including the death assemblage, is

$$
\mathbf{A} = \left(
\begin{array}{ccc|ccc}
F_1 & F_2 & F_3 & 0 & 0 & 0 \\
P_1 & 0 & 0 & 0 & 0 & 0 \\
0 & P_2 & 0 & 0 & 0 & 0 \\
\hline
q_1 & 0 & 0 & 1-\delta_1 & 0 & 0 \\
0 & q_2 & 0 & 0 & 1-\delta_2 & 0 \\
0 & 0 & q_3 & 0 & 0 & 1-\delta_3
\end{array}
\right)
\tag{6.91}
$$

where $q_i = 1 - P_i$ is the mortality rate of age class i and δ_i is the probability that a dead individual in age class i is lost from the death assemblage by decay, dissolution, or other event. The upper-left corner of $\mathbf{A}$ projects the living population, which is independent of the death assemblage. The lower-left corner describes input to the death assemblage from the live population, and the lower-right corner describes the decay of the death assemblage.

Using the methods in Chapter 7, the stable stage distribution can be written as

$$
\left(\frac{\mathbf{w}}{\mathbf{d}}\right) = \left(
\begin{array}{c}
1 \\
P_1 \lambda^{-1} \\
P_1 P_2 \lambda^{-2} \\
\hline
\dfrac{q_1}{\lambda - (1-\delta_1)} \\
\dfrac{P_1 q_2 \lambda^{-1}}{\lambda - (1-\delta_2)} \\
\dfrac{P_1 P_2 q_3 \lambda^{-2}}{\lambda - (1-\delta_3)}
\end{array}
\right)
\tag{6.92}
$$

If $\lambda = 1$, then the ratio of abundances in successive age classes in the death assemblage is

$$
\frac{d_i}{d_{i+1}} = \left(\frac{\delta_{i+1}}{\delta_i}\right)\left(\frac{q_i}{1-q_i}\right)\frac{1}{q_{i+1}}
\tag{6.93}
$$

This ratio depends, naturally enough, on the rates at which individuals enter the death assemblage by mortality and leave it by dissolution.

A little rearranging yields an expression for q_i:

$$
q_i = \frac{q_{i+1}}{q_{i+1} + \dfrac{\delta_{i+1}}{\delta_i}\dfrac{d_{i+1}}{d_i}}
\tag{6.94}
$$

In the absence of information on age-specific dissolution rates, one can assume a common value for all the δ_i (Green et al. 1984). Suppose, in addition, that it can be assumed that, beyond some age ω (perhaps the maximum observed in the death
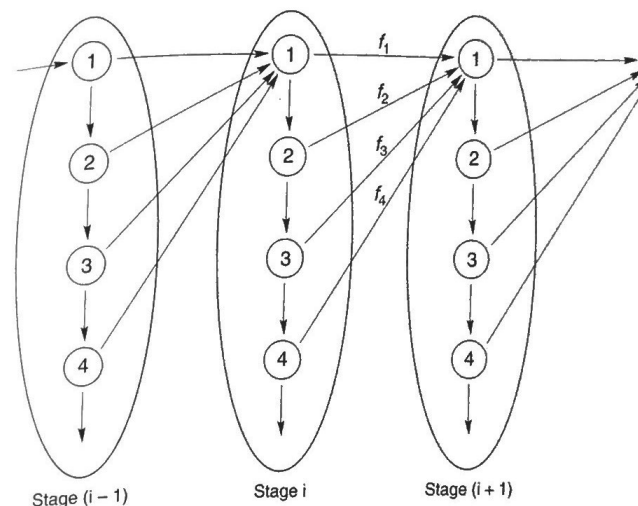
Figure 6.2: A portion of the life cycle graph for three successive stages (e.g., instars) with transition (e.g., molting) probabilities f_i determined by the time spent within the stage (Caswell 1988).

assemblage), all individuals die. This is true in our example for $\omega = 3$. Then $q_\omega = 1$ and (6.94) can be solved iteratively to obtain $q_{\omega-1}, \ldots, q_1$. Green et al. (1984) applied this method to the freshwater clam *Sphaerium striatinum* and found good agreement between mortality estimates from the death assemblage and from the age distribution of the living population.

6.4 Stage-duration distributions

Some of the parameters in the standard size-classified model (Figure 4.1b) can be estimated from information on the duration of the stages or size classes (Caswell 1988). Think of Figure 4.1b as an approximation to Figure 6.2, in which individuals are classified by age *within* stages (Caswell 1983; for an application to insect populations, see Longstaff 1984). The probability of growing to the next stage depends on the time spent in the current stage, but is independent of the time spent in previous stages.

The problem is to obtain information on the probabilities P_i and G_i from information on stage duration. To do this, we separate the processes of survival and growth, both of which appear in P_i and G_i, by defining

$$
\sigma_i = P(\text{survival of an individual in stage } i)
\tag{6.95}
$$

$$\gamma_i = P(\text{growth from } i \text{ to } i+1 \mid \text{survival}) \qquad (6.96)$$

(Caswell 1982a, 1983). In terms of these parameters,

$$G_i = \sigma_i \gamma_i \qquad (6.97)$$
$$P_i = \sigma_i (1 - \gamma_i) \qquad (6.98)$$

We will use the distribution of stage durations to estimate the γ_i; the results, combined with information on survival, can be used to calculate P_i and G_i. The estimates all involve assumptions about the nature of the growth process; all are approximate.

6.4.1 The geometric distribution

The simplest approximation supposes that the probability of "graduating" from stage i to stage $i+1$ is a constant, γ_i, independent of the time spend in stage i. Let T_i be the duration of stage i. Then

$$P(T_i = t) = \gamma_i (1 - \gamma_i)^{t-1} \qquad t = 1, 2, 3, \ldots,$$

which is a zero-truncated geometric distribution with mean $\overline{T}_i = 1/\gamma_i$. Thus

$$\hat{\gamma}_i = \overline{T}_i^{-1} \qquad (6.99)$$

provides an estimate of γ_i. Intuitively, if the average duration of the stage is $\overline{T}_i$, then during each time interval a fraction $\overline{T}_i^{-1}$ of the individuals must grow to the next stage.

6.4.2 Fixed stage durations

Suppose that every individual spends a fixed time T_i in stage i and then graduates to stage $i+1$. The probability of graduating is not constant, but depends on the age distribution within the stage. An approximate constant probability γ_i can be calculated by assuming that the age distribution within the stage is stable.

Assume that survival probability is a constant (σ_i) for all ages within stage i. The within-stage stable age distribution[5] is

$$\mathbf{w} = \begin{pmatrix} 1 \\ (\sigma_i/\lambda) \\ (\sigma_i/\lambda)^2 \\ \vdots \\ (\sigma_i/\lambda)^{T_i-1} \end{pmatrix} \qquad (6.100)$$

[5]The theory needed to derive this will be presented in Chapter 7.

All individuals in the last age class graduate; the proportion is

$$\gamma_i = \frac{\left(\frac{\sigma_i}{\lambda}\right)^{T_i-1}}{1 + \left(\frac{\sigma_i}{\lambda}\right) + \left(\frac{\sigma_i}{\lambda}\right)^2 + \cdots + \left(\frac{\sigma_i}{\lambda}\right)^{T_i-1}} \qquad (6.101)$$

Note that if $\sigma_i/\lambda = 1$, this expression reduces to (6.99). If $\sigma_i/\lambda < 1$, the series in the denominator of (6.101) is

$$\sum_{j=0}^{T_i-1} \left(\frac{\sigma_i}{\lambda}\right)^j = \frac{\left(\frac{\sigma_i}{\lambda}\right)^{T_i} - 1}{\left(\frac{\sigma_i}{\lambda}\right) - 1} \qquad (6.102)$$

so that

$$\gamma_i = \frac{\left(\frac{\sigma_i}{\lambda}\right)^{T_i} - \left(\frac{\sigma_i}{\lambda}\right)^{T_i-1}}{\left(\frac{\sigma_i}{\lambda}\right)^{T_i} - 1} \qquad (6.103)$$

This formula is useful when the "stages" are really groups of age classes. During the interval $(t, t+1]$ all the oldest individuals will graduate to the next stage, and all younger individuals will move up one age class. This model is, in a sense, not "stage-classified" at all, since demography is still determined by age, but it is useful when only relatively crude estimates of the survival are available over broad age ranges.

begin example

Example 6.4 Loggerhead sea turtle demography

Equation (6.103) was used by Crouse et al. (1987) to estimate stage-classified demographic parameters for the loggerhead sea turtle *Caretta caretta*, with the goal of evaluating different strategies for protecting this endangered species. Seven stages were defined (hatchlings, small juveniles, large juveniles, subadults, novice breeders, first-year remigrants, and mature breeders). Estimates of survival probabilities and stage durations were obtained from data collected over 20 years on Little Cumberland Island, Georgia.

Equation (6.103), with $\lambda = 1$, was used to estimate the γ_i. Combined with the survival probabilities σ_i, this allowed estimation of the P_i and G_i. The data and the calculated parameters are as follows:

Stage	σ_i	T_i	γ_i	P_i	G_i
1	0.6747	1	1.0000	0.0000	0.6747
2	0.7857	7	0.0618	0.7371	0.0486
3	0.6758	8	0.0218	0.6611	0.0147
4	0.7425	6	0.0698	0.6907	0.0518
5	0.8091	1	1.0000	0.0000	0.8091
6	0.8091	1	1.0000	0.0000	0.8091
7	0.8091	31	0.0003	0.8088	0.0003

Together with fertility[6] estimates ($F_5 = 127$, $F_6 = 4$, $F_7 = 80$), this is sufficient to generate the population projection matrix. In this case, the approximation $\lambda = 1$ used in estimating the parameters is not far off, since the eigenvalue λ_1 of the completed matrix is 0.945. An iterative procedure that does not rely on the assumption that $\lambda = 1$ is presented in Section 6.4.4.

end example

6.4.3   Variable stage durations

A more realistic approximation describes the distribution of stage durations by its mean $\overline{T}_i$ and its variance $V(T_i)$. The proportion graduating to the next stage at any time depends on the age distribution within the stage. If that age distribution is stable, γ_i can be estimated from $\overline{T}_i$, $V(T_i)$, and σ_i (Caswell 1983).

Consider individuals within stage i. As in Figure 6.2, let f_j be the probability that an individual in age class j graduates, given that it survives, let g_j be the probability density of age at graduation, and let h_j be the probability of not having graduated by age j. The three quantities are related:[7]

$$g_j = f_j \prod_{j=1}^{i-1}(1 - f_j) \qquad g_1 = f_1 \tag{6.104}$$

$$h_j = \prod_{j=1}^{i}(1 - f_j) \qquad h_0 = 1 \tag{6.105}$$

$$f_j = g_j / h_{j-1} \tag{6.106}$$

The stable age distribution $\mathbf{w}$ is

$$\mathbf{w} = \begin{pmatrix} 1 \\ (1 - f_1)(\sigma/\lambda) \\ (1 - f_1)(1 - f_2)(\sigma/\lambda)^2 \\ \vdots \\ \prod_{k=1}^{j-1}(1 - f_k)(\sigma/\lambda)^{j-1} \\ \vdots \end{pmatrix} \tag{6.107}$$

[6]These values are described in Crouse et al. (1987) as numbers of eggs produced per year. That does not, of course, estimate fertility; see Section 6.7. Crowder et al. (1994) repeated the analysis, with fertilities that included both egg production and the transition probabilities of the adults during the year.

[7]If we make an analogy between graduating to the next stage and death, these parameters define a life table, with h_j the survivorship function, g_j the distribution of age at death, and f_j the mortality rate; cf. Section 2.3.1.

The proportion of individuals graduating is

$$\gamma_i = \frac{\sum_j f_j w_j}{\sum_j w_j} \tag{6.108}$$

$$= \frac{\frac{\lambda}{\sigma} \sum_j g_j \left(\frac{\lambda}{\sigma}\right)^{-j}}{\frac{\lambda}{\sigma} \sum_j h_j \left(\frac{\lambda}{\sigma}\right)^{-j}} \tag{6.109}$$

Let $a = \ln(\lambda/\sigma)$. Then we can rewrite (6.109) as

$$\ln \gamma_i = \ln \left(\sum_{j=1} g_j e^{-aj}\right) - \ln \left(\sum_{j=0} h_j e^{-aj}\right) \tag{6.110}$$

The first term on the right-hand side of (6.110) is the cumulant generating function [8] of g_j. The second term differs from a cumulant generating function only because h_j is not a probability density function. However, it can be transformed into one by dividing by the sum of the function h. Define $\hat{h}_i = h_j/\sum_j h_j$. Then (6.110) can be rewritten

$$\ln \gamma_i = \ln \left(\sum_j g_j e^{-aj}\right) - \ln \left(\sum_j \hat{h}_j e^{-aj}\right) - \ln \overline{T} \tag{6.111}$$

where $\overline{T}_i = \sum_j h_j$ is the expected stage duration.

Expanding the cumulant generating functions in (6.111) up to terms of second order in a yields

$$\ln \gamma_i \approx -a \left(\kappa_1(g) - \kappa_1(\hat{h})\right) + \frac{a^2}{2!} \left(\kappa_2(g) - \kappa_2(\hat{h})\right) - \ln \overline{T}_i \tag{6.112}$$

Keyfitz (1977, p. 131) shows that

$$\kappa_1(g) = \overline{T}_i$$
$$\kappa_2(g) = V(T_i)$$
$$\kappa_1(\hat{h}) = \frac{V(T_i) + \overline{T}_i^2}{2\overline{T}_i}$$

[8]The cumulant generating function of a probability density F is $\psi(a) = \ln \int_0^\infty F(z)e^{-az}\, dz$. The cumulants κ_i are defined by the series expansion $\psi(a) = -a\kappa_1 + \frac{a^2}{2!}\kappa_2 - \frac{a^3}{3!}\kappa_3 + \cdots$. The first cumulant κ_1 is the mean, the second cumulant is the variance. Relations between the higher cumulants and the moments of F are given in Kendall and Stuart (1958, p. 71).

where $V(T_i)$ denotes the variance of stage duration. Thus, to first order in a, we can write

$$\ln \gamma_i \approx -a\left(\frac{\overline{T}_i}{2} - \frac{V(T_i)}{2\overline{T}_i}\right) - \ln \overline{T}_i \tag{6.113}$$

or

$$\gamma_i \approx \left(\frac{1}{\overline{T}_i}\right)\exp\left(-a\left(\frac{\overline{T}_i}{2} - \frac{V(T_i)}{2\overline{T}_i}\right)\right) \tag{6.114}$$

From (6.114) we again obtain the approximation $\gamma_i \approx \overline{T}_i^{-1}$, when a is sufficiently small. When $a = \ln(\lambda/\sigma_i) > 0$, $\gamma_i \approx \overline{T}_i^{-1}$ overestimates γ_i, because it overestimates the abundance of old individuals within the instar by neglecting the effects of mortality and population growth in shifting the age distribution toward young individuals. The smaller the variance $V(T_i)$ in stage duration, and the larger the average stage duration $\overline{T}_i$, the greater the overestimate of γ_i.

6.4.4   Iterative calculation

The alert reader will have noted that Equations (6.103) and (6.114) for γ_i depend on λ. However, λ is an eigenvalue of the very matrix whose entries are being estimated, and it cannot be calculated until the estimation is completed!

One solution is to set $\lambda = 1$, as in Crouse et al. (1987). An iterative approach, however, may improve the estimates. Choose an initial value of λ and calculate the entries in $\mathbf{A}$. The eigenvalues of $\mathbf{A}$ yield a second estimate of λ, with which the parameters can be estimated again. If repeated, this process usually (but not always, based on the few calculations I have done) converges to a matrix whose entries are compatible with its own eigenvalues. It is unclear how much difference this makes in practice. For example, when applied to the data of Crouse et al. (1987) on the loggerhead turtle, it changes the estimate of λ from 0.9450 to 0.9644. The uncertainty in the original survival and growth data is certainly greater than this. See Crowder et al. (1994) and Heppell et al. (1994) for applications of this method.

6.4.5   Negative binomial stage durations

The major weakness of the preceding methods is their reliance on the stability of the within-stage age distribution. This section presents a method that approximates the stage duration distribution by a negative binomial distribution (or, in continuous time, a gamma distribution) with specified mean and variance, without assuming that the age distribution is stable. The negative binomial is flexible enough to describe many observed stage duration distributions (Blythe et al. 1984).

Consider a series of k identical stages, in each of which the probability of moving to the next stage is γ. The time T required to grow through all k stages is the time

required for the kth success in a series of identical Bernoulli trials with probability of success γ; this time has a negative binomial distribution

$$P(T = x) = \binom{x-1}{k-1}\gamma^k(1-\gamma)^{x-k}$$

with mean and variance

$$\overline{T} = \frac{k}{\gamma} \tag{6.115}$$

$$V(T) = \frac{k(1-\gamma)}{\gamma^2} \tag{6.116}$$

To produce a life cycle stage whose duration has a negative binomial distribution, we divide the stage into a series of k identical but invisible "pseudostages." These are not ages within the stage; in fact they cannot be identified at all. They appear in the model only to slow down individuals proceeding through the stage so as to produce a distribution of stage durations with a specified mean and variance.[9] The number of pseudostages and their common graduation probability aree calculated from $\overline{T}_i$ and $V(T_i)$ using (6.115) and (6.116):

$$\gamma_i = \frac{\overline{T}_i}{V(T_i) + \overline{T}_i} \tag{6.117}$$

$$k_i = \frac{\overline{T}_i^2}{V(T_i) + \overline{T}_i} \tag{6.118}$$

Mortality and fertility are identical for all pseudostages within a stage. Thus the model is completed by multiplying each transition within the stage by the stage-specific survival probability σ_i. If the stage reproduces, each pseudostage is given the same fertility coefficient F_i.

6.4.6   Duration distributions compared

Consider the life cycle graph in Figure 6.3, which contains an immature stage (n_2) of variable duration. The parameters P_2 and G_2 are determined by the stage duration; let the other parameters be $G_1 = 0.5$, $F_3 = 10$, $\sigma_2 = 0.75$, and let the mean and variance of stage duration be $\overline{T}_2 = 5$, $V(T_2) = 3$. Applying the four methods outlined above [using iteration to obtain λ for (6.103) and (6.114)] produces the following four models

Model 1: Geometric stage-duration distribution: $\gamma_2 = 0.2$, $\lambda = 1.1587$,

$$\mathbf{A} = \begin{pmatrix} 0 & 0 & 10 \\ 0.5 & 0.6 & 0 \\ 0 & 0.15 & 0 \end{pmatrix} \tag{6.119}$$

[9]I do not know the origin of this method, but it was proposed by Cox and Miller (1965).

Model 2: Fixed stage-duration: $\gamma_2 = 0.097$, $\lambda = 1.0246$,

$$\mathbf{A} = \begin{pmatrix} 0 & 0 & 10 \\ 0.5 & 0.677 & 0 \\ 0 & 0.073 & 0 \end{pmatrix} \qquad (6.120)$$

Model 3: Variable stage-duration, stable age distribution: $\gamma_2 = 0.10$, $\lambda = 1.0291$,

$$\mathbf{A} = \begin{pmatrix} 0 & 0 & 10 \\ 0.5 & 0.675 & 0 \\ 0 & 0.075 & 0 \end{pmatrix} \qquad (6.121)$$

Model 4: Negative binomial stage-duration distribution: $\gamma_2 = 0.625$, $k = 3$, $\lambda = 1.0549$.

$$\mathbf{A} = \begin{pmatrix} 0 & 0 & 0 & 0 & 10 \\ 0.5 & 0.2813 & 0 & 0 & 0 \\ 0 & 0.4688 & 0.2813 & 0 & 0 \\ 0 & 0 & 0.4688 & 0.2813 & 0 \\ 0 & 0 & 0 & 0.4688 & 0 \end{pmatrix} \qquad (6.122)$$

The approximation used affects both the asymptotic and transient dynamics of the model (Figure 6.4). Model 1, assuming the geometric distribution of stage durations, has the highest value of γ_2. Because individuals reach adulthood more rapidly, the long-term growth rate is high and transient fluctuations are limited. Only Model 4, with a negative binomial distribution of stage durations, actually delays individuals in their progress through n_2; as a result, it converges to its stable structure much more slowly (and more realistically) than the others.

6.5   Multiregional or age-size models

The parameters in the multiregional age-classified model (4.11) can be estimated by taking advantage of the Leslie-like structure of the matrix to develop matrix analogues of the formulas used in Chapter 2 to parameterize the Leslie matrix from the life table. These calculations are summarized briefly here, following Rogers (1985); for details, see Nour and Suchindran (1984) and especially Schoen (1988). They are equally applicable to the age-size models of Law (1983, Law and Edley 1988).

We begin by defining multiregional survivorship and maternity functions:

$$\mathbf{l}(x) = \begin{pmatrix} l_{1\to 1}(x) & l_{2\to 1}(x) \\ l_{1\to 2}(x) & l_{2\to 2}(x) \end{pmatrix} \qquad (6.123)$$

$$\mathbf{m}(x) = \begin{pmatrix} m_1(x) & 0 \\ 0 & m_2(x) \end{pmatrix} \qquad (6.124)$$

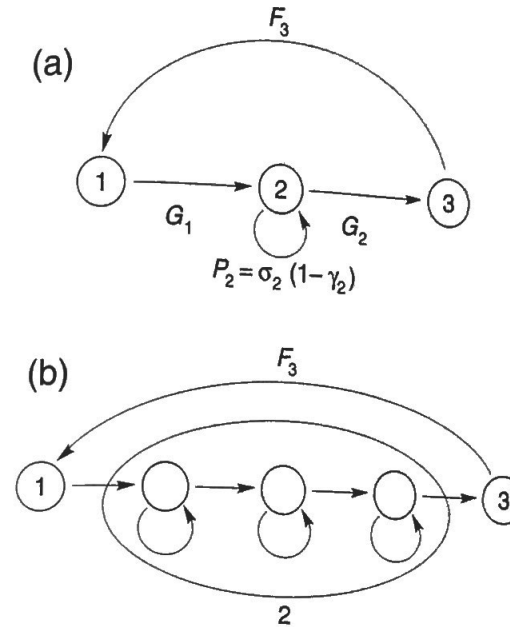**Figure 6.3:** A life cycle graph (a) for a population with an immature stage $\mathcal{N}_2$ of variable duration, with the corresponding graph (b) for a model assuming that the duration of $\mathcal{N}_2$ follows a negative binomial distribution. The second stage now contains three identical "pseudostages"; see text for details (Caswell 1988).

where, e.g., $l_{1\to 2}(x)$ is the probability that an individual born in region 1 is alive and in region 2 at age x, and $m_1(x)$ is the expected offspring production of an individual in region 1 at age x.

The multiregional survivorship function $\mathbf{l}(x)$ integrates mortality and migration information. It can be estimated from age-specific mortality and migration rates as follows (Rogers 1985). Define

$$\mathbf{M}(x) = \begin{pmatrix} M_{1\to d}(x) + M_{1\to 2}(x) & -M_{2\to 1}(x) \\ -M_{1\to 2}(x) & M_{2\to d}(x) + M_{2\to 1}(x) \end{pmatrix} \qquad (6.125)$$

where, e.g., $M_{1\to 2}$ is the migration rate from region 1 to 2 and $M_{1\to d}$ is the mortality rate of individuals in region 1. Then a matrix $\mathbf{p}(x)$ can be defined

$$\mathbf{p}(x) = \left(\mathbf{I} + \frac{1}{2}\mathbf{M}(x) \right)^{-1} \left(\mathbf{I} - \frac{1}{2}\mathbf{M}(x) \right) \qquad (6.126)$$

where the entries $p_{ij}(x)$ of $\mathbf{p}(x)$ give the probability that an individual aged x in region j will be alive and in region i at age $x + 1$. The survivorship function is