Modelling structured populations

4.1 Modelling complex life cycles

The population models in the previous chapters have assumed that all the individuals are the same age or at the same stage in their life cycle. Here we will introduce models which can take account of individuals of different age, stage, or size. In particular we will use matrices to summarize the structure and parameters of a population composed of organisms with complex life histories. There is only space here for a short treatment of what is a rich and fascinating area of ecological modelling (Caswell 2000a).

Individuals of long-lived species may have widely varying patterns of pre-reproductive and reproductive life (Fig. 4.1). It will be assumed that, although generations overlap, reproduction occurs at certain times of year and therefore discrete time models are appropriate. From the perspective of population dynamics there are two important differences between long-lived organisms with overlapping generations and annual or short-lived organisms with separate generations. First, long-lived organisms may delay reproduction for 1 or more years and, second, they may survive after reproduction to reproduce again. In all of these cases the life history of an individual may be categorized according to its age (e.g. time of first reproduction), stage (e.g. adult or juvenile) or size (e.g. only plants over a certain size can reproduce).

Imagine a species, the individuals of which breed once a year, starting at age 3 years and which live to a maximum of 5 years. The reproduction and survival of these organisms can be described by a set of first-order difference equations. These give either the survival of individuals of different age or the reproductive output of individuals aged 3–5 years. Assume that the age-specific fecundity and survival parameter values are density-independent and are constant from year to year. For example, survival from birth to age 1 is described as:

Number of individuals aged 1 (in year $t+1$) = number born (aged 0 in year t)
  × fraction surviving from age 0 to 1

This can be represented algebraically:

$$N_{1,t+1} = N_{0,t}s_{0,1} \tag{4.1}$$
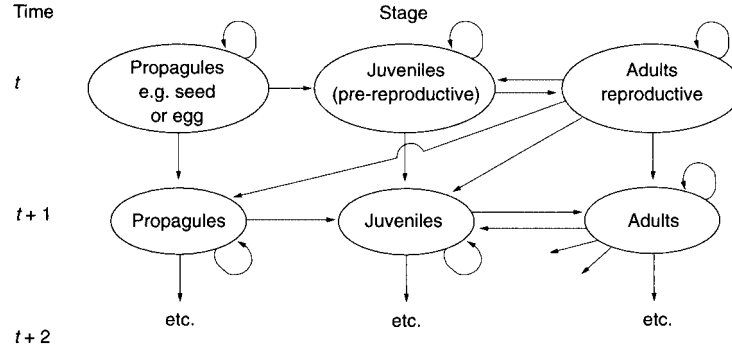
Fig. 4.1 Representations of life cycles of plant and animal species. Arrows show all possible transitions between stages, both within and between years.

In equation 4.1 the double subscript for the number of individuals (N) indicates the age class and the time (year). For the survival parameter (s) the double subscript describes the ages over which survival is considered. We can write similar equations describing the survival for the other age classes:

$$N_{2,t+1} = N_{1,t}s_{1,2} \tag{4.2}$$

$$N_{3,t+1} = N_{2,t}s_{2,3} \tag{4.3}$$

$$N_{4,t+1} = N_{3,t}s_{3,4} \tag{4.4}$$

$$N_{5,t+1} = N_{4,t}s_{4,5} \tag{4.5}$$

The fraction of individuals surviving from birth (age 0) to age 5 is therefore the multiple of the separate survival values from ages 0 to 1, 1 to 2 and so on; that is, $s_{0,1}s_{1,2}s_{2,3}s_{3,4}s_{4,5}$. We will assume that any individuals surviving to reproduce at age 5 then die. Therefore for any given value of N_0, N_5 could be predicted.

An equation is also required for the production of offspring (age 0 individuals in year t) by individuals aged 3–5 in the same year (t):

$$N_{0,t} = N_{3,t}f_3 + N_{4,t}f_4 + N_{5,t}f_5$$

f_3, f_4 and f_5 are age-specific fecundity parameters representing the average number of offspring per individual of that age in year t. Multiplying by $s_{0,1}$ gives an equation determining the number of offspring surviving to age 1 in year $t + 1$ (see equation 4.1):

$$N_{1,t+1} = s_{0,1}(N_{3,t}f_3 + N_{4,t}f_4 + N_{5,t}f_5) \tag{4.6}$$

Equations 4.1–4.6 provide a complete description of the density-independent survival and fecundity of individuals in this age-structured population. We could explore by simulation the dynamics of this population, using these

equations. Alternatively we can employ analytical techniques, in which case it is helpful to rewrite the equations in a different form, employing a matrix structure. As we do so, you might wish to consider whether you expect any fundamental differences in the dynamics of this population to the one described by equation 2.2.

Equations 4.2 to 4.6 can be represented as three matrices:

$$
\begin{pmatrix} N_1 \\ N_2 \\ N_3 \\ N_4 \\ N_5 \end{pmatrix} = \begin{pmatrix} 0 & 0 & s_{0,1}f_3 & s_{0,1}f_4 & s_{0,1}f_5 \\ s_{1,2} & 0 & 0 & 0 & 0 \\ 0 & s_{2,3} & 0 & 0 & 0 \\ 0 & 0 & s_{3,4} & 0 & 0 \\ 0 & 0 & 0 & s_{4,5} & 0 \end{pmatrix} \begin{pmatrix} N_1 \\ N_2 \\ N_3 \\ N_4 \\ N_5 \end{pmatrix} \tag{4.7}
$$
$$
\mathbf{v}_{t+1} \qquad\qquad \mathbf{M} \qquad\qquad \mathbf{v}_t
$$

Three matrices are required to summarize the five difference equations. There are two column matrices representing the number of individuals at ages 1–5 at times $t+1$ and t ($\mathbf{v}_{t+1}$ and $\mathbf{v}_t$ respectively). These column matrices are referred to as the population-structure vectors or age-distribution vectors. There is also one square matrix, $\mathbf{M}$, which gives all of the fecundity and survival values and is known as the population projection matrix. To check that equation 4.7 is equivalent to equations 4.2–4.6 you can multiply out the matrix and population-structure vector on the right-hand side of the equation. For readers unfamiliar with matrix multiplication, you begin by multiplying the five coefficients in the top row of the square matrix $\mathbf{M}$ by the corresponding population sizes in the column matrix $\mathbf{v}_t$ ($0 \times N_1$, $0 \times N_2$, $s_{0,1}f_3 \times N_3$ and so on) and add the resulting five multiplied pairs of values to give N_1 in $\mathbf{v}_{t+1}$. This process is then repeated with the next row, again multiplying by the corresponding values of N_1–N_5 in $\mathbf{v}_t$ and summing the five multiples. This process is repeated for all five rows of the matrix $\mathbf{M}$. Representation of age-structured populations in this manner was first described by Bernardelli (1941), Lewis (1942) and Leslie (1945, 1948).

Matrix equations such as equation 4.7, representing a set of difference equations, can be written in a general form to describe any age- or stage-structured population:

$$
\mathbf{v}_{t+1} = \mathbf{M}\mathbf{v}_t \tag{4.8}
$$

where $\mathbf{v}_t$ and $\mathbf{v}_{t+1}$ are population vectors of the numbers of individuals at different ages (or sizes or stages) at t and $t+1$ respectively, and $\mathbf{M}$ is a square matrix in which the number of columns and rows is equal to the number of age classes. You will see the similarity of this to equation 2.2, $N_{t+1} = \lambda N_t$. This similarity is considered in the next section as we proceed with an analytical study of the dynamics of equation 4.8.

## 4.2 Determination of the eigenvalue and eigenvector

To proceed with the analytical investigation we will take a much simpler age-structured population and then discuss more complicated examples in the light of results from the simpler version. Consider a population of biennial plants (Fig. 4.2). The plant population has two age classes, which correspond to particular developmental stages. In the first year the plant forms rosettes following the germination of over-wintering seed. In the second year the surviving rosettes flower, set seed and then die. We will assume that the plant is a strict biennial: it always flowers in the second year (assuming it survives) and always dies after flowering. This model could also be described as a stage-structured population (Lefkovitch 1965; see Manly 1990 for an overview of matrix models of stage-structured populations) composed of rosettes and flowering plants. It is a coincidence in this case that each stage survives for one unit of time: in most cases this would not be true; for example, a tree species may spend many years at one defined stage. The dynamics of the population can be summarized with two first-order equations:

$$R_{t+1} = f s_{0,1} F_t \tag{4.9}$$

$$F_{t+1} = s_{1,2} R_t \tag{4.10}$$

where R is the number or density of rosette plants, F is the number of flowering plants, f is the average number of viable seed per flowering plant, $s_{0,1}$ represents the fraction of seed surviving between dispersal from the mother plant to rosette formation and $s_{1,2}$ describes the fraction of rosettes surviving until flowering.

　　In constructing such models it is often the case that stages such as seed are omitted. This will depend on the units of time chosen for the model and the census time. For example, we could have examined changes from spring to autumn and autumn to spring in which case seed may need to be included as a specified stage, or at least a seed/small rosette stage.
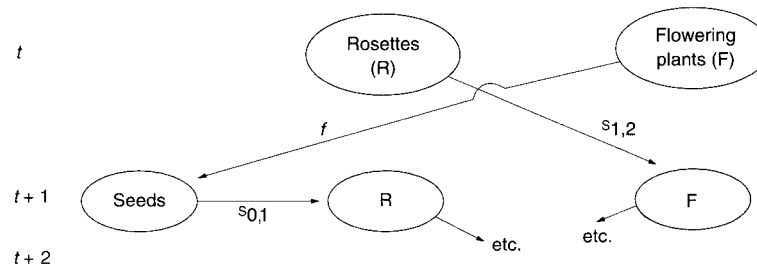
Fig. 4.2 Representation of the life cycle of a biennial plant species with fecundity (f) and survival at two different stages ($s_{0,1}$ and $s_{1,2}$). Seed as a separate stage is not included in this model.

As before, it is possible to write equations 4.9 and 4.10 in matrix notation (the algebraic shorthand for the matrices is indicated below them):

$$\begin{pmatrix} R \\ F \end{pmatrix} = \begin{pmatrix} 0 & fs_{0,1} \\ s_{1,2} & 0 \end{pmatrix}\begin{pmatrix} R \\ F \end{pmatrix} \tag{4.11}$$

$$\mathbf{v}_{t+1} \qquad\quad \mathbf{M} \qquad\quad \mathbf{v}_t$$

We will now describe a mathematical analysis which will reveal two important results. First, it will provide the ratio of R to F, the composition or structure of the population. Second, it will give the finite rate of change of the biennial population, which will be seen to be equivalent to the finite rate of change (λ) in equation 2.2. Therefore this analysis makes the important assumption about the square matrix, $\mathbf{M}$, that it can be replaced by a single value (λ) and therefore that $\mathbf{Mv}_t = \lambda\mathbf{v}_t$. If this is true then the matrix equation 4.11 can be written as the density-independent equation 2.1, except now that $\mathbf{v}_{t+1}$ and $\mathbf{v}_t$ are population vectors rather than single numbers:

$$\mathbf{v}_{t+1} = \lambda\mathbf{v}_t \tag{4.12}$$

You should note that in multiplying the vector, $\mathbf{v}_t$, by λ, that all elements of the matrix are multiplied by λ. (λ is a scalar.) Equating the right-hand side of equations 4.11 and 4.12 – values at time t – we have:

$$\begin{pmatrix} 0 & fs_{0,1} \\ s_{1,2} & 0 \end{pmatrix}\begin{pmatrix} R \\ F \end{pmatrix} = \lambda\begin{pmatrix} R \\ f \end{pmatrix} \tag{4.13}$$

$$\quad\mathbf{M} \qquad\quad \mathbf{v}_t \qquad\quad \mathbf{v}_t$$

It is helpful to have the right-hand side of equation 4.13 in a matrix form similar to the left-hand side. To do this we employ the identity matrix, $\mathbf{I}$. Multiplying any matrix by the identity matrix leaves the matrix unchanged (therefore $\mathbf{M} \cdot \mathbf{I} = \mathbf{M}$ on the left-hand side):

$$\begin{pmatrix} 0 & fs_{0,1} \\ s_{1,2} & 0 \end{pmatrix}\begin{pmatrix} R \\ F \end{pmatrix} = \lambda\begin{pmatrix} 1 & 0 \\ 0 & 1 \end{pmatrix}\begin{pmatrix} R \\ F \end{pmatrix}$$

$$\quad\mathbf{M} \qquad\quad \mathbf{v}_t \qquad\quad \lambda\mathbf{I} \quad\ \mathbf{v}_t$$

Now multiply the identity matrix $\mathbf{I}$ by the scalar λ:

$$\begin{pmatrix} 0 & fs_{0,1} \\ s_{1,2} & 0 \end{pmatrix}\begin{pmatrix} R \\ F \end{pmatrix} = \begin{pmatrix} \lambda & 0 \\ 0 & \lambda \end{pmatrix}\begin{pmatrix} R \\ F \end{pmatrix} \tag{4.14}$$

$$\quad\mathbf{M} \qquad\quad \mathbf{v}_t \qquad\quad \lambda\mathbf{I} \quad\ \mathbf{v}_t$$

We can now find a value for λ. Subtract the right from the left-hand side of equation 4.14:

$$\begin{pmatrix} 0 & fs_{0,1} \\ s_{1,2} & 0 \end{pmatrix}\begin{pmatrix} R \\ F \end{pmatrix} - \begin{pmatrix} \lambda & 0 \\ 0 & \lambda \end{pmatrix}\begin{pmatrix} R \\ F \end{pmatrix} = \begin{pmatrix} 0 \\ 0 \end{pmatrix}$$

$\quad\quad \mathbf{M} \quad\quad \mathbf{v}_t \quad\quad \lambda\mathbf{I} \quad\quad \mathbf{v}_t$

The left-hand side can be simplified by taking out the common vector ($\mathbf{v}_t$) and subtracting the two square matrices:

$$\begin{pmatrix} 0-\lambda & fs_{0,1}-0 \\ s_{1,2}-0 & 0-\lambda \end{pmatrix}\begin{pmatrix} R \\ F \end{pmatrix} = \begin{pmatrix} 0 \\ 0 \end{pmatrix}$$

$\quad\quad\quad \mathbf{M} - \lambda\mathbf{I} \quad\quad\quad \mathbf{v}_t$

to give:

$$\begin{pmatrix} -\lambda & fs_{0,1} \\ s_{1,2} & -\lambda \end{pmatrix}\begin{pmatrix} R \\ F \end{pmatrix} = \begin{pmatrix} 0 \\ 0 \end{pmatrix} \tag{4.15}$$

$\quad\quad \mathbf{M} - \lambda\mathbf{I} \quad \mathbf{v}_t$

If the matrix $\mathbf{M} - \lambda\mathbf{I}$ in equation 4.15 has an inverse then we could multiply both sides of the equation by the inverse matrix:

$$\begin{pmatrix} -\lambda & fs_{0,1} \\ s_{1,2} & -\lambda \end{pmatrix}\begin{pmatrix} a & b \\ c & d \end{pmatrix}\begin{pmatrix} R \\ F \end{pmatrix} = \begin{pmatrix} 0 \\ 0 \end{pmatrix}\begin{pmatrix} a & b \\ c & d \end{pmatrix}$$

$\mathbf{M} - \lambda\mathbf{I} \quad\quad \text{Inverse} \quad \mathbf{v}_t \quad\quad\quad \text{Inverse}$
$\quad\quad\quad \text{of } \mathbf{M} - \lambda\mathbf{I} \quad\quad\quad \text{of } \mathbf{M} - \lambda\mathbf{I}$

Multiplying the square matrix $\mathbf{M} - \lambda\mathbf{I}$ by its inverse on the left-hand side would give the identity matrix, $\mathbf{I}$ (by definition), whereas the right-hand side would reduce to 0:

$$\begin{pmatrix} 1 & 0 \\ 0 & 1 \end{pmatrix}\begin{pmatrix} R \\ F \end{pmatrix} = \begin{pmatrix} 0 \\ 0 \end{pmatrix}$$

$$\begin{pmatrix} R \\ F \end{pmatrix} = \begin{pmatrix} 0 \\ 0 \end{pmatrix}$$

This is unhelpful as we are left with the trivial solution that R and F are equal to 0. To overcome this problem we need to assume that the matrix $\mathbf{M} - \lambda\mathbf{I}$ does *not* have an inverse. This is true if the *determinant of the matrix is equal to 0*. This assumption can then be used to find a value for λ:

$$\begin{vmatrix} -\lambda & fs_{0,1} \\ s_{1,2} & -\lambda \end{vmatrix} = 0 \tag{4.16}$$

The determinant in equation 4.16 is referred to as the *characteristic determinant*. The whole equation 4.16 is called the *characteristic equation*. We can now evaluate the characteristic determinant and therefore solve the characteristic equation:

$$(-\lambda \cdot -\lambda) - fs_{0,1}s_{1,2} = 0$$

$$\lambda^2 = fs_{0,1}s_{1,2} \tag{4.17}$$

We are now left with a quadratic equation (4.17). Initially this poses a problem because a quadratic equation has two solutions (or roots); in other words, λ can have two values. But earlier we had assumed that the square matrix **M** could be replaced by a single value, λ. Effectively this becomes true as the larges of the two λ values, referred to as the *dominant root*, has most influence on the dynamics. Note that the dominant root may be complex or negative. A negative dominant root is biologically meaningless in this application (but see Chapter 7) whereas complex roots are discussed in Chapter 7. In mathematics the values of λ are called the *eigenvalues* and the corresponding values of R and F are the *eigenvectors*. The eigenvalues may also be referred to as the latent roots or the characteristic values of the matrix, **M**. Similarly, the eigenvectors are known as the latent or characteristic vectors. (In passing it is worth noting that in finding values for R and F we have found solutions for the equations 4.9 and 4.10. Matrix methods have a wide application in the solving of simultaneous equations.) Finally, it may be helpful to know that equations 4.13–4.16 can be written in a general mathematical shorthand for any size of matrix **M** and vector **v** (as equation 4.8):

$$\mathbf{M}\mathbf{v}_t = \lambda \mathbf{v}_t$$

$$\mathbf{M}\mathbf{v}_t - \lambda \mathbf{I}\mathbf{v}_t = 0$$

$$(\mathbf{M} - \lambda \mathbf{I})\mathbf{v}_t = 0$$

The requirement for the non-trivial solution is that

$$|\mathbf{M} - \lambda \mathbf{I}| = 0$$

with values of λ being found by solution of the characteristic equation.

To reinforce all these theoretical points let us consider a specific example. If $f = 100$, $s_{0,1} = 0.1$ and $s_{1,2} = 0.5$ then from equation 4.17:
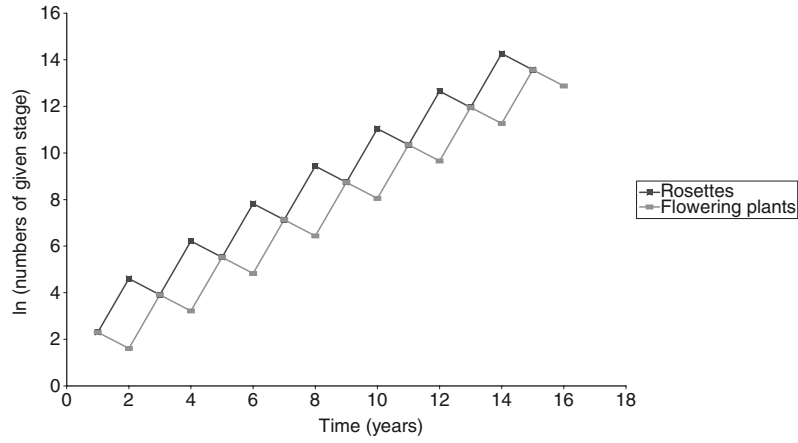
$$\lambda^2 = 100 \times 0.1 \times 0.5$$

$$\lambda^2 = 5$$

$$\lambda = \pm\sqrt{5}$$

$+\sqrt{5}$ is both the larger value (and therefore the dominant root) and the one which is ecologically meaningful. We can now use this value of λ to produce a prediction of the rate of increase of R and F (based on equation 4.12):

$$\mathbf{v}_{t+1} = \sqrt{5}\mathbf{v}_t$$

or

Fig. 4.3 Simulation of population dynamics of rosettes and flowering plants (equations 4.9 and 4.10) with values of $f = 100$, $s_{0,1} = 0.1$ and $s_{1,2} = 0.5$.

$$\begin{pmatrix} R \\ F \end{pmatrix} = \sqrt{5}\begin{pmatrix} R \\ F \end{pmatrix}$$

$$\mathbf{V}_{t+1} \qquad \mathbf{V}_t$$

It is important to note that the model predicts that both R and F increase at the same rate of $\sqrt{5}$, and therefore predicts that they maintain the same ratio of R to F over time; that is, that they maintain a stable age structure. A quirk of this model is that it produces oscillations from year to year (Fig. 4.3). The yearly increase by $\sqrt{5}$ (λ) therefore needs to be viewed over a 2-year period; for example, from years 4 to 6 the rosette numbers increase 5-fold from 500 to 2500, equivalent to two yearly increases ($\sqrt{5} \times \sqrt{5}$).

We can quantify the eigenvector and therefore determine the ratio of R to F as follows, using equation 4.13:

$$\begin{pmatrix} 0 & fs_{0,1} \\ s_{1,2} & 0 \end{pmatrix}\begin{pmatrix} R \\ F \end{pmatrix} = \sqrt{5}\begin{pmatrix} R \\ F \end{pmatrix}$$

Using the given values for f, $s_{0,1}$ and $s_{1,2}$ and multiplying out the left- and right-hand sides:

$$\begin{pmatrix} 10F \\ 0.5R \end{pmatrix} = \begin{pmatrix} \sqrt{5}R \\ \sqrt{5}F \end{pmatrix}$$

In effect we now have two equations: $10F = \sqrt{5}R$ and $0.5R = \sqrt{5}F$. These two equations are equivalent because rearrangement of either produces $R = 2\sqrt{5}F$.

We have now achieved both parts of the analysis described at the beginning of this section: we have found a value for λ, the finite rate of change, by determining the eigenvalue of the matrix and we have calculated the ratio of R to F by quantifying the eigenvector.

These techniques can be applied to more complex examples in which there are more than two ages, stages or sizes of organisms. The number of eigenvalues is equivalent to the number of rows or columns and therefore the number of ages, stages or sizes in the projection matrix **M**. Although the determination of eigenvalues becomes more difficult as the matrix increases in size, the principle continues to hold that it is the dominant eigenvalue that is important. However large the projection matrix is, it can always be reduced to the dominant eigenvalue to describe the dynamics of the component stages of the population. Furthermore, the assumption of a stable age structure continues, given by the values in the eigenvector. Although we have focused on an age-structured population, it should be noted that many of the details of construction and results of the model are also relevant to stage- or size-structured populations.

The modelling of structured populations can be progressed by investigating the contributions of the various survival and fecundity values to the overall rate of change summarized by the eigenvalue (λ). These analyses have applications in harvesting and conservation of populations (Caswell 2000b). Sensitivity and elasticity are two related methods for determining contributions to the change in λ. Sensitivity quantifies the absolute changes in λ while elasticity quantifies relative changes in λ in response to proportional changes in elements of the projection matrix (de Kroon et al. 2000). Because the elasticity values sum to 1 the different components of the projection or transition matrix, such as the fecundity values, can be contrasted to show their importance to λ. This property has been used in comparative studies of life history across different taxa (e.g. Franco & Silvertown 2004).

4.3 Stochastic matrix models and succession

In Chapter 3 we saw how deterministic models of the form $N_{t+1} = \lambda N_t$ introduced in Chapter 2 can be developed by incorporating stochastic processes. Similarly, the deterministic matrix models outlined above have a stochastic counterpart (Fieberg & Ellner 2001) in which the various components of the matrix fluctuate in response to environmental change. These fluctuations are usually assumed to be like those of the random-walk example in Chapter 3; that is, independent and drawn from the same probability distribution. This type of process is referred to as a Markov process or Markov chain. The precise probability distribution used may vary within a given matrix or the probability distribution may be the same but the size of fluctuation may vary. There is also the possibility of including a deterministic signal. Fieberg and