malthus model equation (2.4). For a faithful model of population growth, we take more terms in the series for f(x). We take the intrinsic growth rate as

$$g(x) = a_1 + a_2 x = r\left(1 - \frac{x}{k}\right) \qquad \qquad \dots \qquad (2.11)$$

where $a_1 = r,$ $\quad k = -\left(\frac{a_1}{a_2}\right)$ $\qquad \qquad \dots \qquad (2.12)$

The growth equation (2.3) then becomes,

$$\frac{dx}{dt} = r x\left(1 - \frac{x}{k}\right) \qquad \qquad \dots \qquad (2.13)$$

which is the famous logistic model equation of population growth.

Carrying Capacity :

From equation (2.13) we see that

$$\frac{dx}{dt} = 0 \qquad \text{when } x = k.$$

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Thus $x = k$ is a steady-state or equilibrium state of the logistic equation (2.13). We also note that

$$\left.\begin{array}{ll} \dfrac{dx}{dt} > 0, & \text{for } x < k \\[3mm] \dfrac{dx}{dt} < 0, & \text{for } x > k \end{array}\right\} \qquad \ldots \quad (2.14)$$

The quantity k represents the carrying capacity of the environment of the species.

Example (2.3) : Solve the equation (2.13) i.e. the equation

$$\frac{dx}{dt} = r\,x\left(1 - \frac{x}{k}\right), \quad x(0) = x_0 \qquad \ldots \quad (2.13)$$

To solve we write the equation (2.13) in the form

$$\frac{dx}{x\left(1 - \dfrac{x}{k}\right)} = r\,d\,t$$

Rearrange the equation to show that the solution is given by

$$x(t) = \frac{x_0 k}{x_0 + (k - x_0)e^{-rt}} \qquad \ldots \quad (2\text{-}15)$$

The solution (2.15) shows that for $t \to \infty$, the population size approaches the carrying capacity k. It is easy to show that when the initial population x_0 is very small, the population initially appears to grow exponentially at a rate r.
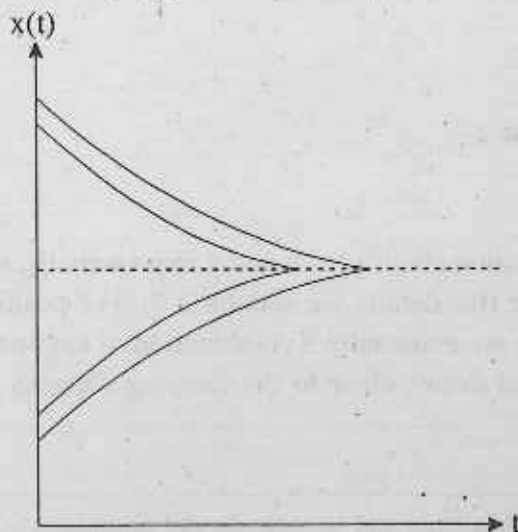

Fig. (2.4): Logistic growth curve

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Intra-species Competition

The competition among the individuals of a species for limited food, habitat and other resources compel an increase in the net population mortality under crowded conditions. Such effects are prominent when there are frequent encounters between individuals. The equation (2.13) can be written as

$$\frac{dx}{dt} = r\,x - \frac{r}{k}x^2 \qquad \qquad \text{...} \qquad (2.16)$$

The second term depicts a mortality proportional to the rate of paired encounters. The equation (2.13) is thus a modification of Malthus growth equation (2.4) by taking a term (the second term in the r.h.s of (2.16)) representing intra-species interaction which stops the exponential growth.

Behaviour near Equilibria

The logistic equation (2.13) has two equilibria, $x^* = 0$ and $x^* = k$. Near $x^* = 0$, x^2/k is small compared to x so that

$$\frac{dx}{dt} \approx r\,x \qquad \qquad \text{...} \qquad (2.17)$$

For $r > 0$, small perturbation about $x^* = 0$ grows exponentially; the equilibrium $x^* = 0$ is unstable. Close to $x^* = k$, we put $y = x - k$ in equation (2.13) to give us

$$\frac{dx}{dt} = -r\,y - \frac{r}{K}y^2$$

Since y is small, we have

$$\frac{dx}{dt} \approx -ry$$

For $r > 0$, small perturbation about $x^* = k$ decay exponentially, the equilibrium $x^* = k$ is asymptotically stable (for details see section 2.7). For positive r, solutions of the logistic equation (2.13) are essentially a combination of exponential growth, close to zero, and of exponential decay, close to the carrying capacity (see Fig. 2.4).

2.5 ❑ Allee Effect

A further extension of Malthus and logistic model equations is an assumption of the form

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$$g(x) = a_1 + a_2 x + a_3 x^2$$
$$\text{with } a_2 > 0 \text{ and } a_3 < 0 \tag{2.17}$$

When this condition is satisfied we obtain Allee effect, which represents a population that has a maximal intrinsic growth rate at intermediate density. This effect may stem from the difficulty of finding mate at very low density. The Fig. (2.5) below is an example of density dependent form of $g(x)$ that predicts the Allee effect. Its general characteristic can be summarized by the inequalities :

$$g'(x) > 0, \quad \text{for } x < \eta$$
$$g'(x) < 0, \quad \text{for } x > \eta \tag{2-18}$$

where η is the density for optimal reproduction.
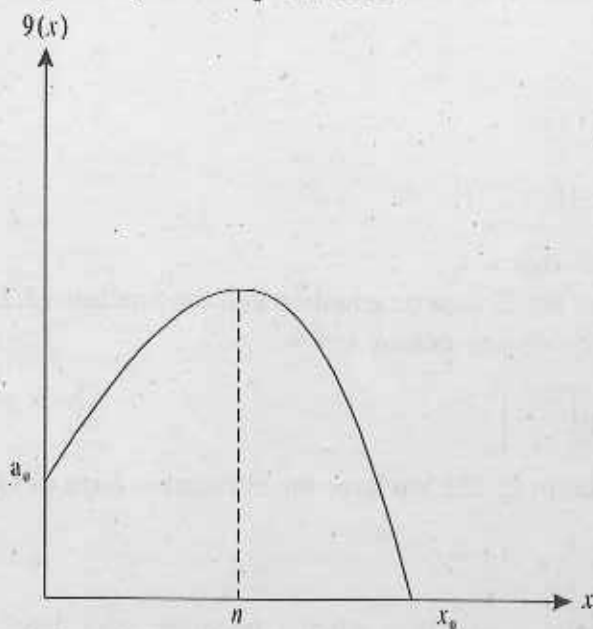
Fig. (2.5) : In the Allee effect the rate of reproduction is maximal at intermediate density

2.6 ❑ Gompertz Population Model

In the case of Malthus model the population grows exponentially and becomes ridiculously large. The exponential model finally becomes meaningless, since really the population never goes to infinity. In an attempt to construct a growth model more realistically we device the following Gompertz model : We assume a growth phenomena in which the growth coefficient is no longer constant, but vary with time t. Thus, in the case of exponential growth, we commence with the differential equation

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$$\frac{dx}{dt} = rx \qquad \qquad \cdots \qquad (2.19)$$

where the growth coefficient r is assumed to change with time according to the relation

$$\frac{dr}{dt} = -\alpha r \qquad \qquad \cdots \qquad (2.20a)$$

where α is a decaying coefficient of r and we assume $\alpha > 0$. With the initial condition $r(o) = r_0$, the solution of (2.20a) is

$$r = r_0 e^{-\alpha t} \qquad \qquad \cdots \qquad (2.20b)$$

So the main feature of Gompertz growth model is the inclusion of an exponentially decreasing growth coefficient. Substituting (2.20b) in (2.19), we have

$$\frac{dx}{dt} = r_0 e^{-\alpha t} x \qquad \qquad \cdots \qquad (2.21)$$

The solution of (2.21) is

$$x(t) = x_o \exp\left[\frac{r_0}{\alpha}\left(1 - e^{-\alpha t}\right)\right] \qquad \cdots \qquad (2.22)$$

with initial condition $x(o) = x_o$.

The equation (2.21) is the Gompertz equation and the function (2.22) is the Gompertz function. From (2.22) we see that as $t \rightarrow \infty$,

$$x \rightarrow x^{\pm} \quad x_o \exp\left[\frac{r_0}{\alpha}\right] \qquad \qquad \cdots \qquad (2.23)$$

Substituting this value in (2.22), we have the alternative form of Gompertz function :

$$x(t) = x^* \exp\left[-\frac{r_0}{\alpha} e^{-\alpha t}\right] \qquad \cdots \qquad (2.24)$$

The quantity x^* is the value of x when t becomes very large, that is, it is the asymptotic value of x. In this sense it is the carrying capacity. Again using (2.24) in (2.21), we have the alternative form of Gompertz equation as

$$\frac{dx}{dt} = -\alpha x \log \frac{x}{x^*} \qquad \qquad \cdots \qquad (2.25)$$

We note that the specific growth rate $\frac{1}{x}\frac{dx}{dt}$ is given by the difference of the logarithms of x^* and x.

A comparison is made of exponential, logistic and Gompertz growth curves in the Fig. (2.6) below.
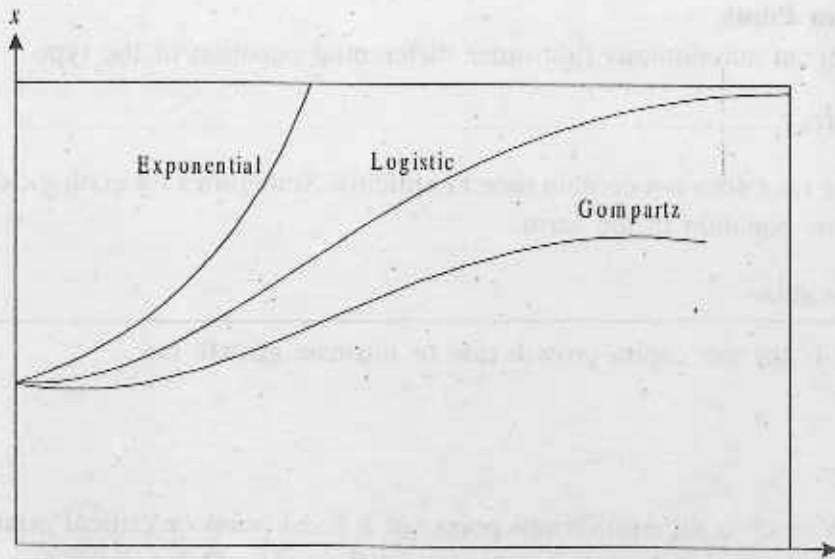
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Fig. (2.6) : Comparison of Exponential, logistic and Gompertz curves.

2.7 ❑ Model Equations : Qualitative Analysis

Having the dynamical equations for model system in our hand, our next problem is to solve these equations. There are two approaches to it. First, we can attempt to find out an analytical solution, that is, a formula relating the value of the state variable at a time t to its value at some initial time t = 0 (say). When analytical solution is available, it provides a complete characterization of the dynamics of the given system. However, except for the simplest models, analytical solutions appear to be impossible. In the other case, an explicit solution can be calculated numerically. A numerical solution of differential equation is more tricky than that of difference equation. Numerical solutions are much less useful than analytical solutions, being valid only for chosen values of the initial state and model parameters. However, they are very easy to compute, and for simple system it is possible to obtain considerable insight by 'numerical experiment'. For more complicated models numerical solution is typically the approach available. In reality, vast majority of investigations proves that it is impossible to obtain complete or near complete information about a dynamical system, either by analytic solution or by numerical experiment. For this reason, over the last century or so mathematicians have developed methods or techniques of determining the qualitative properties of the solutions of the dynamical equations and thus answering many questions of ecological interests, without explicitly solving the model equations concerned.

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Equilibrium Point:

We consider an autonomous first-order differential equation of the type

$$\frac{dx}{dt} = f(x) \qquad\qquad \cdots \qquad (2.26)$$

in which the r.h.s does not contain time t explicitly. Sometimes for ecological systems we write this equation in the form,

$$\frac{dx}{dt} = x\, g(x) \qquad\qquad \cdots \qquad (2.27)$$

where $g(x)$ is the per capita growth rate or intrinsic growth rate.

Definition :

The point $x = x^*$ is an equilibrium point (or a fixed point or critical point or rest point or steady-state point) of the model equation (2.26) if $f(x^*) = 0$. If $x(t)$ is a solution of the differential equation (2.26) that tends to a limit as $t \to \infty$, then it is not difficult to show that its limiting value must be equilibrium point. In fact, for a first-order differential equation every solution must either tend to an equilibrium point as $t \to \infty$ or be unbounded. However, not every equilibrium is a limit of non-constant solutions. For example, the only solution of the logistic equation that tends to zero as $t \to \infty$ is the identically zero solution.

Linearization :

In order to describe the behaviour of solution near equilibrium we introduce the process of linearization. If x^* be an equilibrium point of the equation (2.26) so that $f(x^*) = 0$, we make the change of variable $u(t) = x(t) - x^*$ representing the deviation of the solution from the equilibrium value. Putting this in equation (2.26) we have

$$\frac{du}{dt} = f(x^* + u(t)) + f(x^*)u(t) + \frac{f'(c)u(t^2)}{2}$$

where $x^* < c < x^* + u(t)$.

Since $f(x^*) = 0$, we have $\qquad \dfrac{du}{dt} = f'(x^*)u(t) + h(u)$

where $h(u) = \dfrac{f'(c)u^2(t)}{2}$

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For u (t) very small we can neglect h(u) so that we have the linear equation,

$$\frac{du}{dt} = f'(x^*)u \qquad \qquad \qquad \dots \qquad (2.28)$$

The importance of linearization lies in the fact that the behaviour of its solution is easy to analyse and this behaviour also describes the behaviour of the solution of the original equation (2.26) near equilibrium. We have, infact, the theorem :

Theorem 2.1 :

If all solutions of the linearization (2.28) at equilibrium x^* tends to zero as $t \to \infty$, then all solutions of (2.26) with the initial point $x(o)$ sufficiently close to x^*, tends to the equilibrium point x^* as $t \to \infty$.

Stability :

The process of linearization plays an important role in the study of the stability of the equilibrium point or state. For this, let us first give a formal definition of stability.

Definition :

An equilibrium point x^* is Lyapunov stable if for any arbitrary small $\varepsilon > 0$, there exists a $\delta > 0$ (depending on ε) such that, for all initial condition $x(o) = x_0$ satisfying $|x_0 - x^*| < \delta$, we have $|x(t) - x^*| < \varepsilon$ for all $t > 0$. In other words, an equilibrium point is stable if starting close (enough) to equilibrium guarantees that you will stay close to equilibrium. An equilibrium point x^* is asymptotically stable if it is stable and if in addition $|x_0 - x^*| < \delta$ implies $\lim_{t \to \infty} x(t) = x^*$

Remark :

In biological applications, we will ordinarily require asymptotic stability rather than stability. This is because asymptotic stability can be determined form the linearization, while stability cannot and again this is because asymptotic stable equilibrium is not disturbed greatly by a perturbation of the differential equation. In term of asymptotic stability we may restate the theorem (2.1) as follows :

Theorem 2.2 :

An equilibrium point x^* of (2.26) is asymptotically stable, if $f(x^*) < 0$ and unstable if $f(x^*) > 0$.

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Exercises

(1) Investigate the asymptotic stability of the equilibrium points of the following model equations.

    (i) $\dfrac{dx}{dt} = r\, x \left(1 - \dfrac{x}{k}\right)$ [Logistic model]

    (ii) $\dfrac{dx}{dt} = -r\, x \log \dfrac{x}{k}$ [Gompertz model]

    (iii) $\dfrac{dx}{dt} = \dfrac{r\, x\,(k - x)}{k + a\, x}$ [Smith model]

(2) Show that if $r < 0$, $k < 0$, every solution of the logistic equation with $x(o) \geq 0$ approaches zero as $t \to \infty$.

(3) A population is governed by the equation

$$\frac{dx}{dt} = x\,(e^{3-x} - 1)$$

Find all equilibria and determine their stability.

(4) Discuss the model

$$\frac{dx}{dt} = r\, x \left(1 - \frac{x}{k}\right)\left(\frac{x}{k_o} - 1\right)$$

where $0 < k_o < k$. Find all limits of solutions with $x(o) > 0$ as $t \to \infty$ and find the set of initial values corresponding to each limit.

(5) Show that for every choice of the constant c, the function

$$x = \frac{k}{1 + c\, e^{-rt}}$$

is a solution of the logistic differential equation.

(6) Consider the logistic equation

$$\frac{dx}{dt} = r(t)\left(1 - \frac{x}{k}\right), \qquad x(o) = x_o$$

with time—dependent intrinsic growth rate $r(t)$. Show that the solution is given by

$$x(t) = \frac{k x_o}{x_o + (k - x_o)\, e^{-\int_0^t r(s)\,ds}}$$

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2.8 ❑ Harvest Models :

We wish to study the effect on a population model of the removal of members of the population at a specified rate. If a population modeled by the differential equation

$$\frac{dx}{dt} = f(x) \qquad \cdots \qquad (2.29)$$

is subjected to a harvest at a rate h(t) member per unit time for some given function h(t), then the harvested population is modeled by the differential equation,

$$\frac{dx}{dt} = f(x) - h(t) \qquad \cdots \qquad (2.30)$$

If the numbers are removed at a constant rate H (constant) per unit time, then the model equation is

$$\frac{dx}{dt} = f(x) - H \qquad \cdots \qquad (2.31)$$

Such type of harvesting is called constant rate or constant yield harvesting. It arises when a quota is specified (for example, through permit as in deer hunting seasons in many states or by agreement as sometimes in whaling). If the population is governed by logistic equation, then the harvest model equation is,

$$\frac{dx}{dt} = r\, x\left(1 - \frac{x}{k}\right) - H \qquad \cdots \qquad (2.32)$$

The equilibrium points are given by

$$r\, x\left(1 - \frac{x}{k}\right) - H = 0 \text{ or } x^2 - kx + \frac{kH}{r} = 0$$

$$\text{or } x_1 = \frac{1}{2}\left\{ k - \sqrt{k^2 - \frac{4Hk}{r}} \right\} \text{ and } x_2 = \frac{1}{2}\left\{ k + \sqrt{k^2 - \frac{4Hk}{r}} \right\} \dots \ (2.33)$$

provided $k^2 - \frac{4kH}{r} \geq 0$ or $h \leq \frac{rk}{4}$. If $H > \frac{rk}{4}$ both roots are complex, $x'(t) < 0$ for all x, and every solution crashes, hitting zero in finite time. If a solution reaches zero in finite time, we consider system to have collapsed. If $0 \leq H < \frac{rk}{4}$, there are two equilibria : x_1 which increases from 0 to k/2 as H increases from 0 to rk/H and x_2, which decreases from k to k/2 as H increases. The stability of an equilibrium x^* of $\dot{x} = F(x) - H$ requires $F^1(x^*) < 0$, which for logistic model means $x^* > k/2$. Thus x_1 is always unstable and x_2 is always asymptotically stable. When H increases to the critical value $H_c = rk/4$, there is a discontinuity in the behaviour of the system - the two equilibria coalesce and annihilate each other. For $H < H_c$ the population size

tends to an equilibrium size that approaches k/2 as $H \to H_c$ (provided the initial population size is at least x_1), but for $H > H_c$ the population size reaches zero in finite time for all initial populations sizes (see Fig. (2.8a) below). Such a discontinuity is called a (mathematical) <u>Catastrope</u>; the biological implications are catastropic to species being modeled.

For a general model $x' = f(x) - H$ equilibria are given by $f(x) - H = 0$, that is, by finding values x^* of x for which the growth curve $y = f(x)$ and the harvest curve $y = H$ (a horizontal line) intersect. An equilibrium x^* is asymptotically stable if $(f(x) - H)'|_{x=x^*} = f'(x^*) < 0$, that is, if at such an intersection the growth curve crosses the harvest curve from above to below as x in increases (see fig. (2.8b)). From fig (2.8b) it is clear that if $H > \max f(x)$ there is no equilibrium, and the critical harvest rate H_c at which two equilibria coalesce and disappear is max $f(x)$.

There are other models of harvesting for example, the harvest rate $h(t)$ may be a linear function of population size : $h(t) = Ex$ and in that case it is known as constant effort harvesting. Harvesting plays an important role in fishery and forestry and has economic and commercial importances.

2.9 ❏ Summary

(i) We have first stated basic biological and mathematical postulates necessary for the development for the continuous-time models of populations,

(ii) We have set up a general model equation for single-species populations. We have studied some basic single-species population growth models, namely Malthus growth model, Logistic growth model, Allee effect, Gompertz growth model and Harvest model etc.

(iii) For the qualitative analysis of the model equations we have discussed a autonomous first order differential equations, its equilirium (or fixed) points and criteria of local stability of equilibrium points.

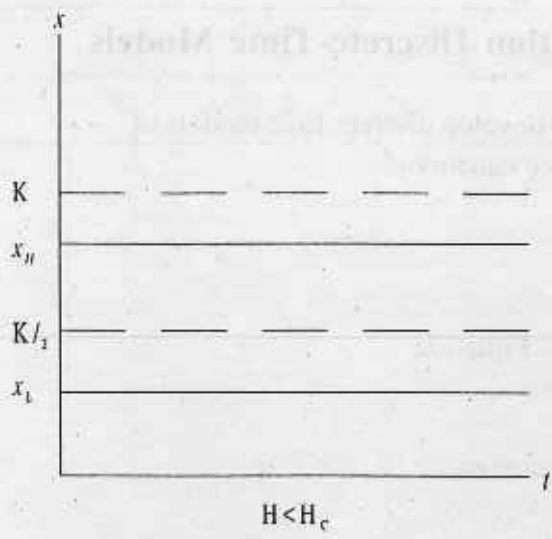(iv) As illustrative examples, we have discussed some problems related to the model equations.
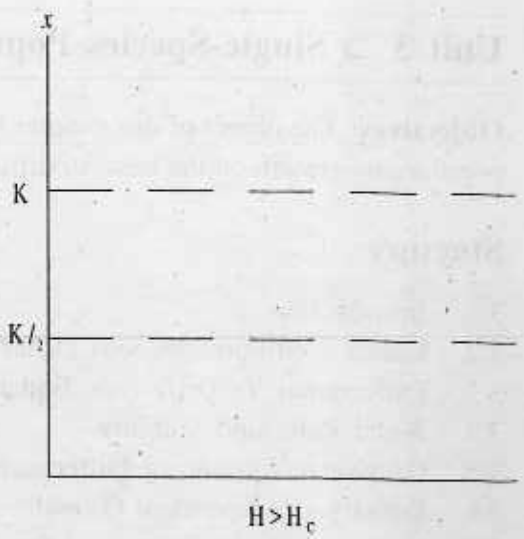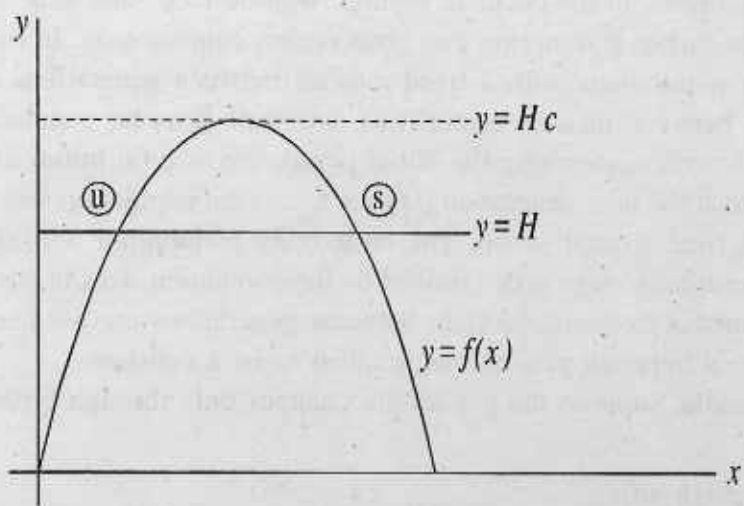
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Fig. (2.8a)

Fig. (2.8b)

FIGURE : 2.8b Intersections of the growth curve with the line of constant yield

Unit 3 ❑ Single-Species Population Discrete-Time Models

Objectives: The object of this chapter is to develop discrete-time models of populations growth on the basis of difference equations.

Stucture

3.1 ❑ Introduction

For many organisms, births occur in regular, well-defined 'breeding seasons'. This contradicts our earlier assumption that birth occurs continuously. In this chapter we shall consider populations with a fixed interval between generations or possibly a fixed interval between measurement. Thus, we shall describe population size by a sequence $\{x_n\}$, with x_0 denoting the initial population size (at initial time t_0), x_1 the population size at the next generation (at time t_1), x_2 the population size at the second generation (at time t_2) and so on. The underlying assumption will always be that population size at each stage is determined by the population sizes in past generations; but that intermediate population sizes between generations are not needed. Usually the time interval between generations is taken to be a constant.

For example, suppose the population changes only through births and deaths, so that

$$x_{n+1} - x_n = (b - d)x_n \qquad \qquad \cdots \qquad (3.1)$$

where bx_n is the number of births and dx_n is the number of deaths in the time-interval (t_n, t_{n+1}); b and d (assumed constants) are the birth and death rates respectively. From (3.1) we thus have

$$x_{n+1} = (1 + b - d)x_n = rx_n, x(t_o) = x_0 \qquad \qquad \cdots \qquad (3.2)$$

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which is a first-order linear homogeneous difference equation. The growth rate $r = 1 + b - d$ is a parameter of the equation. In general, we can write a first-order difference equation as

$$x_{n+1} = f(x_n), \text{ with } x(t_o) = x_o \qquad \qquad (3.3)$$

In such an equation the new value of x is determined completely by the previous value. In higher-order difference equation we would require information about several previous values to determine the current value. For example, the Kepler recursion relation

$$x_{n+1} = x_n + x_{n-1} \qquad \qquad (3.4)$$

is a second-order difference equation as it requires two previous values x_n and x_{n-1} to find out the exact value of x_{n+1}. Such type of difference equation appears in the case of over lapping generations as in the case of Snow Geese in Baffin Island. The function f in (3.3) is called a map or iteration. A map f is linear if f is of the form $f(x) = ax$, for some constant a Otherwise the equation (3.3) is non-linear (or density — dependent in biology).

Example (3.1) : Logistic Difference Equation

Let x_n be the size of a population of a certain species at time t_n. Let r be the rate of growth of population from generation to generation. Then from (3.2) we have

$$x_{n+1} = rx_n, \qquad r > 0 \qquad \qquad (3.2)$$

with initial population $x(to) = x_0$.
Then by simple iteration we find that

$$x_n = r^n x_o \qquad \qquad (3.5)$$

is the solution of (3.2). If $r > 1$, the population increases without any bound to infinity. If $r = 1$, $x_n = x_0$, the population stays constant forever. If $r < 1, \lim_{n \to \infty} x_n = 0$, the populations eventually becomes extinct.

We observe that for most species the above model is not realistic, the population increases until it reaches a threshold. Then limited resources would force the members of the species to fight and compete with others. This competition is proportional to the number of squabbles x^2_n among them. A more realistic model is, therefore,

$$x_{n+1} = rx_n - bx^2_n \qquad \qquad (3.6)$$

where b is the proportionality constant of interaction among the members of the species. Writing $y_n = \frac{b}{r}x_n$, we hvae

$$y_{n=1} = ry_n(1 - y_n) \qquad \qquad (3.7)$$

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The equation (3.7) is the discrete logistic equation and the map $f(y) = ry(1 - y)$ is called the logistic map. It is a reasonably good model in which generations do not overlap. The logistic equation (3.7) is very important, by varying the value of the parameter r, this simple and innocent looking equation exhibits somewhat complex behaviours.

3.2 ◻ Linear Non-homogeneous Difference Equation

Consider the first-order linear non-homogeneous difference equation

$$x_{n+1} = a x_n + b, \qquad x(t_o) = x_o \qquad \qquad \dots \qquad (3.8)$$

The equation can be solved by successive iterations,

$$x_1 = ax_o + b$$
$$x_2 = ax_1 + b$$
$$= a(ax_o b) + b = a^2 x_o + ab + b$$

By induction, we can show that

$$x_3 = ax_2 + b = a(a^2 x_o + ab + b) + b$$
$$= a^3 x_o + a^2 b + ab + b$$

By induction, we can show that

$$x_n = a^n x_o + \sum_{j=o}^{n-1} a^{n-j-1} b$$

$$= a^n x_o + b\left(\frac{a^n - 1}{a - 1}\right), \text{ if } a \neq 1 \qquad \qquad \dots \qquad (3.9)$$

The above formula (3.9) is an important result having many applications. As an application let us consider the following problem.

Example (3.2) :

A drug is administered every six hours. Let $D(n)$ be the amount of the drug in the blood system at the nth interval. The body eliminates a certain fraction p of the drug during each time interval. If the initial blood administered is D_o, find $D(n)$ and $\lim_{n\to\infty} D(n)$.

Solution :

The first step is to write down the difference equation that relates the amount of drug in the patient blood system $D(n+1)$ at the time interval $(n + 1)$ with $D(n)$. The

resulting equation is

$$D(n) = (1-p) D(n) + D_o,$$

Using the formula (3.9). We have

$$D(n) = (1-p)^n D_o + D_o \left[\frac{1-(1-p)^n}{p} \right]$$

$$= \left[D_o - \frac{D_o}{p} \right] (1-p)^n + \frac{D_o}{p} .$$

Thus $\lim_{n \to \infty} D(n) = \dfrac{D_o}{p}$

3.3 ❑ Differential Vs Difference Equation

Consider the differential equation

$$\frac{dx}{dt} = g(x(t)), \qquad x(t_o) = x_o \qquad \qquad \dots \quad (3.10)$$

For many differential equations such as (3.10), it may not be possible to find a 'closed form' of solution. In that case, we resort to numerical method to approximate the solution of (3.10). In Euler algorithm, for example, we start with a discrete set of points $(t_o, t_1, .. t_n)$ with $h = t_{n+1} - t_n$ as the step size. Then for $t_n < t < t_{n+1}$ we approximate $x(t)$ by $x(t_n)$ and dx/dt by

$$\frac{dx}{dt} = \frac{x(t_{n+1}) - x(t_n)}{h}$$

The equation (3.10) then leads to the equation

$$x(t_{n+1}) = x(t_n) + h \, g(x(t_n))$$

or in simple form

$$x_{n+1} = x_n + h \, g(x_n) \qquad \qquad \dots \quad (3.11)$$

where $x_n = x(t_n)$

The equation (3.11) is of the form (3.3) with

$$f(x) = x + h \, g(x) \qquad \qquad \dots \quad (3.12)$$

Given initial data $x(t_0) = x_0$, we may use the equation (3.11) to generate the values $x(t_1), x(t_2).....x(t_n)$. These values approximate the solution of the differential equation (3.10) at the grid points $t_1, t_2.........t_n$ provided that h is sufficiently small.

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3.4 ◻ Fixed (or Equilibrium) Point and Stability

When the map f is linear it is possible to obtain 'closed form' of solution of the first-order difference equation (3.3). However, the situation changes drastically when the map f is non-linear. Since we can not solve all the non-linear difference equations, it is important to develop qualitative or graphical method of finding the behaviour of the solutions. Of particular importance is the finding the fixed points or equilibrium points or steady-states.

Definition : A point x^* is said to be a fixed point or an equilibrium point of the difference equation $x_{n+1} = f(x_n)$ if $f(x^*) = x^*$.

One of the objectives in the theory of dynamical system is the study of the behaviour of the system, that is, the behaviour of solutions of a difference equation near the fixed or equilibrium point. Such a program of investigation is called stability theory. Let us now explain the concept of stability of a fixed point.

Definition : Let x^* be a fixed (or equilibrium) point of the difference equation

$$x_{n+1} = f(x_n), \qquad x(t_o) = x_o.$$

Then

(i) x^* is said to be stable if for any $\varepsilon > 0$ there exists $\delta > 0$ such that $| x_0 - x^* | < \delta$ implies $| x_n - x^* | < \varepsilon$ for all positive integers n and for all x in the domain of definition. Otherwise the point x^* will be unstable.

(ii) x^* is said to be attracting if there exists $\eta > 0$ such that $| x_0 - x^* | < \eta$ implies
$$\lim_{n \to \infty} x_n = x$$

(iii) x^* is asymptotically stable (sometimes called a sink) if it is both stable and attractive. If in (ii) $\eta = \infty$, then x^* is said to be globally asymptotic stable.
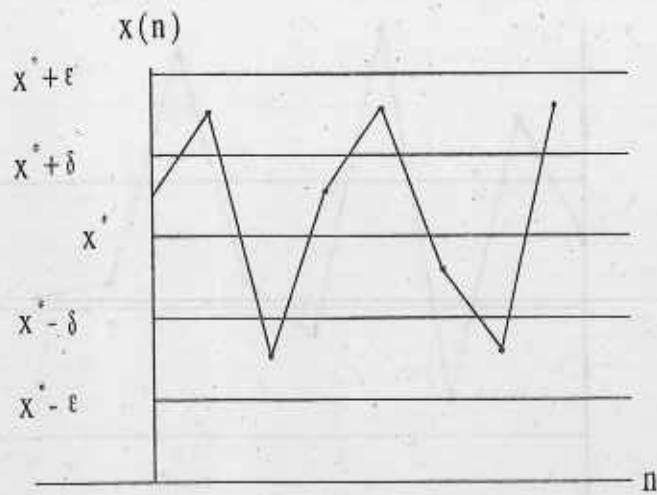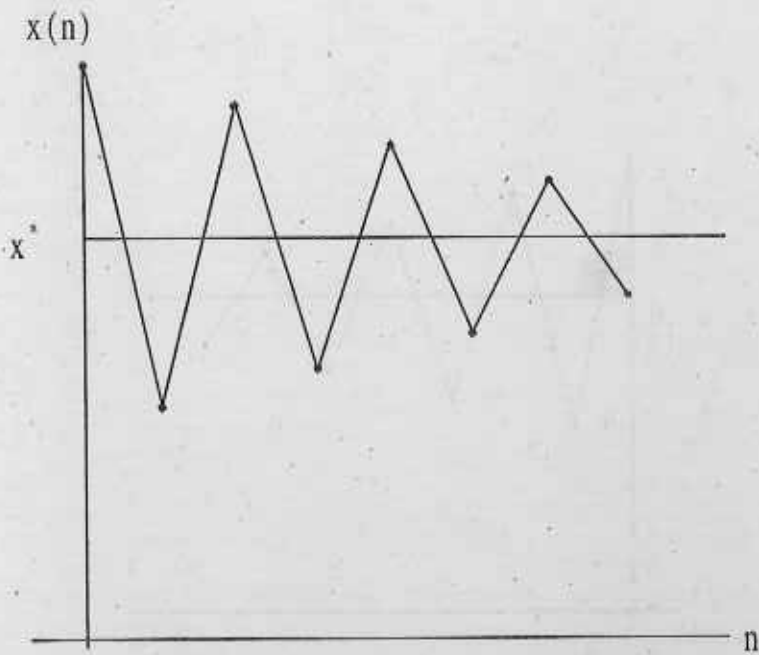
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Fig. 3.1 : Stable fixed point x*

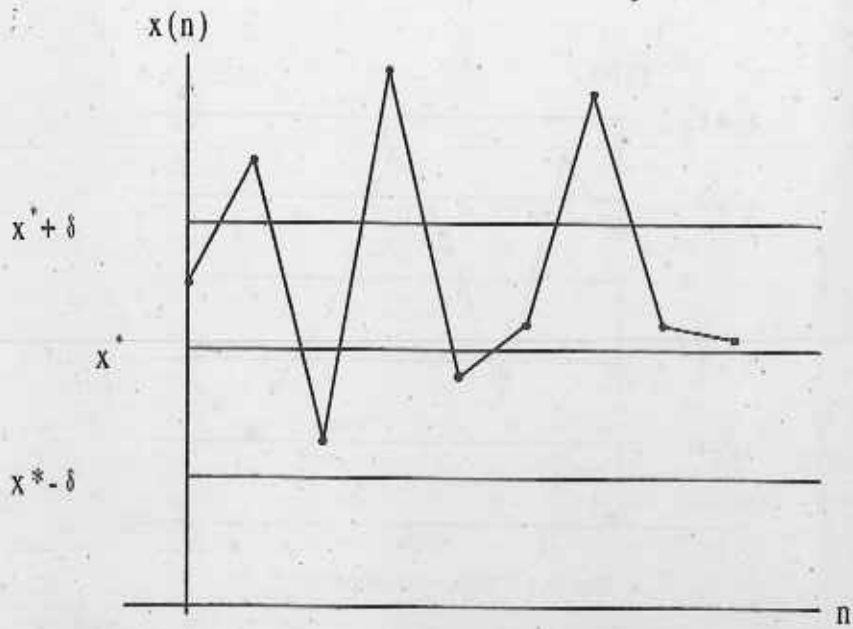Fig. 3.2 : Unstable fixed point

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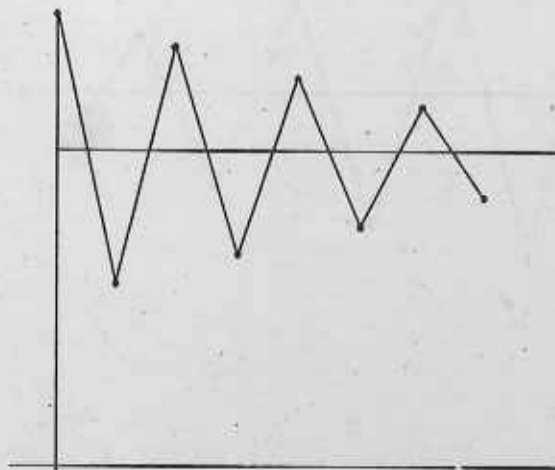Fig. 3.3 : Attractive, but unstable fixed point x

Fig. 3.4 : Asymptotically stable fixed point x

3.5 ❑ Graphical Solution of Difference Equation

In example (3.2) we have explained the method of solving a first-order linear difference equation. Let us now describe a graphical method of solving difference equation of the form $x_{n+1} = f(x_n)$ by a graphical method; called "Cobweb diagram". It is also one of the effective graphical iteration methods to determine the stability of fixed point.

Cobweb Diagram :

We start with an initial point x_0. Then we move vertically until we hit the graph $y = f(x)$ at the point $(x_0, f(x_0))$. We then travel horizontally to meet the line $y = x$ at the point $(f(x_0), f(x_0))$. This determines $f(x_0) = x_1$ on the x-axis. To find out the next iterated value $x_2 = f(x_1) = f(f(x_0)) = f^2(x_0)$, we move again vertically until we strike the graph $y = f(x)$ at the point $(f(x_0), f^2(x_0))$; and then move horizontally to meet the line $y = x$ at the point $(f^2(x_0), f^2(x_0))$. This determines $x_2 = f^2(x_0)$ on the x-axis. Proceeding in this way, we can evaluate all of the iterated values $\{x_1, x_2....x_n...\}$. Let us explain this method with a simple example and show how it can be used to test the stability of a fixed point. Note that fixed point is the point of intersection of the curve $y = f(x)$ and the line $y = x$.
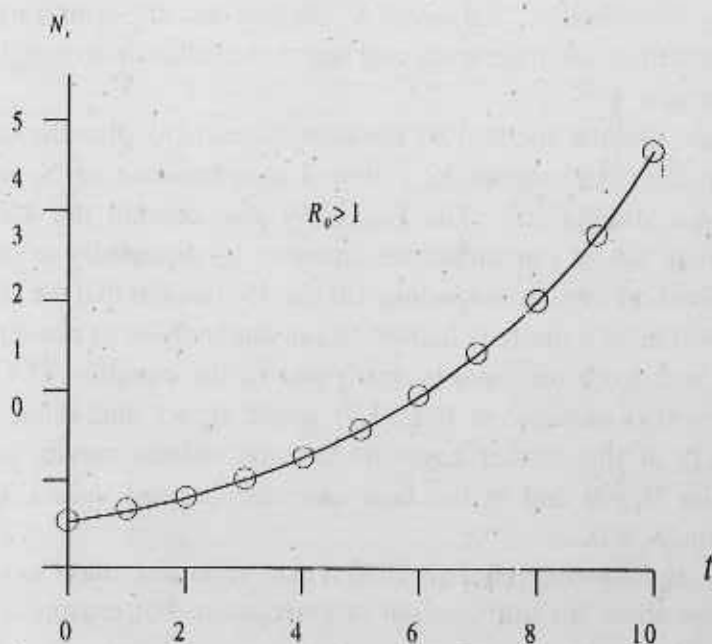

Fig. : 3.5 Geometric growth.

3.6 ❑ Density — Independent Growth

Let N_t be the size of the population in year (or generation) t. We will census the population each year at the same stage of the life cycle. Imagine that each individual leaves Ro offsprings before dying. We shall call Ro the net reproductive rate. It follows that

$$N_{t+1} = R_o N_t \qquad \qquad \text{...} \qquad (3.13)$$

The equation (3.13) is linear, first-order, constant - coefficient difference equation. The solution is given by (see 3.5)

$$N_t = R^t_o N_o \qquad \qquad \text{...} \qquad (3.14)$$

The solution is thus one of geometric growth or decay. If Ro > 1, each individual leaves more than one descendant, and the population grows geometrically (see Fig. 3.5).

If $0 < R_o < 1$ the individuals leave, on average, fewer than one descendant, and the population declines geometrically (see Fig. 3.6). These figures resemble those for exponential growth and decay. Individuals cannot leave a negative number of offspring. However, nothing can prevent us from pondering this possibility mathematically. For $-1 < R_o < 0$, we get decaying oscillations (Fig. 3.7). For $R_o < -1$, we get growing oscillation (Fig. 3.8). Figures (3.5) to (3.8) suggest that the solutions approach the origin if Ro is less than 1 in magnitude and that these solution diverge if Ro is greater than 1 in magnitude.

Let us now use the method of cobweb diagram to plot the solution of the equation (3.13). Fig. (3.9) shows N_{t+1} plotted as a function of N_t for $R_o > 1$. The curve is clearly a straight line. The Fig. (3.9) also contain the 45° dashed line, $N_{t+1} = N_t$. We may iterate our difference equation by repeatedly (a) moving up (or down) to the curve and then (b) bounching off the 45° line (so that we reset $N_{t+1} = N_t$). This approach will be of extremely helpful late in our analysis of non-linear difference equation. Zero is a fixed (or equilibrium) point of the equation (3.13). The trivial equilibrium $N_t = 0$ is unstable in Fig. (3.9) where $R_o > 1$ and stable in Fig. (3.10) where $0 < R_o < 1$; in the former case the iterated values moves away from the equilibrium point $N_t = 0$ and in the later case the iterated values approaches the equilibrium point $N_t = 0$.

A linear, density-independent difference equation may have a non-zero equilibrium if we allow for immigration or emigration. For example, the difference equation

$$N_{t+1} = \frac{3}{4} N_t + 10 \qquad \qquad \text{...} \qquad (3.15)$$

has an equilibrium $N^* = 40$.

We now introduce a new variable $x_t = N_t - 40$

Then the equation (3.15) becomes $x_{t+1} = \frac{3}{4} x_t$

So that $x_t = x_o \left(\frac{3}{4} \right)^t$

or, $N_t = 40 + (N_o - 40) \left(\frac{3}{4} \right)^t$ ... (3.16)

The small perturbation about the equilibrium decay; the equilibrium is asymptotically stable. This stability also comes out in Cobweb analysis [see Fig.(3.9) (3.12)].
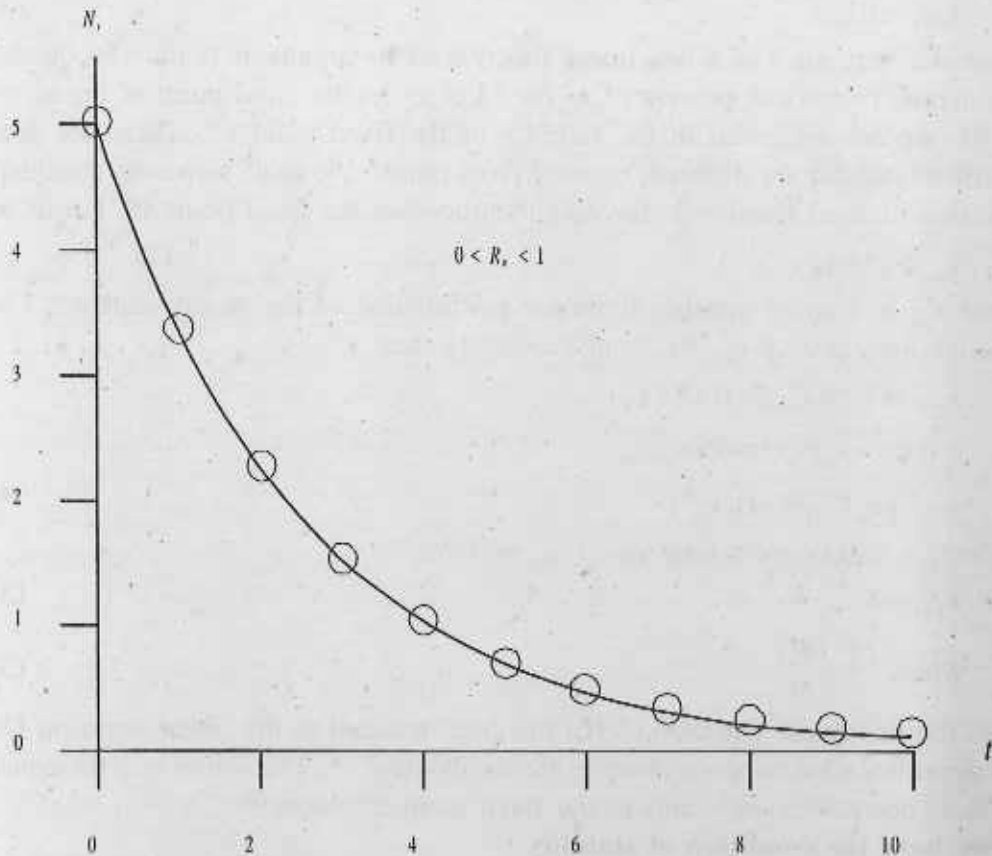

Fig. : 3.6 Geometric decay.

3.7 ❑ Steady-state : Criteria of Stability

The stability is of fundamental importance in biology. When a steady-state (or an equilibrium state) is unstable, great changes may about to happen : a population may crash, homeostasis may be disrupted or else the balance in number of competing groups may shift in favour of a few. Thus, even if an exact analytical solution is not easy to come by, qualitative information about whether change is imminent is of potential importance.

Let us now find out the criteria of stability of a fixed equilibrium point or a steady-state. We consider the non-linear first-order difference equation of the form (3.3) :

$$x_{n+1} = f(x_n) \qquad \qquad \ldots \qquad (3.16)$$

where the function f is a non-linear function of its argument (f may be quadratic, exponential reciprocal, powers of x_n etc.) Let x^* be the fixed point of the equation (3.16). We are interested in the stability of the fixed point x^*. There are general criteria of stability for different types of fixed points. We shall, however, consider the condition of local stability in the neighbourhood of the fixed point x^*. Let us write

$$x_n = x^* + x_n' \qquad \qquad \ldots \qquad (3.17)$$

where x'_n is a small quantity termed a perturbation of the steady state x^*. Let us linearise the equation (3.16) about the steady state x^*

$$x_{n+1} = x^* + x'_{n+1} = f(x^* + x'_n)$$

$$= f(x^*) + x'_n f'(x^*) + O(x_n'^2)$$

$$= x^* + x'_n f'(x^*) + O(x_n'^2)$$

Neglecting higher-order term $O(x_n'^2)$, we have

$$x'_{n+1} = a\, x'_n \qquad \qquad \ldots \qquad (3.18)$$

$$\text{where} \quad a = \left.\frac{df}{dx}\right|_{x=x^*} \qquad \qquad \ldots \qquad (3.19)$$

Thus, the non-linear equation (3.16) has been reduced to the linear equation (3.18) that describes what happens close to the steady-state x^*. The solution of the equation (3.18) is decreasing and tends to the fixed point x^* wherever $|a| < 1$.

So we have the condition of stability :

The fixed point or steady-state x^* is asymptotically stable if and only if

$$|f'(x^*)| < 1 \qquad \qquad \ldots \qquad (3.20)$$

Note that whenever $|f'(x^*)| = 1$, then $(x'_{n+1} - x'_n)$ implying a constant deviation is unable to decrease x'_n to reach the fixed point. More formally, we have the theorem.

Theorem :

Let x* be a fixed point of the difference equation (3.16). Suppose that f(x) is continuously differentiable and $|f'(x^*)| \neq 1$. Then, the fixed point x* is asymptotically stable if $|f'(x^*)| < 1$ and unstable if $|f'(x^*)| > 1$.

Example (3.3) :

The growth of a population satisfies the following difference equation

$$x_{n+1} = \frac{kx_n}{b + x_n}, \quad b, k > 0,$$

Find the steady-state (if any). If so, is that stable ?

Solution : Let x* be the steady-state value of x_n.

Then $\quad x^* = x_{n+1} = x_n$

So that $\quad x^* = \dfrac{kx^*}{b + x^*}, \quad$ or $\quad x^* = 0, k - b$

The steady-state makes sense only if $x^* > 0$ i.e., if $k > b$, since negative population is biologically meaningless. To study the stability, we consider the equation

$$x'_{n+1} = a\, x'_n$$

where $\quad a = \dfrac{df}{dx}\Big|_{x^*} = \dfrac{d}{dx}\left(\dfrac{kx}{b+x}\right)\Big|_{x^*=k-b} = \dfrac{b}{k}$

So the steady-state $x^* = k - b$ is stable if $\left|\dfrac{b}{k}\right| < 1$. Since both k and b are positive, the condition of stability reduces to $k > b$. The study of stability of $x^* = 0$ is left as an exercise.

Excercise :

(1) Find the non-negative equilibrium of a population governed by

$$x_{n+1} = \frac{2x_n^2}{x_n^2 + 2}$$

and check the stability.

(2) A population is governed by the equation

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$$x_{n+1} = x_n c^{3-x_n}$$

show that all equilibria are unstable.

Example (3.4) :

Logistic Difference Equation Revisited

Consider the following equation

$$x_{n+1} = r x_n (1 - x_n).$$

Investigate the stability of the steady-state.

Solution : Let x^* be the steady-state value of x. Then

Then $\qquad x^* = r x^* (1 - x^*)$

So that $\qquad x_1^* = 0, \qquad x_2^* = 1 - \dfrac{1}{r}.$

Perturbation about x_2^* satisfies.

$$x'_{n+1} = a \, x'_n$$

where $\quad a = \dfrac{df}{dx}\Big|_{x_2^*} = r(1 - 2x)\Big|_{x_2^* = 1 - \frac{1}{r}} = 2 - r$

Thus, $x_2^* = 1 - \dfrac{1}{r}$ is stable whenever $|a| < 1$ which implies $|2 - r| < 1$ or $1 < r < 3$. Then

the stability of the steady-state $x^* = 1 - \dfrac{1}{r}$ is conditioned on a parameter r. If r is

greater or small than certain critical values (here 3 and 1); the steady-state $x_2^* = 1 - \dfrac{1}{r}$
is not stable. Such critical parameter values, often called <u>bifurcation values</u>; are points of demarcation for abrupt behaviour of the equation of the system it models. There may be multitude of such transitions, so that as increasing values of the parameter are used, one encounters different behaviours. In fact, if we increase the value of r beyond 3 the equation will exhibit the complex behaviour of period doubling and chaos. This is, however, beyond our discussion.

Example (3.5) :

Density-Dependent Growth

An assumption that growth rate depends on the density of the population leads us to consider models of the following form :
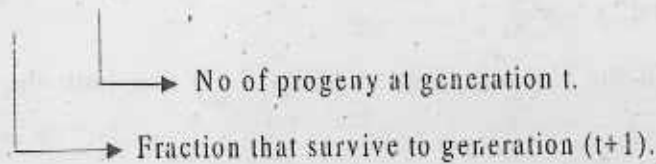
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$$N_{t+1} = f(N_t)$$

where $f(N_t)$ is some non-linear function of the population density. Quite often, single-species populations (insects, for example) are described by such equation. We consider the following model.

Let the single-species population satisfies the equation

$$N_{t+1} = \left(\frac{\lambda}{\alpha}\right) N_t^{1-b}$$

where λ is the reproductive rate, assumed to be greater than 1. The equation is best understood in the form

$$N_{t+1} = \left(\frac{1}{\alpha} N_t^{-b}\right) (\lambda \ N_t)$$

$\longrightarrow$ No of progeny at generation t.

$\longrightarrow$ Fraction that survive to generation (t+1).

where α, b, $\lambda > 0$. Since the fraction of survivors can not exceed 1, we see that the population must exceed a certain size N_c for this model to be biologically applicable. The steady-state population size is given by

$$N^* = \frac{\lambda}{\alpha} N^{*1-b} \quad \text{or} \quad N^* = \left(\frac{\lambda}{\alpha}\right)^{\frac{1}{b}}$$

We write $f(N) = \left(\frac{\lambda}{\alpha}\right) N^{1-b}$ then $\left.\frac{df}{dN}\right|_{N=N^*} = 1-b$ so the stability of the steady-state

$N^* = \left(\frac{\lambda}{\alpha}\right)^{\frac{1}{b}}$ requires $|1-b| < 1$ or $0 < b < 2$.

We note that $b = 0$ is a situation in which the survivorship is not density dependent; then the population grows at the rate $\left(\frac{\lambda}{\alpha}\right)$. Thus, lower-bound for stabilizing values of b makes sense.

Excercise :
(3) : Investigate the stability of the steady-state of the model equation

$$N_{t+1} = N_t \exp\left\{r\left(1 - \frac{N_t}{k}\right)\right\}$$

(4) : Consider the tent map f :

$$f(x) = \begin{cases} 2x \text{ for } 0 \le x \le \frac{1}{2} \\ 2(1-x), \text{ for } \frac{1}{2} x \le 1 \end{cases}$$

Write down the difference equation corresponding to the map f defined above. Find out the fixed points, draw the Cobweb diagram and investigate the stability.
The fixed points are obtained by the equations

$$2x = x \quad \text{and} \quad 2(1-x) = x$$

so the fixed points are

$$x^*{}_1 = 0 \quad \text{and} \quad x^*{}_2 = \frac{2}{3}$$

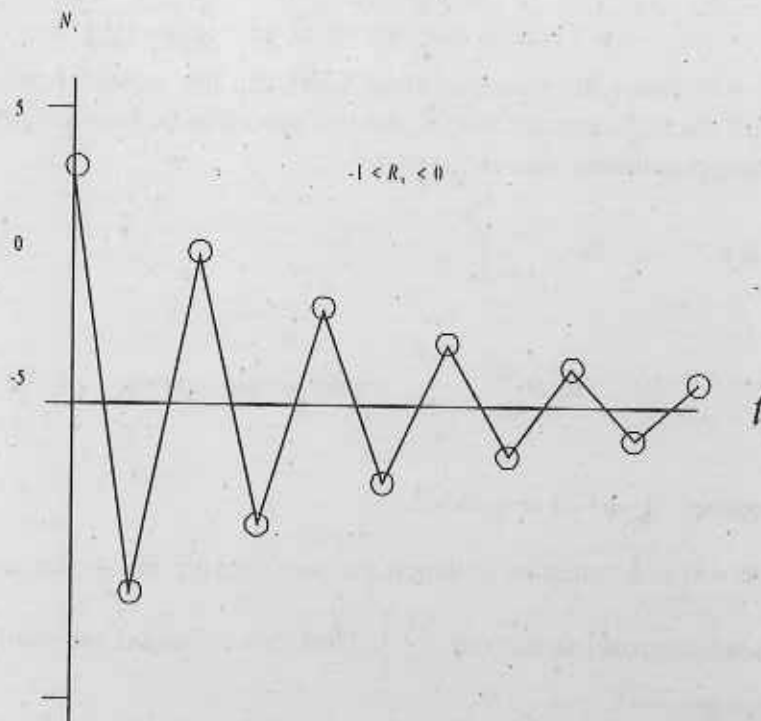We observe from the Cobweb diagram (Fig. 3.12) that both the fixed points are unstable.

Fig. : 3.7 Decay oscillations.

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3.8 ☐ Second-Order Difference Equation and Application

Let us now consider a second-order difference equation of the form

$$x_{n+1} = f(x_n, x_{n-1}) \qquad \qquad \cdots \qquad (3.20)$$

where the function f is now a function of two immediate preceding values x_n and x_{n-1}. The function f may be linear or non-linear. We shall, however, be confined to linear functions only. For simplicity, we shall consider a linear, homogeneous second-order difference equation of the form :

$$a_0 x_{n+1} + a_1 x_n + a_2 x_{n-1} = 0 \qquad \qquad \cdots \qquad (3.21)$$

To solve the equation (3.21) let us take a solution of the form : $x_n = C\lambda^n$. Putting this value in equation (3.21), we have,

$$a_0 \lambda^2 + a_1 \lambda + a_2 = 0 \qquad \qquad \cdots \qquad (3.22)$$

which is known as the characteristic equation of the equation (3.21). The general solution of the equation (3.21) is a linear superposition of the basic solutions of the equation. Let λ_1 and λ_2 be the two solutions of the characteristic equation i.e. the two eigenvalues. Then the generals solution of the difference equation is given by

$$x_n = A_1 \lambda_1^n + A_2 \lambda_2^n \qquad \qquad \cdots \qquad (3.23)$$

where A_1 and A_2 are two constants to be determined from two initial values of x. If the eigenvalues λ_1 and λ_2 are complex conjugates, we can transform the solution in polar-coordinates. Let $\lambda_1, \lambda_2 = a \pm i b$ and write $a = r \cos\phi$, $b = r \sin\phi$. So that

$$r^2 = (a^2 + b^2), \quad \phi = \tan^{-1}\frac{b}{a}.$$

Then $\quad a + i b = r(\cos\phi + \sin\phi) = re^{i\phi}$.

$$a + i b = r(\cos\phi - \sin\phi) = re^{i\phi}.$$

So the general solution is

$$x_n = A_1 (a + i b)^n + A_2 (a - ib)^n \qquad \qquad \cdots \qquad (3.24)$$

$$= A_1 r^n (\cos n\phi + i \sin n\phi) + A_2 r^n(\cos n\phi - i \sin n\phi)$$

$$= B_1 r^n \cos n\phi + i B_2 r^n \sin n\phi$$

where B_1 and B_2 are two constants

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$R_a < 1$
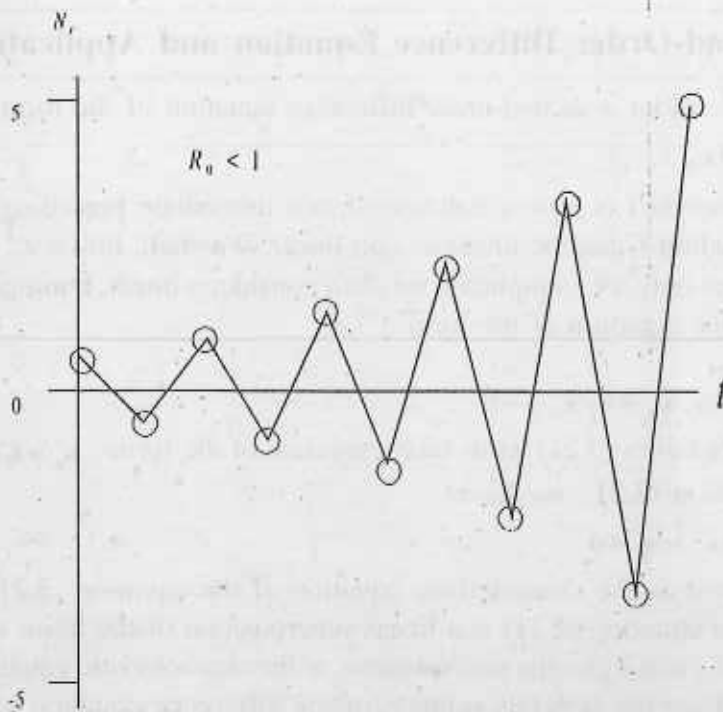
Fig. : 3.8 Growing oscillations.

3.9 Rabbit Problem : Fibonacci Sequence

Let us consider the linear second-order homogeneous difference equation

$$x_{n+1} = x_n + x_{n-1} \qquad \cdots \qquad (3.25)$$

which stems from Fibonacci work and the sequence $\{x_n\}$ is known as Fibonacci sequence. Let us put $x_n = c\lambda^n$ in (3.25) to have the characteristic equation

$$\lambda^2 = \lambda + 1 \qquad \cdots \qquad (3.26)$$

so that the eigenvalues are $\lambda_1 = \dfrac{1-\sqrt{5}}{2}, \lambda_2 = \dfrac{1+\sqrt{5}}{2}$ The general solution of the equation (3.25) is then given by

$$x_n = A_1 \lambda_1^n + A_2 \lambda_2^n = A_1\left(\frac{1-\sqrt{5}}{2}\right)^n + A_2\left(\frac{1+\sqrt{5}}{2}\right)^n$$

Suppose we start write $x_0 = 0$, $x_1 = 1$ (initial condition).

So, $\quad 0 = A_1 \lambda_1^0 + A_2 \lambda_2^0 = A_1 + A_2$

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$$1 = A_1 \lambda_1 + A_2 \lambda_2 = A_1 \left(\frac{1 - \sqrt{5}}{2} \right) + A_2 \left(\frac{1 + \sqrt{5}}{2} \right)$$

These give $A_1 = -\dfrac{1}{\sqrt{5}}, \quad A_2 = \dfrac{1}{\sqrt{5}}$

Then the general solution is $x_n = -\dfrac{1}{\sqrt{5}} \left(\dfrac{1 - \sqrt{5}}{2} \right)^n + \dfrac{1}{\sqrt{5}} \left(\dfrac{1 + \sqrt{5}}{2} \right)^n$ ... (3.27)

We observe that $\lambda_2 > 1, \quad -1 \triangleleft \lambda_1 < 0$

Thus the dominant eigenvalue is $\lambda_2 = \dfrac{1 + \sqrt{5}}{2}$ and its magnitude guarantees that the Fibonacci numbers $\{x_n\}$ form an increasing sequence. Since the eigenvalue λ_1 is negative, but of magnitude smaller than 1, its only effect is to superimpose a slight oscillation that dies out as n increases. It can be concluded that for large n the effect of λ_1 is negligible, so that

$$x_n \approx \frac{1}{\sqrt{5}} \lambda_2^n$$

So the ratio of the successive Fibonacci numbers x_{n+1/x_n} converges to

$$\frac{x_{n+1}}{x_n} = \lambda_2 = \frac{1 + \sqrt{5}}{2}$$

This limiting value known as Golden mean is, therefore, given by
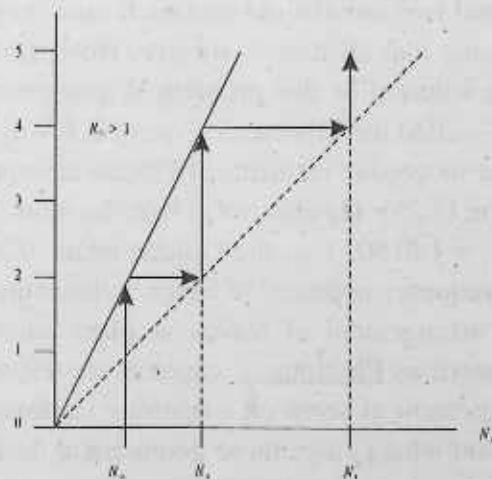
$$\tau = \frac{1 + \sqrt{5}}{2} = 1.618033...$$ ... (3.28)

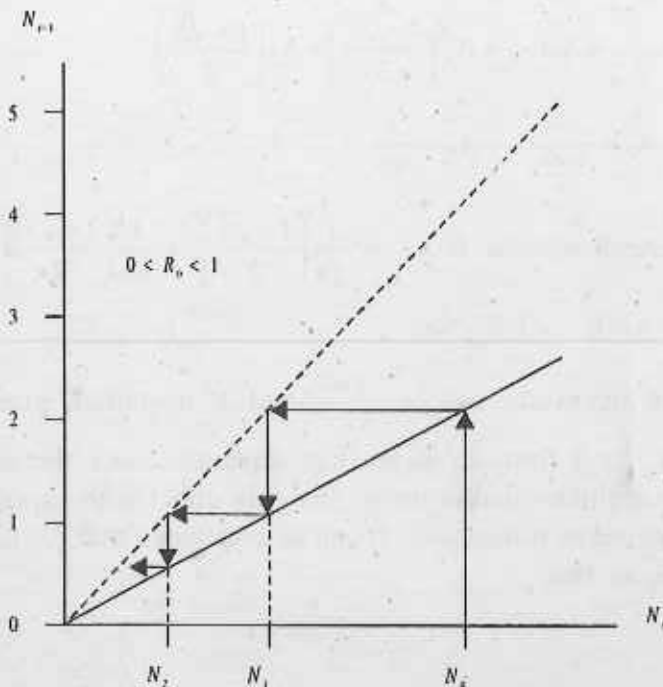Fig. : 3.9 Geometric growth á la cobweb.

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Fig. : 3.10 Geometric decay á la cobweb.

Historical Notes :

In 1202 Leonardo of Pisa (1175 – 1250), an Italian mathematician more affectionately known as Fibonacci (son of good nature), proposed the following problem (known as Rabbit Problem) : "Suppose that every pair of rabbits can produce only twice, when they are one and two months old and each time they produce exactly one new pair of rabbits. Assume that all rabbits survive. How many pairs will there be after n generation ?" The solution of this problem is a sequence of numbers (0, 1, 1, 2, 3, 5, 8, 13, 21 ....) — called the Fibonacci sequence. It was Kepler (1571 - 1630) who first observed that the successive elements of Fibonacci sequence satisfies the recursion or difference equation (3.25). He also noted that the ratio 2 : 1, 3 : 2, 5 : 3, 8 : 5........ approach the value τ = 1.618033 ..., the Golden mean. The manifestation of Golden mean and Fibonacci sequence appeared in Greek architecture, and in different biological forms. The regular arrangement of leaves or plant parts along the stem, apex or flower of a plant known as Phyllotaxis, captures the Fibonacci numbers. A striking example is the arrangement of seeds on a ripening sunflower. Biologists have not yet agreed conclusively on what causes these geometrical designs and patterns in plants, although the subject has been persued for over three centuries.

3.10 Summary

In this chapter we have discussed discrete-time models of populations on the basis of difference equations. The following are the problems discussed, (i) We have first discussed first-order linear difference equation with applications. (ii) We have next discussed the qualitative behaviors such as the stability of equilibrium (or fixed) points of first-order non-linear difference equations, (iii) We have then discussed the method of numerical and graphical solution namely Cobweb diagram method of finding the solution, determination of equilibrium points and their stabilities; (iv) We have next discussed second order linear difference equations and its application in the overlapping population growth, in particular ,in the study of Rabbit problem and Fibonacci sequence.

Exercise : A population obeys the following growth equation

$$x_{n+2} - 2x_{n+1} + 2x_n = 0$$

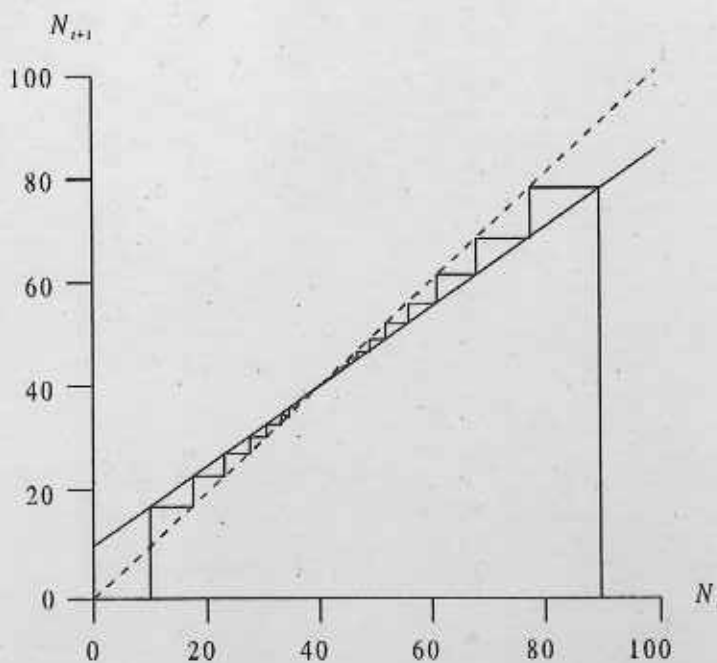Find the population in generation n. Find the steady-state (if it exists). If so, is that stable?
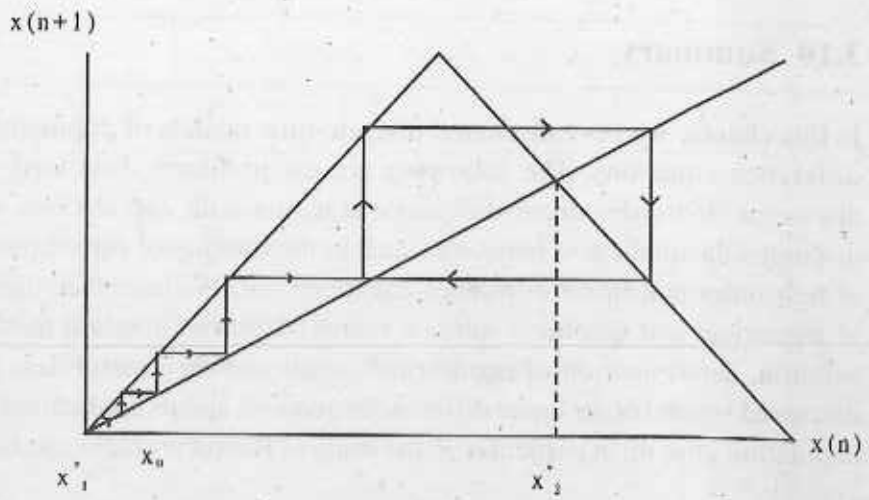

Fig. : 3.11 Cobwebbing to a stable equilibrium.

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FIGURE : 3.12

Both equilibrium points $x^*_1 = 0$ and $x^*_2 = 2/3$ are unstable.

Unit 4 □ Delay Population Models

Objectives: The object of this chapter is to discuss delay differential equation model of population to take effect of time delay or time lag in the population growth.

Structure

4.1 □ Introduction

So far we have assumed that the rate at which a population is growing at time t depends on the magnitude of the population size (or density) at that same time. For example, consider the Malthus (or exponential) growth equation

$$\frac{dx(t)}{dt} = rx(t), \qquad x(o) = x_0 \qquad \qquad \dots \qquad (4.1)$$

Now what happens if we know that the present growth rate depends, not on the present magnitude but on the magnitude at an earlier time? For example, the present growth rate of a colony of flies depends not on the number of flies right now but rather on the number of flies laying a certain number of eggs a week or so ago. In that case we write

$$\frac{dx(t)}{dt} = rx(t - \tau) \qquad \qquad \dots \qquad (4.2)$$

where τ, the average incubation period of the eggs, is a time delay or time lag. As we shall see, this almost trivial change in the differential equation, greatly complicate the analysis and can produce drastic changes in the final answer.

4.2 □ Types of Delay Equations

There are two types of delay equations : (a) discrete-time delay equation and (b) distributed time delay equations.

(a) Discrete-time delay equation :
A more generalized delay equation for Malthus growth is

$$\frac{dx(t)}{dt} = r_1 x(t) + r_2 x(t - \tau) \qquad \qquad \dots \quad (4.3)$$

where r_1 and r_2 are constants. This is an example of differential - difference equations. Another important discrete-time delay equation is the logistic delay equation

$$\frac{dx(t)}{dt} = rx(t)\left(1 - \frac{x(t-\tau)}{x^*}\right)$$

where x^* is the carrying capacity.

(b) Distributed-time delay equation :

For distributed (or continuous) time delay, the logistic equation

$$\frac{dx(t)}{dt} = rx(t)\left(1 - \frac{x(t)}{x^*}\right)$$

becomes

$$\frac{dx(t)}{dt} = rx(t)\left(1 - \frac{1}{x^*}\int_{-\infty}^{t} K(t - \tau)x(\tau)d\tau\right) \qquad \dots \quad (4.6)$$

which is an example of integro-differential equation, the function $K(t - x)$ is the delay function.

4.3 ❏ Discrete-time Delay Models

Consider a model equation of the form

$$\frac{dx(t)}{dt} = r(t)g(x(t - \tau)) \qquad \qquad \dots \quad (4.7)$$

An equilibrium point of the equation (4.7) is a value x^* such that $x^* g(x^*) = 0$ so that $x(t) = x^*$ is a constant solution of the differential-difference equation (4.7). The delay logistic equation (4.4) has two equilibrium points $x = 0$ and $x = x^*$.

Linearization about an Equilibrium Point:

Let us write $u(t) = x(t) - x^*$. Putting this in equation (4.7) and using Taylor series expansion, we have,

$$\frac{du(t)}{dt} = (x^* + u(t))g((x^* + u(t - \tau))$$

$$= (x^* + u(t))\{g(x^*) + g'(x^*)u(t - \tau) + \frac{g''(c)}{2!}u^2(t - \tau)\}$$

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$$= x^* g(x^*) + g(x^*) u(t) + x^* g'(x^*) u(t-\tau) + h(u(t), u(t-\tau))$$
$$= g(x^*) u(t) + x^* g'(x^*) u(t-\tau) + h(u(t), u(t-\tau))$$

where c lies between x^* and $x^* + u(t-\tau)$ and $h(u(t), u(t-\tau)) = g'(x^*) u(t) u(t-\tau) +$

$x^* \dfrac{g''(c)}{2!} u^2(t-\tau)$ is a small quantiy when $u(s)$ is small for $t-\tau \leq s \leq t$. So the

differential-difference equation (4.7) reduces to the linear form

$$\frac{du(t)}{dt} = g(x^*) u(t) + x^* g'(x^*) u(t-\tau) \qquad \qquad \dots \qquad (4.8)$$

obtained by neglecting the light order terms collected in $h(u(t), u(t-\tau))$. We have then the theorem :

Theorem 4.1: If all the solutions of the linear equation

$$\frac{du(t)}{dt} = g(x^*) u(t) + x^* g'(x^*) u(t-\tau) \qquad \qquad \dots \qquad (4.9)$$

tends to zero as $t \to \infty$, then every solution $x(t)$ of the equation (4.7) with $|x(t)-x^*|$ sufficiently small tends to the equilibrium point x^* as $t \to \infty$.

Asymptotic Stability :

For the differential equation

$$\frac{dx(t)}{dt} = xg(x) \qquad \qquad \dots \qquad (4.9)$$

which is the case $\tau = 0$ of the equation (4.7) an equilibrium point x^* is asymptotically stable if and only if

$$\frac{d}{dx}(xg(x))\bigg|_{x=x^*} = (xg(x))'|_{x=x^*} = x^* g'(x^*) + g(x^*) < 0 \quad \dots \quad (4.10)$$

So the equilibrium point $x^* = 0$ is asymptotically stable if $g(0) < 0$ and an equilibrium point $x^* > 0$ is asymptotically stable if $g'(x^*) < 0$, since $g(x^*) = 0$. The study of asymptotic stability of the fixed point x^* of the differential difference equation (4.7) is a bit difficult. It requires the condition

$$(xg(x))'|_{x=x^*} < 0 \qquad \qquad \dots \qquad (4.11)$$

This is, however, not sufficient for the delay equation (4.7). For this, another condition is required and this condition is provided by the theorem of linearization :

(a) For equilibrium point $x^* = 0$, the linearization is $u'(t) = g(o) u(t)$. Since $g(o) > 0$ for most models of this type, the equilibrium point $x^* = 0$ is unstable, since $u(t)$ increases with time t.

(b) For equilibrium point $x^* > 0$, $g(x^*) = 0$ and the linearization is

$$\frac{dx(t)}{dt} = bu(t - \tau) \qquad \dots \quad (4.13)$$

where $b = x^* g'(x^*)$. In order to determine whether all solutions of the linear differential difference equation (4.13) tends to zero as $t \to \infty$ we take a solution of the form

$$u(t) = Ce^{\lambda t}, \text{ (C is a constant)} \qquad \dots \quad (4.14)$$

Putting this value in (4.13) we have,

$$\lambda = be^{-\lambda t} \qquad \dots \quad (4.15)$$

This is a transcendental equation for τ having infinitely many roots. A basic result, which we assume without proof, is that if all roots of the characteristic equation (4.15) have negative real parts, then all solutions of the differential - difference equation (4.13) tends to zero on $t \to \infty$. This result is analogous to the corresponding result for differential equation. However, it is very difficult to analyse transcendental equation (4.15) in the delay case. In the delay case, with $\tau > 0$, it is possible to show that the condition that all roots of the characteristic equation (4.15) have negative real parts is

$$0 < -b\tau < \frac{\pi}{2} \qquad \dots \quad (4.16)$$

The condition (4.16) implies $b < 0$ and in addition, that the time lag τ not to be too large. Combining the analysis with the above theorem we see that an equilibrium point $x^* > 0$ of the differential - difference equation

$$\frac{dx(t)}{dt} = x(t) g\left(x(t - \tau)\right) \qquad \dots \quad (4.17)$$

is asymptotically stable if

$$0 < -x^* g'(x^*)\tau < \pi/2 \qquad \dots \quad (4.18)$$

Example (4.1) : For delay—logistic equation

$$\frac{dx(t)}{dt} = rx(t)\left(1 - \frac{x(t - \tau)}{x^*}\right)$$

the stability condition (4.18) becomes,

$$0 < r\tau < \pi/2$$

Thus in addition to the stability condition. $(xg(x))'|_{x=x^*} < 0$ for ordinary differential equation, we must have additional requirement that the delay time τ be sufficiently small.

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Example (4.2) : Show that the equilibrium point x = K of the delay equation

$$\frac{dx(t)}{dt} = rx(t) \log\left(\frac{K}{x(t-\tau)}\right)$$

is asymptotically stable if $0 \le r\tau < \frac{1}{2}$.

4.4 ❑ Distributed Delay Models :

In the previous section we have studied the discrete-time delay model of the type

$$\frac{dx(t)}{dt} = x(t)\, g\, (x(t-\tau))$$

This model equation can be generalized to the form

$$\frac{dx(t)}{dt} = x(t) \int_0^s g(x(t-s))\, p(s)\, ds \qquad \dots \quad (4.19)$$

describing a distributed delay. Here p(s) ds represents the probability of a delay between s and s + ds, so that

$$\int_0^s p(s)\, ds = 1 \qquad \dots \quad (4.20)$$

The average delay is then, by definition

$$T = \int_0^s s\, p(s)\, ds \qquad \dots \quad (4.21)$$

<u>Definition</u>: An equilibrium point of the integro-differential equation

$$\frac{dx(t)}{dt} = x(t) \int_0^\tau g\,[x(t-s)]\, p(s)\, ds \qquad \dots \quad (4.22)$$

is a value x* such that

$$x * \int_0^s g(x*)\, p(s)ds = x * g(x*) = 0$$

We see that x* = 0 is an equilibrium point and equilibria x* > 0 are given by

$$g(x^*) = 0 \qquad \qquad \qquad \qquad \qquad \qquad \ldots \quad (4.23)$$

Linearization about an equilibrium point

To linearize (4.22) about an equilibrium point x^*, we put $u(t) = x(t) - x^*$ so that, we have,

$$\frac{du(t)}{dt} = (x^* + u(t)) \int_0^* (g(x^*) + g'(x^*) u(t-s) + \ldots) \, p(s)ds$$

$$= (x^* + u(t)) \left\{ g(x^*) + g'(x^*) \int_0^* u(t-s)p(s)ds + \ldots \right\}$$

$$= x^* g(x^*) + g(x^*) u(t) + x^* g'(x^*) \int_0^* u(t-s) \, p(s)ds + \ldots \quad \ldots \quad (4.24)$$

As with other types of equations such as differential equations, difference equations, differential-difference equations, the behaviours of solution near an equilibrium point is thus described by the behaviours of solutions of the linearized equation. We are thus led to study the linear integro-differential equation of the form,

$$\frac{du(t)}{dt} = a \, u(t) + b \int_0^* u(t-s) \, p(s)ds \qquad \qquad \ldots \quad (4.25)$$

where $p(s) \geq 0$, for $0 \leq s \leq *$ and $\int_0^* p(s)d = 1$. To study the behaviour of solution of the equation (4.25) for a specific kernel $p(s)$, we look for solution

$$u(t) = Ce^{\lambda t} \qquad \qquad \qquad \qquad \ldots \quad (2.26)$$

and construct the characteristic equation,

$$\lambda = a + b \int_0^* e^{-\lambda s} \, p(s)ds = a + b \, L\{p(\;)\} \qquad \qquad \ldots \quad (4.27)$$

where $L\{p(\lambda)\}$ is the Laplace Transform of the function $p(s)$ evaluated at λ. We shall

consider two specific choices of p, both normalized so that $\int_0^r p(s) = 1$ and $\int_0^s sp(s)\,ds = T$

(average delay). We shall make use of the following formulae whenever necessary :

(a) $\int_0^x e^{-a\,s}ds = \frac{1}{a}$, (b) $\int_0^s se^{a\,s}ds = \frac{1}{a^2}$, (c) $\int_0^s s^2 e^{a\,s}ds = \frac{2}{a^3}$ ... (4.28)

Example (4.3) : Let us take $P_1(s) = \frac{4s}{T^2}e^{-2s/T}$, so that $p(o) = 0$ and rising to a maximum at $s = T/2$, then falling exponentially. We have

$$L\{p_1(\lambda)\} = \int_0^s e^{-\lambda\,s}p_1(s)ds$$

$$= \frac{4}{T^2}\int_0^s se^{-(\lambda+2/T)s}ds = \frac{4}{T^2\lambda^2+4T\lambda+4}$$

The characteristic equation is

$$a + \frac{b}{T^2\lambda^2+4T\lambda+4} = \lambda$$

or, $\lambda^3 + \left(\frac{4T-aT^2}{T^2}\right)\lambda^2 + \left(\frac{4-4aT}{T^2}\lambda\right) - \frac{4(a+b)}{T^2} = 0$ ...   (4.29)

The stability of the equilibrium requires all the roots of the polynomial equation (4.29) to have negative real parts. By Routh-Hurwitz condition all the roots of the cubic equation

$$\lambda^3 + \alpha\lambda^2 + \beta\lambda + \gamma = 0$$ ...   (4.30)

have negative real parts if and only if

$\alpha > 0, \gamma > 0$ & $\gamma >$ ...   (4.31)

Here $\alpha = \frac{4-aT}{T}, \beta = \frac{4-4aT}{T^2}, \gamma = -\frac{4(a+b)}{T^2}$

and the stability conditions are

$a+b<0$, $aT<4$ and $-bT<(2-aT)^2$ ...   (4.32)

For the equation (4.25), $a = g(x^*)$, $b = x^* g'(x^*)$

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(i) If the equilibrium is $x^* = 0$, then $b = x^* g'(x^*) = 0$. The condition of stability reduces to $a = g(x^*) < 0$ which is satisfied in population models only if there is an Allee effect (see Chapter - II).

(ii) If the equilibrium $x^* > 0$ then $a = 0$, since the equilibrium point satisfies the condition $x^* g(x^*)=0$. Then the stability condition (4.32) redues to
$$0 < -x^* g'(x^*) T < 4.$$

Example (4.4) :

Take $P_2(s) = \dfrac{1}{T} e^{-s/T}$

Then $L\{p(\lambda)\} = \displaystyle\int_0^\infty e^{-\lambda s} p_2(s)ds$

$$= \dfrac{1}{T}\int_0^\infty e^{-\left(\frac{1}{T}+\lambda\right)s} ds = \dfrac{1}{\lambda T+1}$$

The characteristic equation is

$$a + \dfrac{b}{\lambda T+1} = \lambda$$

or, $\lambda^2 + \dfrac{1-aT}{T^2}\lambda - \dfrac{(a+b)}{T^2} = 0$

The stability condition that both the roots of this quadratic equation have negative real parts is

$1 - aT > 0$
$-(a + b) > 0$

From (4.24) we have $a = g(x^*)$, $b = x^* g'(x^*)$.

(i) If $x^* = 0$, then the stability condition reduces to $g(x^*) < 0$, which is not satisfied.
(ii) If $x^* > 0$, the stability condition is just $g'(x^*) < 0$, since $a = 0$. We thus see that for stability there is no requirement that the average delay T not be too large. Hence, in both the cases the stability criteria are satisfied independently of T. From the above example we come to the following conclusion :

"With distributed delay each delay kernel p must be examined in its own right. It is not true that increasing the average delay always destroys stability."

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4.5. ❑ Summary:

In this chapter we have described both the types of discrete-time and continuous time delay models of populations. We have discussed the process of linearization about equilibrium and studied the criteria of stability for both the types of delay equations with illustrative examples.

Unit 5 ❑ Two-Species Models and Qualitative Analysis

Objectives: The object of this chapter is to make a qualitative analysis of two-species interacting model equations.

Structure

5.1 ❑ Introduction

The model equations of interacting populations are usually non-linear. Analytical solutions of these equations are, in general, very difficult. The dynamical behaviors of such can be studied qualitatively. We can find out the criteria of stability of stationary (or equilibrium) states, we can find out the criteria of existence of periodic solutions and limit cycles without solving the equations exactly.

5.2 ❑ Two-Species Model Equations Linearization and Stability

We consider a population of two interacting species with population sizes (or densities) $x(t)$ and $y(t)$. As in the case of continuous single-species models, we assume that both $x(t)$ and $y(t)$ are continuously differentiable functions of time t. Let the model equations for the interacting system be of the form,

$$\frac{dx}{dt} = F(x,y) \qquad \qquad \cdots \qquad (5.1a)$$

$$\frac{dx}{dt} = G(x,y) \qquad \qquad \cdots \qquad (5.1b)$$

Although in models we neglect many factors of importance of real populations, they are useful first step and may represent real populations quite well.

Definition :

An equilibrium point (x^*, y^*) of the system of equations (5.1a) and (5.1b) is a solution of the equations $F(x, y) = 0$, $G(x, y) = 0$. Thus, an equilibrium is a constant solution of the system of equations (5.1a) and (5.1b) Geometrically, an equilibrium is a point in the phase-space that is the orbit of a constant solution.

Linearization :

One of the main tools in studying continuous models for two interacting populations is linearization at equilibria, just as for models for single population. However, as linearization results can only give information about the behaviour of solutions near an equilibrium, they will not enable us to examine such questions as the existence of periodic orbits. However, for the study of local behaviours about the equilibrium the linearization is an important tool in dynamical theory.

Let us linearise the system of equations (5.1) about the equilibrium point (x^*, y^*). We write $u = x - x^*$ and $v = y - y^*$ and transform the system of equations (5.1) to the form

$$\frac{du}{dt} = G(x^* + u, y^* + v)$$

$$\frac{dv}{dt} = G(x^* + u, y^* + v)$$

Using Taylor's series expansion, we have

$$F(x^* + u, y^* + v) = F(x^*, y^*) + F_x(x^*, y^*) u + F_y(x^*, y^*) v + h_1$$

$$G(x^* + u, y^* + v) = G(x^*, y^*) + G_x(x^*, y^*) u + G_y(x^*, y^*) v + h_2$$

where h_1 and h_2 are functions that are small for small deviations (or perturbations) and v in the sense that

$$\lim_{\substack{u \to 0 \\ u \to 0}} \frac{h_1(u, v)}{\sqrt{u^2 + v^2}} = \lim_{\substack{u \to 0 \\ u \to 0}} \frac{h_2(u, v)}{\sqrt{u^2 + v^2}} = 0$$

Neglecting higher-order terms $h_1(u, v)$ and $h_2(u, v)$, we have the linear system of equations.

$$\frac{du}{dt} = F_x(x^*, y^*) u + F_y(x^*, y^*) v \qquad \qquad \dots \qquad (5.2a)$$

$$\frac{du}{dt} = G_x(x^*, y^*) u + G_y(x^*, y^*) v \qquad \qquad \dots \qquad (5.2b)$$

The coefficient matrix of the system (5.2)

$$A = \begin{bmatrix} F_x(x^*, y^*) & F_y(x^*, y^*) \\ G_x(x^*, y^*) & G_y(x^*, y^*) \end{bmatrix} \qquad \cdots \qquad (5.3)$$

is called the community matrix of the system at equilibrium (x^*, y^*). It describes the effect of the size of each species on the growth rates of itself and the other species at equilibrium. In matrix form the system of linear equation (5.2) can be written as

$$\begin{bmatrix} \dot{u} \\ \dot{v} \end{bmatrix} = \begin{bmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{bmatrix} \begin{bmatrix} u \\ v \end{bmatrix} \qquad \cdots \qquad (5.4)$$

where
$$a_{11} = F_x(x^*, y^*), \qquad a_{12} = F_y(x^*, y^*)$$
$$a_{21} = G_x(x^*, y^*), \qquad a_{22} = G_y(x^*, y^*) \qquad \cdots \qquad (5.5)$$

are the elements of the community matrix A.

Stability of Equilibrium

Definition :

An equilibrium point (x^*, y^*) is said to be stable if every solution $(x(t), y(t))$ with $(x(o), y(o))$ sufficiently close to the equilibrium remains closed to the equilibrium for all $t > 0$. An equilibrium (x^*, y^*) is asymptotically stable if it is stable and if, in addition, the solution $(x(t), y(t))$ tends to the equilibrium (x^*, y^*) as $t \to \infty$. These definitions are natural extensions of the definitions given earlier for a single-species population.

Let us now find the explicit form of the criteria of stability. For this, we look for the solution of the linearized equations (5.4). The characteristic (or eigenvalue) equations of the system of linear equations (5.4) is given by

$$\begin{vmatrix} a_{11} - \lambda & a_{12} \\ a_{21} & a_{22} - \lambda \end{vmatrix} = 0$$

or $\lambda^2 - (a_{11} + a_{22}) + (a_{11} a_{22} - a_{12} a_{21}) = 0$

or $\lambda^2 - p + q = 0$ $\qquad \cdots \qquad (5.6)$

where $p = a_{11} + a_{22} = \mathrm{Tr}\, A$, $q = (a_{11} a_{12} - a_{12} a_{21}) = \mathrm{Det}\, A$ $\quad \cdots \qquad (5.7)$

The stability of the equilibrium point (x^*, y^*) can be determined from the eigenvalues

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λ of the system of equation (5.4) or the community matrix A given by (5.3). Infact, we have the theorem.

Theorem 5.1 :

The equilibrium (x^*, y^*) is asymptotically stable if the roots of the characteristic equation (5.6), that is, the eigenvalues λ have negative real parts. According to Routh-Hurwitz criterion the necessary sufficient conditions for the eigenvalues λ to have negative real parts are

$$p = \text{Tr } A < 0, \qquad q = \det A > 0 \qquad \qquad \cdots \qquad (5.8)$$

The conditions (5.8) are the sufficient conditions of asymptotic stability. The trace and determinant determine the eigenvalues λ. We classify the equilibrium points corresponding to the different nature of eigenvalues :

(i)   If the two eigenvalues (λ_1, λ_2) are real and negative, the equilibrium is a stable node.

(ii) If the eigenvalues (λ_1, λ_2) are real and positive the equilibrium is an unstable node.

(iii) If (λ_1, λ_2) are real and of opposite sign, the equilibrium is a saddle point.

(iv) If the eigenvalues are complex with negative real parts, we have a stable focus,

(v)   If the eigenvalues are complex with positive real parts, we have an unstable focus.

(vi) Finally, if the eigenvalues are purely imaginary, the linearised system will have a center but the original non-linear system will have a center or a stable or unstable focus, depending on the exact nature of the non-linear terms, [see Fig. (5.1)]
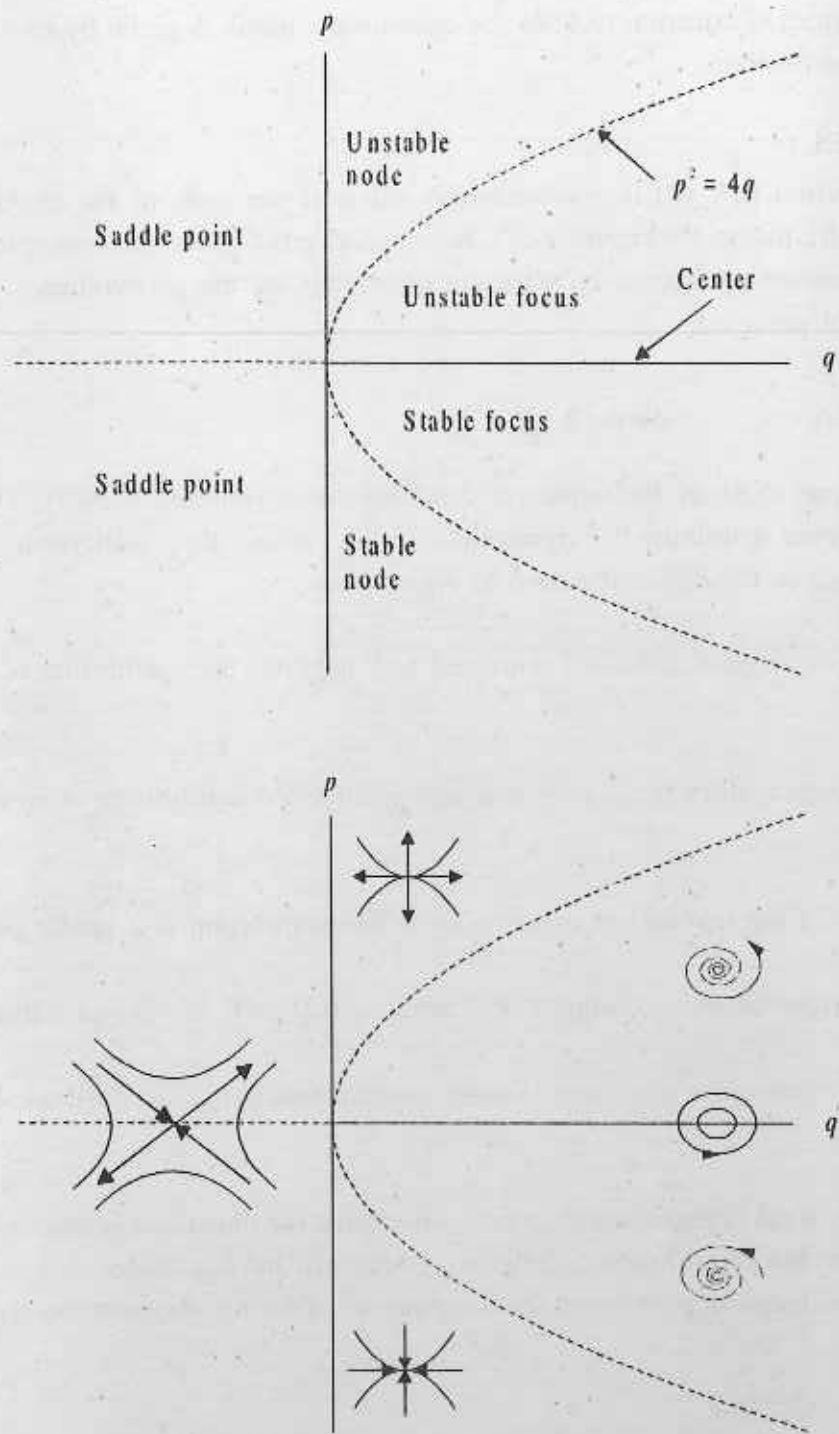
Fig. 5.1 Classification of equilibria.

Exercises :

1. The following two-dimensional non-linear differential equations have been proposed as a model of cell differentiation

$$\frac{dx}{dt} = y - x$$

$$\frac{dx}{dt} = \frac{5x^2}{4 + x^2} - y.$$

(i) Determine the equilibrium points.

(ii) Linearize the system of equations each equilibrium point.

(iii) Determine the local stability of each positive equilibrium point and classify the equilibrium points.

2. The following system of equations (in dimensionless form) appear as a model of plant - harvivore system

$$\frac{dx}{dt} = 1 - kxy(y - 1)$$

$$\frac{dx}{dt} = \alpha \, y\left(1 - \frac{y}{x}\right).$$

show that there is only one equilibrium and determine its stability.

5.3 ❑ Periodic Solution and Limit Cycles

In the preceding section we have analysed the behaviour of solutions starting near an equilibrium point. We now consider the case where the solution does not begin near the equilibrium; in particular we want to examine the behaviour of solutions of systems that have no asymptotic stable equilibrium. Such system can arise in the models of predator-prey system. We consider the two-dimensional system

$$\frac{dx}{dt} = F(x, y)$$

$$\frac{dx}{dt} = G(x, y).$$

Definition :

Let $(x(t), y(t))$ be a solution that is bounded as $t \to \infty$. The positive semi-orbit C^+ of this solution is defined to be the set of points $(x(t), y(t))$ for $t \geq 0$ in the

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(x, y) plane. The limit set $L(C^+)$ of the semi-orbit is defined to be the set of all points $(\bar{x}, \bar{y})$ such that there is a sequence of times $t_n \to \infty$ with $x(t_n) \to \bar{x}, y(t_n) \to \bar{y}$ as $n \to \infty$. For example, if the solution $(x(t), y(t))$ tends to an equilibrium point (x^*, y^*) as $t \to \infty$, then the limit set consists of the equilibrium point (x^*, y^*). If $(x(t), y(t))$ is a periodic solution so that the semi-orbit C^+ is a closed curve, then the limit set $L(C^+)$ consists of all points of the semi-orbit C^+. It is not difficult to show that the limit set of a bounded semi-orbit is closed, bounded and a connected set.

Definition :

An invariant set for the system (5.9) is a set of points in the plane which contains the positive-semi orbit through every point of the set. Thus, for example, an equilibrium is an invariant set, and a closed orbit corresponding to a periodic solution is an invariant set. It is possible to prove, making use of continuous dependence of solutions of differential equation on initial conditions, that the limit set of a bounded semi-orbit is an invariant set.

The results stated above are valid for autonomous differential equations in all dimensions, but in two dimensions more information on the structure of limit sets is available. The reason for this involves the topological properties of the plane, especially the Jordan curve theorem which states that a simple closed curve in the plane divides the plane into two disjoint regions - which is not valid in more than two dimensions. The fundamental result on the behaviour in the large of solutions of autonomous systems in the plane is the Poincare' — Bendixson theorem.

Theorem 5.2 (Poincare' - Bendixson Theorem :

If C^+ is a bounded semi-orbit whose limit set $L(C^+)$ contains no equilibrium points, then either C^+ is a periodic orbit and $L(C^+) = C^+$ or $L(C^+)$ is a periodic orbit, called a limit cycle, (which C^+ approaches spirally, either from inside or from outside.) We shall not go to the proof of the theorem, which may be found in many standard books on differential equations and dynamical system. We conclude the section by stating a theorem - due to Bendixson giving a criterion implying that there can not be a periodic orbit in a given region.

Theorem 5.3 : (Bendixson's negative criterion) :

Consider the system (5.9), that is

$$\frac{dx}{dt} = F(x, y), \quad \frac{dy}{dt} = G(x, y)$$

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where F and G are continuously differentiable function of (x, y) defined on some simply connected domain $D \subset R^2$ (by simply connected, we mean that the domain has no 'holes' or disjoint portion.) If

$$\nabla . (F,G) = \left(\frac{\partial F}{\partial x} + \frac{\partial G}{\partial y} \right) \qquad \qquad \dots \quad (5.10)$$

is of one sign in D, there can not be a closed orbit contained in D.

Proof : The proof is by contradiction . Suppose that we do have a closed orbit C, with interior Ω , contained in D that satisfies the equations (5.9). Suppose also that the right-hand side of equation (5.10) is of one sign. If follows that

$$\iint_\Omega \left(\frac{\partial F}{\partial x} + \frac{\partial G}{\partial y} \right) dxdy \neq 0 \qquad \qquad \dots \quad (5.11)$$

Applying Green's theorem we transform the surface integral (5.11) to the form of line integral. we have then

$$\oint_c (F\,dy - G\,dx) \neq 0 \qquad \qquad \dots \quad (5.12)$$

The last integral may be written as

$$\oint_c \left(F\frac{dy}{dt} - G\frac{dx}{dt} \right) dt \qquad \qquad \dots \quad (5.13)$$

and since C has been assumed to satisfy system (5.9), we may transform (5.13) to the form

$$\oint_c (FG - GF)dt = \oint_c 0.dt = 0 \qquad \qquad \dots \quad (5.14)$$

which contradict (5.12); and so we have been mistaken in assuming the existence of a closed orbit C (contained in D) that satisfies the system of equations (5.9). If the divergence is of one sign, there can not be such an orbit.

Remark : Since a periodic solution corresponds to a closed orbit and vice-versa, the above theorem also provides the criterion of existence of a periodic solution of the system of equations (5.9).

The French mathematician H. Dulac made the useful observation that the last system (5.9) is a member of the family of dynamical systems

$$\left. \begin{array}{l} \dfrac{dx}{dt} = B(x,y)\, F(x,y) \\[2mm] \dfrac{dy}{dt} = B(x,y)\, G(x,y) \end{array} \right\} \qquad \qquad \dots \quad (5.15)$$

that share the same phase - portrait. If one can disprove the existence of a closed orbit for any member of the family, one can disprove the existence of a closed orbit for every member of the family (5.15). This leads to a minor, but powerful extension of Bendixson's negative criterion.

Theorem 5.4 : (Bendixson-Dulae negative criterion) :

Let B be a smooth function on $D \subset R^2$ (with all other assumptions as before). If

$$\nabla \cdot (F,G) = \frac{\partial (BF)}{\partial x} + \frac{\partial (BG)}{\partial y} \qquad \qquad \dots \quad (5.16)$$

is of one sign, then no closed orbit contained within D.

The above theorem does not tell us how to find B(x, y). There is no general method for constructing B. However, we are lucky enough to find such a function.

Example (5.1) : Consider the system

$$\frac{dx}{dt} = x(1 - x - y)$$

$$\frac{dx}{dt} = \beta\, (x - \alpha\,)y.$$

Let $B = \dfrac{1}{xy}$, then $B\,F = \dfrac{1-x-y}{y}$, $BG = \dfrac{\beta\,(x - \alpha\,)}{x}$ and $\dfrac{(BF)}{\partial x} + \dfrac{\partial (BG)}{\partial y} = -\dfrac{1}{y}$

The last expression is strictly negative in the interior of the first quadrant of the (x, y)-plane. Thus, there cannot be a closed orbit that satisfies the above system of equations and that lies entirely within the interior of the first-quadrant. So, the system of equation contains no periodic solution within the first quadrant.

Example (5.2) : Investigate the qualitative behaviour of the solution of the system

$$\frac{dx}{dt} = x\left(1 - \frac{x}{30}\right) - \frac{xy}{x+10}$$

$$\frac{dx}{dt} = y\left(\frac{x}{x+10} - \frac{1}{y}\right)$$

Solution : There are three equilibrium points $(x^*, y^*) = (0, 0), (30, 0), (5, 12.5)$. The community matrix at $(0, 0)$ is

$$A = \begin{pmatrix} 1 & 0 \\ 0 & -\frac{1}{3} \end{pmatrix}$$

Since det $A < 0$, the equilibrium point $(0, 0)$ is unstable. The community matrix at $(30, 0)$ is

$$A = \begin{pmatrix} -1 & -\frac{3}{4} \\ 0 & -\frac{5}{12} \end{pmatrix}$$

This equilibrium $(30, 0)$ is also unstable, since det $A < 0$.
The community matrix at $(5.12.5)$ is

$$A = \begin{pmatrix} \frac{1}{9} & -\frac{3}{4} \\ \frac{5}{9} & 0 \end{pmatrix}$$

Here tr $A > 0$, det $A > 0$ so $(5, 12.5)$ is also unstable. If we add the two equations of the model, we obtain

$$\frac{d}{dt}(x+y) = x\left(1 - \frac{x}{30}\right) - \frac{1}{3}$$

Thus $(x + y)$ is decreasing except in the bounded region $\frac{y}{3} < \left(1 - \frac{x}{30}\right)$. In order that an orbit be unbounded, we must have $(x + y)$ unbounded. However, this is impossible, since $(x + y)$ is decreasing whenever $(x + y)$ is large. Thus every orbit of the system is bounded. Since all equilibria are unstable, the Poineare'-Bendixson theorem implies that there must be a periodic orbit arround $(5, 12.5)$ to which every orbit tends as $t \to \infty$.

Exercises :

(1) Determine the behaviour of the solutions in the first quadrant of the system

$$\frac{dx}{dt} = x(100 - 4x - 2y)$$

$$\frac{dy}{dt} = y(60 - x - y)$$

(2) Consider the system

$$\frac{dx}{dt} = x(ax + by)$$

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$$\frac{dy}{dt} = y(cx + dy)$$

(i) show that every trajectory with $x(0) \geq 0$, $y(0) \geq 0$ satisfies $x(t) \geq 0$, $y(t) \geq 0$ for all $t > 0$ (i.e. trajectories starting in the first quadrant remain in the first quadrant foroever

(ii) use Dulac criterion with $B(x, y) = 1/xy$ to show that there are no periodic orbits if $ac > 0$.

*Mathematical Note : Routh-Hurwitz Criterion

It is difficult or impossible to find explicitly all the roots of the characteristic equation of a multi-dimensional system. There is, however, a general criterion for determining whether all roots of a polynomial equation have negative real parts. This criterion known as Routh-Hurwitz criterion gives conditions on the coefficient of a polynomial equation

$$\lambda^n + a_1 \lambda^{n-1} + a_2 \lambda^{n-2} + \dots + a_n \lambda_1 + a_n = 0$$

under which all roots have negative real parts. For $n = 2$, the Routh-Hurwitz condition are

$$a_1 > 0, \quad a_2 > 0.$$

which is equivalent to the conditions : tr $A < 0$, det $A > 0$. For $n = 3$, the conditions are

$$a_3 > 0, \quad a_1 > 0, \quad a_1 a_2 > a_3$$

For a polynomial of degree n, there are n conditions. This criterion is useful on occasions, it is, however, complicated for problem of many dimensions.

5.4 □ Summary:

This chapter consists of two parts:

    (i)   In the first part we have introduced general model equations of two interacting species, we have found out equilibrium states and reduced model equations to the linear form. On the basis of linear equations we have investigated the criteria of asymptotic stability (local) of the system.

    (ii)   The second part deals with the systems that have no asymptotic stable equilibria. For such systems we have investigated the criteria of existence of periodic solutions and limit cycles.

Unit 6 ❑ Two-Species Models : Lotka-Volterra Systems

Objectives: The chapter consists of an account of Lotka-Volterra dynamical models of interacting poplations.

Structure

6.1 ❑ Introduction

When two or more species interact the population dynamics of each species is effected. In general, the is a whole web of interacting species, called the tropic web which make structurally complex communities. The dynamical models of such interacting species are provided by Lotka-Volterra systems of equations and there are three types of model equations dealing with interactions. Three models are (i) predator-prey model (ii) competition model and (iii) mutualistic model.

In this chapter we shall study the dynamical processes involved in each type of model systems.

6.2 ❑ Predator-Prey Models

6.2.1 Classical Lotka-Volterra Model

Let us consider a prey-predator system. Let $x(t)$ be the number (or density) of prey and $y(t)$ be the number (or density) of predators. Lotka-Volterra model equations for the system are

$$\frac{dx}{dt} = \lambda x - bxy \qquad \qquad \dots \quad (6.1a)$$

$$\frac{dy}{dt} = -\mu y + cxy \qquad \qquad \dots \quad (6.1b)$$

The first term on the right-hand side of (6.1a) implies that the prey will grow exponentially in the absence of the predator : the prey are limited by predator. The second term describes the loss of prey due to predators. This loss is assumed to be proportional to both the numbers of prey and predators, resulting in what is often described as a mass-action term. Turning to the right hand side of equation (6.1b), we see that the loss of prey heads to the production of new predators, and that the predator population decreases exponentially in the absence of prey. The system of equations (6.1) cannot be solved analytically, but we can obtain some information about the behaviour of its solutions by studying the orbits or trajectories of solutions in the (x, y) plane. Eliminating t from the Lotka-Volterra equations (6.1), we have

$$\frac{dy/dt}{dx/dt} = \frac{dy}{dx} = \frac{y(-\mu + cx)}{x(\lambda - by)}$$

We may solve this equation by separation of variables

$$\int \left(\frac{-\mu + cx}{x} \right) dx = \int \left(\frac{\lambda - by}{y} \right) dy$$

or $-\mu \log x - \lambda \log y + ex + by = h$

where h is a constant of integration. Let us write

$$V(x,y) = -\mu \log x - \lambda \log y + cx + by \qquad \dots \quad (6.2)$$

So that the orbit of the system is given by

$$V(x,y) = h \qquad \qquad \dots \quad (6.3)$$

The minimum of the function V(x, y) is given by $\frac{\partial V}{\partial x} = 0$ and $\frac{\partial V}{\partial y} = 0$, that is, by

$(x,y) = \left(\frac{\mu}{c}, \frac{\lambda}{b} \right)$. This is also the equilibrium position (x^*, y^*) of the Lotka-Volterra

system (6.1), that is, $x^* = \frac{\mu}{c}, y^* = \frac{\lambda}{b}$.

So $V(x,y)\big|_{min} = V(x,y)\big|_{\substack{x-x^* \\ y-y^*}} = -\mu \log \frac{\mu}{c} - \lambda \log \frac{\lambda}{b} + \mu + \lambda = h_o$

Every orbit of the system is given implicitly by an equation V(x, y) = h for some

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constant $h \geq h_o$, which is determined by some initial conditions. We make the change of variables :

$$x = x^* + u = \frac{\mu}{c} + u$$

$$y = y^* + v = \frac{\lambda}{c} + v$$

Then $V(x, y)$ becomes,

$$V(x, y) = -\mu \log\left(\frac{\mu}{c} + u\right) - \lambda \log\left(\frac{\lambda}{b} + v\right)$$

$$+ c\left(\frac{\mu}{c} + u\right) + b\left(\frac{\lambda}{b} + v\right) = h$$

We observe that

$$\log\left(\frac{\mu}{c} + \mu\right) = \log\frac{\mu}{c} + \log\left(1 + \frac{cu}{\mu}\right)$$

If $(h - h_o)$ is small, we may use the approximation $\log(1 + x) \sim = x - \frac{x^2}{2}$ so that, we have

$$\log\left(\frac{\mu}{c} + u\right) = \log\frac{\mu}{c} + \frac{cu}{\mu} - \frac{c^2 u^2}{\mu^2}$$

$$\log\left(\frac{\lambda}{b} + v\right) = \log\frac{\lambda}{b} + \frac{bu}{\lambda} - \frac{b^2 c^2}{\lambda^2}$$

Then the orbits $V(x, y) = h$ are approximated by

$$-\mu \log\frac{\mu}{c} - cu + \frac{c^2}{\mu}u^2 - \lambda \log\frac{\lambda}{b} - bv + \frac{b^2}{\lambda}v^2 + \mu + cu + \lambda + bv = h$$

or, $$\left(\frac{c^2}{\mu}\right)u^2 + \left(\frac{b^2}{\lambda}\right)v^2 = h + \mu \log\frac{\mu}{c} + \lambda \log\frac{\lambda}{b} - \mu - \lambda = h - h_o ... \qquad (6.4)$$

which represents an ellipse (if $h > h_o$) with equilibrium $(x^*, y^*) = \left(\frac{\mu}{c}, \frac{\lambda}{b}\right)$ as its centre.

This shows that for $(h - h_o)$ small and positive the orbits are closed curves around the equilibrium point, since the solutions run around closed orbit they must be periodic. It is easy to see that the maximum prey population comes one quarter of a cycle

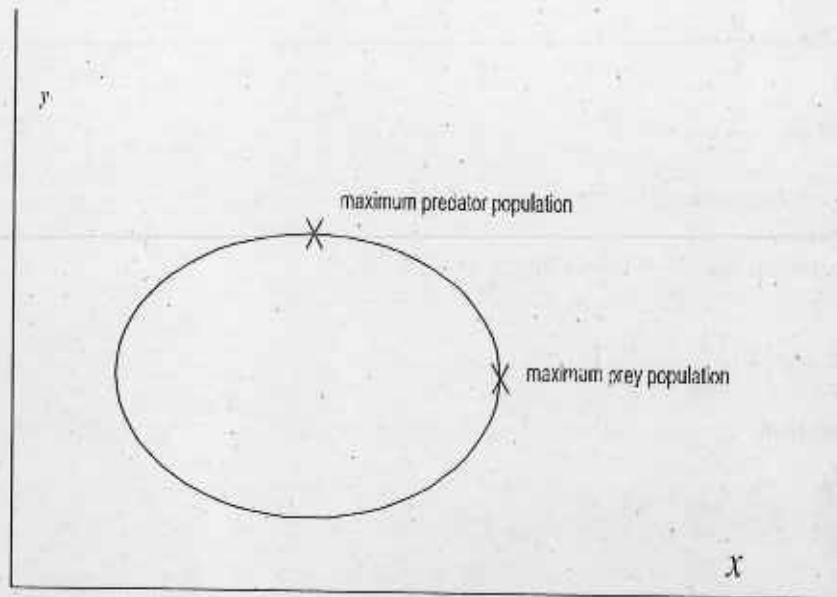before the maximum predator population (see Fig. 6.1).

Figure : 6.1

Historical Background :

How did this model (Volterra model) arise ? In the mid-1920s Umberzto D'Ancona, an Italian marine biologist, performed a statistical analysis of the fish that were sold in the markets of Trieste, Fiume and Venice between 1910 and 1923. Fishing was largely suspended in the upper Adriatic during the First World War, from 1914 to 1978. D'Ancona observed the increase of relative frequency of some species like Selachians (old name of Sharks and Shark - like fish) during the war years and decrease with the increase of fishing. The relative abundance of prey, in turn, followed the opposite pattern. Why did this happen? At that time Umberto was engaged to Luisa Volterra an ecologist. Umberto posed this question to Vito Volterra, his future father-in-law and a famous mathematician. Volterra (1926) constructed a model known as Lotka-Volterra model (because A. J. Lotka (1925) constructed a similar model in a different context about the same time) based on the assumption of that fish and sharks were in predator-prey relationship.

Example (6.1): Show that the period of Oscillation of prey and predator population sizes of Lotka-Volterra system is $2\pi/\lambda\mu$

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Solution : Linearing the system of equation (6.1) about the non-trivial equilibrium $\left({}^{u}\!/_{c}, {}^{1}\!/_{b}\right)$ we have the linear equations

$$\frac{du}{dt} = -\frac{b\mu}{c} V \qquad \qquad \dots \qquad (6.5a)$$

$$\frac{dv}{dt} = -\frac{\lambda c}{b} u \qquad \qquad \dots \qquad (6.5b)$$

It is easy to combine both the equations (6.5a) and (6.5b) to give

$$\frac{d^2 u}{dt^2} = -\lambda \mu\ u \qquad \qquad \dots \qquad (6.6)$$

which is the equation of a simple-harmonic Osillator with frequency $\frac{2\pi}{\lambda\mu}$.

6.2.2 Predator-Prey System : A Realistic Model

The Lotka-Volterra model represented one of the triumphs of early attempts at mathematical modelling in population biology. The dynamics of predator-prey system modelled by Volterra is interesting, but it is unrealistic and there are some flaws in the model. The model is structurally unstable and is extremely sensitive to perturbation. A small change in the initial population size may produce a change to a different periodic orbit, while the addition of a perturbing term to the system of differential equation may eliminate the balanced neutrally stable family of periodic orbits that we have observed. We, therefore, need to look at other predator-prey models.

We now consider a more realistic model of predator-prey system by assuming that in the absence of predators, the prey species grow logistically

$$\frac{dN}{dT} = rN\left(1 - \frac{N}{k}\right) - cNP \qquad \qquad \dots \qquad (6.7)$$

$$\frac{dN}{dT} = bNP - mP$$

where N is the prey-population size, P that of predators, we have written time as T (rather than t) because we will soon rescale this variable. To ease the analysis, we non-dimensionalize all the variables step and by step.

We use the first dimensionless variable

$$x = \frac{N}{K} \qquad \qquad : \qquad \dots \qquad (6.8)$$

Then the system (6.7) becomes

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$$\frac{dx}{dT} = rx(1-x) - cxP \qquad \qquad \cdots \qquad (6.9a)$$

$$\frac{dP}{dT} = bkxP - mP \qquad \qquad \cdots \qquad (6.9b)$$

To simplify (6.9b), we use the dimensionless variable

$$y = \frac{c}{r}p \qquad \qquad \cdots \qquad (6.10)$$

and eliminate P, to have

$$\frac{dx}{dT} = rx(1-x-y) \qquad \qquad \cdots \qquad (6.11a)$$

$$\frac{dy}{dT} = bkxy - my \qquad \qquad \cdots \qquad (6.11b)$$

Finally, we write $t = r\,T$ $\qquad \qquad \cdots \qquad (6.12)$

and note that $\dfrac{d}{dt} = \dfrac{d}{dt}.\dfrac{d}{dt} = r\dfrac{d}{dt}$ $\qquad \cdots \qquad (6.13)$

Then the system of equations (6.11a) and (6.11b) takes the form

$$\frac{dx}{dt} = x(1-x-y) \qquad \qquad \cdots \qquad (6.14a)$$

$$\frac{dy}{dt} = \frac{bk}{r}y\left(x - \frac{m}{bk}\right) \qquad \qquad \cdots \qquad (6.14b)$$

we write $\alpha = \dfrac{m}{bk}$, $\beta = \dfrac{bk}{r}$ $\qquad \qquad \cdots \qquad (6.15)$

With these, we have the system of equations

$$\frac{dx}{dt} = x(1-x-y) \qquad \qquad \cdots \qquad (6.16a)$$

$$\frac{dx}{dt} = \beta(x-\alpha)y \qquad \qquad \cdots \qquad (6.16b)$$

The simplified model (6.16) has three equilibria : $(x^*, y^*) = (0, 0), (1, 0), (\alpha, 1-\alpha)$. These equilibria occur at the intersections of the prey and predator zero growth isoclines*. [see Fig. (6.2)]
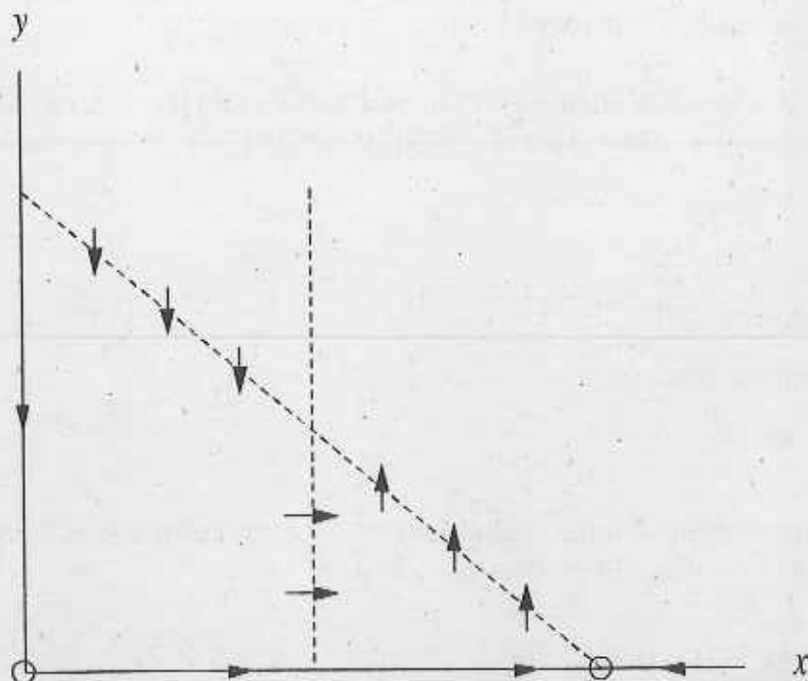
Fig. (6.2) : Predator and Prey zero growth isoclines.

[Zero-growth isoclines are the curves in the (x, y) plane or phase-plane along which $\dfrac{dx}{dt} = 0$ and $\dfrac{dy}{dt} = 0$. These curves should properly be called nullclines.]

The community matrix of the system (6.16) is

$$A = \begin{bmatrix} 1-2x-y & -x \\ \beta & \beta\,(x \neq \ ) \end{bmatrix}_{(x^*,y^*)}$$

At $(x^*, y^*) = (0, 0)$ the community matrix is

$$A = \begin{bmatrix} 1 & 0 \\ 0 & -\beta\alpha \end{bmatrix} \qquad \qquad \dots \quad (6.18)$$

Eigenvalues $\lambda = 1, -\beta\alpha$

Let det $A = -\beta\alpha < 0$. So $(0, 0)$ is a saddle point (Fig. 6.3). At $(x^*, y^*) = (1, 0)$, the community matrix is

$$A = \begin{bmatrix} -1 & -1 \\ 0 & \beta\,(1-\alpha\ ) \end{bmatrix} \qquad \qquad \dots \quad (6.19)$$

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Eigenvalues $= -1, \beta(1-\alpha)$, det $A = \alpha(\alpha - 1)$.

If $\alpha > 1$, det $A > 0$ which implies $(1, 0)$ to be a stable node. If $\alpha < 1$, det $A < 0$ which implies $(1, 0)$ to be a saddle point (Fig. 6.4) At $(x^*, y^*) = (\alpha, 1 - \alpha)$, the community matrix is

$$A = \begin{bmatrix} -\alpha & -\alpha \\ \beta(1-\alpha) & 0 \end{bmatrix} \qquad \qquad \dots \quad (6.20)$$

The characteristic equation is

$$\lambda^2 + \alpha\lambda + \alpha\beta(1-\alpha) = 0 \qquad \qquad \dots \quad (6.21)$$

By Routh-Hurwitz criterion the equilibrium $(\alpha, 1 - \alpha)$ is stable if $\alpha < 1$ end unstable if $\alpha > 1$ (Fig. 6.5). The eigenvalues are given by

$$\lambda = \frac{-\alpha \pm \{\alpha^2 - 4\alpha\beta(\alpha - 1)\}^{1/2}}{2} \qquad \qquad \dots \quad (6.22)$$

If we examine the discriminant, we see that we have a node if

$$\alpha > \frac{4\beta}{1 + 4\beta} \qquad \qquad \dots \quad (6.23)$$

and a focus if

$$\alpha < \frac{4\beta}{1 + 4\beta} \qquad \qquad \dots \quad (6.23)$$

The model does not show any periodic orbits — in contrast to classical Lotka-Volterra system. The addition of a small amount of prey-density dependence has destroyed the family of periodic orbits that we have observed in the classical Lotka-Volterra model. It leads to the conclusion that the classical Lotka-Volterra system is structurally unstable.
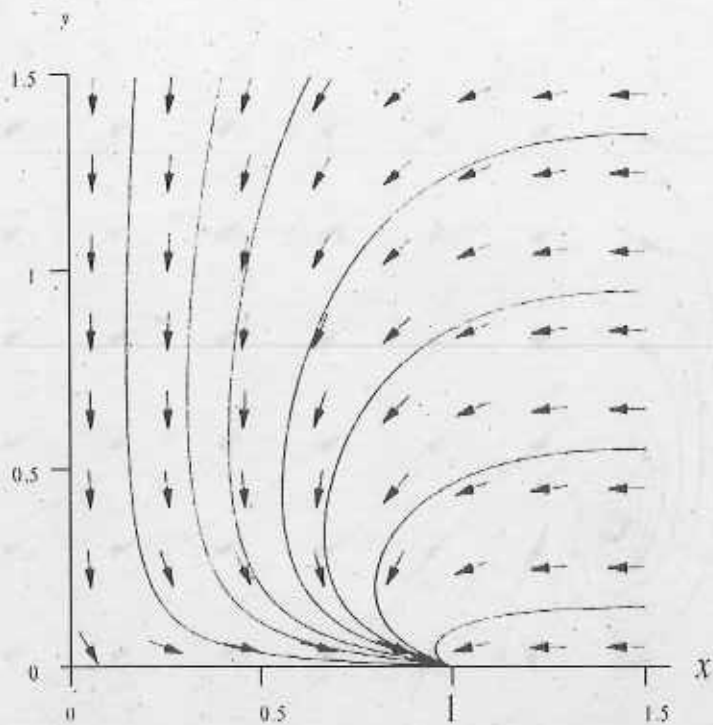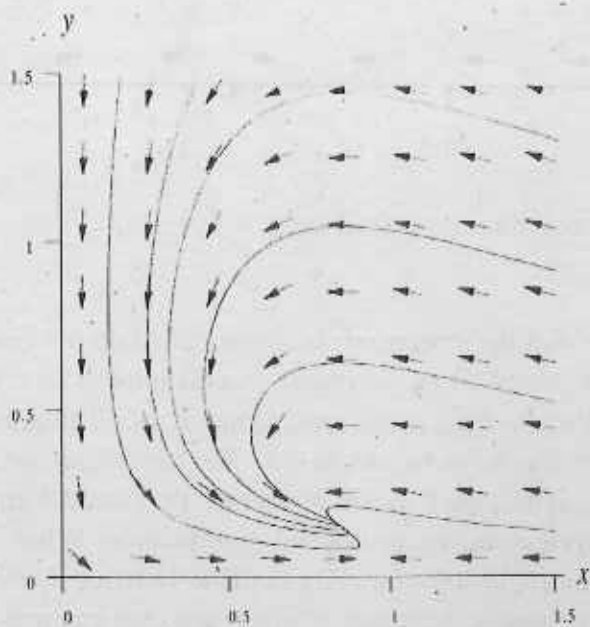
Fig. 6.3 Phase portrait for a > 1.

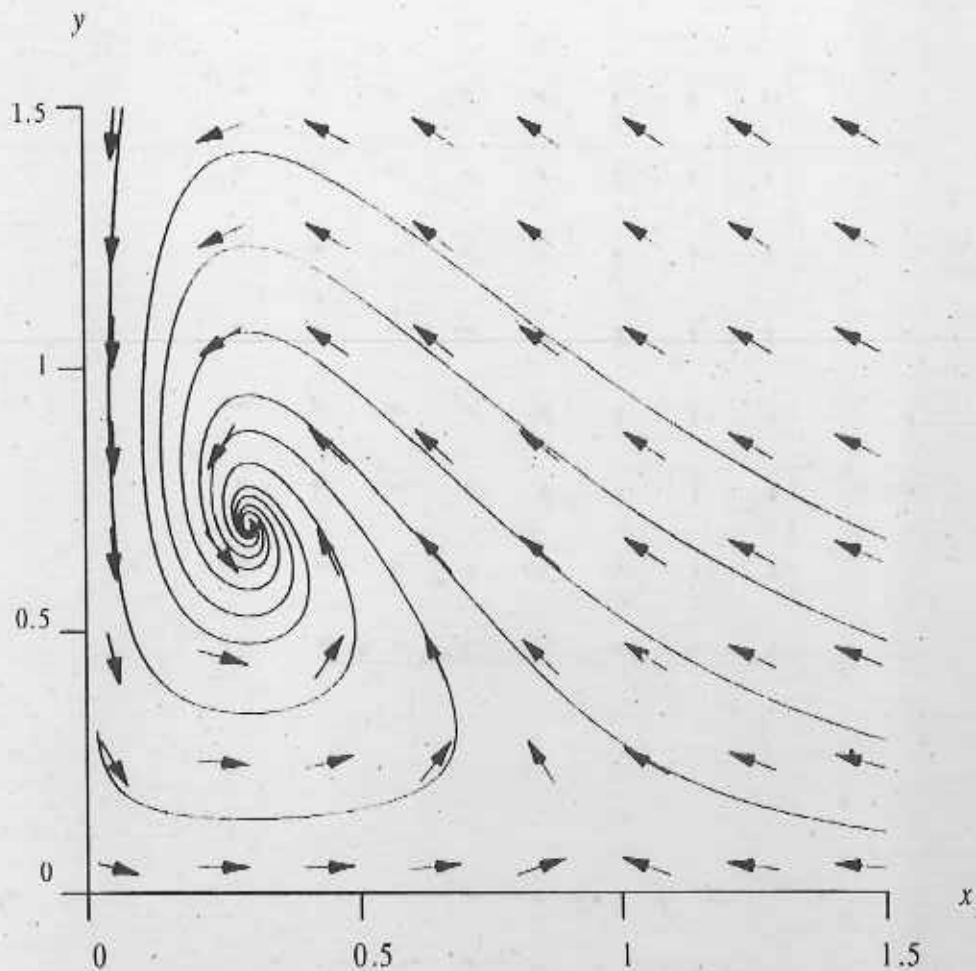Fig. 6.4 Phase portrait for a < 1, a > 4β/(1+4)

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Fig. 6.5 Phase portrait for $a < 1$, $a < 4\beta(1+4)$

Example (6.2) : Show that the system of equations (6.16) do not contain any periodic solution in the first quadrant of (x, y) plane, (see example (5.1), Chapter-V).

Remarks : Predator-Prey system is the most dynamic of all interacting populations. There are many other things to be discussed. We have discussed the criterion of periodic orbit and its significance in the predator - prey model equations. We have not discussed limit cycles and its ecological significance. What biological factors create limit cycles? The inclusion of a more realistic functional response is one such factor. The functional response is the rate at which predator captures prey. Heretofore, the functional response was a linearly increasing function of prey density. However,

predator may become satiated. They may also be limited by the handling time of catching and consuming their prey. This limit on the predator's ability can have a profound effect on the dynamics of a predator-prey model. There are four different functional response curves. Predator - Prey models with functional responses can exhibit limit cycles, bifurcation and chaotic behaviour in the dynamics of the systems. These are, however beyond the introductory course.

Example (6.3) :

Determine the qualitative behaviour of a predator-prey system modelled by

$$\frac{dx}{dt} = x\left(1 - \frac{x}{30}\right) - \frac{xy}{x+10}$$

$$\frac{dy}{dt} = y\left(\frac{xy}{x+10} - \frac{1}{3}\right)$$

Solution :

We have studied this system in Example (5.2) of Chapter - V and shown that every orbit approaches a periodic orbit around the (unstable) equilibrium (5, 12.5). Thus the species co-exist with oscillations.

Exercises :

(1) Determine the equilibrium behaviour of a predator-prey system modelled by

$$\frac{dy}{dt} = y\left(\frac{x}{x+10} - \frac{3}{5}\right)$$

$$\frac{dx}{dt} = x\left(1 - \frac{x}{13}\right) - \frac{xy}{x+10}$$

(2) Show that the equilibrium (x^*, y^*) with $x^* > 0$, $y^* > 0$ of the predator-prey model

$$\frac{dx}{dt} = rx\left(1 - \frac{x}{k}\right) - \frac{axy}{x+A}$$

$$\frac{dy}{dt} = sy\left(\frac{ax}{x+A} - \frac{aB}{A+B}\right)$$

is unstable if $k > A + 2B$ and asymptotically stable if $B < k < A + 2B$.

(3) Investigate the stability of the equilibrium of the chemostat modelled by the equations

$$\frac{dy}{dt} = \frac{acy}{C+A} - ay$$

$$\frac{dc}{dt} = q(c^{(b)} - c) - \frac{\beta\, acy}{C+A}$$

where y is the number of bacteria and c is the concentration of nutrient in the chemostat.

6.3 ❑ Competition Models

6.3.1 Lotka-Volterra Classical Competition Model

We consider the classical model of competition due to Lotka and Volterra. The Lotka-Volterra competition model is an interference competition model : two species are assumed to diminish each others per capita growth rate by competition.

We begin with two species, with population sizes $x_1(t)$ and $x_2(t)$ at any time t. We assume that each species grows logistically in the absence of the other. The model equatiors are

$$\frac{1}{x_1}\frac{dx_1}{dt} = r_1\left(1 - \frac{x_1}{k_1} - \frac{\alpha_{12}}{k_1}x_2\right) \qquad \text{... (6.25a)}$$

$$\frac{1}{x_2}\frac{dx_2}{dt} = r_2\left(1 - \frac{x_2}{k_2} - \frac{\alpha_{21}}{k_2}x_1\right) \qquad \text{... (6.25b)}$$

Each individual of the second species causes a decrease in the per capita growth of the first species; and vice versa. To parameterize this effect, we have introduced a pair of competition coefficients α_{12} and α_{21}, that describe the strength of the effect of the species 2 on the species 1 and of species 1 on the species 2 respectively. The system of equations (6.25) can be rewritten as

$$\frac{dx_1}{dt} = \frac{r_1}{k_1}x_1(k_1 - x_1 - \alpha_{12}x_2) \qquad \text{... (6.26a)}$$

$$\frac{dx_2}{dt} = \frac{r_1}{k_2}x_2(k_2 - x_2 - \alpha_{21}x_1) \qquad \text{... (6.26b)}$$

The complete characterization of the dynamics of the equations (6.26) revolves around the orientations of zero-growth isoclines. The x_2 – zero growth isoclines given by $\frac{dx_2}{dt} = 0$, are

$$x_2 = 0 \qquad \text{... (6.27a)}$$

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and $x_2 = k_2 - a_{21}x_1$ ...   (6.27b)

[see Fig. (6.6)]. Below the line given by (6.27b), x_2 increases; above this line, x_2 decreases. The x_1 - zero growth isoclines in turn, given by $\dfrac{dx_1}{dt} = 0$, are

$$x_1 = 0 \quad\quad\quad\quad ... \quad\quad (6.28a)$$

and $x_1 = k_1 - a_{12}x_2$ ...   (6.28b)

Below the line given by (6.28b), x_1 increases; above this, x_1 decreases (see Fig. 6.6)
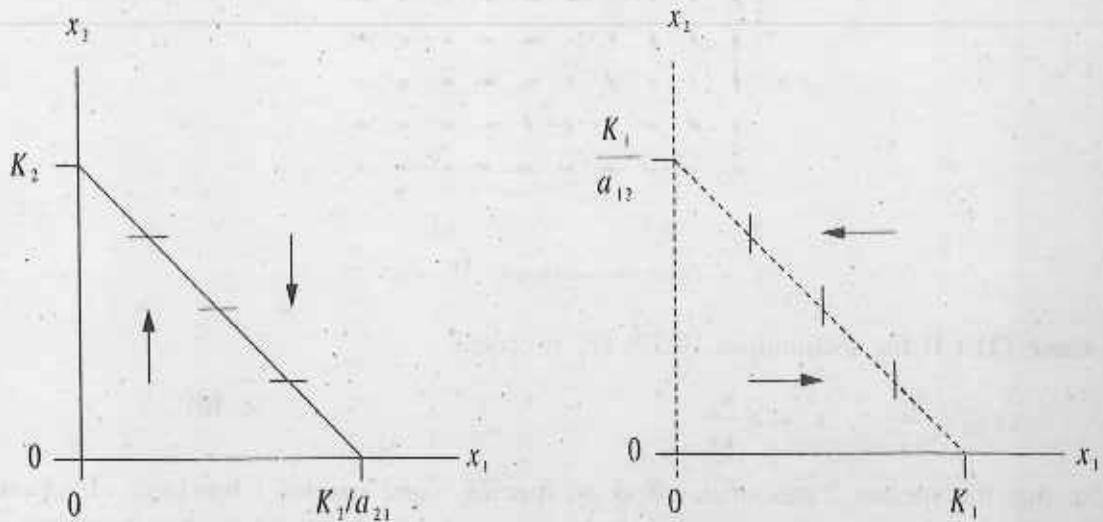

Fig. 6.6 : Zero-growth isoclines.

One of the isoclines (6.27b) and (6.28b) may be entirely above the other. Alternatively they may cross each other. There are four classes, depending on the relative position of x_1 and x_2 intercepts of these two zero growth isoclines. Each case corresponds to a different phase-portrait. Let us consider each one in turn.

Case (1) : If each intercept of the lines given by (6.27b) is greater than the corresponding intercept of that for (6.28b), so that

$$k_2 > \frac{k_1}{a_{12}} \quad \text{or} \quad a_{12} > \frac{k_1}{k_2}$$

$$\frac{k_2}{a_{21}} > k_1 \quad \text{or} \quad a_{21} < \frac{k_2}{k_1} \quad\quad ... \quad (6.29)$$

x_2 excludes x_1 [see Fig. 6.7]. Thus, if species 2 has a relatively large effect on species 1 and species 1 has a relatively small effect on species 2, we expect that the species 1 will go extinct and the species 2 will approach its carrying capacity.
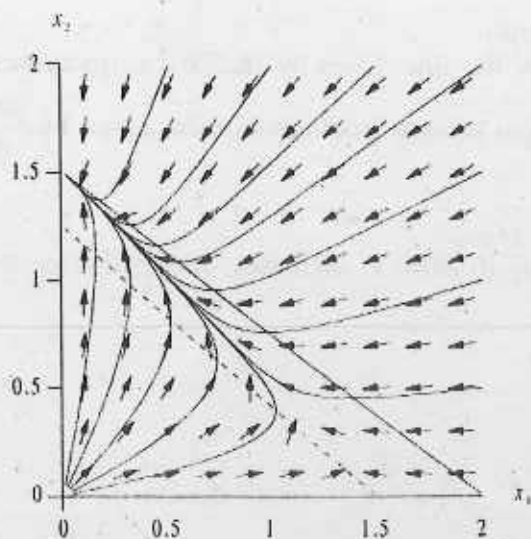
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Fig. 6.7 Phase portrait for $a_{12} > \dfrac{K_1}{K_2}$, $a_{21} < \dfrac{K_2}{K_1}$.

Case (2) : If the inequalities (6.29) are reversed

$$\alpha_{12} < \frac{k_1}{k_2} \quad , \quad \alpha_{21} > \frac{k_2}{k_1} \qquad \qquad \dots \quad (6.30)$$

so that the species 2 has small effect on species 1 and species 1 has large effect on species 2, the competitive outcome is also reversed : species 1 approaches its carrying capacity and species 2 goes to extinction (see Fig. 6.8).
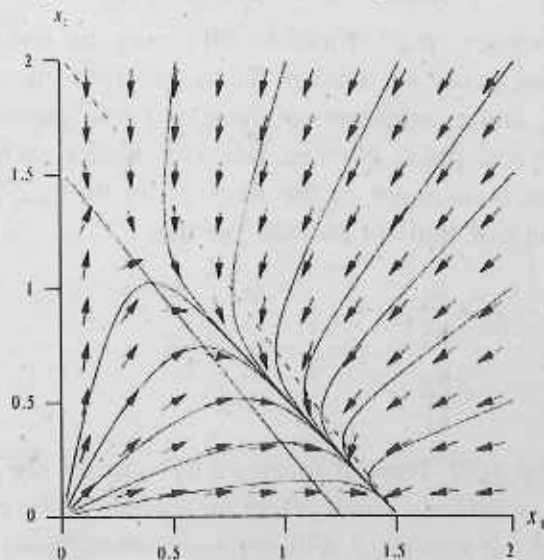

Fig. 6.8 Phase portrait for $a_{12} < \dfrac{K_1}{K_2}$, $a_{21} > \dfrac{K_2}{K_1}$.

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Case (3) : If $\alpha_{12} > \dfrac{k_1}{k_2}$, $\alpha_{21} > \dfrac{k_2}{k_1}$ ... (6.31)

In this case both the isoclines cross each other. In this case interspecific effects are large for both species. Two equilibria $(k_1, 0)$ and $(0, k_2)$ corresponding to the exclusions of one or the other species, are now both stable nodes (see Fig. 6.9). One or the other of the species will go extinct, depending on the initial conditions. There is a saddle point that lies between the two nodes.

Case (4) : If $\alpha_{12} < \dfrac{k_1}{k_2}$, $\alpha_{21} < \dfrac{k_2}{k_1}$ ... (6.32)

the equilibria $(k_1, 0)$ and $(0, k_2)$ are unstable saddle points and trajectories are drawn towards a stable node in the interior of the first quadrant. (Fig. 6.10).
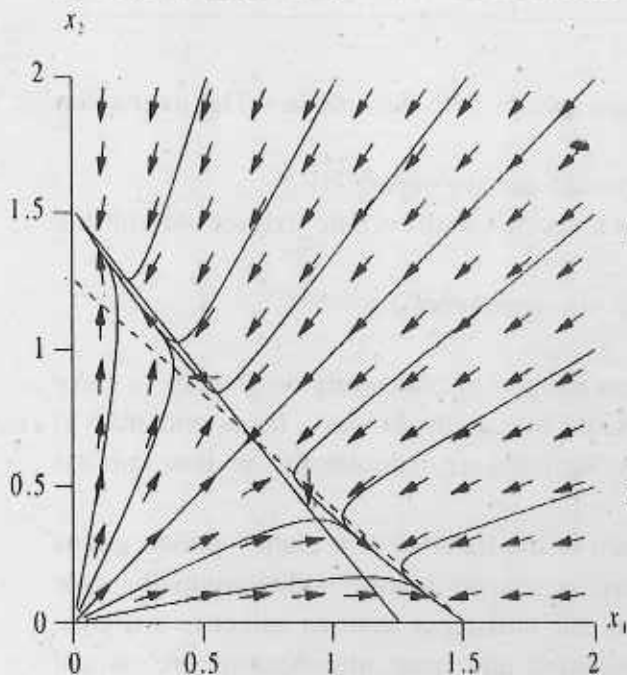

fig. (6.9) : $\alpha_{12} > \dfrac{k_1}{k_2}$

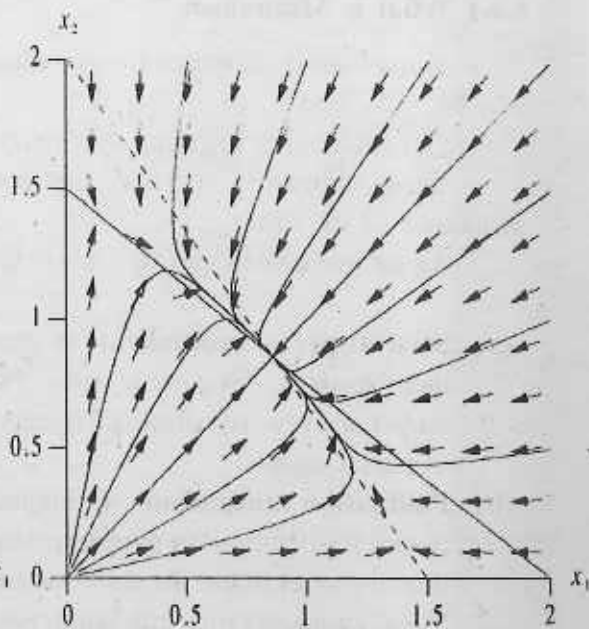$\alpha_{21} > \dfrac{k_2}{k_1}$

fig. (6.10) : $\alpha_{12} < \dfrac{k_1}{k_2}$

$\alpha_{21} < \dfrac{k_2}{k_1}$

Example (6.5) : For the competition model (6.26) show that there is no closed orbits (or periodic solution) within the first quadrant of (x_1, x_2) - plane.

Solution : Recall Bendixson - Dulac negative criterion. Let $B(x_1, x_2) = \dfrac{1}{x_1 x_2}$ Since the divergence

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$$\frac{\partial}{\partial x_1}(Bx_1) + \frac{\partial}{\partial x_2}(Bx_2) = -\frac{r_1}{k_1}\frac{1}{x_1} - \frac{r_2}{k_2}\frac{1}{x_2} \qquad \dots \quad (6.23)$$

is strictly negative in the interior of the first quadrant, we can be sure that there are no closed orbits (or periodic solutions) contained entirely within the first quadrant.

For three out of the four cases we have considered, one species successfully excludes the other. Only in case (4), where interspecific effects were weak relative to intraspecific effects, did the two species coexist. This is the basis for Gause's "Principle of Competitive Exclusion". The experimental evidence is somewhat equivocal and there is considerable doubt about the universability of the principle.

6.4 Mutualism Models

6.4.1 What is Mutualism

Mutualism is an interaction in which species help one another. The interaction may be

    (i) facultative meaning that two could survive separately

or (ii) obligatory, meaning that each species will become extinct without the assistance of the other.

    Again mutualism can be classified into four types :

(a) **Seed-dispersal mutualism** : A great number of plants rely on animals to carry their seeds to favourable sites. Plants frequently produce fruits and nuts to attract and rewards dispersal agents. Squirells are undoubtedly the most familiar dispersal agents.

(b) **Pollination mutualism** : Pollination is the transfer of a plants' pollen grains before fertilization. In gymnosperms, the transfer is from pollen producing cone directly to an ovule. In angiosperms, the transfer is from an anther to a stigma. Most gymnosperms are wind pollinated and most angiosperms are animal pollinated. Angiosperm flowers often reward pollinators with nectar.

(c) **Digestive mutualism** : The guts of many animals are filled with bacteria, yeast and protozoa that help to breakdown food. Often, the host is unable to digest the food on its own. Cattle, deer and sheep rely on bacteria to breakdown plant cellulose and hemi cellulose into digestive sub-units.

(d) **Protection mutualism** : In 1874, the famous naturalist, Thomas Belt, described a remarkable mutualism - between ants and acacias. The genus Acacia contains a large number of trees and shrubs native to warm parts of both hemispheres.

Many of the plants in this genus house, support and employ ants. The ants guard the acacia against hervivores predators.

6.4.2 Lotka-Volterra Model of Mutualism :

Let us consider a simple model for a one-to-one facultative mutualism. This will be followed by obligatory mutualism. These two models are Lotka-Volterra competition models equation in which the negative competitive interactions has been turned into positive mutualistic interaction.

Let us consider a system of two species with population sizes (or densities) x_1 and x_2. Each species grows logistically in the absence of the other. Each species has per capita growth rate that decreases linearly with size (or density)

$$\frac{1}{x_1}\frac{dx_1}{dt} = r_1\left(1 - \frac{x}{k}\right) \qquad \ldots \quad (6.34a)$$

$$\frac{1}{x_2}\frac{dx_2}{dt} = r_2\left(1 - \frac{x_2}{k_2}\right) \qquad \ldots \quad (6.34b)$$

The introduction of mutualism between the species leads to the equations.

$$\frac{1}{x_1}\frac{dx_1}{dt} = r_1\left[1 - \frac{(x_1 - \alpha_{12}x_2)}{k_1} - \right] \qquad \ldots \quad (6.35a)$$

$$\frac{1}{x_2}\frac{dx_2}{dt} = r_2\left[1 - \frac{(x_2 - \alpha_{21}x_1)}{k_2} - \right] \qquad \ldots \quad (6.35b)$$

where the parameters α_{21} and α_{12} measure the strength of positive effect of species 2 on species 1 and of species 1 on species 2 respectively. The system of equations (6.35a) and (6.35b) can be written as

$$\frac{dx_1}{dt} = \frac{r_1}{k_1}x_1(k_1 - x_1 + \alpha_{12}x_2) \qquad \ldots \quad (6.36a)$$

$$\frac{dx_2}{dt} = \frac{r_2}{k_2}x_2(k_2 - x_2 + \alpha_{21}x_1) \qquad \ldots \quad (6.36b)$$

This is a model of facultative mutualism so far as

$$r_1 > 0, r_2 > 0. \ k_1 > 0, k_2 > 0 \qquad \ldots \quad (6.37)$$

Each species can, in other words, survive without its mutualist.
Let us look at the zero-growth isoclines for this system. The x_2 - zero growth isoclines given by $\frac{dx_2}{dt} = 0$ are

$$x_2 = 0 \qquad \qquad \qquad \cdots \quad (6.38a)$$
$$\text{and} \quad x_2 = k_2 + a_{21} x_1 \qquad \qquad \cdots \quad (6.38b)$$
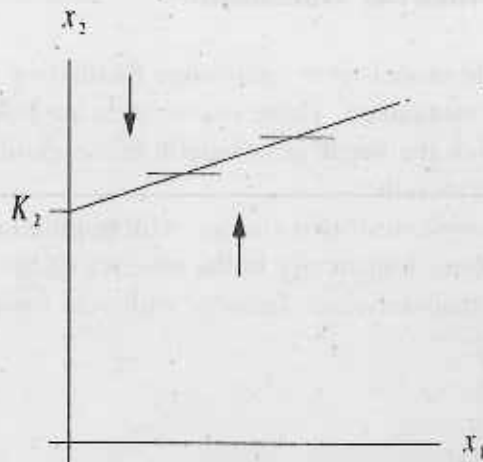
[see Fig. (6.11)].

Fig. (6.11): x_2 - zero growth isoclines, $k_2 > 0$.

Below line (6.38b), x_2 increases; above this line, x_2 decreases.

The x_1 - zero growth isoclines given by $\dfrac{dx_1}{dt} = 0$, are

$$x_1 = 0 \qquad \qquad \qquad \cdots \quad (6.39a)$$
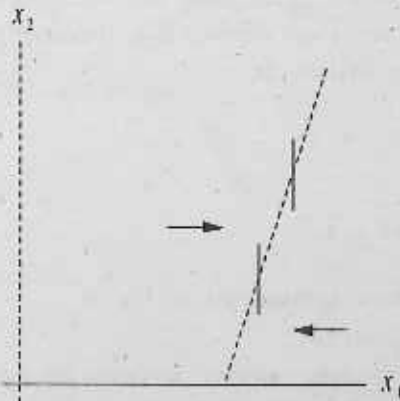$$\text{and} \quad x_1 = k_1 + a_{12} x_2 \qquad \qquad \cdots \quad (6.39b)$$
(see Fig. 6.12)

Fig. 6.12 : x_1 zero-growth isoclines; $k_1 > 0$.

To the left of line (6.39b), x_1 increases; to the right of this line, x_1 decreases. The

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zero-growth isoclines (6.38b) and (6.39b) may either converge or divergence. They converge if

$$\frac{1}{\alpha_{12}} > \alpha_{21}$$

or $\alpha_{12}\alpha_{21} > 1$ ...   (6.40)

In this case, the two isoclines cross each other and orbits approach a stable node in the interior of the first quadrant (see Fig. 6.13). Since the slopes of the zero-growth isoclines are positive, the coordinates of this equilibrium are greater than the carrying capacity k_1 and k_2; each species surpasses its carrying capacity because of its mutualist. If $\alpha_{12}\alpha_{21} < 1$ ...   (6.41)

zero-growth isoclines (6.38b) and (6.39b) diverges. Now, the zero-growth isoclines do not cross and there is no non-trivial equilibrium in the first quadrant. The population undergo unlimited growth (see Fig. 6.14) in what has been called "an orgy of mutual benefaction".
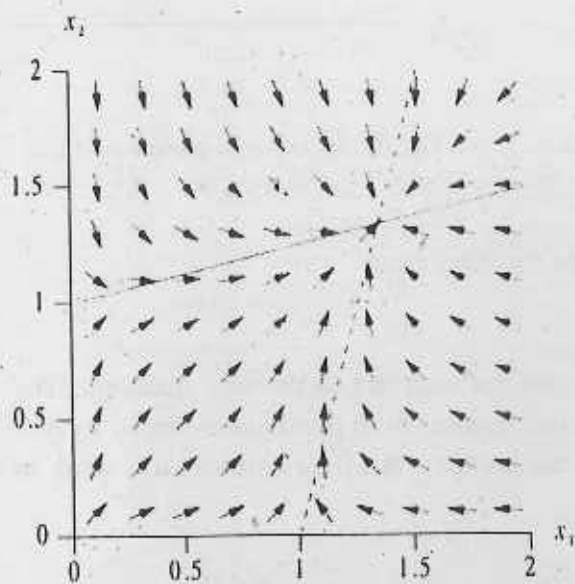
Fig. (6.13): Facultative mutuatism for $\alpha_{12}\alpha_{21} < 1$

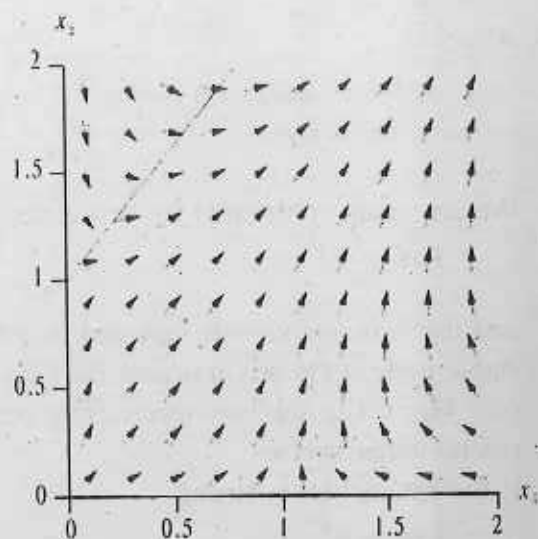Fig. (6.14): Facultative mutuatism for $\alpha_{12}\alpha_{21} > 1$

Equations (6.36a) and (6.36b) can be used as a model for obligate mutulism if we assume that

$$r_1 < 0 , r_2 < 0 . k_1 < 0 , k_2 < 0 \qquad ... \qquad (6.42)$$

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Neither species can now survive on its own; each species is banking on the other to save it. Equations (6.38) and (6.39) are still the correct equations for x_2 and x_1 zero-growth isoclines. However, since k_1 and k_2 are negative, the lines (6.38b) and (6.39b) look rather different [see Fig. 6.15 and 6.16]
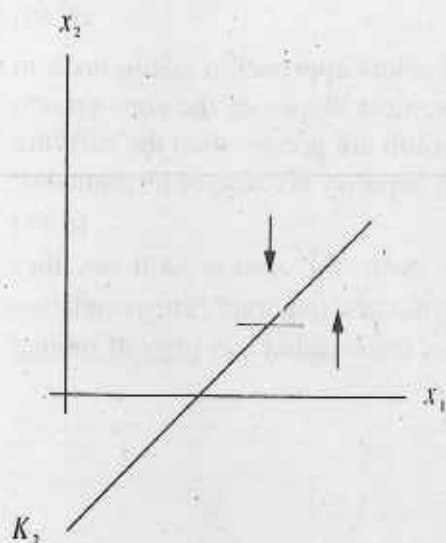

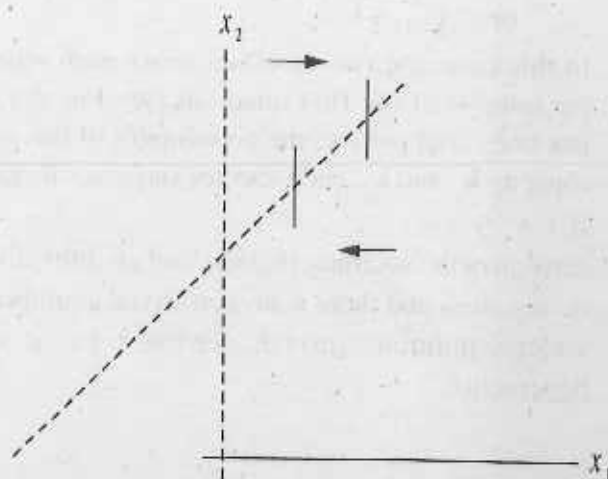Fig. (6.15) : x_2 zero-growth isoclines.
$$k_2 < 0$$

Fig. (6.16) : x_1 zero-growth isoclines.
$$k_1 < 0$$

We are again confronted by two cases. In the first case

$$\alpha_{12}\,\alpha_{21} < 1 \qquad\qquad \dots \quad (6.43)$$

and the two isoclines (6.38b) and (6.39b) do not intersect in the first quadrant. The stable node at the origin is now the only equilibrium. Both populations decay to zero (see Fig. 6.17). the two species rely on one another, but interaction is too weak to rescue either species.

If the interaction is strong

$$\alpha_{12}\,\alpha_{21} > 1 \qquad\qquad \dots \quad (6.44)$$

the isoclines (6.38b) and (6.39b) do intersect in the first quadrant (see Fig. 6.18). There is now a saddle point in the first quadrant. If mutualist densities are low, both populations go extinct : the interaction is strong but there are too few mutualists to rescue either population. If mutualist densities are high, both species increase in another "orgy of mutual benefaction". Orbit now divergence to infinity
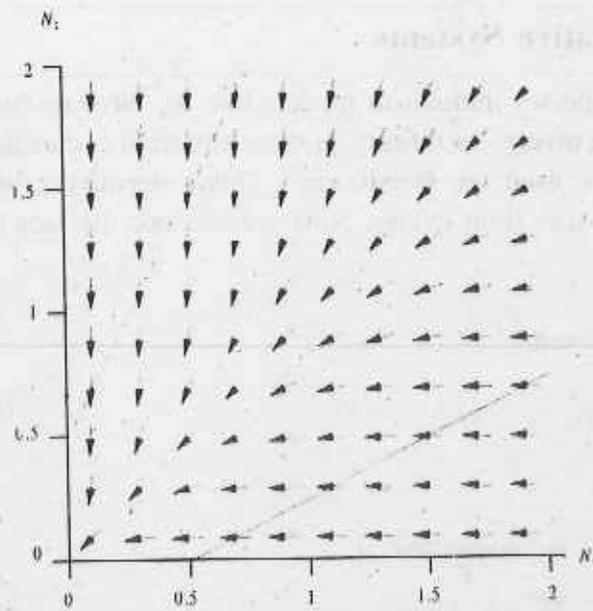
[see Fig.6.18]

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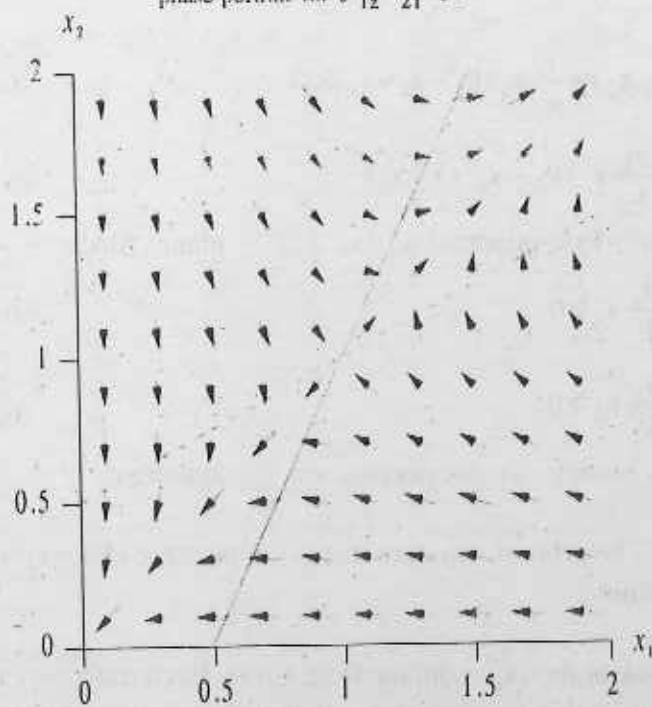Fig. (6.17): Obligate mutualism phase
phase-portrait for $\theta_{12} \theta_{21} < 1$

Fig. (6.18) Obligate mutualism phase
phase-portrait for $\theta_{12} \theta_{21} > 1$

6.4.3 ☐ Cooperative Systems

All orbits of two-species mutualism models that we have discussed appear to tend to equilibrium or to diverge to infinity. Is there any limit cycles that we have missed? Previously we have used the Bendixson - Dulac negative criterion to prove that systems do not possess limit cycles. Now we can use the fact that our models are cooperative.

Definition : The system

$$\frac{dx_1}{dt} = f(x_1, x_2)$$ ... (6.45a)

$$\frac{dx_2}{dt} = g(x_1, x_2)$$ ... (6.45b)

defined on $D \subset R^2$, is cooperative if

$$\frac{\partial f}{\partial x_2} \geq 0 \quad , \quad \frac{\partial g}{\partial x_1} \geq 0$$ ... (6.46)

for all $(x_1, x_2) \in D$

Example (6.6) :

Let $$f(x_1, x_2) = \frac{r_1}{k_1} x_1 (k_1 - x_1 + \alpha_{12} x_2)$$ ... (6.47a)

$$g(x_1, x_2) = \frac{r_2}{k_2} x_2 (k_2 - x_2 + \alpha_{21} x_1)$$ ... (6.47b)

on the (invariant*) first quadrant x_1 (xi, x_2) — plane. Since

$$\frac{\partial f}{\partial x_2} = \alpha_{12} \frac{r_1}{k_1} x_1 \geq 0$$ ... (6.48a)

$$\frac{\partial g}{\partial x_1} = \alpha_{21} \frac{r_2}{k_2} x_2 \geq 0$$ ... (6.48b)

those mutualism models are cooperative on this quadrant.

Theorem (6.3) : The orbit of a system that is cooperative either converge to equilibria or diverge to infinity.

Proof : Let us look at the $(\dot{x}_1, \dot{x}_2)$ plane (Fig. 6.19). Each trajectory of a planer system generates an orbit in this $(\dot{x}_1, \dot{x}_2)$ plane. If the planer system that we are looking at is everywhere cooperative, the first quadrant of the $(\dot{x}_1, \dot{x}_2)$ plane is invariant*. To see

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this, we consider an orbit that attempts to leave the first quadrant by crossing the positive $\dot{x}_2$ - axis, In the light of the equation (6.45a) and our definition of cooperative system,

$$\frac{d}{dt}(\dot{x}_1) = \frac{d^2 x_1}{dt^2} = \frac{\partial f}{\partial x_1} \cdot \frac{dx_1}{dt} + \frac{\partial f}{\partial x_2} \cdot \frac{dx_2}{dt} \qquad \cdots \qquad (6.49a)$$

$$= \frac{\partial f}{\partial x_2} \cdot \frac{dx_2}{dt} > 0 \ (\text{since } \dot{x}_1 = \frac{dx_1}{dt} \text{ is zero on } \dot{x}_2 - \text{axis}) \qquad \cdots \qquad (6.49b)$$

on the positive $\dot{x}_2$ - axis. The orbit cannot cross the positive $\dot{x}_2$ - axis; for when the orbit crosses the positive $\dot{x}_2$ - axis, we must have $\dot{x}_1 = \frac{dx_1}{dt} = 0$ so that $\dot{x}_1$ can not. increase with time. By a similar argument the orbit can not cross the positive $\dot{x}_1$ - axis. Finally, the orbit cannot cross through the origin, since this would imply that the original trajectory passes through a rest point. Similar argument also shows that the third quadrant is also invariant*.

Ultimately (as $t \to \infty$) $\dot{x}_1$ and $\dot{x}_2$ are of constant sign. If we start in the first or third quadrant, we will stay there forever. If we start from the second or fourth quadrants, we may either stay in those quadrants or we may enter the first or third quadrants; which are invariants. Either way, x_1 and x_2 are ultimately monotonic function at time. This precludes limit cycles and implies that trajectoris either approach equilibria or diverge to infinity.
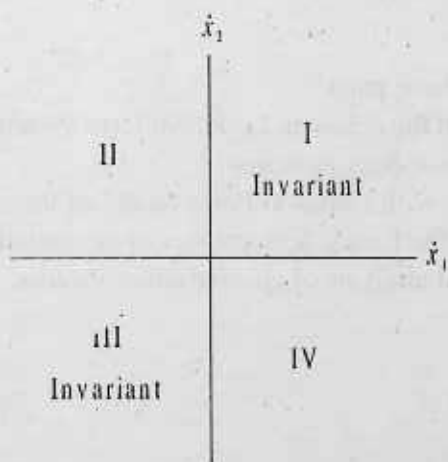
Fig. (6.19): $(\dot{x}_1, \dot{x}_2)$ plane

* A set (a region) is invariant if an orbit starting from this set (or region) will stay there forever.

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Exercises :

1. Determine the outcome of the competition the system

$$\frac{dx}{dt} = x(100 - 4x - y)$$

$$\frac{dx}{dt} = y(60 - x - y).$$

2. What is the outcome of a competition modelled by the system

$$\frac{dx}{dt} = x(2 - x - x^2 - y).$$

$$\frac{dy}{dt} = y(16 - 2x - x^2 - y).$$

3. For the mutualistic system

$$\frac{dx}{dt} = x(-20 - x + 2y)$$

$$\frac{dy}{dt} = y(-50 + x - 2y).$$

Find the equilibrium points and determine their stabilities.

6.5 ❑ Summary

This chapter consists of three parts' :

(i) The first one deals with the classical Lotka-Volterra system and the modification for a realistic model of predator-prey systems.

(ii) The second part deals with Lotka-Volterra model of the competition system,

(iii) The third deals with the Lotka-Volterra model of mutualism or symbiosis. It also includes the mathematical analysis of co-operative systems.

Unit ❑ 7 : Ecosystem Models

7.1 Introduction : Functional Groups

Objectives. The chapter consists of a brief account of dynamical modeling of ecosystems.

Structure:

Two useful tools of studying a natural system are the laws of conservation of energy and mass. The study of ecosystem form the point of view of energy-flow (or energeties) was advocated by Odum and Odum (1975). The early ecosystem models, which used energy as the currency were not successful everywhere. Although energy inflows to many systems can be estimated quite accurately, the outflows are, however, hard to define and measure precisely. More recent works reveal that the energy flows inside an ecosystem occur in the form of chemically bound energy and are thus accompanied by flows of elemental nutrients. The inflows and outflows of nutrients are more easier to define and measure than their energetic counterpart. Modern ecosystem models thus adopt one or more essential elements, usually carbon, nitrogen or phosphorus, as their 'currency'. For the study of the flow of nutrient we focus from populations to functional groups - that is, groups of species which cause the passage of nutrient from one place to another. For example, in a model of grassland ecosystem we might skate over wealth of biological details and differentiate only between plants which are edible by harvivores and those which are not.

7.2 Linear Food-chain : Constant Production

(i) One Level system :

We consider an ecosystem with a single functional group, which we shall call 'plants'. We take carbon biomass as our currency and write the current carbon biomass density of plants as $P(t)$ gc/m^2. We assume that photosynthesis produces new biomass at a rate ô gc/m^2/day and that a plant of carbon mass û loses carbon through mortality and respiration at a rate δ_pû gc/day. The dynamics of this very simple system is described by a single equation

$$\frac{dP}{dt} = \varphi - \delta_p P \qquad \qquad \cdots \qquad (7.1)$$

which has the steady-state,

$$P* = \frac{\varphi}{\delta_p} \qquad \qquad \cdots \qquad (7.2)$$

Thus the steady-state carbon density of plant (called steady-state standing stock) is given by the product of the primary production rate P and the average residence time of a carbon atom in a plant $\left(\frac{1}{\delta_p}\right)$. Let $P = P* + p$, p being the deviation from the steady-state value, then the equation (7.1) reduces to

$$\frac{dp}{dt} = -\delta_p p \qquad \qquad \cdots \qquad (7.3)$$

implying the stable steady-state for $\delta p > 0$.

(ii) Two-level System :

We now add a second functional group ('hervivores') to our ecosystem. Let $H(t)$ gc/m^2 be the carbon biomass density of these organisms. We assume that respiration and mortality remove hervivore carbon at a per-capita rate δ_h/day, that hervivores feed exclusively on plants, with a linear functional response characterized by an attack rate α_h m^2/day/gc. This implies that in the presence of plant carbon density P, a hervivore of weight α consumes plant carbon at a rate $\alpha_h P\varphi$ gc/day. The system dynamics is described by a pair of coupled differential equations

$$\frac{dP}{dt} = \varphi - \delta_p P + \alpha_h PH \qquad \qquad \cdots \qquad (7.4)$$

$$\frac{dH}{dt} = \alpha_h PH - \delta_h H \qquad \qquad \cdots \qquad (7.5)$$

This system has two steady-states :

$$P* = \frac{\delta_h}{\alpha_h}, \qquad H* = \frac{1}{\delta_h}(\varphi - \delta_p P*) \qquad \cdots \qquad (7.6)$$

$$P* = \frac{\varphi}{\delta_p}, \qquad H* = 0 \qquad \qquad \cdots \qquad (7.7)$$

Let us interpret the biological significance of the first-steady state (7.6). For a biologically possible or sensible solution, $H* > 0$. As a result we have,

$$\frac{\varphi}{\delta_p} \geq \frac{\delta_h}{\alpha_h} \qquad \qquad \cdots \qquad (7.8)$$

which implies the decrease of steady-state standing stock of primary production with the presence of harvivores.

To study the local stability, we put

$$H = H^* + h \qquad P = P^* + p \qquad \qquad \cdots \qquad (7.9)$$

Putting these values in (7.4) and (7.5) we have the linearised equations,

$$\left. \begin{aligned} \frac{dh}{dt} &= \alpha_h H^* P \\ \frac{dp}{dt} &= -(\delta_p + \alpha_h H^*) \, p + \alpha_h P^* h \end{aligned} \right\} \qquad \cdots \qquad (7.10)$$

Seeking the solutions like $e^{\lambda t}$ shows that the eginevalues λ must satisfy the characteristic equation

$$\lambda^2 + (\delta_p + \alpha_h H^*) \, \lambda + \alpha_h^2 P^* H^* = 0 \qquad \cdots \qquad (7.11)$$

The constant term and the coefficient of λ are both unequivocally positive for biologically sensible (positive) steady-state. For the stability of the steady state (7.6), the eginevalues, that is, the roots of the characteristic equation (7.11) must have negative real parts.

The system of linear food-chains can be extended to a three-level system by addition of a functional group of 'consumers' which eat (only) hervivores.

7.3 Logistic Primary Production

The models discussed in section (7.2) are based on the assumption of constant primary production. Although these models are acceptable approximations for some systems, for many other the rate of primary production depends on the standing stock of primary producers. To investigate the implication of this, we shall modify our model of linear food-chain by assuming that in the absence of hervivory, the plant carbon biomass grow logistically to a carrying capacity k, that is,

$$\frac{dP}{dt} = rp\left(1 - \frac{P}{k}\right) \qquad \cdots \qquad (7.12)$$

Two - level System :

We investigate a very simple system, in which the hervivores are the only additional tropic levels. We retain all other assumptions of section (7.2), so that the system dynamics are described by the equations,

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$$\frac{dP}{dt} = r\, p\left(1 - \frac{P}{k}\right) - \alpha_h\, PH$$

$$\frac{dH}{dt} = \alpha_h\, PH - \delta_h\, H \qquad \cdots \qquad (7.13)$$

This system is mathematically identical to the predator-prey model with logistic prey and linear predator functional response. It has two steady-states $(K, 0)$ and (P^*, H^*) where

$$P^* = \frac{\delta_h}{\alpha_h}, \qquad H^* = \frac{r}{\alpha_h}\left(1 - \frac{P^*}{K}\right) \qquad \cdots \qquad (7.14)$$

The co-existence steady-state (P^*, H^*) is biologically sensible, that is, $P^* > 0$ and $H^* > 0$, provided the required plant carbon biomass is less than the carrying capacity, that is,

$$K \geq \frac{\delta_h}{\alpha_h} \qquad \cdots \qquad (7.15)$$

Small deviations about steady-state (P^*, H^*) are described by

$$\frac{dp}{dt} = \frac{rP^*}{K}p - \alpha_h\, P^*h$$

$$\frac{dh}{dt} = \alpha_h\, H^*p \qquad \cdots \qquad (7.16)$$

and hence a characteristic equation,

$$\lambda^2 + \frac{rP^*}{K}\lambda + \alpha_h^2\, P^*H^* = 0 \qquad \cdots \qquad (7.17)$$

Since both the constant terms and the coefficient of λ in this characteristic equation (7.17) are positive for all biologically sensible steady-states, we see that all such steady-states are necessarily stable. We can extend the model by addition of a consumer functional group to our logistic primary production model.

With a basic discussion of linear food chain and logistic primary production we close up the chapter on ecosystem. The models of food-chain and many other ecosystem problems are similar in both structure and dynamics to those which we have set out to describe interacting groups of unstructured population. We can, therefore, use our knowledge of such models to inform our view of the likely properties of ecosystem models.

7.4 ❏ Material Cycling : Linear Tropic Interaction :

In the previous sections we have considered the passage of elemental matter such as carbon, phosphorus or nitrogen, and resumed the primary production rate either to be a constant or a logistic function. The primary production is limited by some factors other than the elements being modelled : for example light. However, in closed system the elemental matter needed for primary production must be provided through recycling - by mortality and respiration in the case of carbon, or by mortality and excretion in the case of phosphorus and nitrogen. Few ecosystems outside the laboratory are closed to carbon, so in this section we explain the dynamic implications of closure of an elemental nutrient (i.e. nitrogen and phosphorus).

A Nutrient - Plant System :

The system model is very simple, it consists of a nutrient compartment, containing limiting nutrient at density $N(t)$, and the plant functional group, which we now characterise by its limiting nutrient density $P(t)$. We assume that the plants have a linear response, with slope ap and a mortality excretion rate δp. The system is closed, so any nutrient taken up by the plants is lost to the free nutrient pool, and all nutrient lost by plants due to death and excretion is immediately (or instantaneously) added to the nutrient pool. With these assumptions, the system dynamics are,

$$\left. \begin{aligned} \frac{dp}{dt} &= \alpha_p NP - \delta_p P \\ \frac{dN}{dt} &= \delta_p P - \alpha_p PN \end{aligned} \right\} \qquad \dots \quad (7.18)$$

Equations (7.18) imply that

$$\frac{dN}{dt} + \frac{dP}{dt} = \frac{d}{dt}(P + N) = 0 \qquad \dots \quad (7.19)$$

In other words, the total quantity of nutrient contained in the system is constant as it should be for a closed system. Representing the total amount of bound and unbound nutrient by S, the dynamical equations (6.18) reduce to

$$\frac{dP}{dt} = \alpha_p NP - \delta_p P, \quad N(t) + P(t) = S \qquad \dots \quad (7.20)$$

Eliminating N, from (7.20), we have,

$$\frac{dP}{dt} = (\alpha_p S - \delta_p) P \left[1 - \frac{\alpha_p}{\alpha_p S - \delta_p} P \right] \qquad \dots \quad (7.21)$$

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Writing $r_p = a_p S - \delta_p$, $K_p = \dfrac{r_p}{a_p}$, the equation (7.21) reduces to the form of logistic equation

$$\frac{dP}{dt} = r_p P\left[1 - \frac{P}{K_p}\right] \qquad \qquad \dots \qquad (7.22)$$

From (7.22), we can conclude that the model has an unstable steady-state at $P = 0$ and a globally stable steady state at $P = K_p = (S - \delta_p / a_p)$.

7.5 ❑ Summary

In the introduction (section 7.1) we have explained the concept of functional groups for the modeling of ecosystems. In sections (7.2) we have discussed the linear food-chain model of ecosystem with constant production. In section (7.3) we have modified the constant production model to the logistic primary production model. In section (7.4) we have discussed the basic concept of material cycling in functioning in ecosystems.

"For dealing with any natural phenomena-especially one of a vital nature, with all the complexity of living organism in type and habit— the mathematician has to simplify the conditions until they reach the attenuated character which lies in the power of this analysis"

—Kerl Pearson

Glossary of Ecological Terms

Abiotic : not biological or not relating to living organisms.

Abundance : large amount or large number of something.

Algae : tiny plants living in water or in moist condition.

Allele : one of two or more alternative forms of a gene; which can imitate each others form.

Allelopathy : harm caused by one plant to another plant, usually by producing a chemical substance.

Anther : part of a stamen which produces pollen.

Biomass : all living organisms in a given area or at a given tropic level expressed in terms of living or dry weight.

Biome : large ecological region characterized by similar vegetation and climate (such as desert, the tundra etc.).

Bion : single living organism in an ecosystem.

Biota : flora and fauna of a region.

Bloom : (a) flower; the blooms on the orchids have been ruined by frost (b) algae bloom = mass of algae which develop rapidly in a lake. 2. Verb, to flower. The plant blooms at night, some cacti only bloom once every seven years.

Carrying Capacity : maximum number of individuals of a species that can be supported in a given area.

Cellulose : carbohydrate which makes up a large percentage of plant matter.

Community : group of different organisms which live together in an area, and which are usually dependent on each other for existence.

Diversity : richness of the number of species in an area.

Ecology : study of relationship among organisms and the relationship between them and their physical environment.

Deep ecology : extreme form of ecological thinking where humans are considered as only one species among many in the environment.

Ecological balance (or balance of nature) : situation where relative number of organisms remain more or less constant.

Ecological succession : series of communities of organisms which follow on one after the other, until a climax community is established.

Ecospecies : subspecies of a plant.

Ecosphere : biosphere, part of the earth and its atmosphere where living organism exist.

Ecosystem : system which includes all organisms of an area and the environment in which they live.

Etholog : study of the behaviour of living organisms.

Evolution : heritage changes in organisms, which take place over along period involving many generation.

Genetics : study of the way the characteristics of an organism are inherited through genes.

Genome : all the genes in an individual.

Genotype : genetic composition of an organism.

Genus : group of closely-related species.

Green house : building made mostly of glass, used to raise and protect plants.

Green house effect : effect produced by accumulation of carbon dioxide crystals and water vapour in the upper atmosphere, which insulates the earth and raises the atmosphere temperature by preventing heat loss.

Habitat: type of environment in which an organism lives.

Heredity : occurrence of physical or mental characteristics in offspring which are inherited from their parents.

Immune : protected against an infection or allergic disease.

Niche : place in an ecosystem which a species is specially adapted to fit.

Ecological Niche : all the characters (chemical, physical and biological) that determine the position of an organism or species in an ecosystem, (commonly called the "role" or "profession" of an organism e.g. an aquatic predator, a terrestrial hervivore.

Omnivore : animal which eats any thing, both vegetation and meat.

Phenotype : physical characteristics of an organism which its genes produce, such as brown eye, height etc. compare genotype.

Pisci culture : fish farming; the breeding fish for food in special enclosures.

Terrestrial: referring to land; terrestrial animals : animals which live on dry land.

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মানুষের জ্ঞান ও ভাবকে বইয়ের মধ্যে সঞ্চিত করিবার যে একটা প্রচুর সুবিধা আছে, সে কথা কেহই অস্বীকার করিতে পারে না। কিন্তু সেই সুবিধার দ্বারা মনের স্বাভাবিক শক্তিকে একেবারে আচ্ছন্ন করিয়া ফেলিলে বুদ্ধিকে বাবু করিয়া তোলা হয়।

— রবীন্দ্রনাথ ঠাকুর

ভারতের একটা mission আছে, একটা গৌরবময় ভবিষ্যৎ আছে, সেই ভবিষ্যৎ ভারতের উত্তরাধিকারী আমরাই। নূতন ভারতের মুক্তির ইতিহাস আমরাই রচনা করছি এবং করব। এই বিশ্বাস আছে বলেই আমরা সব দুঃখ কষ্ট সহ্য করতে পারি, অন্ধকারময় বর্তমানকে অগ্রাহ্য করতে পারি, বাস্তবের নিষ্ঠুর সত্যগুলি আদর্শের কঠিন আঘাতে ধূলিসাৎ করতে পারি।

—সুভাষচন্দ্র বসু

Any system of education which ignores Indian conditions, requirements, history and sociology is too unscientific to commend itself to any rational support.

— Subhas Chandra Bose