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AUTUMN COURSE ON MATHEMATICAL ECOLOGY

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POPULATION DYNAMICS IN A SPATIALLY HOMOGENEOUS ENVIRONMENT

1. Introduction to Population Theory
2. Discrete Models of Populations

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Thomas G. Hallam

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1.0 Introduction

Ecology, freely translating from the Greek expression, means "the study of the household of nature". A population is a collection of organisms, usually of the same species, that occupy a prescribed region and function together as an ecological entity. While most populations consist of a single species, the definition of a population is intended to be sufficiently broad to include assemblages of species such as those that can interbreed to produce viable hybrids or lichen populations where the algae and fungi are so closely associated that they function as a single species. Population ecology, in the sense meant here, refers to the structure and function of a collection of organisms as an autecological unit and, as such, addresses the more purely biological aspects of ecology.

The relationship between a population and its biogeochemical environment is often an intricate one. Populations are seldomly dominated by their physical environment; indeed, they are often able to modify and even regulate, within constraints, their environment. The biology of the population, the biogeochemical characteristics of the environment and the feedback mechanisms between the collection of organisms and the environment are important aspects of population ecology.

1.1 Characteristics of a Population

Before embarking on a study of population models, it is useful to have a compilation of the terminology that is employed to describe a population.

There are many traditional, physical characteristics of populations that even a casual observer can delineate. These include the size and distribution of the population. The density of the population is the number of individual organisms per unit of space. The density of the population can be computed from a population census; it is, of course, a nontrivial task to accurately census most natural populations. The manner in which organisms are distributed in space is referred to as the dispersion of the population. In the subsequent models, it will be assumed that the population is uniformly dispersed throughout the region. This situation is termed spatially homogeneous; hence, the origin of the title of this chapter.

There are ways that population size can fluctuate. Natality can occur; new organisms can arise from seeds, spores, or eggs. It is customary to refer to the rate of addition of new individuals to a population by reproduction as the birth rate. Mortality decreases population size; the rate at which organisms are lost from the population by death is called the death rate. Another change in population size can be effected through immigration and emigration. The rate at which organisms immigrate to or emigrate from the region used to define the population is called the dispersal rate of the population.

There are many other attributes of a population that help to characterize it. These include the sex, age, and organism size distributions as well as genetic characteristics. The proportion of organisms of different ages (or sizes) is often a fundamental characteristic of populations and this feature subsequently will be explored in detail in Dr. Frauenthal's lectures. Another important trait of a population that will be discussed later are the evolutionary aspects of population ecology.

1.2 Modelling Aspects of Populations

The use of the language of mathematics to model or represent a phenomenon has several advantages. This interdisciplinary approach allows the usage of tools from two disciplines - those of the scientific area plus those of mathematics. A traditional view of the use of mathematical models is to "predict" the behavior of a system. In biology, while prediction is highly desirable, this objective is probably one of the least fruitful avenues of research. Among the uses of mathematical modelling, many of which will be illustrated in these notes, are

1. Clarification of definitions of compartments, flows, and pathways,
2. Generation of hypotheses about the system,
3. Suggestion of experiments to validate these hypotheses,
4. Assistance in research planning,
5. Identification of poorly understood system mechanisms.

In any modelling process the objectives of the effort must be clearly delineated. When the objectives are specified, the representation of the scientific phenomenon in the language of mathematics results in a model. This procedure requires basic laws which, in ecology, are not plentiful. The contrast between existence of fundamental laws in the physical sciences and the lack of corresponding laws in biological sciences is striking. However, this is one reason modelling in the biological sciences is fascinating and is evolving at a high rate. After the model is formulated, it must be solved. A specific problem can sometimes be solved analytically but often it is necessary to study the model numerically. In the modelling process, the next step is to interpret the solution in terms of the ecology of the system and, then, quite possibly start the process over by redefining the objectives.

When the model is suitable, according to the objectives, an important aspect of modelling is the control of the biological system. It is frequently necessary to modify or optimize system behavior (as in an agricultural production) so the development of the theory of control of systems is fundamental.

Some steps (and perhaps, all of these) in the modelling process will be evident in the presentations of this course.

1.3 Continuous and Discrete Models

If the domain of the deterministic dynamical system is a continuous set (usually $\mathbb{R}_+ = [0,\infty)$) then the model is called briefly, a continuous model. In these notes, a continuous model will refer to an ordinary differential equation. If the domain of the model is a discrete subset of the integers, the model is said to be discrete. The discrete models discussed here will be difference equations. Examples of quantities measured continuously include inflation and temperature while the census of a population is a discrete measurement. It is traditional to model certain discrete phenomena in a continuous manner. Notable physical examples include gas and hydrology measurements. As we will see, it is often convenient to model populations by a continuous model. If a population model has as a state variable the number of individual organisms, this would seem to force the model to be discrete. However, if the population is very large, the addition of another individual is a small change relative to the population size. In this situation, it might be reasonable to model the population in a continuous manner (often not only continuity but differentiability is assumed for such variables). Another justifiable way to view population state variables as continuous is to use biomass as the measured quantity.

1.4 Quantitative Behavior of Populations

To motivate the subsequent development, the time-evolution of the structure of some laboratory and natural populations is presented.

How do Populations Behave at Densities that Allow Substantial Growth?

Figures 1.1, 1.2, and 1.3 indicate that some populations grow rapidly from certain initial population sizes. From this realized growth, it can be inferred that the population is not at a level where some resource factor (such as a limiting nutrient or a restricted space requirement) is drastically hindering the growth of the population. A reasonable but tautological definition of a population density which promulgates at a high growth rate is that there are no constraints to severely limit expansion of the population. There exist certain constraints on densities of this type; in particular they need not be very low densities (compare Figures 1.3a and 1.3b). The Allee principle states that undercrowding can be a limiting factor in population regulation. Limitations at low population densities might occur if the population is so widely dispersed that reproductive contacts are restricted and infrequent.

One of the simplest ways to model a rapid growth employing a minimal number of parameters is to fit it exponentially. Two parameters are required here: one to indicate the initial size of the population and the second to represent the rate of increase.

How do High Density Populations Grow?

As in the case of a growing population, our terminology describes a situation that is relative to another comparative one. A high density population refers to a population that is limited by the availability of

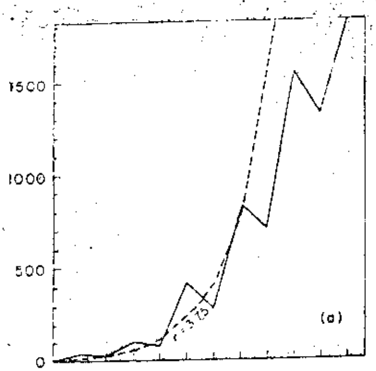


Fig. 1.1 Population of pheasant (Phasianus colchicus torquatus) introduced onto Protection Island and followed during the early part of its development; plotted arithmetically against time (data of Einarsen). Broken lines indicate hypothetical exponential growth. (Hutchinson)

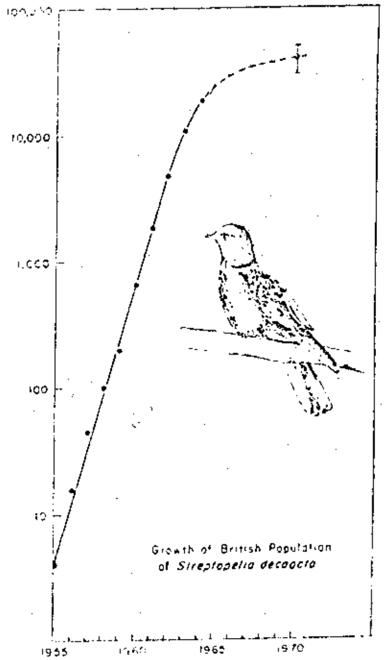


Fig. 1.2 Estimates of population of the collard turtledove (Streptopelia decaocto) in Great Britain since 1955. logarithm scale. Note exponential increase in first 8 years, with rapid decline in rate of increase after 1963. (Hutchinson)

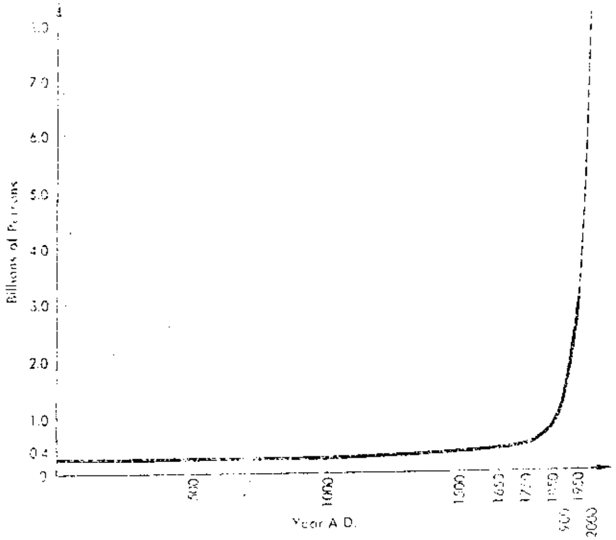


Fig. 1.3a World population in the first two milennia of the Christian Era. Figures represent billions of persons. The dotted portions of the curve represent estimates of what may occur in the near future if present rates continue. The consensus of present opinion foresees a human population of 6 or 7 billion by the next millennium. (Boughey)

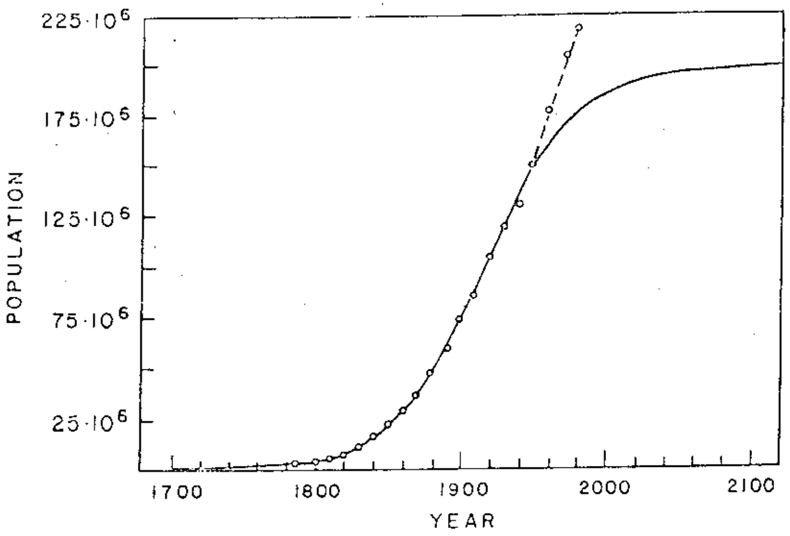


Fig. 1.3b Logistic (solid line) fitted to the human population of the U.S. from censuses up to and including that of 1940, by Pearl, Reed, and Kish, with actual points from later censuses, following the broken line.

some resource. The degree of limitation should affect the growth of the population until there is a balance between available limiting resource and population utilization of that resource. This should lead to a steady state population assuming that no other limiting factor becomes critical or another ecological change occurs.

Figures 1.4, 1.5, 1.6, 1.7, 1.8, 1.9, 1.10, 1.11, 1.12, and 1.13 all reflect an exponent-type growth for some low initial densities and, then, a saturation effect at high densities.

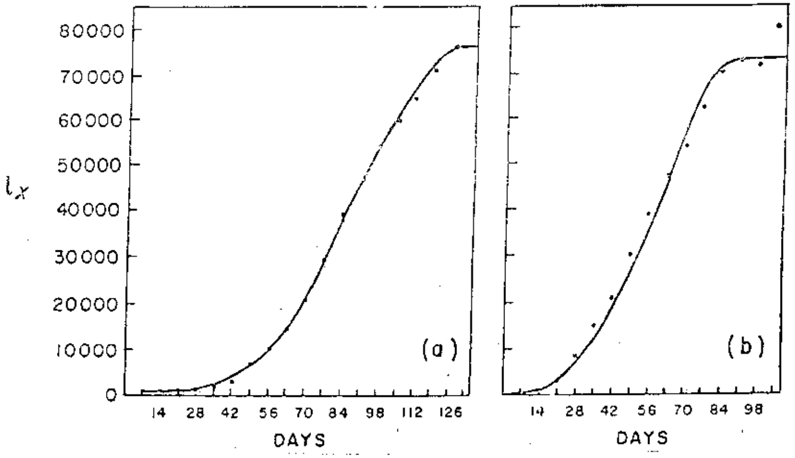
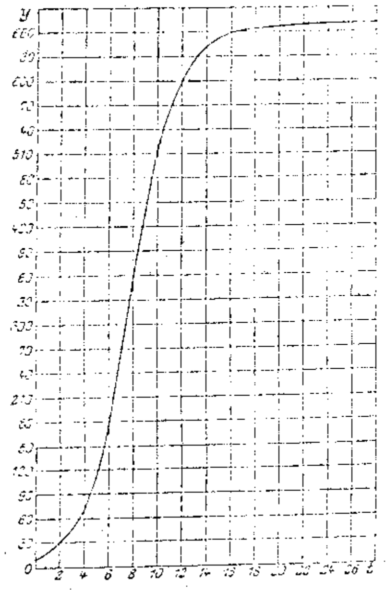


Fig. 1.4 Logistic growth of colonies, (a) of Cyprian and (b) of Italian cultivars of the honeybee (Apis mellifera) near Baltimore, Maryland, showing almost identical values of K (76, 328, and 74,000) determined ultimately by hive size. (Bodenheimer, from the data of Nolan).



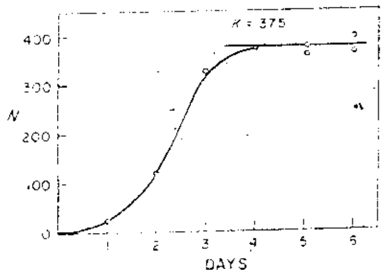


Fig. 1.6 Growth of a population of Paramecium caudatum, fitted to a logistic curve. (Gause).

Fig. 1.5 Growth of Saccharomyces cerevisiae as plotted by Carlson. This curve, plotted arthimetically, seems to be the first one for an actual population drawn to show the sigmoid form.

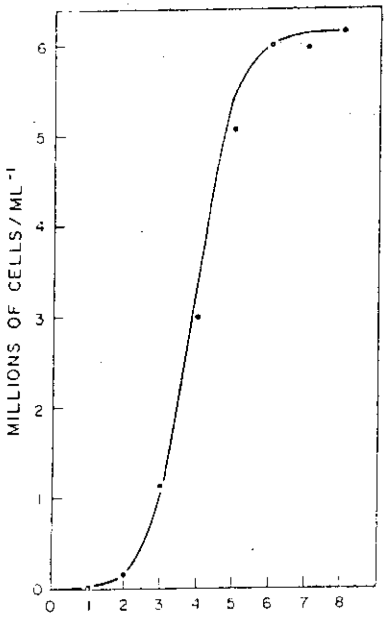


Fig. 1.7 Growth of Escherichia coli at 37°C in peptone broth, from the data of M'Kendrick and Kesava Pai, with their calculated curve, which they plotted logarithmically, for which r is taken as implying division every 22.3 minutes.

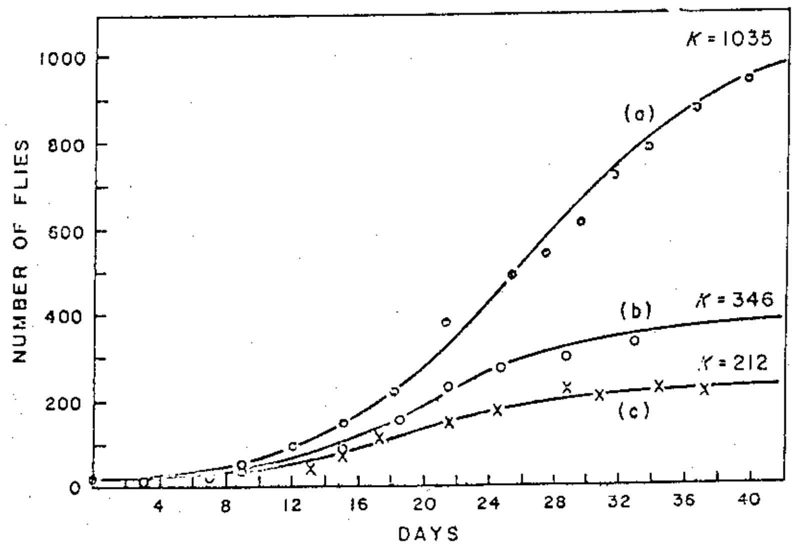


Fig. 1.8 Growth of populations of Drosophila melanogaster, (a) wild type in a pint bottle; (b) stock homozygous or hemizygous for five recessives including vestigial wing, in same-sized bottle; (c) wild type in a half-pint bottle (Pearl).

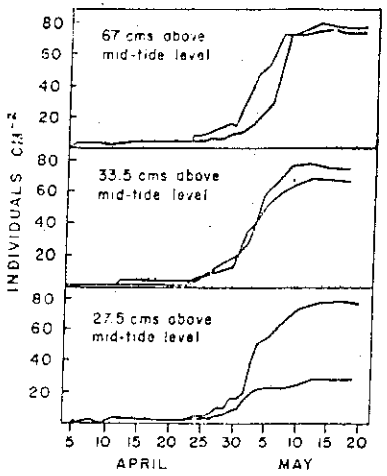


Fig. 1.9 Sigmoid curve of settling of populations of Balanus balanoides on the shore of Great Cumbrae Island in the Firth of Clyde, April-May 1954. Populations on two stones are shown for three levels relative to mean tide level (Connell).

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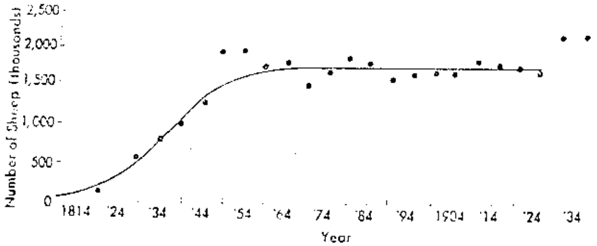

Fig. 1.10 Population growth of sheep introduced into Tasmania. The dots represent average numbers over five-year periods. From J. Davidson, Transactions of the Royal Society of South Australia, 62: 342-346 (1938)

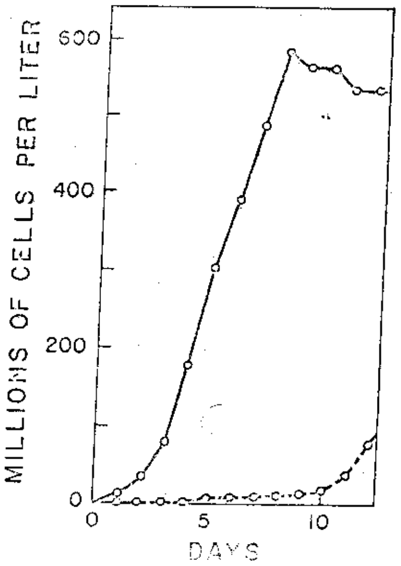

Fig. 1.11 Growth of the marine diatom (Nitzschia closterium) in culture prior to the appearance of a significant number of senescent [illegible] cells (Riley)

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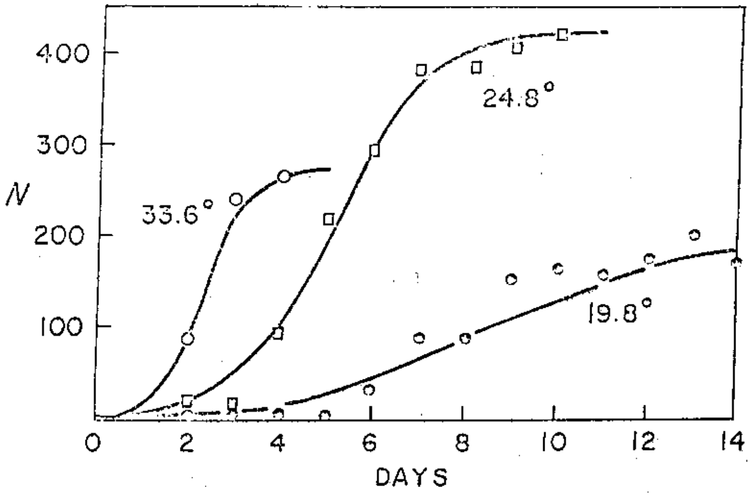

Fig. 1.12 Growth of populations of Moina macrocopa at three temperatures. (Hutchison)

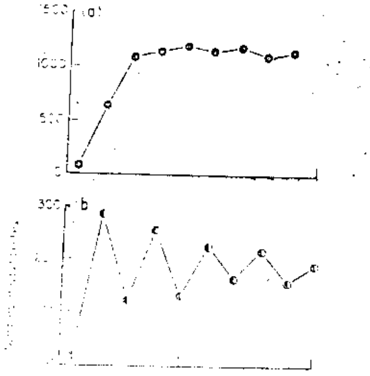

Fig. 1.13 Population changes in laboratory cultures of three different strains of stored-product beetles, displayed as number of adult beetles in successive generations: (a) Callosobruchus chinensis (after Fujii, 1968); (b) C. maculatus (after Utida, 1967); (c) C. maculatus (after Fujii, 1968).

Variation in Populations

Many variables, including environmental and genetic fluctuations, can change the behavior of a population. Figures 1.10, 1.11, 1.12, and 1.13 represent populations that exhibit some oscillatory behavior. Figure 1.14 represents a Drosophila population with some genetic regulation present. Figures 1.15, 1.16, 1.17 and 1.18 demonstrate that oscillations are a viable behavior made for some populations.

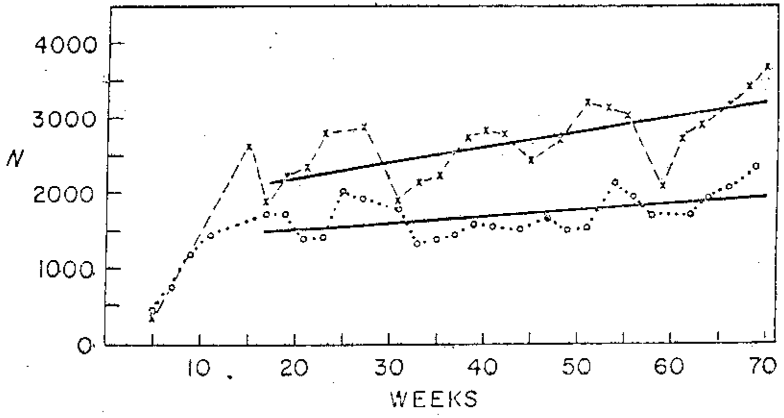

Fig. 1.14 Populations of Drosophila birchi, reared at 19 C: one (o) from Popondetta, New Guinea; and one (x) a strain derived from mass hybridization of the Popondetta strain and of another from 200 km north of Sydney, Australia. The solid lines are the regression lines on time, starting 17 weeks after initiation of the populations. (Ayala)

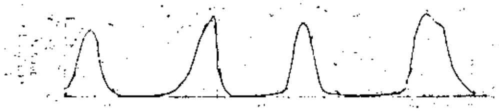

Fig. 1.15 Shelford's (1943) data on the lemming population in the Churchill area in Canada (expressed as numbers of individuals per hectare).

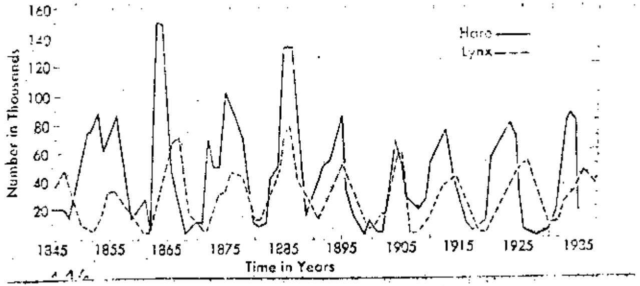

Fig. 1.16 Changes in the abundance of lynx and snowshoe hare. This is a classic example of the cyclic oscillation in population density and illustrates the correlation between fluctuations in numbers of prey (hare) and numbers of predator (lynx). After D.A. MacLulich, University of Toronto Studies; Biological Series No. 43. 1937. pp. 1-136.

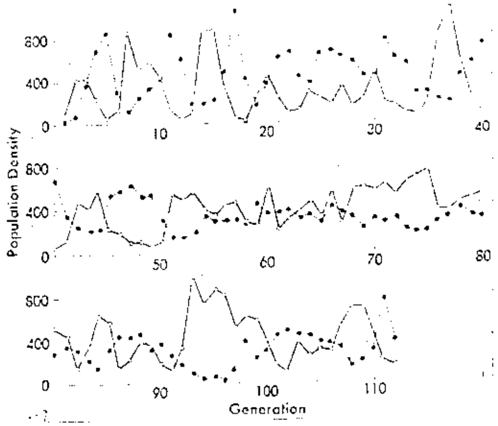

Fig. 1.17 Fluctuation in population density of interacting populations of a host, the bean weevil Callosobruchus chinensis (solid line) and a parasite, the abracenid wasp Heterospilus prosopidis (broken line). From S. Utida, Ecology, 38: 442-449 (1957.

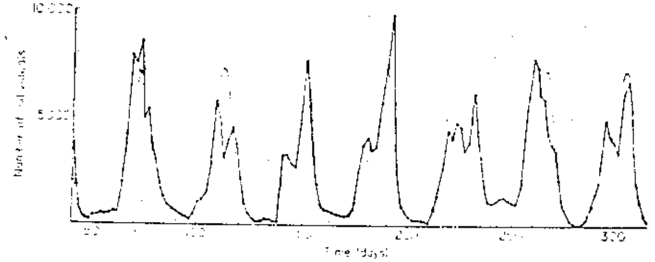

Fig. 1.18 Fluctuations in a blowfly population (Nicholson).

Why Don't all Populations Behave Nicely?

The sample populations presented in this section have behaviors that range from nice (Figures 1.4 - 1.12) to wild oscillations (Figures 1.16 - 1.17). There are many factors that determine the behavior of a population. Ironically, while the biology of a population is important, it is often secondary to the ecological system of which that population is a component. If a population goes to extinction (and they do with a high frequency) the void it leaves in the ecosystem does not go unnoticed. Through a process sometimes called ecological release, another population (or combination of populations) will assume the function of the removed population.

To understand the dynamics of a population is to understand the ecosystem of which it is a component. At the current state of knowledge of population ecology, and ecosystem ecology, there remains much to be done before the governing principles of populations can be delineated.

2. Discrete Models of Populations

2.0 Introduction to Exponential Growth

A population in which generations do not overlap or population size is not large should probably be modelled in a discrete manner. Suppose that the time variable is scaled so that the generation time is one and let y_n represent the number of individual organisms in the population at time n. Then, the population size at time $n + 1$ is given by a conservation law as

$$(2.1) \quad y_{n+1} = y_n + by_n - dy_n + e_n,$$

where the terms on the right in (2.1) are respectively, the population size of the previous generation; the number of individuals born in the nth time interval; the number of individuals that died (or were removed for example, by predators) in the nth time interval; and the net number of individuals that emigrate from and immigrate to the region defining the population.

Let $r = 1 + b - d$; r may not be constant over an extended period of time. It varies with the environment, food supply, predation pressure, and many other factors that can affect the population. Let's explore the modelling effects of various hypotheses about the population as they are reflected through the net growth rate parameter r.

If r is a function of the population size, the model (2.1) is said to have a density dependent growth rate. To be biologically realistic models of growth processes, certain restrictions on r are necessary. For example, suppose that the net exogeneous input, e_n, is zero for all n, and $r(y_n) \ge \alpha > 1$ or $r(y_n) \le \delta < 1$ for all n (or for all n sufficiently large). These hypotheses have important implications for the growth of the population.

If $r(y_n) \ge \alpha > 1$, then $y_{n+1} = r(y_n)y_n \ge \alpha y_n \ge \alpha^n y_0$, $n = 1, 2, \ldots$ Thus, $\lim_{n \to \infty} y_n = \infty$ and the population grows beyond bounds imposed by physical constraints. The alternate hypothesis, $r(y_n) \le \delta < 1$, results in extinction of the population; hopefully, no population is operating under these conditions.

The hypothesis above that led to exponential growth for the model yields conclusions that are, at best, ridiculous. MacArthur and Connell ( ) demonstrate this by considering a single organism, such as a bacterium, that reproduces by dividing into daughter organisms every twenty minutes. Assuming exponential growth, this bacterium and its progeny can produce a population that is one foot deep over the entire earth in a 36 hour period. This population would, in a few thousand years, weigh as much as one universe and be expanding outward at the speed of light.

Braun (1975) has performed some interesting calculations about exponential growth and the world's population. Although done for the differential equation analog of the difference equation we are considering, he finds, by assuming people are able to live as members of aquatic communities as well as terrestrial ones, that in approximately 500 years, each of us will have only 9 feet of surface area; in 600 years, only one square foot per person; and in another 35 years, someone will have to stand on each person's shoulders.

Clearly, with these kinds of numerics, there is something that is wrong with the model. Is there anything that can be saved? There is certainly evidence that populations can explode and, even some evidence, that this explosion can be exponential for at least a finite time period. Swarms of grasshoppers, massive outbreaks of agriculture pests, multitudes of tent caterpillars, gypsy moths, and spruce budworms provide examples of the occurance of exponential growth. Many of the populations illustrated in Figures 1.1-1.13 exhibit an exponential growth for low densities of the populations. Minimally, we observe that at small population sizes, the population growth can be approximated by an exponential function.

2.1 Density Dependence and Delays in Population Models

Returning to the model (1) and noting the above restrictions, what form might a generic density dependent growth rate take? If population size is small, the organisms could be sparsely distributed in its habitat, mating encounters could be infrequent, survival and development might be difficult. This could be reflected in $r(y_n)$ by requiring that $r(y_n) < 1$ if $y_n << 1$. On the other hand if $y_n >> 1$ overcrowding is likely since intraspecific competion will be strong and the assumption $r(y_n) < 1$ seems reasonable. As we noted above there should be a population size where $r(y_n) > 1$, otherwise extinction is automatic. Figure 2.1 illustrates a generic density dependent growth rate.

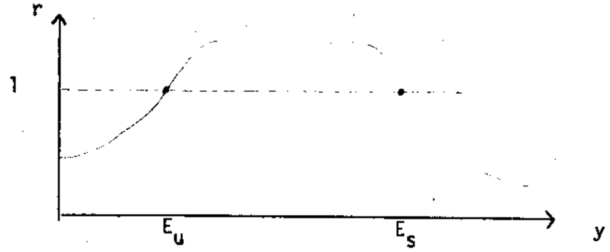

Fig. 2.1 A generic per capita growth rate reflecting effects of density dependence.

The points E_u and E_s of Fig. 2.1 where $r(E_u) = r(E_s) = 1$ are important for the analysis of

$$(2.2) \qquad y_{n+1} = r(y_n)\, y_n;$$

namely, they are equilibrium values of (2.2) where the population size remains constant for all n $(r(y_n) = 1)$, $n = 1,2,\ldots$ The fact that a state is at equilibrium tells very little about the dynamical system. A needle standing on its point is in equilibrium but it probably won't stay there long. Certain stability properties of the equilibrium would be desirable information.

A standard technique used in the stability analysis of an equilibrium is that of linearization. This process is now briefly described. Let E represent an equilibrium. Translate the equilibrium to the origin: $y_n - E = Y_n$. Using Taylor's Theorem, linearize the system ignoring all higher order terms. Study the linearized system for stability since most nonlinear systems behave locally about an equilibrium like an associated linear system (Coddington and Levinson, 1955).

Employing this procedure leads to

$$r(y_n) \cong r(E) + r'(E)\,(y_n - E) = 1 - Er'(E) + r'(E)y_n;$$

hence, the resulting linearized equation is

$$(2.3) \qquad Y_{n+1} = \lambda Y_n \qquad n = 1, 2, \ldots$$

where $\lambda = 1 + r'(E)\,E$. The asymptotic behavior of the first order equation (3) with constant coefficients is indicated in Figure 2.2; the solution of (3) is $Y_n = Y_0\,\lambda^n$, $n = 1, 2, \ldots$

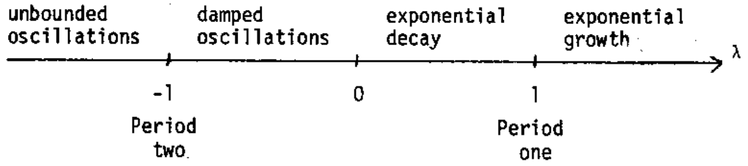

Fig. 2.2 Description of the asymptotic behavior of the first order difference equation $Y_{n+1} = \lambda Y_n$ as a function of λ.

If λ satisfies either of the inequalities $-1 < \lambda < 0$ or $0 < \lambda < 1$ then E is locally asymptotically stable. If $|\lambda| > 1$ then the equilibrium is unstable. Translating this information to E_u, since $r'(E_u) > 0$, this point is unstable. At E_s, some information about relative magnitude of $E_s r'(E_s)$ is needed to guarantee asymptotic stability. For example, if $E_s r'(E_s) > -2$ then linearization indicates stability results.

When the actions of a previous generation regulate the growth of population, the resulting model might be governed by the model

$$(2.4) \qquad y_{n+1} = r(y_{n-1})\,y_n, \qquad n = 1, 2, \ldots$$

The equation (2.4) is a second order difference equation. As a first approximation to study the behavior of (2.4), suppose an equilibrium E exists; that is, $r(E) = 1$. Linearization results in the equation

$$(2.5) \qquad Y_{n+1} - Y_n - Er'(E)\,Y_{n-1} = 0, \quad n = 1,2,\ldots$$

The behavior of a general second order difference equation with constant coefficients is expressed in Figure 2.3.

The numerical value of $Er'(E)$ again determines the growth or decay of solutions starting close to E. For example, if $r'(E) > 0$, growth occurs; if $0 < -Er'(E) \leq \frac{1}{4}$ decay results; hence stability can be determined in this manner.

Figure 2.4 compares the differences in behavior of solutions difference euqations due to delay effects in the growth rate. In general, this modelling exercise indicates that the population might be regulated

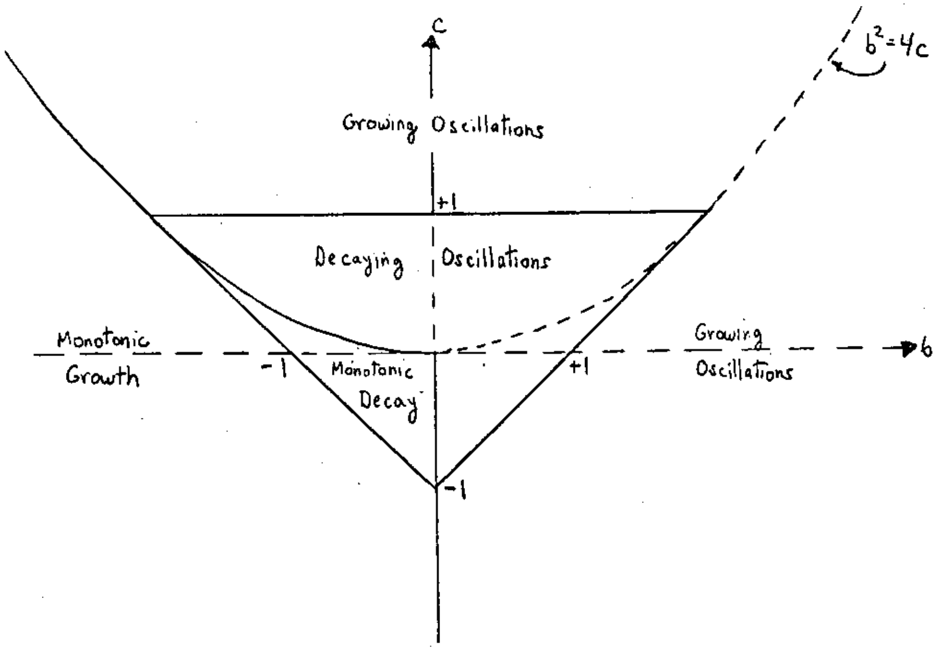

Fig. 2.3 The asymptotic behavior of the homogeneous second order linear difference equation

$$Y_{n+2} + b\,Y_{n+1} + c\,Y_n = 0$$

as a function of its coefficients.

more efficiently by using current data. It is also apparent that additional delays induce oscillations.

one period delay in r	oscillatory growth	oscillatory decay		monotonic decay	monotonic growth
two period delay in r	monotonic growth	monotonic decay	oscillatory decay	oscillatory growth	

-Er'(E)

Fig. 2.4 A comparison of the effects of delay in the difference equations $X_{n+1} = r(x_n)x_n$ and $x_{n+1} = r(x_{n-1})\,x_n$ in terms of the parameter Er'(E).

2.2 Discrete Logistic Equation

One of the simplest models that contains a formulation which represents effects of overcrowding is when r is a linear function of population size: $r(y_n) = 1 + \frac{r_o}{E}(E - y_n)$. Because of the name of the continuous analogue, this equation is often referred to as the discrete logistic equation. Scaling the variable y_n by the transformation $Z_n = r_o(1 + r_o)^{-1} y_n \, 1/E$ gives a canonical form

$$(2.6) \qquad Z_{n+1} = \alpha Z_n (1 - Z_n)$$

The behavior of solutions of equation (2.6) is a function of the parameter α. This behavior, while it is complex and fascinating, also has several disturbing attributes. Only for $0 \leq \alpha \leq 4$ does (2.6) make sense with Z_n measuring a nonnegative quantity. If $\alpha < 0$, then small Z_o results in $Z_1 < 0$; when $\alpha > 4$, then small Z_o forces Z_2 to be negative. For $0 \leq \alpha \leq 4$ the solution sequence Z_n, $n = 0, 1, 2, \ldots$ does not change sign and remains less than or equal to one provided Z_o satisfies $0 \leq Z_o \leq 1$.

To study the sensitivity of the solutions to changes in the parameter α it is convenient to decompose the interval [0, 4] further. For $0 < \alpha < 1$ extinction of the population can occur since $Z_{n+1} \leq \alpha^n Z_o$: hence, $\lim_{n \to \infty} Z^n = 0$. When $\alpha = 1$, $Z_n = Z_o$, $n = 1, 2, \ldots$ For $1 < \alpha < 3$, as may be demonstrated by linearization, $Z_n = \frac{\alpha - 1}{\alpha}$ is an asymptotically stable equilibrium. The character of the approach is monotone decay if $1 < \alpha < 2$ and oscillatory decay for $2 < \alpha < 3$. The value $\alpha = 3$ results in a

neutral oscillation about the equilibrium.

The solution behavior when $\alpha > 3$ becomes more interesting. There is no longer just a single stable equilibrium that governs the dynamics of the population; periodic solutions can emerge. The existence of a neutral oscillation of period two and its stability is now discussed. It is convenient to use (2.6) and write

$$(2.7) \qquad Z_{n+2} = \alpha^2 Z_n [1 - (\alpha + 1) Z_n + 2\alpha Z_n^2 - \alpha Z_n^3]$$

Suppose Z_n bounces between V_1 and V_2 then when $Z_n = V$ (either V_1 or V_2), $Z_{n+2} = V$. This leads to

$$\alpha V^3 - 2\alpha V^2 + (\alpha + 1) V + (\alpha^{-2} - 1) = 0$$

One root must be $(\alpha - 1)/\alpha$ so

$$(V - \frac{\alpha - 1}{\alpha}) \quad (\alpha V^2 - (\alpha + 1) V + (1 + \alpha^{-1}) = 0$$

The quadratic factors into roots

$$V = \frac{\alpha + 1 \pm [\alpha^2 - 2\alpha - 3]^{1/2}}{2\alpha}$$

The assumption that $\alpha > 3$ implies both roots, V_1 and V_2, are real; in fact, it can be seen that they are positive. These oscillations exist but are they stable? For example, if Z_n is close to V, does this mean that Z_{n+2} is closer to V? For certain α, this is the case. From

(2.7), the relationship

$$Z_{n+2} - Z_n = -\alpha^3 Z_n \left(Z_n - \frac{\alpha - 1}{\alpha}\right)(Z_n - V_1)(Z_n - V_2)$$

results. Writing $Z_n = V_1 + P_n$, linearizing, and doing some algebra, the equation

$$P_{n+2} = [\,1 - (\alpha + 1)(\alpha - 3)\,]\,P_n$$

is found to determine the stability of V_1. Hence, α must satisfy $0 < (\alpha + 1)(\alpha - 3) < 2$ (or $3 < \alpha < 1 + \sqrt{6}$) for local asymptotic stability. A similar argument establishes the stability of V_2. The asymptotic behavior of equation (2.6) as discussed to the present is indicated in Figure 2.5.

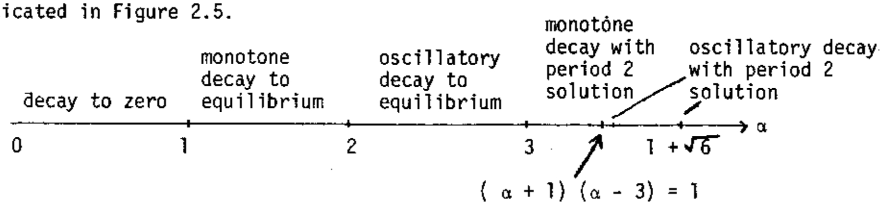

Fig. 2.5 Asymptotic behavior of the discrete logistic equation $Z_{n+1} = \alpha Z_n (1 - Z_n)$ as a function of the parameter α.

At $\alpha = 1 + \sqrt{6}$, the onset of double-double oscillations occurs; that is a periodic solution of period 4 emerges. This is expressed in a classical bifurcation diagram in Fig. 2.6. Notice the traditional exchange of stability at the points of bifurcation.

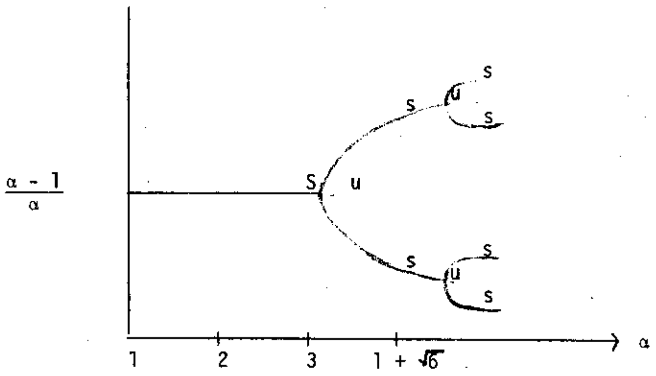

Fig. 2.6 A bifurcation diagram for the discrete logistic equation. S indicates an asymptotically stable solution while u indicates an unstable solution.

You can undoubtedly predict what happens next as α increases. A periodic solution of period 8 arises, then one of period 16, and, in general, one of period 2^n. This all transpires on a compact interval and there is a limit point on the α axis where this sequence of periodic solutions terminates. The value of $\alpha = 3.570$ seems prevalent for this behavior, although others have different numbers (e.g. Roughgarden). This value of α signals the onset of periodic solutions with odd period, beginning with very long periods, and as r increases, the period decreases to three. As r continues to increase, periodic solutions with arbitrary period and asymptotically aperiodic solutions occur. The behavior of this innocent looking equation has been termed "chaotic". Several authors have indicated the outcome of this deterministic population model should be regarded as stochastic (e.g. May, 1976).

There do seem to be some redeeming features of the model (2.6). Smale and Williams (1976) have demonstrated that for almost all $\alpha \in (3,4)$

there exists a single solution that is an attractor for almost all trajectories.

The remaining case $\alpha = 4$ is of interest also; not so much for its unusual behavior, but because it can be solved analytically (Steeb and Bromba, 1982). The function

$$Z_n = \frac{1}{2} - \frac{1}{2} \cos \left(2^n \arccos \left(1 - 2 x_0\right)\right)$$

is a solution of (2.6) with $\alpha = 4$. This solution oscillates, except for the initial conditions $x_0 = \frac{1}{2} - \frac{1}{2} \cos \frac{n\pi}{2^m}$, for n and m positive integers, in which case it tends to a limit.

2.3 Reflections on the Relevance of Discrete Models to Population Ecology

As May (1976) has pointed out, if models with chaotic behavior are relevant to populations, then wild oscillations of a population need not necessarily be the consequence of random environmental fluctuations but might be intrinsic to the population. An important question is "Do biological population exhibit chaotic behavior"? Hassell *et al* (1976) find little evidence to support an affirmative answer certainly the question is unresolved at present.

The utility of chaotic type models has been questioned by several authors. Smith and Mead (1980) employed a stochastic model and conclude that deterministic behavior is not biologically meaningful. O'Neill et al (1982) use an error analysis approach to demonstrate that uncertainty in growth rate is as important in determining the regularity of the system as the mean value. In spite of the negative aspects of these works on models with a rich spectrum of behavior the resulting discussions have been enriching to both population ecology and mathematics.

2.4 Summary

Discrete models, discussed here as difference equations, appear to be natural models to use to estimate the size of a population. Difference equations are innocent looking but they can be dynamic monsters. While the behavior of some populations can be mimicked by these simple models, it is not clear if these models are extremely useful tools in population ecology. The behavioral spectra of the simplest nonlinear model is extremely broad. Bifurcations can occur with extremely small perturbation of parameters. This phenomena of chaotic behavior is not unique to the discrete logistic equation. These are, in the literature, models with other than the logistic which exhibit chaotic motions and do not have some of the deficiencies, such as a restricted parameter range for biological significance, of the logistic. These include the widely applied Ricker model

$$X_{t+1} = X_t \exp r(1 - X_t/K)$$

among others (see May (1976); Levin (1981)).

Chaotic behavior is not restricted to difference equations. It can occur in ordinary differential equations (Gilpin, 1979) but not for systems of order less than two. This behavior can be demonstrated for first order delay-differential equations (Mackey and Glass, 1977).