

# ONE-DIMENSIONAL LINEAR AND LOGISTIC HARVESTING MODELS

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**Abstract**—Some of the results in the literature on simple one-dimensional, density-dependent, discrete and continuous models—with and without harvesting—are reviewed. Both deterministic and stochastic models are included. Some comparisons of the various models are made, and the results are discussed in terms of their ramifications in population model building.

## 1. INTRODUCTION

Understanding population dynamics has been a major objective in anthropology, cell biology, genetics and demography. Early mathematical models of population growth and development were necessarily highly simplified in nature. The usual simplifying assumptions were that adjustment to changes in the environment all took place simultaneously, all of the terms in the equations were linear, and the only variables in the equations were the population numbers (or population densities). Although analytic solutions to some of the simplified equations have been obtained, the situations described by these solutions are often far from those observed in reality. Frequently, the controlled growth behavior of laboratory populations has been quite different from that predicted by the theoretical models that were proposed to describe the specific behavior (Witten[1]). Despite these problems, population models abound in the literature.

This paper deals with the specific case of one-species, density-dependent, population models—of the logistic type—which undergo either constant or density-dependent harvesting procedures. We consider an assortment of models of this type, having either constant or stochastically varying parameters. Our purpose is to summarize some of the recent work on the formulation, analysis and interpretation of such models, and to point out deficiencies or open questions concerning them. However, due to lack of space, we have had to omit much. For example, we have not included considerations of maximum sustainable yield and of economic optimization.

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In the next section we discuss continuous density-dependent models of the logistic form and their variants. Although this material is elementary and is quite familiar, it is included both for the sake of completeness and because we will want to contrast features of the variants.

In subsequent sections we treat the logistic equation with constant harvesting and with proportional harvesting. We introduce the concept of sequential–continuous models and contrast the predictions of this class of models with previously discussed harvest equations. We then discuss harvesting of the logistic population in a random world. The second portion of this review covers much of the same ground for the discrete logistic population equation. We close our discussion by posing some yet to be answered questions.

Those readers who have further interesting material on this subject, who have material which we have missed, or who wish to make commentary on this paper, are encouraged to contact the authors.

## 2. CONTINUOUS DENSITY DEPENDENT MODELS

### 2.1. The logistic equation

The original formulation of density dependence, in populations, is due to Pearl and Reed[2] and Verhulst[3]; with an extensive discussion in Lotka[4]. In this formulation, the population grows exponentially for small values of population size. However, as the population becomes large enough, crowding, food shortage and environmental effects come into play, in a manner which limits population growth. The generalized density-dependent model takes on the form

$$\begin{aligned}\frac{dN(t)}{dt} &= b(t)N(t)g(t, N(t)), \\ N(t_0) &= N_0,\end{aligned}\tag{2.1}$$

where  $N(t)$  is the number of individuals at time  $t$ ,  $b(t)$  is the net reproductive rate (average numbers of births minus deaths per person), and  $g(t, N(t))$  is the density interaction term. The logistic equation of Pearl and Verhulst has the specialized form

$$\begin{aligned}\frac{dN(t)}{dt} &= b(t)N(t) \left( \frac{K(t) - N(t)}{K(t)} \right), \\ N(t_0) &= N_0,\end{aligned}\tag{2.2}$$

where  $K(t)$  is the time-dependent *environmental carrying capacity*.

### 2.2. Variants of the logistic equation

One may rewrite Eq. (2.2) in the following forms:

$$\begin{aligned}\frac{dN(t)}{dt} &= b(t)N(t) \left( 1 - \frac{N(t)}{K(t)} \right), \\ N(t_0) &= N_0, \\ \frac{dN(t)}{dt} &= b_1(t)N(t)[K(t) - N(t)],\end{aligned}\tag{2.3}$$

$$b_1(t) = \frac{b(t)}{K(t)}, \quad (2.4a)$$

$$N(t_0) = N_0.$$

Finally, one may rescale Eq. (2.4a) by substituting  $b_1(t) dt = dt'$ ,  $N(t) = N(t')$ , and  $K(t) = \mathcal{K}(t')$ . Then, dropping the script notation, we have

$$\begin{aligned} \frac{dN(t')}{dt'} &= N(t')[K(t') - N(t')], \\ N(t'_0) &= N_0. \end{aligned} \quad (2.4b)$$

This rescaling is valid provided that  $b_1(t) dt = dt'$  constitutes a valid change of variables, meaning that the correspondence between  $t$  and  $t'$  is one-to-one. One can show that, for this to be true, we need

$$\frac{dt'}{dt} \quad \text{to be of fixed sign.}$$

If  $b_1(t) > 0$  for all  $t$ , this will be true. It is not true if  $b_1(t)$  changes sign. This can happen, as the function

$$b_1(t) = \frac{b(t)}{K(t)}$$

may fluctuate into negative values if the net reproductive rate  $b(t)$  is sometimes positive and sometimes negative.

It should be pointed out that a number of other continuous density-dependent models have been proposed to describe the growth of a single-species population. These are often of the form (2.1), but with a different choice of the function  $g$ . Other models are much more complicated and incorporate mathematical representations of age structure, time delays, and other characteristics which we mention below in Section 4. Because this is intended as an introductory article, we have not attempted to survey these other models.

Equations (2.4a) and (2.4b) provide convenient reformulations of Eq. (2.2), particularly when one wishes to perform white noise analyses of the effects of stochastically varying birth rate or environmental carrying capacity. In an upcoming section, we discuss why these variants may lead to nonequivalent results.

It is possible to obtain analytic solutions to Eqs. (2.3) and (2.4). These are illustrated in Table 1. The most common application of Eq. (2.2) is in the situation where both  $b(t)$  and  $K(t)$  are assumed to be constants. In this case, the solution is given by

$$N(t) = \frac{K}{1 + \left(\frac{K}{N_0} - 1\right) \exp[-b(t - t_0)]}, \quad (2.5)$$

and the trajectories are illustrated in Fig. 1. For details see, for example, Haberman[5]. A classic illustration of just how well the logistic equation may describe a real population can be found in Maynard Smith[6], who discusses the logistic equation and its application to the growth of yeast in culture. Coleman[7] analyzed the behavior of solutions of (2.3)

Table 1. Analytic solutions for the logistic equation and its variants are illustrated in this table. Note that, for ease of typesetting,  $t_0$  has been set to zero, and  $N(t_0)$  has become  $N(0)$

|           | MODEL  | SOLUTION   |
|-----------|--|--|
| Eq (2.3)  | $\frac{dN(t)}{dt} = b(t)N(t) \left[ 1 - \frac{N(t)}{K(t)} \right]$ | $N(t) = \frac{N(0)e^{\int_0^t b(\tau) d\tau}}{\left[ 1 + N(0) \int_0^t \frac{b(s)e^{\int_0^s b(\tau) d\tau}}{K(s)} ds \right]}$        |
| Eq (2.4a) | $\frac{dN(t)}{dt} = b_1(t)N(t)[K(t) - N(t)]$                       | $N(t) = \frac{N(0)e^{\int_0^t b_1(\tau)K(\tau) d\tau}}{\left[ 1 + N(0) \int_0^t b_1(s)e^{\int_0^s b_1(\tau)K(\tau) d\tau} ds \right]}$ |
| Eq (2.4b) | $\frac{dN(t)}{dt} = N(t)[K(t) - N(t)]$                             | $N(t) = \frac{N(0)e^{\int_0^t K(\tau) d\tau}}{\left[ 1 + N(0) \int_0^t e^{\int_0^s K(\tau) d\tau} ds \right]}$                         |

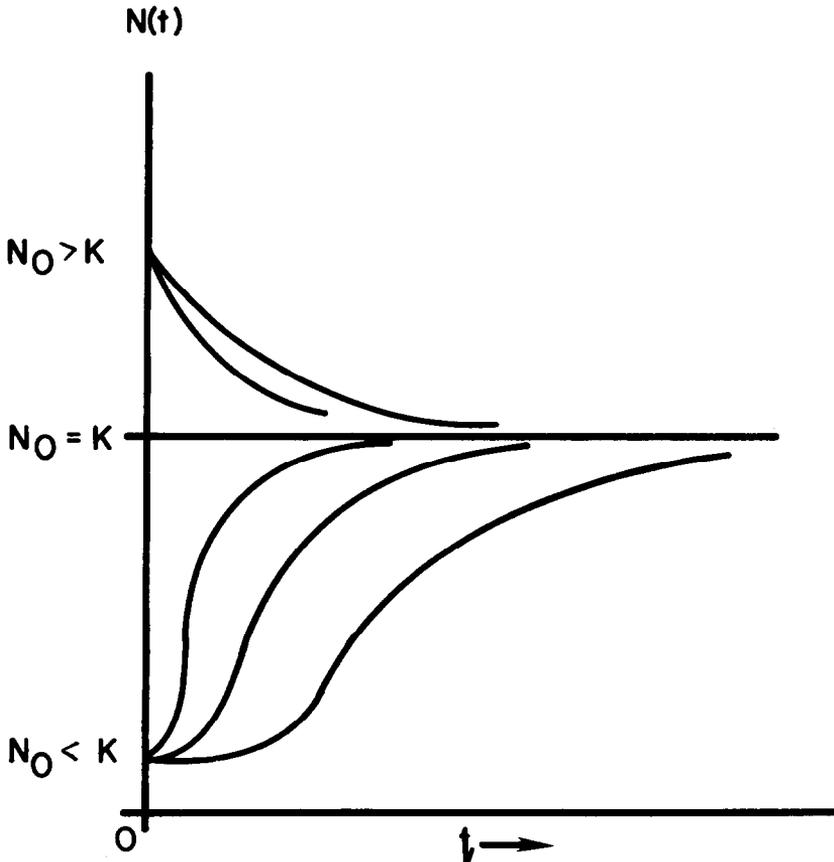


Fig. 1. Solution trajectories for the logistic equation (2.5), for the case  $b(t)$  and  $K(t)$  constant, are qualitatively illustrated for the three critical cases:  $K < N(0)$ ,  $K = N(0)$  and  $K > N(0)$ .

for arbitrary positive functions  $b(t)$  and  $K(t)$ . He showed that there is one solution  $N^*(t)$  (called the canonical solution) with the property that every solution  $N(t)$ , whatever its initial value  $N_0$ , approaches  $N^*(t)$  as  $t \rightarrow \infty$ . Logistic equations with periodic coefficients have been discussed by several authors: see deMottoni and Schiaffino[8]. For a discussion of the application of the nonautonomous (that is, with nonconstant  $b$  and  $K$ ) logistic equation to populations in a deteriorating environment, see Hallam and Clark[9].

### 2.3. Problems in using some of the variants

The use of Eqs. (2.4a and 2.4b) instead of (2.3) is not always justifiable. One possible misuse arises in the following manner. Sometimes a modeler will assume that  $b_1(t)$  is constant [in Eq. (2.4a)] and let  $K(t)$  vary. This approach is often used, when one wishes to perform white-noise analysis in a fluctuating environment represented by stochastic  $K(t)$ . This leads to a problem as  $b_1(t) = b(t)/K(t)$  and hence  $b_1(t)$  must vary if  $K(t)$  varies. One cannot make use of Eq. (2.4a) as equivalent to Eq. (2.3) if one assumes  $b_1$  is fixed, unless  $K$  and  $b$  vary together. This inconsistency is further compounded in using Eq. (2.4b), which assumes that  $b_1(t)$  is of constant sign, in order to eliminate the net reproduction rate. An example of this may be found in May[10]. Thus, one must be careful about the assumptions one is operating under when one is making use of a logistic equation variant. Similar considerations apply to logistic models with harvesting, as we shall now see.

### 2.4. The logistic equation with density-dependent harvesting

The harvesting procedures most commonly modeled are constant-rate harvest and density-dependent harvest. Density-dependent or proportional harvesting in the logistic equation introduces the term  $H_p N$ , where  $H_p$  is the harvest proportionality constant, yielding the system

$$\begin{aligned} \frac{dN(t)}{dt} &= b(t)N(t) \left( 1 - \frac{N(t)}{K(t)} \right) - H_p N(t), \\ N(t_0) &= N_0. \end{aligned} \quad (2.6)$$

The term  $H_p$  is often called the harvesting *effort*, and its magnitude depends upon the resources devoted to the harvest.

If one wished to discuss enrichment of the population, Eq. (2.6) would be rewritten

$$\begin{aligned} \frac{dN(t)}{dt} &= b(t)N(t) \left( 1 - \frac{N(t)}{K(t)} \right) + H_p N(t), \\ N(t_0) &= N_0. \end{aligned} \quad (2.7)$$

It is easy to demonstrate that Eq. (2.6) may be rewritten as follows [if  $b(t) \neq 0$ ]:

$$\begin{aligned} \frac{dN(t)}{dt} &= b'(t)N(t) \left( 1 - \frac{N(t)}{K'(t)} \right), \\ b'(t) &= b(t) - H_p, \\ K'(t) &= \frac{K(t)b'(t)}{b(t)}, \\ N(t_0) &= N_0. \end{aligned} \quad (2.8)$$

Figure 2 illustrates some sample solution trajectories for Eq. (2.8). Table 2 illustrates the analytic solutions to the logistic equation with density-dependent harvesting, along with its variants.

It is easy to see that Eq. (2.8) is simply a shifted form of Eq. (2.2) in which, for the case  $K'$ ,  $b'$  and  $H_p$  constant, we have

$$N(t) = \frac{K'}{1 + \left(\frac{K'}{N_0} - 1\right) \exp[-b'(t - t_0)]}. \quad (2.9)$$

Solution trajectories for Eq. (2.9) are similar to those of Eq. (2.5) when  $b' > 0$ , and  $N(t) \rightarrow K'$  as  $t \rightarrow +\infty$ . Observe that the limiting population  $K'$  is  $1 - (H_p/b)$  times the unharvested carrying capacity  $K$ , and that the population can be driven to extinction if  $H_p > b$ .

### 2.5. Constant-rate harvesting in the logistic equation

Instead of density-dependent or proportional harvesting, one might wish to have a constant harvest rate, denoted  $H_c$  (not to be confused with  $H_p$ ). Here one obtains the differential equation system

$$\begin{aligned} \frac{dN(t)}{dt} &= b(t)N(t) \left(1 - \frac{N(t)}{K(t)}\right) - H_c, \\ N(t_0) &= N_0. \end{aligned} \quad (2.10)$$

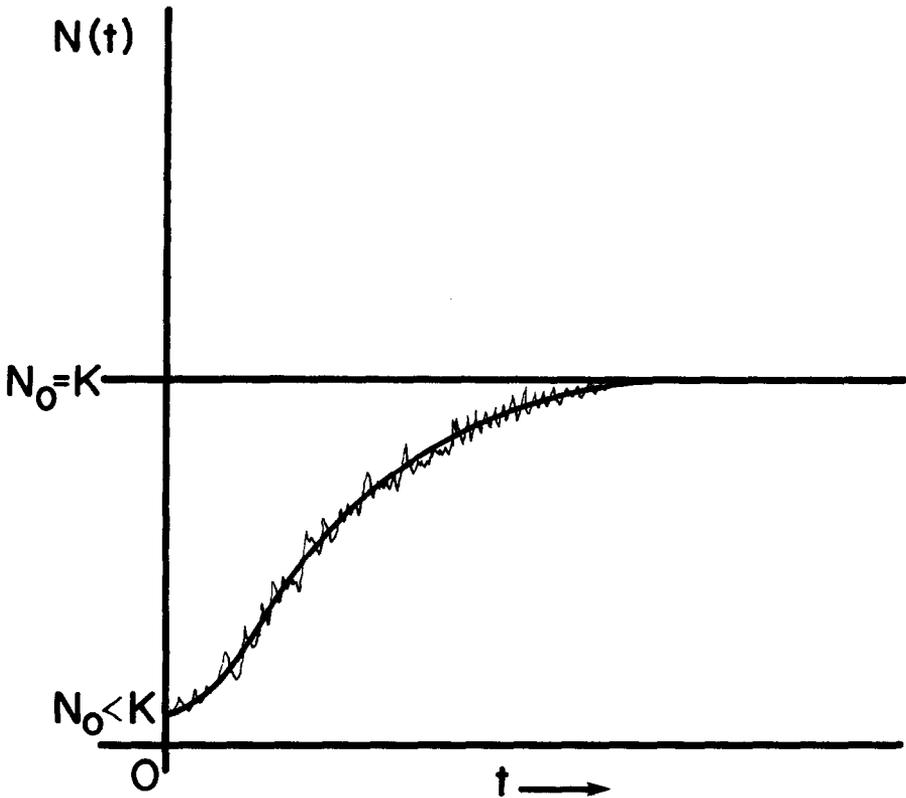


Fig. 2. Solution trajectories for the proportionally harvested logistic equation (2.8), for the case  $K(t)$  and  $b(t)$  constant,  $N(0) < K$  and  $H_p$  varied.

Table 2. Analytic solutions for the proportional harvesting procedure in logistic growth populations and their variants are illustrated in this table

| <i>MODEL</i>  |   |
|---|---|
| $\frac{dN}{dt} = b(t)N \left[ 1 - \frac{N}{K(t)} \right] - H_p N$ | $N(t) = \frac{N(0)e^{\int_0^t [b(\tau) - H_p] d\tau}}{\left[ 1 + N(0) \int_0^t \frac{[b(s) - H_p] b(s) e^{\int_0^s [b(\tau) - H_p] d\tau}}{K(s)[b(s) - H_p]} ds \right]}$ |
| $\frac{dN}{dt} = b_1(t)N[K(t) - N] - H_p N$                       | $N(t) = \frac{N(0)e^{\int_0^t [K(\tau)b_1(\tau) - H_p] d\tau}}{\left[ 1 + N(0) \int_0^t b_1(s) e^{\int_0^s [K(\tau)b_1(\tau) - H_p] d\tau} ds \right]}$                   |
| $\frac{dN}{dt} = N[K(t) - N] - H_p N$                             | $N(t) = \frac{N(0)e^{\int_0^t [K(\tau) - H_p] d\tau}}{\left[ 1 + N(0) \int_0^t e^{\int_0^s [K(\tau) - H_p] d\tau} ds \right]}$  |

If  $b(t)$  and  $K(t)$  are constant, Eq. (2.10) may be directly integrated to yield

$$N(t) = \frac{(D - b) + A(D + b) \exp(Dt)}{\frac{2b}{K} (A \exp(Dt) - 1)} \tag{2.11}$$

where

$$\begin{aligned} D &= \sqrt{b^2 - \frac{4bH_c}{K}}, \\ A &= \frac{b - D + J}{b + D + J} \exp(-Dt_0), \\ J &= -\frac{2bN_0}{K}. \end{aligned} \tag{2.12}$$

In general case, an explicit solution of Eq. (2.10) is apparently unknown. The behavior of solutions may be determined by the following analysis, when  $b$  and  $K$  are constant.

If we assume that  $D$  is real and positive, then Eq. (2.10) may be written in the factored form

$$\frac{dN(t)}{dt} = -\frac{b}{K} [N(t) - N_1][N(t) - N_2],$$

where the roots  $N_1$  and  $N_2$  are given by

$$\begin{aligned} N_1 &= \frac{K(b - D)}{2b}, \\ N_2 &= \frac{K(b + D)}{2b}. \end{aligned}$$

Since we are assuming that  $b$ ,  $K$  and  $H_c$  are positive, we can see that  $D < b$ , and therefore

$0 < N_1 < N_2$ . Consequently, it follows from the differential equation that

$$\begin{aligned} \frac{dN}{dt} &> 0 && \text{for } N_1 < N < N_2, \\ \frac{dN}{dt} &< 0 && \text{for } N < N_1 \text{ or } N > N_2. \end{aligned}$$

It follows that if  $N_0 > N_2$ , the solution  $N(t)$  decreases and has limit  $N_2$ . If  $N_1 < N_0 < N_2$ , the solution  $N(t)$  increases and has limit  $N_2$ . If  $N_0 < N_1$ , the solution  $N(t)$  decreases, becomes negative and, in fact, has a vertical asymptote at the value of  $t$  given by

$$Dt = \log \frac{1}{A}.$$

In this case, this gives a positive time  $t$ , since

$$\begin{aligned} b - D + J &> b - D - \frac{2bN_1}{K} = 0, \\ b + D + J &> b - D + J. \end{aligned}$$

In any event, a positive equilibrium  $N_2$  exists when  $H_c < Kb/4$  so that  $D > 0$ . But if the initial population  $N_0$  is less than  $N_1$ , extinction occurs because the birth rate is insufficient to overcome harvesting. If  $H_c > Kb/4$ , then  $D$  is imaginary, and the quadratic form  $-(b/K)N^2 + bN - H_c$  has the same negative sign for all values of  $N$ . Therefore  $dN/dt < 0$ , and  $N(t)$  becomes negative for any value of  $N_0$ .

### 2.6. Sequential–continuous model for harvesting

The concept of sequential–continuous dynamical models was independently developed by Busenberg and Cooke[11] for models of vertically transmitted diseases, Witten[1, 12] for models of asynchronously dividing cellular systems, and by Coffman and Coleman[13], for a model of growth of a population with age structure and periodic variations in the environment.

The essential feature of sequential–continuous systems is that during certain periods of time, the system dynamics is governed by continuous equations (differential or partial-differential equations), and during the other periods, the system is governed by sequential (discrete or probabilistic) equations. This type of model is particularly applicable to harvesting.

The harvesting procedure is seldom continuous; it either occurs at definite time points or else it is on/off over certain time intervals. We will first consider discrete time-point harvesting. Let  $t_1, t_2, \dots$ , be an increasing sequence of time points satisfying  $t_1 < t_2 < t_3 < \dots$ . At each time point  $t_i$ , assume that a constant harvest  $H_c$  is instantaneously removed from the population. During the time intervals between the harvest times, assume that the population is governed by the continuous logistic model. Let

$$N(t_i^-) = \lim_{t \uparrow t_i} N(t), \quad N(t_i^+) = \lim_{t \downarrow t_i} N(t).$$

Then the model takes on the form

$$\begin{aligned} \frac{dN(t)}{dt} &= b(t)N(t) \left( 1 - \frac{N(t)}{K(t)} \right) \quad \text{for } t_{i-1} < t < t_i, \\ N(t_0) &= N_0, \\ N(t_i^+) &= N(t_i^-) - H_c \quad \text{for } i = 1, 2, \dots \end{aligned} \tag{2.13}$$

Note that  $H_c$  is no longer a *removal rate*, as it was in Eq. (2.10), but rather, the *number removed*. More generally, we could envisage seasonal harvesting, in which there is a fixed harvest period or open season, occurring periodically. If we assume that the unit of time is one year and that harvesting is permitted each year during a time interval of length  $h$ , then a model might have the following form—in which  $H_c$  is again a removal rate.

$$\begin{aligned} \frac{dN(t)}{dt} &= b(t)N(t) \left( 1 - \frac{N(t)}{K(t)} \right) - H_c \quad \text{for } n < t < n + h, \\ \frac{dN(t)}{dt} &= b(t)N(t) \left( 1 - \frac{N(t)}{K(t)} \right) \quad \text{for } n + h < t < n + 1, \\ N(t_0) &= N_0. \end{aligned} \tag{2.14}$$

Here  $N(t)$  is required to be continuous at all the points  $t = n$  and  $t = n + h$  for  $n = 0, 1, 2, \dots$ . In other words, there is a harvesting “window” of length  $h$ . In fact, the two differential equations making up Eq. (2.14) may be considered a special case of the equation

$$\frac{dN(t)}{dt} = b(t)N(t) \left( \frac{1 - N(t)}{K(t)} \right) - H(t), \quad 0 < t,$$

where  $H(t)$  is given by the discontinuous periodic function

$$H(t) = \begin{cases} H_c & \text{for } n < t < n + h, \\ 0 & \text{for } n + h < t < n + 1, \end{cases} \quad n = 0, 1, 2, \dots$$

Brauer and Sánchez[14] have discussed constant rate population harvesting, while Sánchez[15] has treated seasonal harvesting for a model of linear age-dependent population growth. In our paper we shall not consider explicit dependence upon age. Related issues have been discussed by Sánchez[16]. Both Eqs. (2.13) and (2.14) are also easily extended to include more general expressions for harvesting. For example, Eq. (2.13c) could be replaced by

$$N(t_i^+) = N(t_i^-) - f(N(t_i^-), t_i). \tag{2.15}$$

For purposes of illustration and later comparison, we shall—from this point on—discuss Eq. (2.13) with  $K$  and  $b$  constant. During the period  $t \in (t_{n-1}, t_n)$  the population process is governed by Eq. (2.13a). Hence we may obtain the following solution for  $N(t_n^-)$ :

$$N(t_n^-) = \frac{K}{1 + \left( \frac{K}{N(t_{n-1}^+)} - 1 \right) \exp[-b(t_n - t_{n-1})]}. \tag{2.16}$$

From Eq. (2.13c), we obtain

$$N(t_n^+) = \frac{K}{1 + \left(\frac{K}{N(t_{n-1}^+)} - 1\right) \exp[-b(t_n - t_{n-1})]} - H_c. \tag{2.17}$$

If we let  $t_n = n$ , for example, and let  $N(n) = N(t_n^+)$ ,  $n = 0, 1, 2, \dots$ , we see that the whole behavior of the process is governed by the recursive equation (difference equation)

$$N(n + 1) = \frac{K}{1 + \left(\frac{K}{N(n)} - 1\right) \exp[-b]} - H_c. \tag{2.18}$$

By definition, the points  $N(n) = N(n^+)$  must lie on the solution trajectory of Eq. (2.13) at the time points  $t_n$ . Further discussion of this model will be given in Section 3.5.

For proportional harvesting, Eq. (2.13c) would be replaced by  $N(t_i^+) = (1 - H)N(t_i^-)$  and Eq. (2.18) would be modified to

$$N(n + 1) = \frac{K(1 - H)}{1 + \left(\frac{K}{N(n)} - 1\right) \exp[-b]}, \tag{2.19}$$

where  $H$  is the harvested fraction. Notice immediately that Eq. (2.13) could be turned into an enrichment process by modification of Eq. (2.13c) as follows:

$$N(t_i^+) = N(t_i^-) + H_c. \tag{2.20}$$

The concept of persistence times of populations undergoing logistic growth with random density-dependent and -independent disasters was considered in Hanson and Tuckwell[17, 18]. In these papers, they considered a logistic growth population undergoing Poisson-like catastrophic harvest (disaster) in a stochastic differential equation of the form

$$\begin{aligned} dN(t) &= bN(t) \left(\frac{1 - N(t)}{K}\right) dt - HN(t) d\Pi(t; \lambda), \\ N(t_0) &= N_0, \\ b > 0; H &\in (0, 1), \end{aligned} \tag{2.21a}$$

where  $d\Pi(t; \lambda)$  is the differential of a Poisson process with rate parameter  $\lambda$ . Hanson and Tuckwell also consider a constant harvest catastrophe by modifying the stochastic differential equation (2.21a) to read

$$\begin{aligned} dN(t) &= bN(t) \left(1 - \frac{N(t)}{K}\right) dt - H d\Pi(t; \lambda), \\ N(t_0) &= N_0, \\ b > 0; H &\in (0, 1). \end{aligned} \tag{2.21b}$$

Currently, research is ongoing in the investigation of systems of type (2.21), where  $H$  is replaced by  $H(t)$ , some predetermined distribution in time (Hanson, private communi-

cation). Similar issues are addressed by Gripenberg[19], for a model of the growth of a population subject to random catastrophes, and by Reed[20].

### 2.7. Harvesting the logistic equation in a noisy environment

The next generalization of logistic growth with constant environment  $K$  and net reproductive rate  $b$  is to an equation in which  $K(t)$  and  $b(t)$  are fluctuating functions of time. The usual assumption is that

$$\begin{aligned} K(t) &= K_0 + \gamma_K(t), \\ b(t) &= b_0 + \gamma_b(t), \end{aligned} \quad (2.22)$$

where  $K_0$  and  $b_0$  are the means of  $K(t)$  and  $b(t)$ , respectively, and  $\gamma_K(t)$ ,  $\gamma_b(t)$  are white noise with mean zero and variance  $\sigma_K^2$ ,  $\sigma_b^2$ , respectively. For an excellent introduction to the discussion in this section, including the ideas of Ito and Stratonovich calculi, see Roughgarden ([21], Chap. 20) or Nisbet and Gurney ([22], Chaps. 6, 7).

One of earliest investigations into the behavior of a population in a randomly varying environment was by Lewontin and Cohen[23]; see also Ludwig[24]. Lewontin and Cohen first consider a discrete population growing according to the rule

$$\begin{aligned} N(n+1) &= N(n)b(n), \\ N(0) &= N_0, \end{aligned} \quad (2.23)$$

where  $b(n)$  is a random variable. It is straightforward to demonstrate that the solution to Eq. (2.23) is given by

$$N(n) = N_0 \prod_{i=1}^n b(i). \quad (2.24)$$

Their discussion of this model leads them to the conclusion that, even though the expectation of the population size,  $E[N(n)]$ , may grow infinitely large with time, the extinction probability for the population can approach one.

The next paper on the subject of population growth in random environments is due to Levins[25]. In this paper, Levins investigates populations living in random environments and undergoing both density-dependent and density-independent growth. In particular, he investigates the two equations

$$\frac{dN(t)}{dt} = b(t)N(t)$$

and

$$\frac{dN(t)}{dt} = b(t)N(t) \left( 1 - \frac{N(t)}{K} \right),$$

where  $b(t)$  is of the form given in Eq. (2.22). He is able to rigorously demonstrate the following results. Sampling variance increases the expected size of density-dependent populations. However, the addition of density-dependent growth with capacity  $K$  results in a bimodal distribution. Further, variation in the net rate of increase  $b$  does not alter the expected value of  $\ln[N(t)]$ , in the case of density-independent growth. In the case of

density-dependent growth, there is a concentration of population values near  $K$  if  $\sigma_b^2$  is less than the mean of  $b(t)$ . Otherwise, a varying  $b$  results in a bimodal distribution with populations clustering near  $K$  and 0. Finally, if  $K$  varies,  $N$  is equal to a weighted harmonic mean of the  $K$ 's. In this case, greater weight is given to more recent  $K$  values, and the rate at which the effects of previous  $K$  values are damped out is a function of the size of  $b$ ; the larger the  $b$  value, the more rapid the washout effect. For further details, see Levins[25].

The question of stochastically varying environments came to the foreground with the work of May[26, 10]. In these papers, May considers the logistic variant

$$\begin{aligned}\frac{dN(t')}{dt'} &= N(t')[K(t') - N(t')], \\ N(0) &= N_0,\end{aligned}\tag{2.25}$$

where  $K(t)$  is as described in Eq. (2.22). It is important to remember that, in order to make use of Eq. (2.25), the function  $K(t)$  in Eq. (2.25) fluctuates not as a function of  $t$  but rather as a function of  $t'$ , where

$$t' = \int b_1(t) dt = \int \frac{b(t)}{K(t)} dt.$$

Hence, if  $K(t)$  in Eq. (2.3) has the form in Eq. (2.22),  $K(t')$  in Eq. (2.25) need not be of the same form.

Making use of the Fokker-Plank (also called Chapman-Kolmogorov) equation [see Eq. (2.61) below], May is able to demonstrate that the equilibrium probability distribution for  $N(t)$ , denoted  $p^*(n)$ —where  $p^*(n)$  is a solution to the time-independent form of Eq. (2.61)—where  $N(t)$  is governed by Eq. (2.25), is given by

$$p_I^*(n) = C_I n^{(2K_0/\sigma_K^2)-2} \exp[-(2n/\sigma_K^2)].\tag{2.26}$$

Equation (2.26) describes a Pearson Type-III gamma distribution and  $C_I$  is an integration constant. While the results of this analysis are of interest, care must be taken in their application. More details on this model may be found in May[10] and Witten[1].

The conclusion of May's analysis is that persistence in a stochastically varying environment involves a balance between the randomness of the environment and the spontaneous tendency to return to the equilibrium of the deterministic equation. This result may be restated in terms of the difference between  $K_0$  and  $\sigma_K^2/2$ . If the difference between  $K_0$  and  $\sigma_K^2/2$  is large, then the probability of extinction is zero. Should the difference be small, the population is doomed to extinction with probability one. This particular point has stirred up much discussion in the literature. For various alternative approaches to this problem, see Ricciardi[27], Ricciardi and Capocelli[28], Keiding[29], Karlin and Levikson[30], Gillespie[31] and Feldman and Roughgarden[32].

It is relevant to pause and mention one of the major points of the Feldman and Roughgarden[32] paper. Namely, depending upon whether one uses the Stratonovich calculus or the Itô calculus, one obtains different stationary probability distributions for  $p^*(n)$ . If we interpret May's problem in the Stratonovich sense, we obtain the following equilibrium probability distribution

$$p_S^*(n) = C_S n^{(2K_0/\sigma_K^2)-1} \exp[-(2n/\sigma_K^2)].\tag{2.27}$$

Clearly, the equilibrium distributions under the two different calculi are different. Hence the interpretations of the population dynamics will be different. Thus one must be careful about the choice of stochastic calculus one uses in addressing these problems. An elegant discussion may be found in Braumann[33]. Other discussions concerning exact equilibrium solutions to various stochastic differential equation models of population growth may be found in Kiester and Barakat[34], Tuckwell[35] and Sawyer and Slatkin[36].

The first work concerning the harvesting of natural populations in a randomly fluctuating environment may be found in the work of May[37]. In this paper, May considers the results of letting  $b(t)$  be stochastic in a logistic growth proportional harvest model of the form

$$\frac{dN(t)}{dt} = b(t)N(t) \left( 1 - \frac{N(t)}{K} \right) - H_p N(t). \tag{2.28}$$

He assumes that the randomness appears only in the density-independent growth portion of Eq. (2.28). This yields, after substitution and rearrangement, the following equation:

$$\frac{dN(t)}{dt} = [\gamma_b(t) + b_0 - H_p]N(t) - \frac{b_0 N^2(t)}{K}. \tag{2.29}$$

Making use of the Itô calculus, May[37] demonstrates that

$$\begin{aligned} p_I^*(n) &= \beta \exp \left( - \frac{2b_0}{K\sigma_b^2} n \right), \\ \beta &= \frac{2b_0 \left( \frac{2b_0 n}{K\sigma_b^2} \right)^\alpha}{K\sigma_b^2 \Gamma(\alpha + 1)}, \\ \alpha &= \frac{2(2b_0 - H_p - \sigma_b^2)}{\sigma_b^2}. \end{aligned} \tag{2.30}$$

We wish to point out that the noise may be introduced into the density-dependent term, yielding a stochastic differential equation of the form

$$\begin{aligned} \frac{dN(t)}{dt} &= (b_0 - H_p)N - \frac{b_0 + \gamma_b(t)}{K} N^2(t), \\ N(t_0) &= N_0. \end{aligned} \tag{2.31}$$

If we apply the Itô calculus, the drift term of Eq. (2.61)—which appears as  $M(n, t)$  in that equation—is given by

$$M_I(n, t) = (b_0 - H_p)n \left( 1 - \frac{b_0 n}{K(b_0 - H_p)} \right). \tag{2.32}$$

The diffusion coefficient, which appears as  $V(n, t)$  in Eq. (2.61), is given by

$$V_I(n, t) = \frac{\sigma_b^2 n^4}{K^2}. \tag{2.33}$$

Making use of the fact that stationary probability densities (if they exist) will be given by

$$p^*(n) = \frac{C}{V(n)} \exp \left( 2 \int^n \frac{M(n')}{V(n')} dn' \right), \quad (2.34a)$$

and  $C$  is a constant given by

$$C = 1 / \int_0^\infty \left[ \frac{1}{V(n)} \exp \left( 2 \int^n \frac{M(n')}{V(n')} dn' \right) \right] dn. \quad (2.34b)$$

Following the Itô calculus, we obtain the Itô equilibrium distribution

$$p_I^*(n) = \frac{C_I}{n^4} \exp \left[ \frac{2Kb_0}{\sigma_b^2 n} \left( 1 - \frac{K(b_0 - H_p)}{2b_0 n} \right) \right]. \quad (2.35)$$

If we follow the Stratonovich calculus, we obtain

$$M_S(n, t) = M_I(n, t) + \frac{\sigma_b^2 n^3}{K^2}, \quad (2.36)$$

where  $V_S(n) = V_I(n)$ , and

$$p_S^*(n) = \frac{C_S}{n^2} \exp \left[ \frac{2Kb_0}{\sigma_b^2 n} \left( 1 - \frac{K(b_0 - H_p)}{2b_0 n} \right) \right]. \quad (2.37)$$

Both equilibrium distributions always exist (cf. Feldman and Roughgarden[32]).

Let us take a moment to compare Eqs. (2.30), (2.35) and (2.37). Observe that the essential difference, modulo the value of the constant  $C$ , is the fact that

$$p_I^* \sim \frac{1}{n^2} p_S^*.$$

Thus the Itô probability distribution decreases more rapidly than the Stratonovich distribution (for large values of  $n$ ). Both Eqs. (2.35) and (2.37) differ fundamentally from Eq. (2.30). While, for large values of  $n$ , Eq. (2.35) behaves like  $C_I/n^4$ , and Eq. (2.37) behaves like  $C_S/n^2$ ; Eq. (2.30) behaves like  $Cn^\alpha e^{-\epsilon n}$  where the value of  $\alpha$  depends directly upon the values of  $b_0$ ,  $H_p$  and  $\sigma_b^2$ . And it may take on positive, negative or zero values.

It is also of interest to examine the constant-harvest case. Let us first consider constant harvest, logistic growth, and noise in the density-independent term. Here we have the equation

$$\begin{aligned} \frac{dN(t)}{dt} &= [b(t)N(t) - H_c] - \frac{b_0 N^2(t)}{K}, \\ N(t_0) &= N_0. \end{aligned} \quad (2.38)$$

Following the Itô calculus, we obtain

$$M_I(n) = b_0 \left[ n \left( 1 - \frac{n}{K} \right) - \frac{H_c}{b_0} \right], \quad (2.39)$$

$$V_I(n) = \sigma_b^2 n^2,$$

$$p_I^*(n) = C_I n^{(2b_0/\sigma_b^2 - 2)} \exp \left( \frac{2H_c}{\sigma_b^2 n} - \frac{2b_0 n}{\sigma_b^2 K} \right). \quad (2.40)$$

Following the Stratonovich calculus,

$$M_S(n) = M_I(n) + \frac{\sigma_b^2 n}{2}, \tag{2.41}$$

where  $V_S(n) = V_I(n)$  and

$$p_S^*(n) = C_S n^{(2b_0/\sigma_b^2 - 1)} \exp\left(\frac{2H_c}{\sigma_b^2 n} - \frac{2b_0 n}{\sigma_b^2 K}\right). \tag{2.42}$$

Observe that  $p_I^* \sim (1/n)p_S^*$ . Thus, for large  $n$ , the Itô distribution is more rapidly decreasing than the Stratonovich distribution.

Finally we may consider the constant harvest logistic model where the noise is in the density-dependent term. This yields a model of the form

$$\begin{aligned} \frac{dN(t)}{dt} &= (b_0 N - H_c) - \frac{b(t)N^2(t)}{K}, \\ N(t_0) &= N_0. \end{aligned} \tag{2.43}$$

For this case we can demonstrate that

$$\begin{aligned} M_I(n) &= b_0 n \left(1 - \frac{n}{K}\right) - H_c, \\ V_I(n) &= \frac{\sigma_b^2 n^4}{K^2}, \\ p_I^*(n) &= \frac{C_I}{n^4} \exp\left[\frac{2Kb_0}{\sigma_b^2 n} \left(\frac{KH_c}{3b_0 n^2} + 1 - \frac{K}{2n}\right)\right] \end{aligned} \tag{2.44}$$

and

$$\begin{aligned} M_S(n) &= b_0 n \left(1 - \frac{n}{K}\right) - H_c + \frac{\sigma_b^2 n^3}{K^2}, \\ V_S(n) &= V_I(n), \\ p_S^*(n) &= \frac{C_S}{n^2} \exp\left[\frac{2Kb_0}{\sigma_b^2 n} \left(\frac{KH_c}{2b_0 n^2} + 1 - \frac{K}{2n}\right)\right]. \end{aligned} \tag{2.45}$$

For details on the application of stochastic arguments to bioeconomics, the reader is invited to examine May[37].

Stochasticity has also been introduced in  $b(t)$  itself, not just in the density-independent or density-dependent parts. That is, we have an equation of the form

$$\begin{aligned} \frac{dN(t)}{dt} &= b(t)N(t) \left(1 - \frac{N(t)}{K}\right), \\ N(t_0) &= N_0. \end{aligned} \tag{2.46}$$

Equations of logistic growth in a random environment have been discussed, in detail, by Braumann[38]. See also Kiester and Barakat[34], as well as Tuckwell[35]. For a constant

harvest model of the form of (2.46) we have

$$\begin{aligned}\frac{dN(t)}{dt} &= b(t)N(t) \left(1 - \frac{N(t)}{K}\right) - H_c, \\ N(t_0) &= N_0,\end{aligned}\tag{2.47}$$

with

$$\begin{aligned}M_I(n) &= -H_c + b_0 n \left(1 - \frac{n}{K}\right), \\ M_S(n) &= M_I(n) + \frac{\sigma_b^2}{2} n \left(1 - \frac{n}{K}\right) \left(1 - \frac{2n}{K}\right), \\ V_I(n) &= V_S(n) = \sigma_b^2 n^2 \left(1 - \frac{n}{K}\right)^2.\end{aligned}\tag{2.48}$$

This leads to stationary distributions of the form

$$\begin{aligned}p_I^*(n) &= \frac{C_I}{n^2 \left(1 - \frac{n}{K}\right)^2} \Omega_1^\alpha \exp(\Omega_2), \\ p_S^*(n) &= \frac{C_S}{n^2} \Omega_1^{\alpha-1} \exp(\Omega_2), \\ \Omega_1(n) &= \left(\frac{n}{1 - \frac{n}{K}}\right), \\ \Omega_2(n) &= \left[\frac{2H_c}{\sigma_b^2} \left(\frac{1}{n} - \frac{1}{K-n}\right)\right], \\ \alpha &= \frac{2(b_0 - H_c)}{\sigma_b^2}.\end{aligned}\tag{2.49-2.50}$$

Notice that, for this example,

$$p_I^* \sim \frac{\Omega_1}{\left(1 - \frac{n}{K}\right)^2} p_S^*.$$

Finally, in the case where the noise is in the carrying capacity, Feldman and Roughgarden[32] have suggested an alternate model which we modify for constant harvest as follows:

$$\begin{aligned}\frac{dN(t)}{dt} &= bN(t) \left(1 - \frac{N(t)[1 - \gamma(t)]}{K_0}\right) - H_c, \\ N(t_0) &= N_0.\end{aligned}\tag{2.51}$$

This can be shown to have

$$\begin{aligned} M_I &= bn \left( 1 - \frac{n}{K_0} \right) - H_c, \\ M_S &= M_I + \frac{\sigma_K^2 b^2 n^3}{K_0^2}, \\ V_I &= V_S = \frac{\sigma_K^2 b^2 n^4}{K_0^2}, \end{aligned} \tag{2.52}$$

and the equilibrium distributions, assuming that they exist, are given by

$$p_I^*(n) = C_I n^\alpha \exp \left[ \left( \frac{2K_0^2}{\sigma_K^2 b^2 n} \right) \left( \frac{-n}{2n} + \frac{b}{K_0} + \frac{H}{3n^2} \right) \right], \tag{2.53}$$

where

$$\alpha = \left( \frac{2K_0^2}{\sigma_K^2 b} \right) - 2.$$

For the Stratonovich calculus we obtain

$$p_S^*(n) = C_S n^{\alpha-2} \exp \left[ \left( \frac{2K_0}{\sigma_K^2 b} \right) \left( \frac{K_0 H_c}{bn} - n \right) + n^2 \right], \tag{2.54}$$

where  $\alpha$  is as defined above.

This concludes our brief discussion of harvesting processes in a one-dimensional logistic population model with stochastically varying reproductive rate or carrying capacity. One might also investigate the situation in which the harvest term is the stochastically varying parameter. This might be done in the following manner.

$$\begin{aligned} \frac{dN(t)}{dt} &= bN \left( 1 - \frac{N}{K} \right) - [H_c^0 + \gamma(t)], \\ N(t_0) &= N_0. \end{aligned} \tag{2.55}$$

It is straightforward to show that

$$\begin{aligned} M_I &= bn \left( 1 - \frac{n}{K} \right) - H_c^0, \\ M_S &= M_I, \\ V_S &= V_I = \sigma^2. \end{aligned} \tag{2.56}$$

Hence the equilibrium probability distributions may be shown to be

$$p_I(n) = p_S(n) = C_I \exp \left[ \frac{n}{\sigma^2} \left( bn - \frac{2bn^2}{3K} - 2H_c^0 \right) \right]. \tag{2.57}$$

The proportional harvesting model, with stochastic harvesting, takes on the form

$$\begin{aligned}\frac{dN(t)}{dt} &= bN \left(1 - \frac{N}{K}\right) - [H_p^0 + \gamma(t)]N, \\ N(t_0) &= N_0,\end{aligned}\tag{2.58}$$

where

$$\begin{aligned}M_I &= bn \left(1 - \frac{n}{K}\right) - H_p^0 n, \\ M_S &= bn \left(1 - \frac{n}{K}\right) + \frac{\sigma^2}{2} n - H_p^0 n, \\ V_I &= V_S = \sigma^2 n^2.\end{aligned}\tag{2.59}$$

The equilibrium distributions (assuming they exist) are given by

$$\begin{aligned}p_I^*(n) &= C_I n^{\beta-2} \exp\left(-\frac{2n}{K\sigma^2}\right), \\ p_S^*(n) &= C_S n^{\beta-1} \exp\left(-\frac{2n}{K\sigma^2}\right), \\ \beta &= \frac{2(b - H_p^0)}{\sigma^2}.\end{aligned}\tag{2.60}$$

It should be pointed out that one does not always need to find the equilibrium distribution. If we let  $p(n, t)$  be the probability of  $n$  individuals being present at time  $t$ , one can demonstrate that  $p(n, t)$  satisfies the Kolmogorov–Bogoliubov forward diffusion equation (also called the Fokker–Planck equation) given by

$$\frac{\partial p(n, t)}{\partial t} = -\frac{\partial}{\partial n} [M(n, t)p(n, t)] + \frac{1}{2} \frac{\partial^2}{\partial n^2} [V(n, t)p(n, t)],\tag{2.61}$$

where  $M(n, t)$  and  $V(n, t)$  are the time-dependent drift and diffusion coefficients previously introduced. For an excellent discussion of the derivation of Eq. (2.61) and its application see Roughgarden[21]. If we assume that  $p(n, t) = N(n)T(t)$ , that  $M$  and  $N$  are not time dependent, and substitute this into Eq. (2.61), we obtain

$$\frac{1}{T} \frac{dT}{dt} = N^{-1} \left[ \frac{V}{2} \frac{d^2 N}{dn^2} + \left( \frac{dV}{dn} - M \right) \frac{dN}{dn} + \left( \frac{1}{2} \frac{d^2 V}{dn^2} - \frac{dM}{dn} \right) N \right].\tag{2.62}$$

Since the left-hand side of Eq. (2.62) involves only  $t$  and the right-hand side of the equation involves only  $n$ , we may equate both sides to the same constant, say  $-\lambda$ . This allows us to separate the equations. Thus, Eq. (2.62) becomes

$$\begin{aligned}\frac{dT}{dt} &= -\lambda T, \\ \frac{V}{2} \frac{d^2 N}{dn^2} + \left( \frac{dV}{dn} - M \right) \frac{dN}{dn} + \left( \frac{1}{2} \frac{d^2 V}{dn^2} - \frac{dM}{dn} + \lambda \right) N &= 0.\end{aligned}\tag{2.63}$$

Now, for any value of  $\lambda$ , say  $\lambda_i$ , we have

$$T(t, \lambda_i) = \exp(-\lambda_i t). \tag{2.64}$$

And we may hope that we might solve Eq. (2.63) to yield a solution  $N_i = N(n, \lambda_i)$ . Thus the general solution to Eq. (2.61) might be expressed in the form

$$p(n, t) = \sum_{i=0}^{\infty} A_i N_i \exp(-\lambda_i t), \tag{2.65}$$

where  $\lambda_i$  and  $A_i$  are determined from the boundary conditions of the problem to be solved. The complexity of the solution, even in the simplest cases, may be noted in the following example. Let us assume that  $M(n, t) = \alpha_1 n$  and  $V(n, t) = \alpha_2 n$ ,  $\alpha_2 > 0$ . If we assume that  $N(t = 0) = N_0$ , then the solution to Eq. (2.61) may be shown to be given by

$$p(n, t) = \frac{2\alpha_1 \left(\frac{N_0\alpha_3}{n}\right)^{1/2}}{\alpha_2(\alpha_3 - 1)} \exp\left(-\frac{2\alpha_1(N_0\alpha_3 + n)}{\alpha_2(\alpha_3 - 1)}\right) I_1\left(\frac{4\alpha_1(N_0n\alpha_3)^{1/2}}{\alpha_2(\alpha_3 - 1)}\right), \tag{2.66}$$

where  $\alpha_3 = e^{\alpha t}$  and  $I_1$  is a Bessel function of order one. For more details on methods for solving Eq. (2.61), see Sagan[39] and Bharucha-Reid[40].

In the following discussion, we consider models of harvesting a population when the duration of the harvest interval is subject to random fluctuations. This kind of situation arises, for example, if the harvester or predator can harvest only when the weather conditions are favorable. Clearly the length of the favorable period will be subject to random variations.

We consider a single-species population which is assumed to grow according to a deterministic growth law. At first, we analyze the continuous time case; if  $N(t)$  denotes the population at time  $t$ , the growth law has the form

$$\frac{dN}{dt} = g(N(t))$$

for a suitable function  $g(N)$ . We assume that during each year (or other suitable unit of time) harvesting occurs during an interval of time, and that the length of this interval varies randomly. For the sake of mathematical convenience, we shall assume proportional harvesting. Thus we postulate a model of the form

$$\begin{aligned} \frac{dN(t)}{dt} &= g(N) - HN, & S'_i < t < S_i & \quad (i = 1, 2, 3, \dots), \\ \frac{dN(t)}{dt} &= g(N) & \text{otherwise,} & \end{aligned} \tag{2.67}$$

where  $S'_i$  and  $S_i$  are random variables that satisfy  $i - 1 \leq S'_i < S_i \leq i$  ( $i = 1, 2, \dots$ ).

In this discussion we only consider the case in which  $g(N)$  is a linear function,  $g(N) = bN$ , where  $b$  is the net rate of increase (natural birth rate minus natural death rate, which we assume to be fixed constants). This model might be appropriate for cases in which harvesting keeps the population at a low enough level that density-dependent effects are negligible. For example, cell culture growth is density dependent. However, if the

cell density is low enough, then these effects are negligible. The extension of this model to the case in which  $g(N)$  has a logistic form has not been worked out.

We shall examine the following model, which is treated in Capasso *et al.*[41].

$$\begin{aligned} \frac{dN(t)}{dt} &= bN - HN, & i - 1 < t < i - 1 + T_i, \\ \frac{dN(t)}{dt} &= bN, & i - 1 + T_i < t < i, \end{aligned} \tag{2.68}$$

where  $i = 1, 2, 3, \dots$  and with initial condition

$$N(0) = N_0 \tag{2.69}$$

and continuity equations

$$N(i - 1 + T_i^-) = N(i - 1 + T_i^+), \quad i = 1, 2, 3, \dots \tag{2.70}$$

We assume that  $b, H$  and  $N_0$  are given constants. It is easy to write the solution of Eqs. (2.68)–(2.70). We find, by induction, that the following formulae are valid, for  $k = 1, 2, 3, \dots$ :

$$\begin{aligned} N(t) &= N_0 \exp \left[ (b - H)t + H \left( k - \sum_{i=1}^k T_i \right) \right], & k \leq t \leq T_{k+1} + k, \\ N(t) &= N_0 \exp \left( bt - H \sum_{i=1}^{k+1} T_i \right), & k + T_{k+1} \leq t \leq k + 1. \end{aligned} \tag{2.71}$$

In particular, we have

$$\begin{aligned} N(k) &= N_0 \exp \left( bk - H \sum_{i=1}^k T_i \right), \\ N(k + T_{k+1}) &= N_0 \exp \left( b(k + T_{k+1}) - H \sum_{i=1}^{k+1} T_i \right) \end{aligned} \tag{2.72}$$

for  $k = 0, 1, 2, 3, \dots$ . Thus, the problem is to describe the distribution of the random variables  $N(k)$  and  $N(k + T_{k+1})$  under appropriate assumptions about the random variables  $T_i, i = 1, 2, 3, \dots$ . Throughout, we shall make the basic assumption that all of these random variables are independent, but not necessarily identically distributed, unless specifically stated.

If we now take into account that

$$E\{\{\exp(sT_i)\}^r\} = E[\exp(rsT_i)] = M_i(rs), \tag{2.73}$$

where  $T_i$  has moment generating function  $M_i(s) = E[\exp(sT_i)]$  then we can demonstrate that the  $r$ th-order moments  $r = 1, 2, 3, \dots$  are given by

$$\begin{aligned} E\{[N(k)]^r\} &= N_0^r e^{rbk} \prod_{i=1}^k M_i(-rH), \\ E\{[N(k + T_{k+1})]^r\} &= N_0^r e^{rbk} M_{k+1}(rb) \prod_{i=1}^{k+1} M_i(-rH) \end{aligned} \tag{2.74}$$

for  $k = 0, 1, 2, 3, \dots$ . In particular, for the variance, we obtain

$$\text{VAR}[N(k)] = N_0^2 e^{2bk} \left( \prod_{i=1}^k M_i(-2H) - \prod_{i=1}^k M_i^2(-H) \right), \tag{2.75}$$

$$\text{VAR}[N(k + 1)] = N_0^2 e^{2bk} \left( M_{k+1}(2b) \prod_{i=1}^{k+1} M_i(-2H) - M_{k+1}^2(b) \prod_{i=1}^{k+1} M_i^2(-H) \right)$$

for  $k = 0, 1, 2, \dots$ .

Of interest is the asymptotic behavior of the system. We determine this as follows. Let us consider the transformed random variable given by

$$Y(k) = \ln N(k) = \ln N_0 + bk - H \sum_{i=1}^k T_i, \quad k = 1, 2, 3, \dots \tag{2.76}$$

For this random variable, we have that

$$E[Y(k)] = \ln N_0 + bk - H \sum_{i=1}^k E[T_i], \quad k = 0, 1, 2, \dots, \tag{2.77}$$

and if we assume independence of the random variables  $T_i, i = 1, 2, \dots$ , we have that

$$\text{VAR}[Y(k)] = H^2 \sum_{i=1}^k \text{VAR}[T_i].$$

We may assume, for simplicity, that all of the variances of the  $T_i$ 's are equal to  $\sigma^2$ , and that all of the means  $E(T_i) = \mu$ . By the Chebyshev inequality, we have that

$$P[\ln N_0 - (H\mu - b)k - \lambda H\sigma\sqrt{k} < Y(k) < \ln N_0 - (H\mu - b)k + \lambda H\sigma\sqrt{k}] \geq 1 - \frac{1}{\lambda^2} \tag{2.78}$$

for  $k = 0, 1, 2, 3, \dots$ . Observe that

$$\lim_{k \rightarrow \infty} - (H\mu - b)k = \begin{cases} -\infty & \text{if } b < H\mu, \\ 0 & \text{if } b = H\mu, \\ +\infty & \text{if } b > H\mu. \end{cases} \tag{2.79}$$

This gives us the well-known deterministic behavior of the population. On the other hand, we see that, for any  $\lambda > 0$ ,

$$\lim_{k \rightarrow \infty} [\ln N_0 - (H\mu - b)k \pm \lambda H\sigma\sqrt{k}] = \begin{cases} -\infty & \text{if } H\mu > b, \\ \pm\infty & \text{if } H\mu = b, \\ +\infty & \text{if } H\mu < b. \end{cases} \tag{2.80}$$

We can then state that, with probability one,

$$\lim_{k \rightarrow +\infty} Y(k) = \begin{cases} -\infty & \text{if } H\mu > b, \\ +\infty & \text{if } H\mu < b, \end{cases} \tag{2.81}$$

while for  $H\mu = b$ ,  $-\infty < Y(k) < +\infty$ . This implies that, for large  $k$ , with probability one,

$$\lim_{k \rightarrow +\infty} N(k) = \begin{cases} 0 & \text{if } b < H\mu, \\ +\infty & \text{if } b > H\mu, \end{cases} \quad (2.82)$$

as in the deterministic case. For  $b = H\mu$ , the extremes of any confidence interval for  $N(k)$  will tend, respectively, to 0 and  $+\infty$ .

In other words, the stability character of the trivial solution is not influenced by the randomness of the harvesting time if  $b \neq H\mu$ . This randomness, on the other hand, introduces a complete indeterminacy when  $b = H\mu$ . The model described in Eqs. (2.68)–(2.70) was simulated, for the case in which the  $T_i$ 's are identically distributed beta distributions. In all cases the dynamics were as predicted. Details of this analysis may be found in Capasso *et al.*[41].

Before we leave our discussion of harvesting of logistic populations in stochastic environments, it is relevant to mention the question of first passage (exit) from a specified region. That is to say, how long does it take before the population will first cross some upper or lower population boundary size. This is particularly relevant to logistic populations as the solution of the deterministic logistic equation is bounded above by  $K$  and below by zero. Hence, one can ask about first passage from this region. Since the system cannot exit above  $K$ , (cf. Tuckwell[42]), first exit demands extinction. Thus questions of first passage become questions of extinction. The inverse question, namely that of persistence, is also relevant since a population which does not undergo extinction must—by definition—persist. The literature on first passage problems is quite extensive and well-reviewed. For details see Chung[43], Ludwig[38], Tuckwell[42], Keiding[29], Matkowsky and Schuss[44], Teir and Hanson[45] and Hanson and Teir[46]. It is worthwhile to note that many of the articles cited in this section have extensive reference lists.

Let us now turn to discrete one-dimensional models involving logistic growth.

### 3. DISCRETE DENSITY DEPENDENT MODELS

#### 3.1. Deriving the discrete logistic equation

The standard discrete approximation to the continuous logistic equation is given by

$$\begin{aligned} N(n+1) &= b(n)N(n) \left(1 - \frac{N(n)}{K(n)}\right), \\ N(0) &= N_0. \end{aligned} \quad (3.1)$$

Here it is assumed that for small population size,  $N(n)$ , the population increases as a function of its size. However, as the population size increases, a limiting effect comes into play.

#### 3.2. Variants of the discrete logistic equation

The simplest approximation to Eq. (2.3), by finite difference methods, leads to the approximation

$$\mathcal{N}((n+1)\Delta) - \mathcal{N}(n\Delta) = \Delta b(n\Delta)\mathcal{N}(n\Delta) \left(1 - \frac{\mathcal{N}(n\Delta)}{K(n\Delta)}\right).$$

Letting  $N(n) = \mathcal{N}(n\Delta)$ , we obtain

$$N(n + 1) - N(n) = \Delta b_1(n)N(n) \left( 1 - \frac{N(n)}{K_1(n)} \right).$$

This may be arranged to be

$$N(n + 1) = [\Delta b_1(n) + 1]N(n) \left( 1 - \frac{\Delta b_1(n)N(n)}{[\Delta b_1(n) + 1]K_1(n)} \right), \tag{3.2}$$

$$N(0) = N_0,$$

where  $b_1(n) = b(n\Delta)$ , and  $K_1(n) = K(n\Delta)$ . It can be seen that this equation has the form of Eq. (3.1) after appropriate redefinition of  $b$  and  $K$ . Each of the variants, Eqs. (2.4a) and (2.4b), may be approximated in the same manner.

Finally, one may approximate the solutions to the logistic equation and its variants. For the case where  $K$  and  $b$  are constant one obtains, from Eq. (2.5), the following iterative process (in which we have taken  $\Delta = 1$ ).

$$N(n + 1) = \frac{K}{1 + \left( \frac{K}{n(n)} - 1 \right) e^{-b}}. \tag{3.3}$$

For cases where  $K$  and  $b$  are not constant, one can discretize the formulae in Table 1.

### 3.3. Properties of the discrete logistic equation

The literature on the behavior of Eq. (3.1), for the case  $b$  constant and  $K = 1$ , is immense, and we shall merely sketch some salient features. For extensive reviews, see May[47, 48], Guckenheimer, Oster and Ipaktachi[49] and Witten[50–53].

Briefly (for the case  $b$ , a constant, and  $K = 1$ ), the mapping

$$f_b(x) = bx(1 - x) \tag{3.4}$$

maps  $[0, 1] \rightarrow [0, 1]$ , has a maximum at  $x_c = \frac{1}{2}$  with  $f_b(x_c) = b/4$ , and satisfies  $f_b(0) = f_b(1) = 0$ . For  $b \leq 1$ , one can demonstrate that

$$\lim_{n \rightarrow \infty} f_b^n(x_0) = 0 \quad \text{for all } x_0 \in [0, 1], \tag{3.5}$$

where  $f_b^n(x_0)$  is the  $n$ th iterate of  $x_0$  satisfying  $f_b^n(x_0) = f_b(f_b^{n-1}(x_0))$  and  $f_b^0(x_0) = x_0$ . Further, the way in which the iterates approach zero is topologically equivalent for all  $b \in [0, 1]$  (Witten[53]). A simple case is illustrated in Fig. 3. The point 0 is said to be an attractor for the points  $x_0 \in [0, 1]$ . Think of  $b$  as a parameter that may be varied. As  $b$  becomes greater than 1, a new fixed point  $x_f = (b - 1)/b$  appears. For the values  $b \in (1, 2)$ ,  $x_f$  is an attractor for all values  $x_0 \in (0, 1)$ . That is

$$\lim_{n \rightarrow \infty} f_b^n(x_0) = x_f \quad \text{for } x_0 \in (0, 1); b \in (1, 2). \tag{3.6}$$

This is illustrated in Fig. 4. Thus,  $b \in (1, 2)$  is a separate conjugacy class (Witten[52, 53]). For  $b = 2$ ,  $x_f = x_c$ , and this is a separate conjugacy class even though the dynamics can

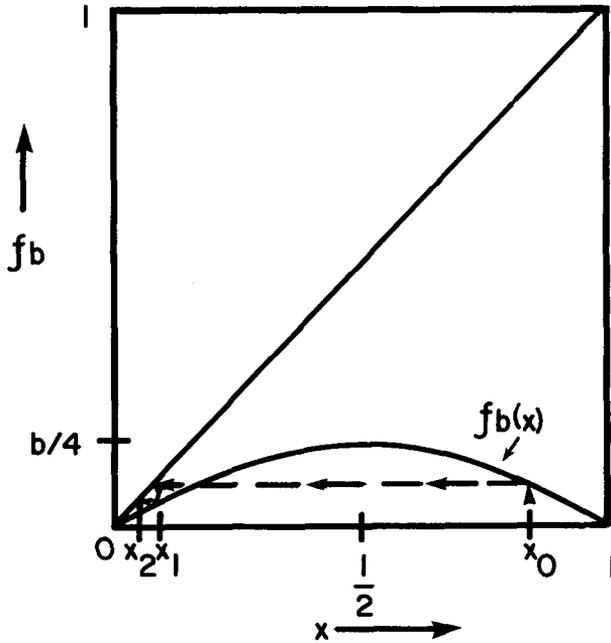


Fig. 3. An illustration of a sample trajectory or orbit of the mapping  $f_b(x)$  for  $b \in (0,1)$ .

be shown to be of the  $b \in (1, 2)$  class. For  $b \in (2, 3)$ ,  $x_f$  is still an attractor, however the dynamics about the fixed point is different. This is illustrated in Fig. 5. As  $b$  approaches 3, the fixed point becomes weakly attracting (Guckenheimer, Oster, Ipaktchi[49]). Finally, as  $b$  becomes greater than three,  $x_f$  becomes an unstable fixed point and two new fixed points of order (period) two appear. That is, two points  $x_1^{(2)}$  and  $x_2^{(2)}$  appear such that  $f_b^2(x_i^{(2)}) = x_i^{(2)}$ ,  $i = 1, 2$ ,  $b > 3$ .

As  $b$  continues to increase, the points  $x_i^{(2)}$  become unstable, and points of period four appear. The appearance of the periodic points, the windows of their stability as a function of the parameter  $b$ , and the passage of the system into what is called chaos are elegantly discussed in May[48]. The reader is directed to the previously mentioned references for more details on the topological dynamics of Li and Yorke’s[54] “simplest dynamical system.”

### 3.4. Harvesting in the discrete logistic equation

The concept of harvesting in the discrete logistic equation was discussed in Sánchez[55]. In this paper, Sánchez considers the general density-dependent model undergoing constant harvest  $H$ :

$$N(n + 1) = N(n)\Phi[N(n)] - H.$$

For  $\Phi = b(1 - N/K)$ , this becomes

$$N(n + 1) = bN(n) \left( 1 - \frac{N(n)}{K(n)} \right) - H. \tag{3.7}$$

The major result of this paper was that the equilibrium of the harvest model was shifted, in an easily predicted manner, from the equilibrium of the unharvested model. On the

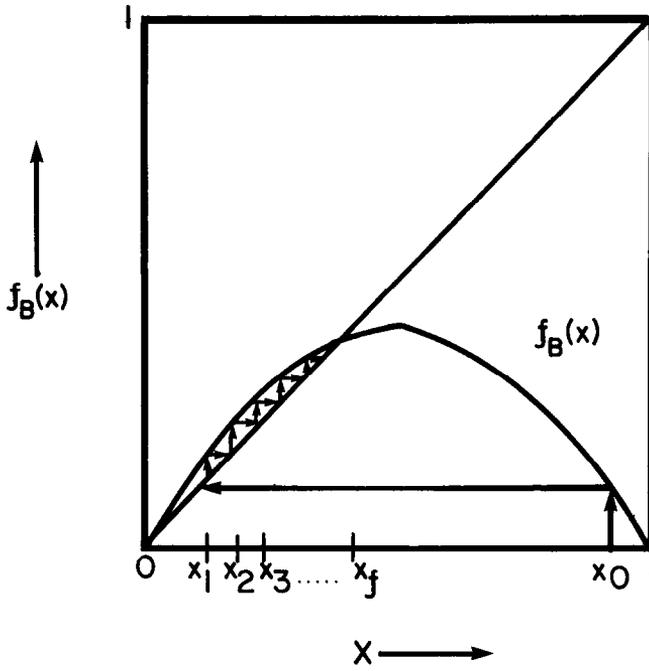


Fig. 4. An illustration of a sample trajectory of the mapping  $f_b(x)$  for  $b \in (1, 2)$ .

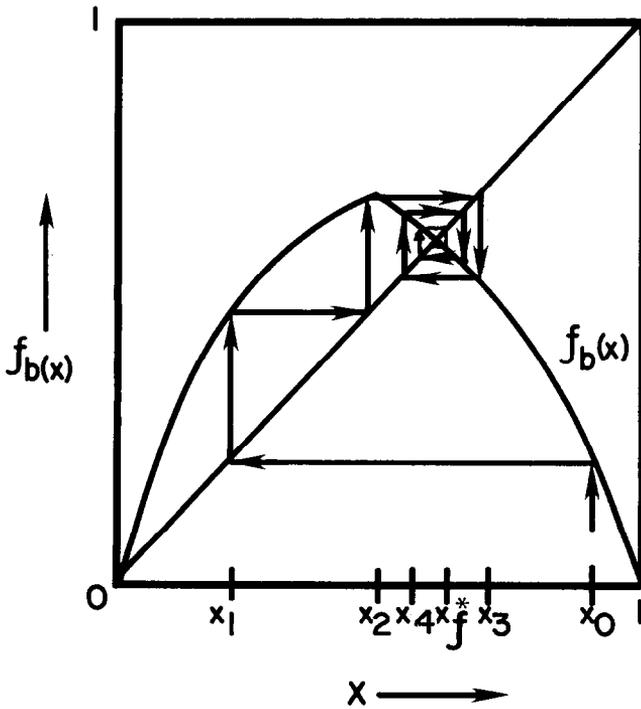


Fig. 5. An illustration of a sample trajectory of the mapping  $f_b(x)$  for  $b \in (2, 3)$ .

other hand, discretization of Eq. (2.10), in a manner analogous to that used to derive Eq. (3.2), leads to the equation

$$N(n + 1) - N(n) = \Delta b_1(n)N(n) \left( 1 - \frac{N(n)}{K_1(n)} \right) - \Delta H. \tag{3.8}$$

Equation (3.7) may be explained in the following manner: the population  $N(n)$  is allowed to grow logistically for one time period, after which  $H$  animals are removed, leaving  $N(n + 1)$  as the result. On the other hand, one can imagine that the order of these operations is reversed. That is,  $H$  animals are removed from  $N(n)$ , the remaining  $N(n) - H$  animals grow logistically. The resulting equation is

$$N(n + 1) = b[N(n) - H] \left( 1 - \frac{N(n) - H}{K(n)} \right). \tag{3.9}$$

Of course, the transformation  $\mathcal{N}(n) = N(n) - H$  reduces Eq. (3.9) to Eq. (3.7). These models present serious problems, since one is not always sure that there will be  $H$  individuals in the population to harvest. Consequently, if one is to use a constant harvest model then one must *worry about the present*. For example, in Eq. (3.9), if  $N(n) > H$ , then one can harvest  $H$ . But, if  $N(n) \leq H$ , then a harvest of  $H$  animals causes population extinction. Thus one must have a *harvest management policy*. The concept of harvest management in iterative density-dependent models is discussed in detail in Witten[56] and Cooke, Elderkin, and Witten[57].

Cooke *et al.*[57] consider a general model of the form

$$\begin{aligned} N(n + 1) &= f[N(n) - H(n; N(n))M_N(n)], \\ N(0) &= N_0, \end{aligned} \tag{3.10}$$

where

$$M_N(n) = \begin{cases} \frac{H_A(n; N(n))}{H(n; N(n))} & N(n) \leq H, \\ 1 & N(n) > H, \end{cases} \tag{3.11}$$

where  $H(n; N(n))$  is the time- and density-dependent harvest, and  $H_A(n; N(n))$  is the time- and density-dependent alternate harvesting policy to be followed when there are not enough animals available for harvest. This model has also been generalized to a model which worries about the effects of a harvest on future populations. We will not discuss the details of this model here. Let us illustrate Eqs. (3.10) and (3.11) using the quadratic mapping equation (3.4), constant harvest  $H$ , with management policy given by

$$M_N(n) = \begin{cases} 0 & N(n) \leq H, \\ 1 & N(n) > H. \end{cases} \tag{3.12}$$

Then Eq. (3.10) becomes

$$\begin{aligned} N(n + 1) &= b\{N(n) - Hu[N(n) - H]\}\{1 - N(n) + Hu[N(n) - H]\}, \\ N(0) &= N_0, \end{aligned} \tag{3.13}$$

where

$$u[N(n) - H] = \begin{cases} 0 & N(n) - H \leq 0, \\ 1 & N(n) - H > 0. \end{cases} \tag{3.14}$$

A sample picture is illustrated in Fig. 6. Here, we have chosen  $H < \frac{1}{2}$  and  $b < 2$ . For the case  $b < 1$ , the iteration sequence starting from any point  $N_0 \in [0, 1]$  tends to zero. This is illustrated in Fig. 7.

For  $H < \frac{1}{2}$ , it is demonstrated in [57] that for  $b$  in the interval  $[(1 - 2H)^{-1}, 2(1 - H)^{-1}]$  there is an absolutely continuous invariant measure on  $[0, 2H]$ , thereby implying the existence of a chaotic regime. Figure 8 illustrates the mappings  $f(N), f^2(N), f^3(N)$ , where  $f(N)$  is given by the right-hand side of Eq. (3.13). These figures were computed on the basis of 50 initial values of  $N$  on the interval  $[0, 1]$ . The apparent piecewise linear nature of these functions is an artifact of the number of points used to calculate the iterates. As  $b$  is further increased, the chaotic regime disappears and a stable first-order fixed point (depending on  $H$ ) may reappear, followed finally by period doubling and possibly chaos. For further details, see [57].

The most common alternate form in harvesting models is one in which the harvest is some fraction  $H_p$  of the population. Suppose that the population size is  $N(n)$  and then there is a proportional harvest  $H_p N(n)$ . Then the growth over the next time interval is given by

$$\begin{aligned} N(n + 1) &= b(1 - H_p)N(n)[1 - (1 - H_p)N(n)], \\ N(0) &= N_0. \end{aligned} \tag{3.15}$$

Or letting  $\mathcal{N}(n) = (1 - H_p)N(n)$ , we obtain

$$\begin{aligned} \mathcal{N}(n + 1) &= (1 - H_p)b\mathcal{N}(n)[1 - \mathcal{N}(n)], \\ \mathcal{N}(0) &= \mathcal{N}_0. \end{aligned} \tag{3.16}$$

An alternate derivation is to notice that the population at time  $n$  grows to size

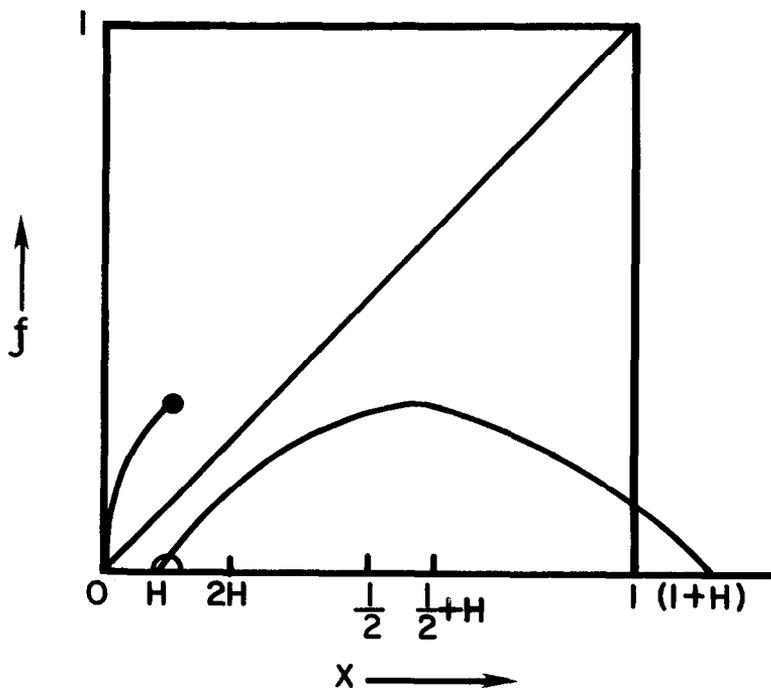


Fig. 6. An illustration of a sample harvest mapping of the type described in Eq. (3.13). Here  $H < \frac{1}{2}$  and  $b < 2$ .

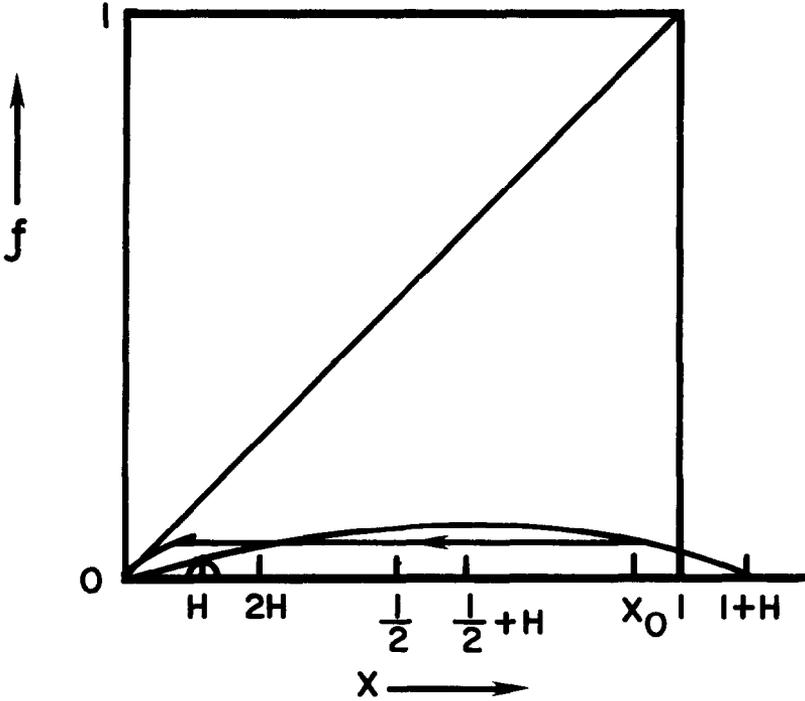


Fig. 7. An illustration of a sample trajectory of the mapping described in Eq. (3.13) with  $H < \frac{1}{2}$  and  $b < 1$ .

$bN(n)[1 - n(n)]$ . Then, the harvest removes  $H_p bN(n)[1 - N(n)]$ . The remaining population size is given by

$$N(n + 1) = (1 - H_p)bN(n)[1 - N(n)], \tag{3.17}$$

which is the same final form as that of Eq. (3.16). System (3.17) is equivalent to Eq. (3.4) and hence follows the same dynamical behaviors with the behaviors of Eq. (3.17) parameterized on the value of  $(1 - H_p)b$  instead of  $b$ . The discussion in Section 3.3 shows that proportional harvesting could result in extinction if  $(1 - H_p)b < 1$ .

On the other hand, harvesting could eliminate erratic periodicities or chaos, present in the absence of harvest, if  $(1 - H_p)b$  falls into the appropriate range; namely, 1 to 3.

### 3.5. Comparison of discrete harvesting and sequential-continuous harvesting models

Up to this point we have discussed a number of different discrete, continuous and discrete (sequential)-continuous formulations of a constant harvest in a density-dependent growth model without comparing them. One interesting method of comparison is to examine the location of  $N_{SS}$  (the steady states or equilibria) for each of the models in the case of time-independent parameters. Table 3 illustrates the four major logistic growth, constant harvest equation models and the location of their respective steady states. It is of interest to note that Eqs. (3.8) and (2.10) have the same steady-state populations if we identify  $b$  with  $b_1$ . It is also of interest to note that Eq. (2.13) has steady states [determined from Eq. (2.18)] which reduce to those of Eqs. (3.8) and (2.10) in the limit of small  $b$  and  $H$ . However, for  $b$  and  $H$  large enough, they give different results. On the basis of the preceding analysis, we are led to the conclusion that Eq. (2.13) can be said to embed the

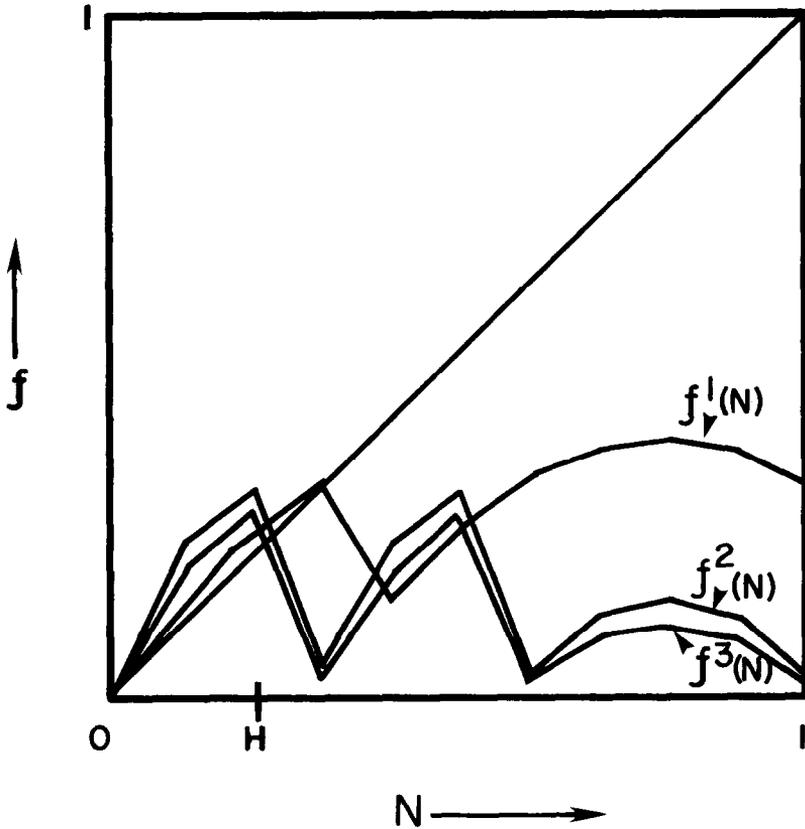


Fig. 8. An illustration of  $f(N)$ ,  $f^2(N)$  and  $f^3(N)$ , where  $f(N)$  is the right-hand side of Eq. (3.13), demonstrating the existence of a distinct period three point.

Table 3. A summary of the four major logistic growth, constant harvest equations and the location of their respective steady states

|        | MODEL  | STEADY-STATE   |
|--------|--|--|
| (2.13) | $\begin{cases} \frac{dN}{dt} = bN \left(1 - \frac{N}{K}\right); & N(0) = N_0 \\ N(t_i^+) = N(t_i^-) - H \end{cases}$ | $N_{SS} = (K - H) \times \left[ \frac{1}{2} \pm \sqrt{\left(\frac{1}{2}\right)^2 - \frac{HK}{(K - H)^2} \left(\frac{e^{-b}}{1 - e^{-b}}\right)} \right]$ |
| (2.10) | $\frac{dN}{dt} = bN \left(1 - \frac{N}{K}\right) - H; \quad N(0) = N_0$  | $N_{SS} = K \left[ \frac{1}{2} \pm \sqrt{\left(\frac{1}{2}\right)^2 - \frac{H}{Kb}} \right]$   |
| (3.7)  | $\begin{cases} N(n+1) = bN(n) \left(1 - \frac{N(n)}{K}\right) - H; \\ N(0) = N_0 \end{cases}$                        | $N_{SS} = K \left(\frac{b-1}{b}\right) \left[ \frac{1}{2} \pm \sqrt{\left(\frac{1}{2}\right)^2 - HK \left(\frac{b}{b-1}\right)^2} \right]$               |
| (3.8)  | $\begin{cases} N(n+1) - N(n) \\ = \Delta b_1 N(n) \left[1 - \frac{N(n)}{K_1}\right] - H\Delta \end{cases}$           | $N_{SS} = K_1 \left[ \frac{1}{2} \pm \sqrt{\left(\frac{1}{2}\right)^2 - \frac{H}{K_1 b_1}} \right]$  |

steady-state behaviors of both the discrete and continuous models of constant harvesting, if one passes to the appropriate limits on the parameters of the system.

Before we leave this section, we shall briefly discuss the behavior of the mapping defined by Eq. (2.18). One can demonstrate that the derivative, with respect to  $N$ , of the function on the right-hand side of Eq. (2.18), is

$$\left( \frac{K e^{-b/2}}{K e^{-b} + N(1 - e^{-b})} \right)^2 \geq 0 \quad \text{for all } N, \tag{3.18}$$

hence, that the graph has positive slope for all  $k, b, H$  and  $N$  values. Figures 9 and 10 illustrate the case where the mapping has no fixed point and has two fixed points, respectively. Data for these simulations are illustrated in Tables 4 and 5, respectively.

In the case where there is no fixed point,  $N(n)$  becomes negative after a few steps, no matter what the starting value  $N(0)$  is, and there is extinction of the population. Mathematically, however, the values  $N(n)$  of the sequence will eventually again become positive.

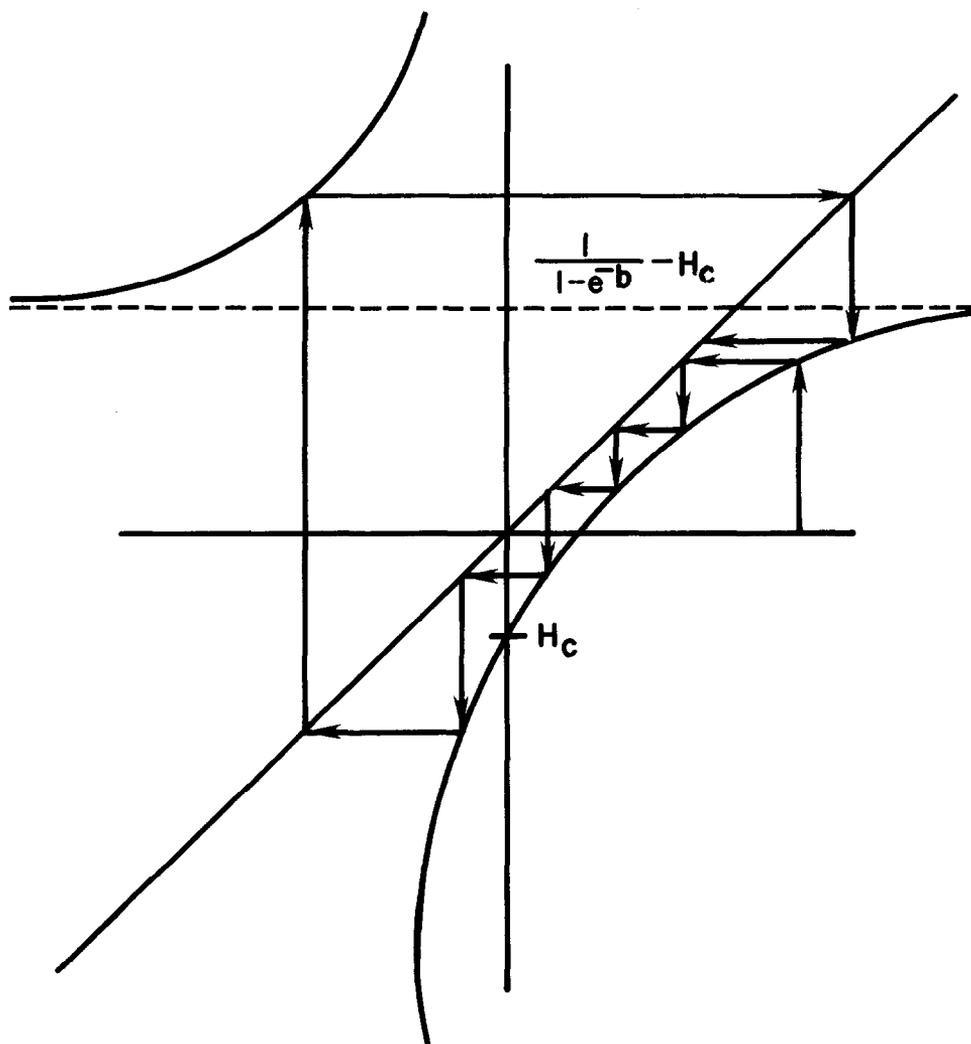


Fig. 9. An illustration of the function in Eq. (2.18) and the possibility of a cyclic behavior in the case of no fixed point behavior. Numerical data is illustrated in Table 4.

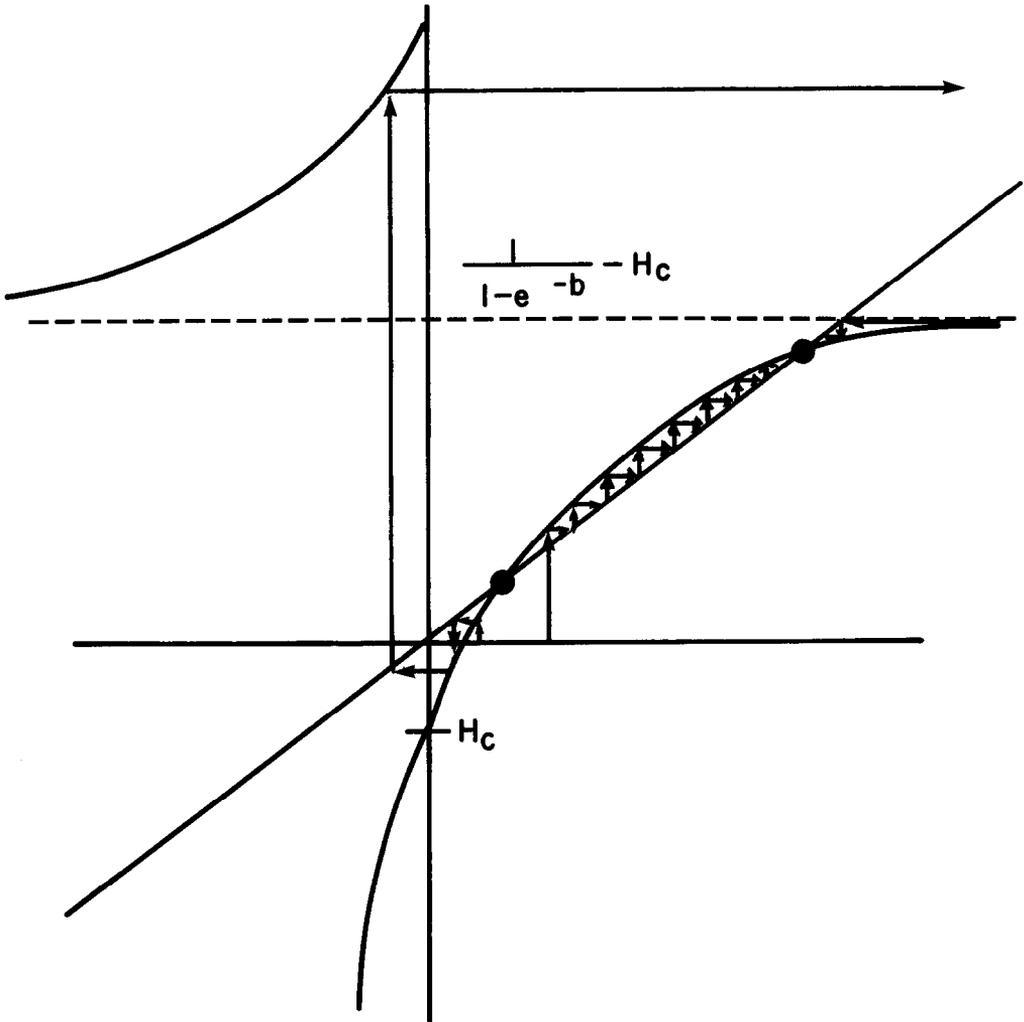


Fig. 10. An illustration of the function in (2.18) and the dynamics of the orbit for the case of two fixed points.

In the case where there are two fixed points, the larger fixed point is stable and attracts all initial points  $N(0)$  larger than the smaller fixed point. Initial points less than the smaller fixed point lead to negative values of  $N(n)$  after a few steps (and then, mathematically, back to positive values and convergence to the larger fixed point). Observe that the derivative equation (3.18) is  $e^b > 1$  at  $N = 0$ . Therefore, if  $H_c$  is small enough, we will have the case of two fixed points. As  $H_c$  is increased, a critical value  $H^*$  is reached at which the two fixed points coincide, and for  $H_c > H^*$  we have no fixed points. In other words,  $H^*$  is a bifurcation value for the parameter  $H_c$ . Figure 11 shows the *bifurcation diagram*. It can be shown that the critical value is given by

$$H^* = K[1 + 2\beta - (4\beta + 4\beta^2)^{1/2}],$$

$$\beta = \frac{e^{-b}}{1 - e^{-b}},$$

and that the fixed points are (when  $H_c < H^*$ ) as given in Table 3.

Table 4. A sample data run for Eq. (2.18) for the case where no fixed points exist

| $n$ | $N(n)$ |
|-----|--------|
| 0   | 300    |
| 1   | 200    |
| 2   | 153    |
| 3   | 122    |
| 4   | 95     |
| 5   | 67     |
| 6   | 32     |
| 7   | -26    |
| 8   | -183   |
| 9   | 10098  |
| 10  | 366    |
| 11  | 221    |
| 12  | 165    |
| 13  | 130    |
| 14  | 86     |
| 15  | 103    |
| 16  | 76     |
| 17  | 45     |
| 18  | -4     |
| 19  | -110   |
| 20  | -906   |
| 21  | 486    |

$K = 300; b = 1; H_c = 100; N(0) = 300$

Table 5. A sample data run for Eq. (2.18) for the case where two fixed points exist

| $n$ | $N(n)$ |
|-----|--------|
| 0   | 300    |
| 1   | 205    |
| 2   | 197    |
| 3   | 168    |
| 4   | 155    |
| 5   | 148    |
| 6   | 144    |
| 7   | 142    |
| 8   | 140    |
| 9   | 139    |
| 10  | 138    |
| 11  | 137    |
| 12  | 137    |

$K = 300; b = 1.5; H_c = 100; N(0) = 300$

It should be noted that for the continuous harvest model [Eq. (2.10)], there is also a bifurcation diagram of the same general appearance as in Fig. 11. The critical value is  $H^* = bK/4$ . For small values of  $b$ , there is very little difference between the critical ratios  $H^*/K$  for the two models and, in fact, they are asymptotically equal as  $b \rightarrow 0$ . However, as  $b \rightarrow \infty$ , the critical ratio for model equation (2.13) tends to 1, whereas it tends to  $\infty$  for the logistic model. This suggests that for fast growing species, being harvested during a short season, use of the logistic model might cause an over estimate of the critical harvest point. Of course, the meaning of  $H$  is different for the two models. For the logistic model [Eq. (2.10)] it is a rate of continuous removal, whereas for Eq. (2.13) it is a removal occurring once per time period.

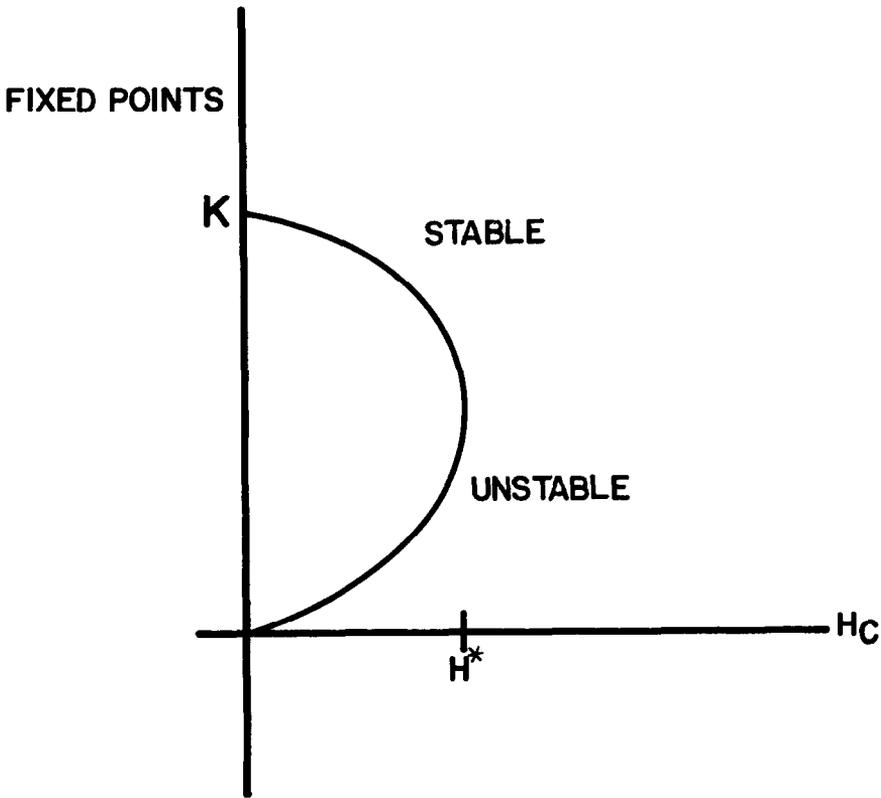


Fig. 11. Bifurcation diagram for Eq. (2.13). When the harvest falls below the critical value  $H^*$ , there are two equilibrium values; the larger of the two equilibria being the stable one.

### 3.6. Harvesting the discrete logistic equation in a random environment

As we have already pointed out, the environment  $K(n)$  can and usually does fluctuate. Further, the reproductive rate  $b(n)$  may also fluctuate. Little if any work has been done in this area. Witten[52] demonstrated that, for the model

$$\begin{aligned}
 N(n + 1) &= b(n)N(n)[1 - N(n)], \\
 N(0) &= N_0 \in [0, 1],
 \end{aligned}
 \tag{3.19}$$

as long as the fluctuations in  $b(n)$  stay within a conjugacy class, the dynamics of the system trajectories (iterative sequences) remain equivalent. Should the  $b(n)$  values pass through different conjugacy classes, the system dynamics might be scrambled. This was illustrated by driving  $b(n)$  by a random number  $r_n \in (-0.5, 0.5)$ , where  $b(n) = 3.157 + r_n$ . Without the  $r_n$  perturbation, all  $N_0 \in (0, 1)$  should tend to a stable two point cycle (see May[48]). However, with this large perturbation, cyclic behavior was not apparent after 10,000 iterations. A detailed analysis of uniform and Gaussian random perturbations may be found in Witten and de la Torre[58, 59], and it was shown that the cyclic dynamics does exist, even under random perturbation. That is, the trajectory generated by  $b(n) = 3.157 + r_n$  contains a two cycle, and the magnitude of the two-cycle contribution to the dynamics is a function of the magnitude of the perturbation  $r_n$ . For a detailed discussion of the effects of random perturbation of the net reproductive rate in a number of models, see Witten and de la Torre[59].

For  $b$  constant and a fluctuating environment  $K(n)$ , the model

$$\begin{aligned} N(n+1) &= bN(n) \left( 1 - \frac{N(n)}{K(n)} \right), \\ N(0) &= N_0, \end{aligned} \tag{3.20}$$

as well as the more general model

$$\begin{aligned} N(n+1) &= b(n)N(n) \left( 1 - \frac{N(n)}{K(n)} \right) - H, \\ N(0) &= N_0, \end{aligned} \tag{3.21}$$

have not been investigated. Figures 12 and 13 show a variety of computer simulation runs for various types of fluctuation in the components, as well as various parameter values. The equation

$$\begin{aligned} N(n+1) &= b(n)N(n) \left( 1 - \frac{N(n)}{K(n)} \right) - H_p N(n), \\ N(0) &= N_0, \end{aligned} \tag{3.22}$$

may be transformed to the quadratic model

$$\begin{aligned} N(n+1) &= [b(n) - H_p]N(n) \left( 1 - \frac{b(n)N(n)}{K(n)[b(n) - H_p]} \right), \\ N(0) &= N_0. \end{aligned} \tag{3.23}$$

We may consider a discrete version of Eqs. (2.68–2.70). Let  $N(j)$  denote the number of individuals in the population at time  $t = j$ . We let  $L$  be a fixed positive integer, and assume that within each time interval of length  $L$  there is first a period during which harvesting occurs and then a period during which it does not occur. Within the  $i$ th interval, harvesting is assumed to occur at the times  $iL, iL + 1, \dots, iL + T_{i+1} - 1$ , and there is no harvesting at times  $iL + T_{i+1}, \dots, (i+1)L - 1$ . We let  $b$  denote the intrinsic growth rate of the population, per individual per unit time, when there is no harvesting, and we let  $a$  denote the net growth rate, per individual per unit time, when there is harvesting. The number  $b - a$  represents the depression of growth rate due to harvesting. The parameters  $a$  and  $b$  must, with our biological interpretation, satisfy  $0 < a < b$ . Thus our model equations have the form

$$\begin{aligned} N(j+1) &= aN(j), & j &= iL, iL + 1, \dots, iL + T_{i+1} - 1, \\ N(j+1) &= bN(j), & j &= iL + T_{i+1}, iL + T_{i+1} + 1, \dots, (i+1)L - 1. \end{aligned} \tag{3.24}$$

In Eq. (3.24),  $i$  represents the number of the *year* or *cycle* ( $i = 0, 1, 2, \dots$ ),  $L$  represents the length or number of time steps in one *year*, and  $T_i$  represents the duration of harvesting (see Fig. 14). If  $T_{i+1} = 0$ , we agree that the first equation in (3.24) shall be absent. In addition to Eq. (3.24), we have the initial condition

$$N(0) = N_0. \tag{3.25}$$

Note that, in the absence of harvesting, the population size will be exponentially in-

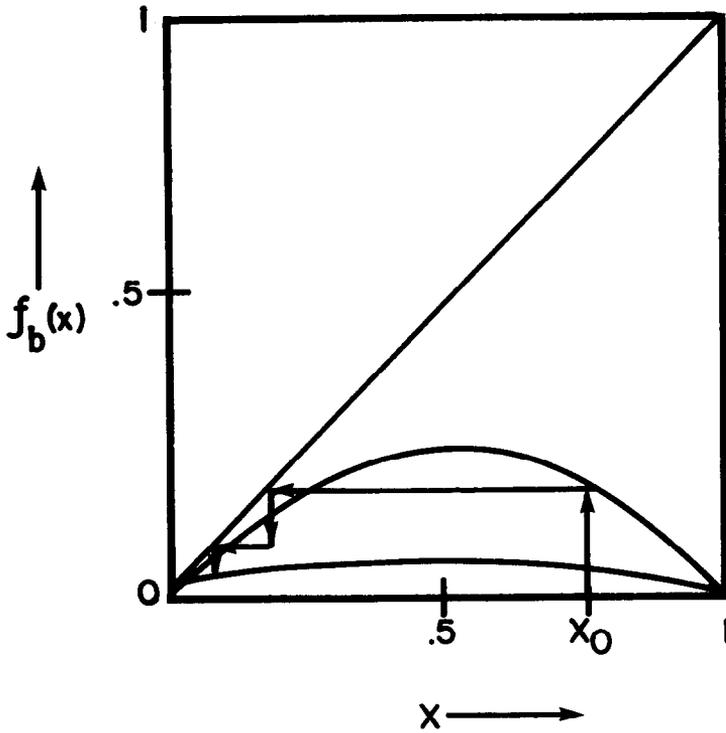


Fig. 12. An illustration of a random iterative process [e.g. Eq. (3.20)] where  $b(n) = b_0 + r_n$ ,  $r_n$  is a uniform random number  $r_n \in [-0.4, 0.4]$ , and  $b_0 = 0.5$ .

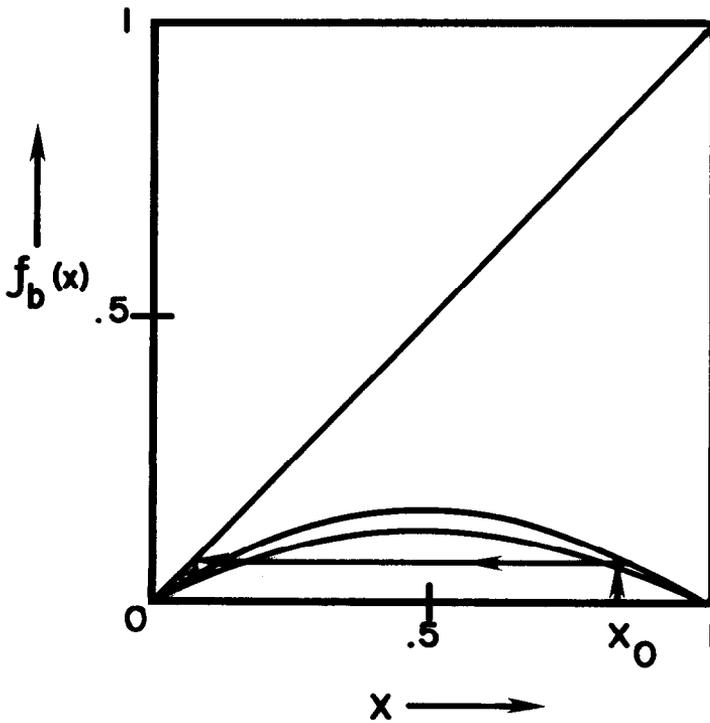


Fig. 13. An illustration of a random iterative process [e.g. Eq. (3.20)] where  $b(n) = b_0 + r_n$ ,  $r_n$  a uniform random number  $r_n \in [-0.01, 0.01]$ ,  $b_0 = 0.5$ .

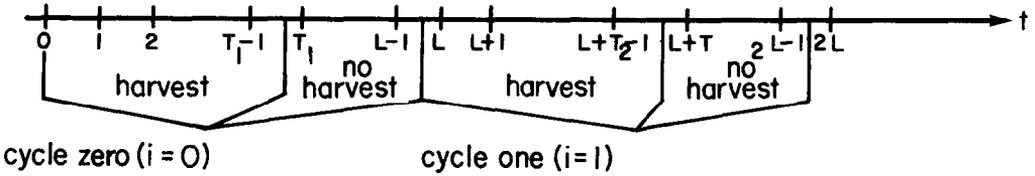


Fig. 14. An illustration of the time line used to describe the sequential-continuous model of Eq. (3.24).

creasing if  $b > 1$ , exponentially decreasing if  $0 < b < 1$ , and constant if  $b = 1$ . In the same way, during harvesting time, the population will be exponentially increasing, exponentially decreasing, or constant if  $a > 1$ ,  $0 < a < 1$ , or  $a = 1$ , respectively. The behavior of the population size over time will evidently depend upon the magnitude of  $a$  and  $b$  and on the lengths of  $T_i$ , the harvesting periods. We shall assume that the  $T_i$ 's are integer-valued random variables with values restricted to lie in the range

$$0 \leq T_i \leq L, \quad i = 1, 2, 3, \dots \tag{3.26}$$

The value  $T_{i+1} = 0$  corresponds to no harvesting during the  $i$ th cycle, whereas  $T_{i+1} = L$  corresponds to harvesting at every time step during the  $i$ th cycle.

Equation (3.24) may be solved recursively. Starting with the initial condition  $N_0$ , and applying Eq. (3.24) with  $i = 0$ , we obtain

$$\begin{aligned} N(j) &= N_0 a^j \quad j = 0, 1, 2, \dots, T_1, \\ N(j) &= N_0 a^j b^{j-T_1}, \quad j = T_1 + 1, T_1 + 2, \dots, L. \end{aligned} \tag{3.27}$$

For  $i = 1, 2, \dots$ , we have

$$\begin{aligned} N(iL + j) &= N(iL) a^j, \quad j = 0, 1, \dots, T_{i+1}, \\ N(iL + j) &= N(iL + T_i) b^{j-T_{i+1}}, \quad j = T_{i+1} + 1, \dots, L. \end{aligned} \tag{3.28}$$

From Eqs. (3.27) and (3.28), by induction, we obtain for  $k = 0, 1, 2, 3, \dots$ ,

$$\begin{aligned} N(kL) &= N_0 b^{kL} \left(\frac{a}{b}\right)^{\sum_{i=1}^k T_i}, \\ N(kL + T_{k+1}) &= N_0 b^{kL} b^{T_{k+1}} \left(\frac{a}{b}\right)^{\sum_{i=1}^{k+1} T_i}. \end{aligned} \tag{3.29}$$

In this form, the analogy with Eqs. (2.72) for the continuous time model is apparent.

As in the continuous case, it will suffice to examine  $N(j)$  at the points  $j$  of the form  $kL$  or  $kL + T_{k+1}$ . Values at other points can then be reconstructed using Eqs. (3.29).

As we did for the continuous case, we may compute the moments of the random variables  $N(kL)$  and  $N(kL + T_{k+1})$ , defined in Eq. (3.29), in the following way. Suppose that all of the harvesting times  $T_i$  are independent. Let

$$G_i(s) = E[s^{T_i}] = \sum_{t=0}^L P(T_i = t) s^t \quad s \in R \tag{3.30}$$

be the probability generating function of the random variables  $T_i$ . Then, for the  $r$ th mo-

ment, we obtain, for any  $r = 1, 2, \dots$ ,

$$E\{[N(kL)]^r\} = N_0^r b^{rkL} E \left\{ \left[ \left( \frac{a}{b} \right)^r \right]^{\sum_{i=1}^k T_i} \right\} = N_0^r b^{rkL} \prod_{i=1}^k G_i \left[ \left( \frac{a}{b} \right)^r \right], \tag{3.31}$$

$$E\{[N(kL + T_{k+1})]^r\} = N_0^r b^{rkL} G_{k+1}(b^r) \prod_{i=1}^{k+1} G_i \left[ \left( \frac{a}{b} \right)^r \right]$$

for  $k = 0, 1, 2, \dots$  and  $r = 1, 2, \dots$ . In particular, we obtain the first moments for  $r = 1$ , and for the variance we obtain

$$\text{VAR}[N(kL)] = N_0^2 b^{2kL} \left\{ \prod_{i=1}^k G_i \left[ \left( \frac{a}{b} \right)^2 \right] - \prod_{i=1}^k G_i^2 \left( \frac{a}{b} \right) \right\},$$

$$\text{VAR}[N(kL + T_{k+1})] = N_0^2 b^{2kL} \left\{ G_{k+1}(b^2) \prod_{i=1}^{k+1} G_i \left[ \left( \frac{a}{b} \right)^2 \right] - G_{k+1}^2(b) \prod_{i=1}^{k+1} G_i^2 \left( \frac{a}{b} \right) \right\} \tag{3.32}$$

for  $k = 0, 1, 2, \dots$ .

We may also determine the asymptotic behavior for the discrete case. As for the continuous case, it is convenient to introduce the following transformed variable:

$$Z(k) = \ln N(kL) = \ln N_0 + kL \ln b + \ln \left( \frac{a}{b} \right) \sum_{i=1}^k T_i \tag{3.33}$$

for  $k = 0, 1, 2, \dots$ . Its expected value is

$$E[Z(k)] = \ln N_0 + kL \ln b + \ln \left( \frac{a}{b} \right) \sum_{i=1}^k E[T_i], \quad k = 0, 1, 2, \dots, \tag{3.34}$$

and if we assume, as usual, the independence of the random variables  $T_i$ , we have for the variance

$$\text{VAR}[Z(k)] = \left[ \ln \left( \frac{a}{b} \right) \right]^2 \sum_{i=1}^k \text{VAR}[T_i]. \tag{3.35}$$

By means of the Chebyshev inequality we obtain, in this case, if  $E(T_i) = \mu$ , and  $\text{VAR}(T_i) = \sigma^2$ ,

$$P \left\{ N_0 \left[ b^L \left( \frac{a}{b} \right)^\mu \right]^k \left( \frac{a}{b} \right)^{\lambda\sigma\sqrt{k}} < N(kL) < N_0 \left[ b^L \left( \frac{a}{b} \right)^\mu \right]^k \left( \frac{a}{b} \right)^{-\lambda\sigma\sqrt{k}} \right\} \geq 1 - \frac{1}{\lambda^2} \tag{3.36}$$

for any  $\lambda > 0$ , and  $k = 0, 1, 2, \dots$ . Now, set  $\gamma = b^L (a/b)^\mu$ . Then

$$\lim_{k \rightarrow +\infty} N_0 \left[ b^L \left( \frac{a}{b} \right)^\mu \right]^k = \begin{cases} +\infty & \text{if } \gamma > 1, \\ N_0 & \text{if } \gamma = 1, \\ 0 & \text{if } \gamma < 1 \end{cases} \tag{3.37}$$

according to the deterministic behavior of the system. On the other hand,

$$\lim_{k \rightarrow +\infty} N_0 \left[ b^L \left( \frac{a}{b} \right)^\mu \right]^k \left( \frac{a}{b} \right)^{\pm \lambda \sigma \sqrt{k}} = \begin{cases} +\infty & \text{if } \gamma > 1, \\ 0 & \text{if } \gamma < 1 \end{cases} \quad (3.38)$$

for any  $\lambda > 0$ . We may then state that, with probability one,

$$\lim_{k \rightarrow +\infty} N(kL) = \begin{cases} +\infty & \text{if } \gamma > 1, \\ 0 & \text{if } \gamma < 1. \end{cases} \quad (3.39)$$

If instead  $\gamma = 1$ , then

$$\lim_{k \rightarrow +\infty} N_0 \gamma^k \left( \frac{a}{b} \right)^{\pm \lambda \sigma \sqrt{k}} = 0 \text{ or } +\infty. \quad (3.40)$$

Again, the stability character of the trivial solution is not affected by the randomness of the harvesting time when  $\gamma \neq 1$ . It introduces a complete indeterminacy when  $\gamma = 1$ .

#### 4. CLOSING COMMENTS

In closing, we would like to summarize by saying that even the simplest one-dimensional models, with very simple harvesting procedures, may exhibit a wide variety of dynamical behaviors. This paper has made an effort to review those models and their associated dynamics. The variety of models brings to the fore an important caveat to the mathematical modeler; namely, one must pick with care a model or models appropriate to the situation being modeled.

Because of the extent of the literature, this review has not covered questions in the areas of harvesting age-dependent discrete and continuous populations, harvesting in time delay models or harvesting in diffusion population models. Further, we have not discussed harvesting in higher-order systems which incorporate competition, predation, mutualism, niche selection and persistence.

Open questions arise in higher-order sequential-continuous (coupled) systems, as well as stochastic sequential-continuous systems. In one-dimensional models, the question of harvesting a population undergoing logistic growth with a stochastic time-lag governed by an equation of the form

$$\begin{aligned} \frac{dN(t)}{dt} &= b(t)N(t) \left( 1 - \frac{N[t - \tau(t)]}{K(t)} \right), \\ \tau(t) &= \tau_0 + \gamma(t), \end{aligned} \quad (4.1)$$

is open. Further, the general iterative models described by Eqs. (3.20)–(3.22), in which the environment is allowed to fluctuate, have not been investigated.

We have not discussed the notion of persistence and/or extinction times. Given an excessive harvesting policy, can one estimate when  $N(t)$  or  $N(n)$  becomes less than zero? Sánchez (private communication) has pointed out that, for the constant harvested logistic equation, the extinction time may be calculated even though an explicit solution is not known.

Needless to say, a myriad of relevant questions still await answers, even in one-dimensional systems.

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