COMPUTER SIMULATION IN BIOLOGY

Initiate your batch cultures with biomass concentrations of 1 mg liter^{-1}. Make your simulation of two parts. First plot the rate of change of biomass, dB/dt, against toxicant concentration from 0 to 0.04 mg l^{-1}, in increments of 0.001 mg l^{-1}. Do this for at least 4 different values of $[S]$. These values should cover a fairly wide range, including much less than K_s, about equal to K_s, greater than K_s, and very much greater than K_s to simulate saturation. Secondly, plot the growth of the culture through time with at least six different concentrations of toxicant: 0, 0.001, 0.01, 0.1, 1, and 10. This log series of toxicant levels will approximate the first-trial procedure of an experimental determination of the reaction to various toxicant levels.

Conclusion

The Monod model provides an alternative to the logistic for describing how homogeneous populations grow in limited environments. Like the logistic, it is based on simple assumptions which are infrequently met even in carefully controlled experiments. A fair amount of printer's ink has been spilled describing the failures of the Monod model. For example, the concentrations of nutrients are known to differ among cells of different ages; some nutrients will affect growth of biomass and others affect rates of cell division; and, the "luxury consumption" of nutrients like phosphorus is not considered.

Like the Verhulst-Pearl logistic, the Monod model is used not because it is a "good" or a "bad" model, but because it is simple. In the present case, it serves as a tractable model that provides the basic starting point for models of microbial growth.

CHAPTER 9

POPULATION MODELS BASED ON AGE-SPECIFIC EVENTS

In the previous two chapters we studied homogeneous populations, with all members of populations assumed to be identical. We essentially ignored birth and death processes, lumping them together as "growth rate". However, age makes a difference in the performance of complex organisms, and this must be considered if we wish to make realistic models of their populations. Ability to reproduce depends on age, with some members of a population more likely to reproduce than others. Death rates change with age of organisms, and age is important in changing the impact of disease, parasitism, predation, etc. on an individual. Age-class models that consider these differences are the subject of this chapter.

9.1 Age-Specific Survival and Reproduction

Members of populations of most organisms do not all die at the same age. (The life insurance industry is based on this observation.) If enough data about age of death can be collected for a population, an overall pattern can be seen for age at death, also called age-specific mortality or survivorship. Three common patterns are diagrammed in Figure 9.1 (Pearl and Miner 1935, Deevey 1947, Slobodkin 1980). Type A is characteristic of species with relatively high death rates for very young individuals, low and constant mortality rates for intermediate ages, and higher mortality rates again for older individuals. This type of curve is found for most human populations and for many mammals. Type B is produced by a constant mortality rate, with a constant percentage of individuals dying for each unit of time. (This is identical with the exponential die-off simulation of Section 1.2.) Adults of some species of birds and bats may follow this curve (Deevey 1947, Keen and Hitchcock 1980). Type C is characteristic of most organisms, with a high rate of mortality early in life, and a relatively low rate for the later periods. This curve is typical of many fish
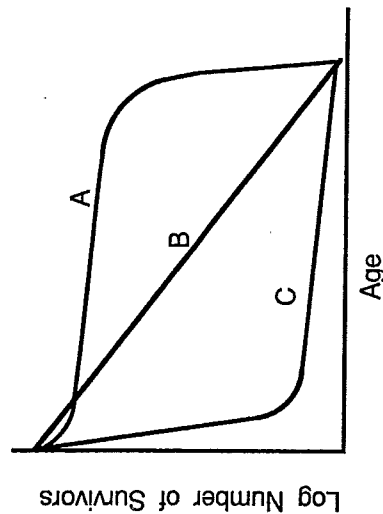
Figure 9.1.   Three common patterns of survival in populations. See text for identification and discussion of these types.

and marine invertebrates and of most plants; an organism surviving the hazards of early life has a good chance of living to a relatively old age.

Just as plants and animals in a population usually die at different ages, so do they reproduce at different ages, producing different numbers of offspring. Figure 9.2 shows three common patterns of variability of reproduction with age. Type A describes organisms that reproduce once in their lifetime. This is common in annual plants, and in species of salmon. Other organisms such as trees and many species of fish show type B, in which young animals do not reproduce, and in which newly reproductive individuals do not produce as many offspring as older individuals. Type C is found in species that show increasing reproductive ability after sexual maturity, and then a decline toward zero reproduction at older ages. This type is typical of most populations of humans.

9.2 Life Tables

A life table presents age-specific information about the survival and reproduction of a population. The table is a handy way of summarizing the data shown in Figures 9.1 and 9.2. The following statistics are usually presented in a life table:

x = the age of the organisms at the beginning of the time interval;
N_x = number of individuals alive at age x;
d_x = number of individuals dying between ages x and $x+1$;
s_x = proportion of individuals alive at x that are also alive at $x+1$;
m_x = number of offspring produced between x and $x+1$ by the average individual alive at x.
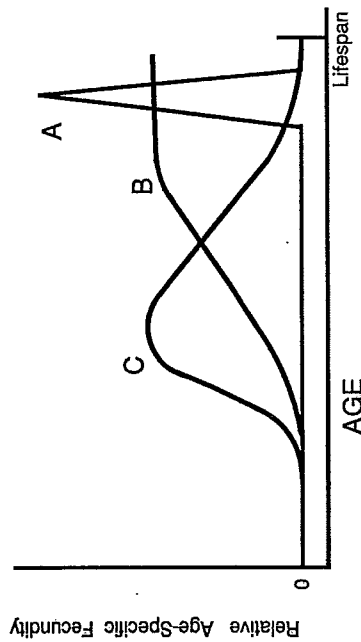
Figure 9.2.   Three common patterns of variation in reproductive capacity with age in populations.

Other terms are frequently incorporated in a life table, depending upon its objective. The terms s_x and m_x are the age-specific survival and natality rates. These two are the terms used in modeling age-structured populations.

The data used to construct a life table may be obtained in a variety of ways. One method involves following the performance of a group of individuals from birth, recording their ages at death and the number of offspring at each age. Another method requires a single census over a unit period of time, looking at the reproductive rates of the different ages present, and the rates of death of the age groups in the population. For either method, the population is assumed to be under fairly stable environmental conditions, so that life table values can be applied through time.

The usual life table is set up for females only. The assumption behind this procedure is that males and females make up constant proportions of the population. In such female life tables, age-specific natality will refer only to female births. Some populations may exhibit significant survival differences between the sexes; certain populations of deer, for example, have higher mortality among older males which are hunted intensively. Adequate models of such populations often require use of a different life table for each sex, as in Section 9.5 below.

Life tables are most often based either on a description of the fate of 1000 births, or on a proportional survivorship basis. Where life tables are used to simulate the performance of populations, more realistic numbers may be employed, based on actual population sizes or densities. However, survival and natality will be expressed as rates, usually as number per

female per unit of time.

Age-specific survival will always be a decimal fraction less than unity, and can be considered as the probability that an organism of age x will survive to age $x + 1$. The idea of probability will be useful in stochastic simulations later. Age-specific natality can be greater or less than unity, depending upon the organism and the time intervals. The units of time used in life tables will vary among different organisms. Life histories of some small invertebrates may be described in hours, and some longer-lived species in years. Life tables for humans are often given with five-year intervals.

Table 9.1 is a sample life table for a population of a common terrestrial crustacean, and contains the information needed to develop an age-class simulation of a population of this animal.

Age in years x	Number living at age x N_x	Number dying x to $x+1$ d_x	Rate of survival x to $x+1$ s_x	Per capita birth rate x to $x+1$ m_x
0	10000	8896	0.1104	0.00
1	1104	989	0.1042	3.13
2	115	99	0.1391	42.53
3	16	14	0.1250	100.98
4	2	2	0.0000	118.75
5	0			

Table 9.1. Life table for females of a California population of a sowbug, *Armadillidium vulgare*. Adapted from data by Paris and Pitelka (1962).

In this chapter we will use an easily understood stepwise approach to simulating events in a population that follows a particular life table. An approach using matrices is simpler to program for computers, but is more complex in concept and will be deferred to Chapter 16.

The equation used to describe the reproduction that takes place in one time period would be

$$\Delta N = \Sigma N_x m_x \tag{9.1}$$
$$= N_0 m_0 + N_1 m_1 + N_2 m_2 + N_3 m_3 + N_4 m_4 \tag{9.2}$$

The survival of each age class is calculated with the following equations, which also move the survivors into the next age class. The order of their solution is important in writing a life table program:

$$N_5 \leftarrow N_4 s_4 \tag{9.3}$$
$$N_{x+1} \leftarrow N_x s_x \tag{9.4}$$
$$N_1 \leftarrow N_0 s_0 \tag{9.5}$$
$$N_0 \leftarrow \Delta N \tag{9.6}$$
$$\Sigma N = N_0 + N_1 + N_2 + N_3 + N_4 + N_5 \tag{9.7}$$

Note that the number of births is calculated first with Equation 9.1, and saved in a temporary variable ΔN. The value of ΔN is assigned to N_0 only after the previous N_0 has been used to find N_1. The total population size ΣN calculated in Equation 9.7 is the total number existing at the end of the time interval, or the start of the next time interval.

Exercise 9-1: Write a program for the simple age-class simulation of a sowbug population that has constant survival and natality characteristics as described in Table 9.1. Set up your simulation to start at time $= 0$ using the values from the N_x column of Table 9.1 as initial values for the various age classes. Generate 12 years of simulation data. For each year from 0 to 12, your program should print out a table that shows the number of individuals in each age class, as well as the total population size. Figure 9.3 is a flowchart to help you set up your simulation.

Exercise 9-2: Populations that follow a fixed schedule of age-specific natality and survival are known to attain a "stable age distribution" after passing through several generations. With a stable age distribution, the size of each age class is a constant proportion of total population size. Alter the program for Exercise 9-1 to follow a sowbug population for 20 years, printing out the size of each age class at the end of the 20-year period. Also print out the proportion of the total size represented by each age class. Perform 20-year simulations with at least four different sets of initial age-class numbers, to demonstrate that the population does in fact attain a stable age distribution. You should be as inventive as possible in selecting your data.

9.3 A Logistic Modification for Life Table Simulations

Simulations that involve fixed natality and survival schedules assume these rates to be independent of density effects produced by growth or shrinkage of the population. The population of sowbugs following the schedule of reproduction and mortality in Table 9.1 will grow exponentially. An age-class model can be modified readily to simulate a logistic growth pattern. We will make one of the easier changes here, using the sowbug example.

We will assume that survival rates are independent of population density, so that only rates of natality are affected by density. As a first step in the modification, natality rates are adjusted so that the population will just replace itself when the age distribution is stable. (See Exercise 9-2 for a description of such stability.) Ideally these rates would be derived from experiment, but here we will simply reduce all the m_x values by a constant fraction, so that $N_0 = \Sigma N_x m_x$ when the population has a stable age distribution. For the sowbugs, the adjusted set of natality rates are: $m_0 = 0$, $m_1 = 3.06$, $m_2 = 41.66$, $m_3 = 98.27$, $m_4 = 115.392$.

The second step in the modification is to change Equation 9.1 of the life-table model so that reproduction is limited to replacement of dying animals when population abundance is at the carrying capacity K:

$$\Delta N = (N_0 m_0 + N_1 m_1 + N_2 m_2 + N_3 m_3 + N_4 m_4) \cdot \left(2 - \frac{\Sigma N}{K}\right) \quad (9.8)$$

The m_x values in this equation must be the modified values given above. The rate-limiting term in the equation has been altered from the $(1 - \Sigma N/K)$ term of the Verhulst-Pearl model of Equation 7.3. In Equation 7.3 the growth constant r includes both birth and death rates. However, in Equation 9.8 the term $(2 - \Sigma N/K)$ is used to modify only the number of population births, ΔN. Here, when $\Sigma N = K$, the rate-limiting term $(2 - \Sigma N/K)$ equals 1 and reproduction is held to the replacement level. When the population size ΣN is less than K, birth rate increases proportionally, reaching a factor of 2 as ΣN approaches zero. If your simulation is likely to encounter total population sizes ΣN much greater than K, your program should include a statement to limit ΔN to zero whenever Equation 9.8 might produce a negative number of births.

Natality at different densities can be modified by changing the logistic term in Equation 9.8. For example, using $(4 - 3 \cdot \Sigma N/K)$ will produce an almost $4\times$ increase in birth rate at low ΣN, and $(1.1 - 0.1 \cdot \Sigma N/K)$ will provide about a $1.1\times$ increase.
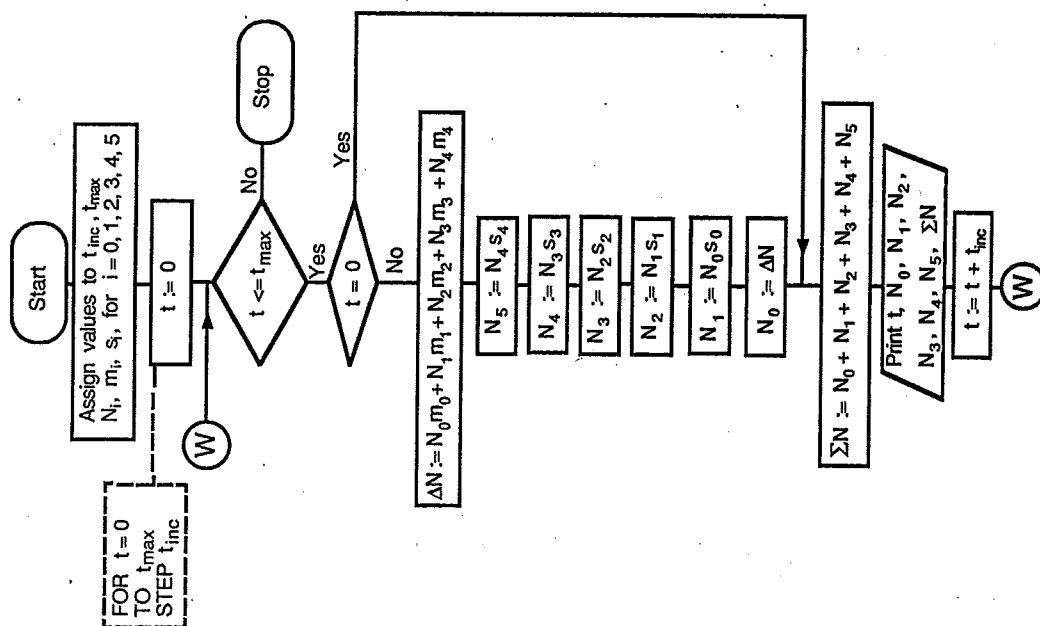

Figure 9.3. Flowchart for program to simulate age-class survival and reproduction in the population of sowbugs discussed in the text.

AGE-SPECIFIC POPULATION MODELS

Age class	Class ages (years)	Number of females (millions)	Age-class survival rate	Age-class natality rate
1	0-4	8.806	0.996	0
2	5-9	8.231	0.999	0
3	10-14	8.340	0.998	0.003
4	15-19	9.107	0.997	0.124
5	20-24	10.479	0.997	0.262
6	25-29	10.865	0.996	0.264
7	30-34	10.171	0.995	0.162
8	35-39	8.967	0.993	0.056
9	40-44	7.116	0.989	0.010
10	45-49	5.969	0.981	0.001
11	50-54	5.660	0.971	0
12	55-59	5.957	0.955	0
13	60-64	5.877	0.932	0
14	65-69	5.151	0.899	0
15	70-74	4.415	0.849	0
16	75-79	3.311	0.777	0
17	80-84	2.293	0.676	0
18	85-89	1.073	0.544	0
19	90-94	0.536	0.385	0
20	95-99	0.268		0

Table 9.2. Age-class data for female population of the U.S.A. in 1985. Survival and natality are for an age group for a 5-year period. (For example, the probability of an individual in age-class 7 surviving to age-class 8 is 0.995, and the probability is 0.162 that an individual in age-class 7 will produce a female offspring in 5 years). Data are derived from U.S. Bureau of the Census (1986).

Exercise 9-3: Substitute the modified m_x values and Equation 9.8 into the simulation of Exercise 9-1. Allow the simulation to proceed for 20 years with a carrying capacity of $K = 12000$. At time interval 21, simulate a single year of poor reproduction by letting ΔN be 25% of the value calculated with Equation 9.8. Allow the simulation to proceed for an additional 20 years after the perturbation. Your output for this simulation should be a plot of ΔN and ΣN over the 40-year period.

9.4 Use of Subscripted Variables in Life Table Simulations

A program for a large age-class model using the stepwise approach involves many equations of almost identical form. Whenever this occurs in writing computer programs, it is a good idea to consider using subscripted variables to reduce the number of programming instructions. The age-class model is a good example where this simplification may be used. The following BASIC program employs subscripted variables to accomplish the same calculations as the sequence of Equations 9.1-9.7.

```
100 REM AGE-CLASS MODEL USING SUBSCRIPTED VARIABLES
110 DN = 0
120 FOR J = 0 TO 4
130   DN = DN + N(J) * M(J)
140 NEXT J
150 SN = 0
160 FOR J = 4 TO 0 STEP -1
170   N(J+1) = N(J) * S(J)
180   SN = SN + N(J+1)
190 NEXT J
200 N(0) = DN
210 SN = SN + N(0)
220 END
```

Although this listing is about the same length as a program that uses the direct approach for the sowbug life table, with minor changes this one could also be used for models having very many age classes. For such larger models, using subscripted variables is always more efficient. Look for other opportunities to use this technique.

Exercise 9-4: The demographic data in Table 9.2 describe the female population of the U.S.A. in 1985. The tabulated rates of survival and natality are based on five-year intervals. Although age classes exist for greater ages, they are ignored for purposes of this exercise. Assume the given rates of survival and natality will hold for 40

years. Write a simulation to predict the female population for each five-year interval from 1985 through the year 2025. Your output for each interval should be in the form of a table showing age class, age group, and number of individuals (in millions). After you have your simulation working properly, send output to the printer for the years 1985, 2010, and 2025.

9.5 Simulating Sex-differentiated Survival and Reproduction: Deer Hunting

Age-specific survival rates will differ for the sexes of most populations. Males of some animals may be more important economically than females, so that a female-only life table does not adequately describe the population. Males of some game animals, for example, are particularly subject to hunting pressure. We will illustrate this with an age-class model of a population of white-tail deer (*Dama virginiana*) hunted under the "bucks only" regulations common to many areas of North America.

The basic life-history information of age-specific survival and natality is given in Table 9.3. The table also presents a hypothetical population composed of the indicated number of males and females, M_x and F_x, for different age groups x, 0 through 12. From the table, $\Sigma M_x = 3351$ and $\Sigma F_x = 4465$. The area involved is assumed to be 200 square miles. Deer are sexually mature at the age of one year, assuming an adequate diet. For convenience in calculations using the model equations below, we will define the number of adult reproductive females F_a and adult males M_a as

$$M_a = \Sigma M_x - M_0 \qquad (9.9)$$

$$F_a = \Sigma F_x - F_0 \qquad (9.10)$$

In working with this model, separate sets of simulation data must be maintained for males and females. Both sexes are assumed to follow the given survival rates in the absence of hunting pressure. With hunting pressure, males are subject to additional mortality.

In most deer populations, male-female ratio at birth is not 1.0, but 1.12. The m_x values of Table 9.3 are age-specific birth rates giving the production of male and female offspring combined. The fraction of these births that are male is about 0.528; 0.472 is the fraction that are female. To find F_0 and M_0, use equations that are analogous to Equation 9.6:

$$F_0 = 0.472 \, \Delta N \qquad (9.11)$$

$$M_0 = 0.528 \, \Delta N \qquad (9.12)$$

x	s_x	m_x	F_x	M_x	P_x
0	0.62	0.00	1000	1000	0.00
1	0.87	0.50	620	694	0.80
2	0.88	0.60	539	543	0.89
3	0.89	0.63	474	406	0.92
4	0.90	0.66	422	289	0.95
5	0.88	0.68	380	195	0.98
6	0.86	0.70	334	120	0.99
7	0.78	0.68	287	62	0.99
8	0.62	0.60	224	29	0.99
9	0.30	0.50	139	11	0.99
10	0.10	0.40	42	2	0.99
11	0.00	0.30	4	0	0.99
12	—	—	0	0	

Table 9.3. Life history information and population sizes for a hypothetical deer herd in an area of 200 square miles. x = age in years; s_x = age-specific rate of survival for unhunted deer of age x; m_x = age-specific rate of production of fawns of both sexes by females of age x, assuming 100 % fertilization; F_x = number of female deer of age x; M_x = number of male deer of age x; P_x = male mortality probabilities for an encounter between a hunter and a male deer of age x. Data are derived from Dahlberg and Guettinger (1956).

The natality rates of Table 9.3 are adjusted to maintain a steady-state population of females, assuming they follow the given survivorship schedule. The hypothetical female population of the table has been set up specifically to demonstrate such a stationary population. If 1000 0-aged females follow the survival schedule given in the table, their numbers at each age will equal those given for each age-group of the hypothetical population. If the hypothetical population reproduces following the given m_x schedule, and ΔN is found as usual with Equation 9.1, then $\Delta N = 2120$. The fraction (0.472) of these births that are females is 1000, which will replace the F_0 age-group and hold the female population at a constant size.

In populations of deer with a small number of males relative to the number of females, some females may not be fertilized during the mating season. Intense hunting pressure may lower sufficiently the density of male deer to cause a decline in female mating success. The deer-hunting

model should account for this source of reproductive failure. We can reasonably assume that mating success is a positive function of the number of reproductive males. We assume that mating success is 0 when M_a is 0; from observation it is known that success is 90% when M_a is about 870. An exponential equation like Equation 7 of Chapter 3 can be used to simulate this process:

$$R = 1 - \exp(kM_a) \qquad (9.13)$$

where R is the fraction of adult females fertilized, M_a is the number of mature breeding males, and the constant $k = -0.002656$. Thus, Equation 9.1 for finding the number of deer born each year is modified to become

$$\Delta N = (\Sigma F_x m_x)\,R \qquad (9.14)$$

This population, that is just capable of replacing itself, is assumed to be at "carrying capacity". One may also assume that as population density declines below this level, the fertility of the deer will increase. This effect can be simulated with a variation of Equation 9.8. We will assume that the annual production of young deer increases by a factor of 2.5 when deer populations are low and food is plentiful. It will be necessary therefore to multiply Equation 9.14 by the type of limiting logistic term introduced in Section 9.3:

$$2.5 - \frac{1.5\,(\Sigma M_x + \Sigma F_x)}{6000}$$

Although both males and females follow the schedule of survival given in Table 9.3, males are also subject to hunting mortality. To account for hunting mortality, an equation must consider the number of male deer and the number of hunters. The predation equations of Chapter 7 are not suitable because the hunting season is brief, not continuous through the year. An equation used by O'Neill et al. (1972) appears suitable (see also Watt 1975 and DeAngelis et al. 1975). The general form of the equation is:

$$\Delta M_H = \frac{P\,H\,M_a}{H + M_a} \qquad (9.15)$$

Here, ΔM_H is the mortality in the males due to hunting, H is the density of hunters, and P is the probability that an encounter between a male deer and a hunter will result in a dead deer. The value of P may be estimated from hunting data. In the northern part of the lower peninsula of Michigan in 1957, 306,000 hunters killed 41,000 of an estimated 75,000 adult male deer (Jenkins and Bartlett 1959). From these data, the value of P is found to be 0.681.

Equation 9.15 cannot be applied directly to an age-class model, because hunting mortality does not occur uniformly for all age classes of males.

Males of age-class-0 are protected by regulation. Hunters encountering a male of age-class-1 or -2 may not recognize it as a male because of its small antlers. Some hunters will pass up a younger male, expecting later to encounter more desirable older males. Table 9.3 indicates for each age class of males a hunter preference value, P_x, which is essentially the probability that an individual male deer will be taken during an encounter with a hunter. These values were developed as weighted averages of the P value above, based on reasonable expectations. For the different age classes of male deer, the annual hunting mortality is found with

$$(\Delta M_x)_H = \frac{M_x H\,P_x}{H + M_a} \qquad (9.16)$$

Hunting mortality must be combined with mortality occurring apart from hunting. However, birth and hunting in deer populations are discontinuous events, while other mortality is continuous through the year. The sequence of calculations for the model is therefore important. You may assume the year starts in the spring with births, that mortality is very low during the summer, that hunting occurs in the fall just after the breeding season, and that non-hunting mortality for both sexes is concentrated in the winter months. The values given in Table 9.3 describe a hypothetical population in the summer. The proper sequence for a deer-hunting simulation would require sequentially calculating (1) the proportion of females fertilized during the breeding season, (2) the hunting mortality of the males, (3) the number of births, (4) the mortality of females and remaining males, moving survivors to the next age class, (5) the proportion of births that are males and females, which are put into age-class-0 for each sex.

Exercise 9-5: A variety of simulations are possible using the deer-hunter model above. As a minimum exploration of the model, write a program to simulate the effects of different hunting pressures on the deer population. As measures of the performance of the deer population, have your program show the total number of deer, the number of births per year, and the proportion of males among adult deer. These measures should reach a steady-state condition after about 25 years at any given hunting pressure. The output of your program should show these three measures at steady-state plotted against the number of hunters. Vary the size of the hunter population from 0 to 10,000 in steps of 1000.

9.6 A Fisheries Age-Class Model

Age-class models are important to fisheries management because fecundity and fishing pressure both vary with the age of fish. Fisheries

management has been based for several decades in the density-dependent stock-and-recruitment model attributed to Ricker. Hall (1988) reviews the model instructively. The key idea of this model is fundamentally that of the logistic model, based on the premise that there is some upper density of the population at which birth rate is balanced by death rate; below this density births exceed deaths, and above it deaths exceed births. Ricker's (1954) model is shown graphically in Figure 9.4, based on this equation:

$$F = P \cdot \exp[(P_r - P)/P_m] \tag{9.17}$$

where F is the density of recruited (i.e. next generation) adults and P is the density of parental stock adults. P_r is the density of parental stock which will produce just sufficient recruits for replacement, and P_m is the parental stock which produces maximal recruitment. (P_r is conceptually equivalent to K in the logistic.) Like the logistic, this model was formulated for homogeneous populations, but can be adapted for age-class models.
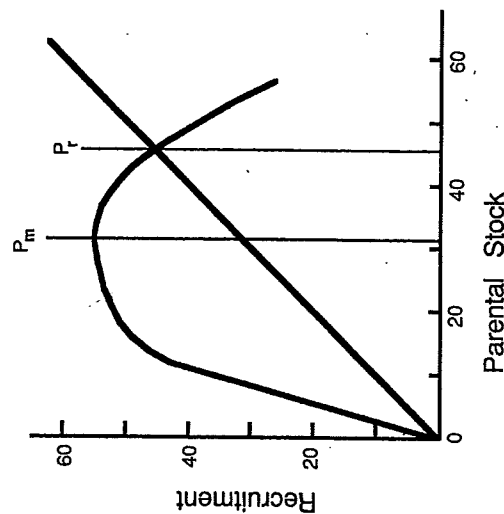

Figure 9.4. Density of recruitment of new adults in a fishery as a function of parental stock density. P_r is the upper limit of density for successful replacement. P_m is the parental density resulting in a maximum recruitment density.

The dynamics of a population of haddock in the North Sea have been modeled with a variation of the stock-recruitment model employing age

classes (Jones and Hall 1973, Cushing 1977). A Ricker-type curve relating egg production of parental stock to recruitment of year-old fish was employed, which may be approximated with the following equation:

$$N_1 = F \cdot E \cdot \exp[(E_r - E)/E_m] \tag{9.18}$$

In this modification of Equation 9.17, N_1 is the density of one-year-old female recruits, and F is a survival factor relating eggs and larvae to number of female fish. E is the density measure of total egg production during a spawning season, E_r is the density of eggs required for replacement, and E_m is the density of eggs required for maximal recruitment. For the North Sea population of haddock, density values were based on 3 square kilometers of pelagic habitat. The constants were as follows:

$$F = 19.2 \times 10^{-6} \text{ females egg}^{-1},$$
$$E_r = 130 \times 10^6 \text{ eggs } (3 \text{ km}^2)^{-1},$$
$$E_m = 80 \times 10^6 \text{ eggs } (3 \text{ km}^2)^{-1}$$

The age-specific survival and fecundity information for the fish are summarized in Table 9.4, and describe the population just before spawning begins.

Age in years x	Density of females at age x N_x	Rate of survival x to $x+1$ s_x	Average number of eggs produced per female of age x m_x
1	2500	0.65	0
2	1630	0.42	0.58×10^5
3	700	0.35	1.4×10^5
4	250	0.33	2.2×10^5
5	90	0.33	3.0×10^5
6	30	0.33	3.8×10^5
7	10	0.30	4.4×10^5
8	5	0.20	5.0×10^5
9	2	0.00	5.5×10^5
10	0		

Table 9.4. Population characteristics of North Sea haddock, adapted from data in Jones and Hall (1973).

Exercise 9-6: With the information given above, develop an age-class simulation of the North Sea population of haddock. Use the fecundity data to determine the total production of eggs, then use the survival equations and data to determine the age classes for the next year, and finally use Equation 9.18 to find the number of first-year recruits. This simulation will show some interesting oscillations in the total population size. It should also show dominant age classes moving through the population. To demonstrate these phenomena, write your program to draw a graph of total population as a function of time for a period of at least 30 years. Then modify your program to produce histograms that show the size of each age class for a given year. Produce 10 such histograms for years 0 through 9 of your simulation.

9.7 Insect Life Stages: Flour Beetles

Flour beetles (*Tribolium* sp.) have been used frequently in laboratory investigations of population dynamics. At usual culturing temperature the stages of the beetle life cycle have the following durations in days: eggs, 4.6; larvae, 22.6; pupae, 6.6; adults, 120. Experiments are usually started with a few adults put into a vial containing 8 grams of whole wheat flour and brewer's yeast. The beetles are allowed to reproduce and grow in this confined volume at constant temperature and humidity. The flour is sifted at 30-day intervals to separate the larvae, pupae and adults; these are counted and put into a fresh supply of flour and yeast. Under these conditions, the data of Table 9.5 are typical of those collected in the classic work of Thomas Park (1948).

The data of the table show that adult beetles will intensely cannibalize two other life stages. Just after the population is founded, there are few adults, and there is little mortality in going from larva or pupa to adult (24 larvae and pupae become 24 adults). However, later in the experiment, there is a very low rate of successful transition from larva or pupa to adult (9-10 larvae and pupae become 5 adults, most of which were probably old surviving adults). Cannibalism appears to be occurring during the pupal stage. The other life stage that is cannibalized is the egg stage. For example, 20 adults should be laying about 250 eggs per day. Over a 30-day period this should result in about 7500 eggs and then 7500 pupae and larvae. However, after day 60, less than one larva and pupa per gram are found. Evidently the rate of cannibalism is intensely directed against the eggs. Park et al. (1965) indicate that cannibalism is the primary mechanism for limiting the population of flour beetles under these conditions. The model described below for cannibalistic control of

the confined flour beetle population illustrates some important features of simulations involving insect life stages.

Culture age in days	Density of larvae + pupae number gram^{-1}	Density of adult beetles number gram^{-1}
0	—	3
30	24.0	3
60	3.0	24
90	1.0	24
120	0.7	23
150	0.7	22
180	2.0	20
210	2.5	14
240	4.0	10
480	9.0	5
960	10.0	5

Table 9.5. Typical data from laboratory cultures of flour beetles (*Tribolium* spp.). See text for further details. Data are derived from Park (1948).

The life cycle of the beetle is divided into four stages. The model is based on an assumption that the egg and pupal stages are equally long. The duration of the egg or pupal stage will represent one unit of time for modeling purposes, so that a simulation based on the model will use physiological time units. The larval stage lasts about three units of physiological time, so for the model the stage will be broken into three consecutive parts. The adult stage will consist of many parts in the model, each a single interval in duration. Adults all will survive successfully through three intervals, and then survive at a constant fractional rate S for each succeeding time interval.

Egg-laying is assumed to be continuous throughout the adult stage, described by a constant R, measured as eggs adult^{-1} time-unit^{-1}. These units presume that the male-female ratio is a constant. Adults are assumed to eat both eggs and pupae. Given the "natural history" of a flour vial, with the adults tunneling through the flour and eating eggs when they encounter them, the simple mass-balance Lotka-Volterra predation term is an adequate descriptor of loss of eggs and pupae:

$$\frac{-dE}{dt} = k \cdot E \cdot A \tag{9.19}$$

$$\frac{-dP}{dt} = K \cdot P \cdot A \tag{9.20}$$

where A is adult density, E is egg density, P is pupal density, and K and k are cannibalism constants for eggs and pupae, and t is actual time, not physiological time. If we assume that the number of adults is constant over a unit of physiological time, then Equations 9.19 and 9.20 can be integrated (following procedures of Chapter 1) over one unit of physiological time:

$$E_u = E_o e^{kA} \tag{9.21}$$

where E_o and E_u are egg densities at the beginning and end of the time unit. Similarly,

$$P_u = P_o e^{KA} \tag{9.22}$$

describes pupal density after one time unit.

The sequential model system is described with the following:

$$A = A_1 + A_2 + A_3 \tag{9.23}$$

$$A_3 \leftarrow A_3 \cdot S + A_2 \tag{9.24}$$

$$A_2 \leftarrow A_1 \tag{9.25}$$

$$A_1 \leftarrow P e^{-KA} \tag{9.26}$$

$$P \leftarrow L_3 \tag{9.27}$$

$$L_3 \leftarrow L_2 \tag{9.28}$$

$$L_2 \leftarrow L_1 \tag{9.29}$$

$$L_1 \leftarrow E e^{-kA} \tag{9.30}$$

$$E \leftarrow R \cdot A \tag{9.31}$$

L_1, L_2 and L_3 are densities of the three parts of the larval stage. A_1, A_2 and A_3 are densities of the three parts of the adult stage. As in Exercise 9-1, the sequence of solution of the model is important, particularly the summation of number of adults before the calculations with Equations 9.26, 9.30 and 9.31.

Exercise 9-7: Implement the simulation described above for cannibalistic regulation of flour beetle populations. Assume the population begins with two adults placed in a closed container with one kilogram of flour (adult density = 0.002). Set the constants as follows:

$R = 100$ $k = 0.30$ gram adult^{-1} time-unit^{-1}
$S = 0.85$ $K = 0.03$ gram adult^{-1} time-unit^{-1}

Your output should plot number of (larvae + pupae) and number of adults over 100 units of physiological time.

The simulation should produce oscillating densities, with high adult densities depressing the abundance of immature stages. The simulation results are quite sensitive to the value of adult survival S. The oscillation is damped with values of S greater than about 0.9. With smaller values, the oscillations are undamped and some rather large excursions of larval densities are possible.

Conclusion

This chapter has covered several different models based on dividing a population into subclasses. The technique is used frequently in developing realistic models of economically important organisms, such as forest trees and insect pests. The increase in realism is obtained at the price of complexity. The modeler must be careful not to let the complexity cloud the central point of the particular model.