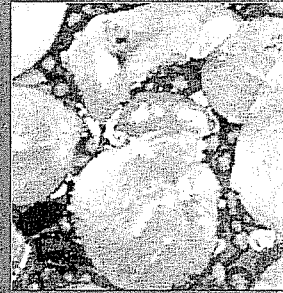


# Chapter 4

## Life, Death and Life Histories



### 4.1 Introduction: an ecological fact of life

In this chapter we change the emphasis of our approach. We will not be concerned so much with the interaction between individuals and their environment, as with the numbers of individuals and the processes leading to changes in the number of individuals.

In this regard, there is a fundamental ecological fact of life:

$$N_{\text{now}} = N_{\text{then}} + B - D + I - E. \quad (4.1)$$

This simply says that the numbers of a particular species presently occupying a site of interest ( $N_{\text{now}}$ ) is equal to the numbers previously there ( $N_{\text{then}}$ ), plus the number of births between then and now ( $B$ ), minus the number of deaths ( $D$ ), plus the number of immigrants ( $I$ ), minus the number of emigrants ( $E$ ).

This defines the main aim of ecology: to describe, explain and understand the distribution and abundance of organisms. Ecologists are interested in the number of individuals, the distributions of individuals, the demographic processes (birth, death and migration) that influence these, and the ways in which these demographic processes are themselves influenced by environmental factors.

### 4.2 What is an individual?

#### 4.2.1 Unitary and modular organisms

Our 'ecological fact of life', though, implies by default that all individuals are alike, which is patently false on a number of counts. First, almost all species pass through a number of *stages* in their life cycle: insects metamorphose from eggs to larvae, sometimes to pupae, and then to adults; plants pass from seeds to seedlings to photosynthesizing adults; and so on. The different stages are likely to be influenced by different factors and to have different rates of migration, death and of course reproduction.

Second, even within a stage, individuals can differ in 'quality' or 'condition'. The most obvious aspect of this is size, but it is also common, for example, for individuals to differ in the amount of stored reserves they possess.

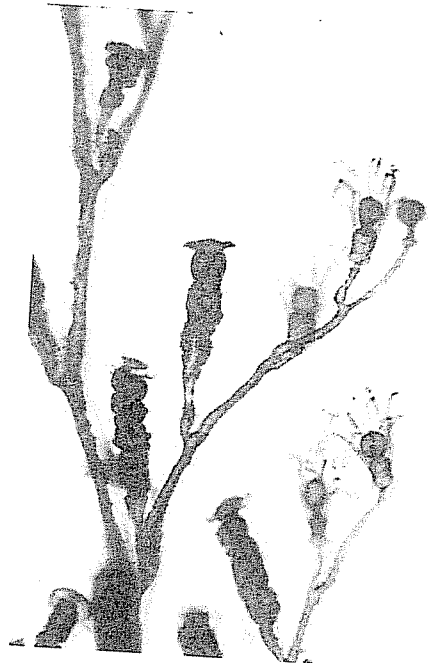
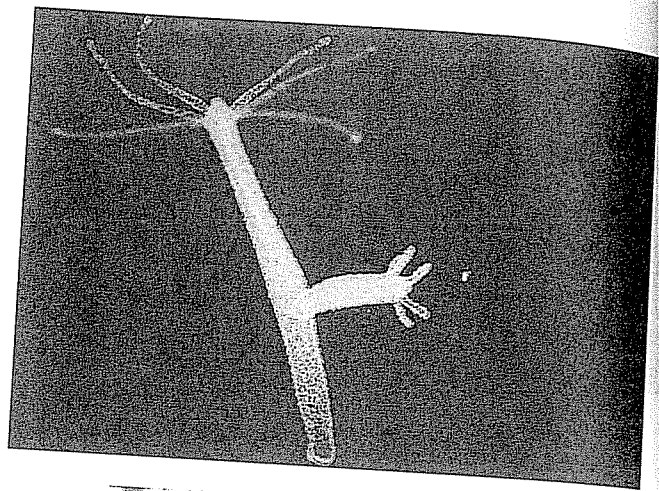
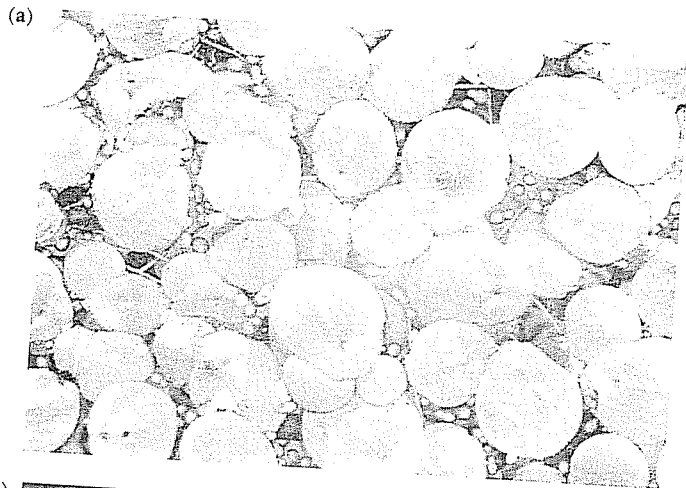
Uniformity amongst individuals is especially unlikely, moreover, when organisms are *modular* rather than *unitary*. In unitary organisms, form is highly determinate: that is, barring aberrations, all dogs have four legs, all squid have two eyes, etc. Humans are perfect examples of unitary organisms. A life begins when a sperm fertilizes an egg to form a zygote. This implants in the wall of the uterus, and the complex processes of embryonic development commence. By 6 weeks the fetus has a recognizable nose, eyes, ears and limbs with digits, and accidents apart, will remain in this form until it dies. The fetus continues to grow until birth, and then the infant grows until perhaps the 18th year of life; but the only changes in form (as opposed to size) are the relatively minor ones associated with sexual maturity. The reproductive phase lasts for perhaps 30 years in females and rather longer in males. This is followed by a phase of senescence. Death can intervene at any time, but for surviving individuals the succession of phases is, like form, entirely predictable.

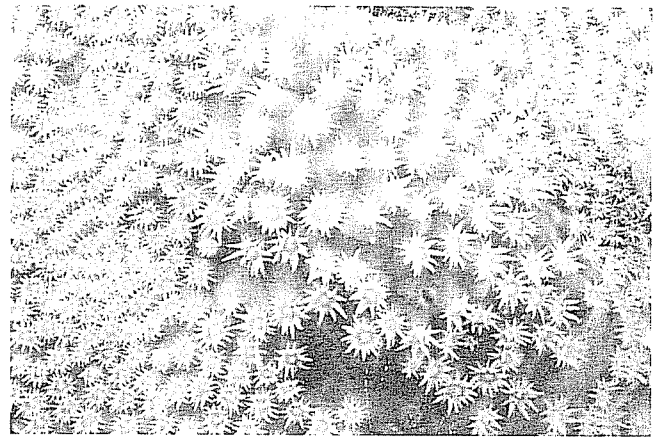
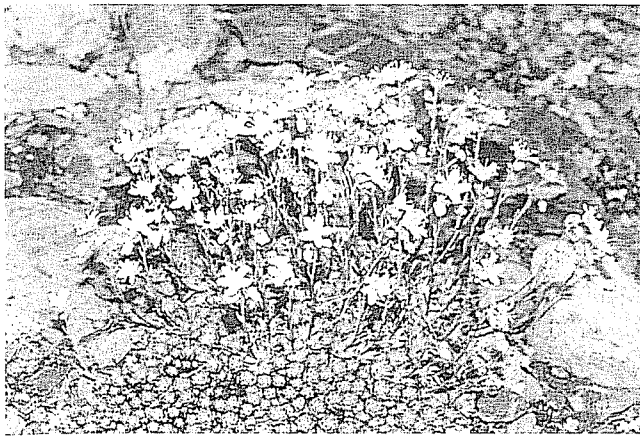
In modular organisms (Figure 4.1), on the other hand, neither timing nor form is predictable. The zygote develops into a unit of construction (a module, e.g. a leaf with its attendant length of stem), which then produces further, similar modules. Individuals are composed of a highly variable number of such modules, and their program of development is strongly dependent on their interaction with their environment. The product is almost always branched, and except for a juvenile phase, effectively immobile. Most plants are modular and are certainly the most obvious group of modular organisms. There are, however, many important groups of modular animals

individuals differ in their life cycle stage and their condition

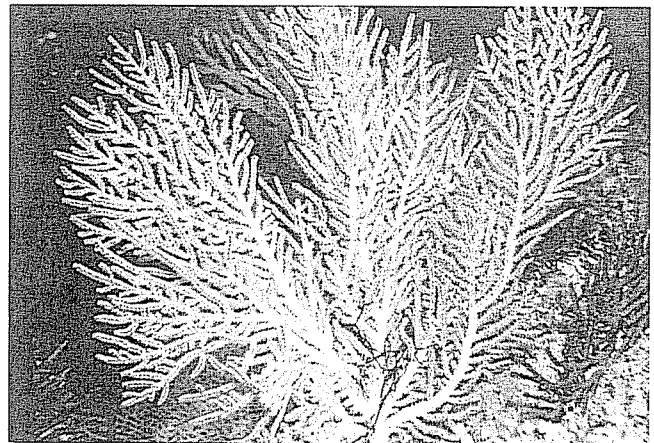
unitary organisms

modular organisms





(d)



(e)

**Figure 4.1** Modular plants (on the left) and animals (on the right), showing the underlying parallels in the various ways they may be constructed. (*opposite page*) (a) Modular organisms that fall to pieces as they grow: duckweed (*Lemna* sp.) and *Hydra* sp. (b) Freely branching organisms in which the modules are displayed as individuals on 'stalks': a vegetative shoot of a higher plant (*Lonicera japonica*) with leaves (feeding modules) and a flowering shoot, and a hydroid colony (*Obelia*) bearing both feeding and reproductive modules. (c) Stoloniferous organisms in which colonies spread laterally and remain joined by 'stolons' or rhizomes: a single plant of strawberry (*Fragaria*) spreading by means of stolons, and a colony of the hydroid *Tubularia crocea*. (*above*) (d) Tightly packed colonies of modules: a tussock of the spotted saxifrage (*Saxifraga bronchialis*), and a segment of the hard coral *Turbinaria reniformis*. (e) Modules accumulated on a long persistent, largely dead support: an oak tree (*Quercus robur*) in which the support is mainly the dead woody tissues derived from previous modules, and a gorgonian coral in which the support is mainly heavily calcified tissues from earlier modules. (For color, see Plate 4.1, between pp. 84 and 85.)

((a) left, © Visuals Unlimited/John D. Cunningham; right, © Visuals Unlimited/Larry Stepanowicz; (b) left, © Visuals Unlimited; right, © Visuals Unlimited/Larry Stepanowicz; (c) left, © Visuals Unlimited/Science VU; right, © Visuals Unlimited/John D. Cunningham; (d) left, © Visuals Unlimited/Gerald and Buff Corsi; right, © Visuals Unlimited/Dave B. Fleetham; (e) left, © Visuals Unlimited/Silwood Park; right, © Visuals Unlimited/Daniel W. Gotshall.

(indeed, some 19 phyla, including sponges, hydroids, corals, bryozoans and colonial ascidians), and many modular protists and fungi. Reviews of the growth, form, ecology and evolution of a wide range of modular organisms may be found in Harper *et al.* (1986a), Hughes (1989), Room *et al.* (1994) and Collado-Vides (2001).

Thus, the potentialities for individual difference are far greater in modular than in unitary organisms. For example, an individual of the annual plant *Chenopodium album* may, if grown in poor or crowded conditions, flower and set seed when only 50 mm high. Yet, given more ideal conditions, it may reach 1 m in height, and produce 50,000 times as many seeds as its depauperate counterpart. It is modularity and the differing birth and death rates of plant parts that give rise to this plasticity.

In the growth of a higher plant, the fundamental module of construction above ground is the leaf with its axillary bud and the attendant internode of the stem. As the bud develops and grows, it produces further leaves, each bearing buds in their axils. The plant grows by accumulating these modules. At some stage in the development, a new sort of module appears, associated with reproduction (e.g. the flowers in a higher plant), ultimately giving rise to new zygotes. Modules that are specialized for reproduction usually cease to give rise to new modules. The roots of a plant are also modular, although the modules are quite different (Harper *et al.*, 1991). The program of development in modular organisms is typically determined by the proportion of modules that are allocated to different roles (e.g. to reproduction or to continued growth).

#### 4.2.2 Growth forms of modular organisms

A variety of growth forms and architectures produced by modular growth in animals and plants is illustrated in Figure 4.1 (for color, see Plate 4.1, between pp. 84 and 85). Modular organisms may broadly be divided into those that concentrate on vertical growth, and those that spread their modules laterally, over or in a substrate. Many plants produce new root systems associated with a laterally extending stem: these are the rhizomatous and stoloniferous plants. The connections between the parts of such plants may die and rot away, so that the product of the original zygote becomes represented by physiologically separated parts. (Modules with the potential for separate existence are known as 'ramets'.) The most extreme examples of plants 'falling to pieces' as they grow are the many species of floating aquatics like duckweeds (*Lemna*) and the water hyacinth (*Eichhornia*). Whole ponds, lakes or rivers may be filled with the separate and independent parts produced by a single zygote.

Trees are the supreme example of plants whose growth is concentrated vertically. The peculiar feature distinguishing trees and shrubs from most herbs is the connecting system linking

modules together and connecting them to the root system. This does not rot away, but thickens with wood, conferring perennality. Most of the structure of such a woody tree is dead, with a thin layer of living material lying immediately below the bark. The living layer, however, continually regenerates new tissue, and adds further layers of dead material to the trunk of the tree, which solves, by the strength it provides, the difficult problem of obtaining water and nutrients below the ground, but also light perhaps 50 m away at the top of the canopy.

We can often recognize two or more levels of modular construction. The strawberry is a good example of this: leaves are repeatedly developed from a bud, but these leaves are arranged into rosettes. The strawberry plant grows: (i) by adding new leaves to a rosette; and (ii) by producing new rosettes on stolons grown from the axils of its rosette leaves. Trees also exhibit modularity at several levels: the leaf with its axillary bud, the whole shoot on which the leaves are arranged, and the whole branch systems that repeat a characteristic pattern of shoots.

Many animals, despite variations in their precise method of growth and reproduction, are as 'modular' as any plant. Moreover, in corals, for example, just like many plants, the individual may exist as a physiologically integrated whole, or may be split into a number of colonies – all part of one individual, but physiologically independent (Hughes *et al.*, 1992).

#### 4.2.3 What is the size of a modular population?

In modular organisms, the number of surviving zygotes can give only a partial and misleading impression of the 'size' of the population. Kays and Harper (1974) coined the word 'genet' to describe the 'genetic individual': the product of a zygote. In modular organisms, then, the distribution and abundance of genets (individuals) is important, but it is often more useful to study the distribution and abundance of modules (ramets, shoots, tillers, zooids, polyps or whatever): the amount of grass in a field available to cattle is not determined by the number of genets but by the number of leaves (modules).

#### 4.2.4 Senescence – or the lack of it – in modular organisms

There is also often no programmed senescence of whole modular organisms – they appear to have perpetual somatic youth. Even in trees that accumulate their dead stem tissues, or gorgonian corals that accumulate old calcified branches, death often results from becoming too big or succumbing to disease rather than from programmed senescence. This is illustrated for three types of coral in

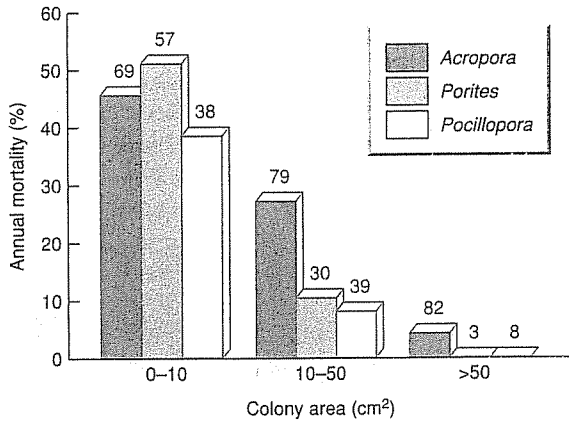


Figure 4.2 The mortality rate declines steadily with colony size (and hence, broadly, age) in three coral taxa from the reef crest at Heron Island, Great Barrier Reef (sample sizes are given above each bar). (After Hughes & Connell, 1987; Hughes *et al.*, 1992.)

the Great Barrier Reef in Figure 4.2. Annual mortality declined sharply with increasing colony size (and hence, broadly, age) until, amongst the largest, oldest colonies, mortality was virtually zero, with no evidence of any increase in mortality at extreme old age (Hughes & Connell, 1987).

At the modular level, things are quite different. The annual death of the leaves on a deciduous tree is the most dramatic

example of senescence – but roots, buds, flowers and the modules of modular animals all pass through phases of youth, middle age, senescence and death. The growth of the individual genet is the combined result of these processes. Figure 4.3 shows that the age structure of shoots of the sedge *Carex arenaria* is changed dramatically by the application of NPK fertilizer, even when the total number of shoots present is scarcely affected by the treatment. The fertilized plots became dominated by young shoots, as the older shoots that were common on control plots were forced into early death.

#### 4.2.5 Integration

For many rhizomatous and stoloniferous species, this changing age structure is in turn associated with a changing level to which the connections between individual ramets remain intact. A young ramet may benefit from the nutrients flowing from an older ramet to which it is attached and from which it grew, but the pros and cons of attachment will have changed markedly by the time the daughter is fully established in its own right and the parent has entered a postreproductive phase of senescence (a comment equally applicable to unitary organisms with parental care) (Caraco & Kelly, 1991).

The changing benefits and costs of integration have been studied experimentally in the pasture grass *Holcus lanatus*, by comparing the growth of: (i) ramets that were left with a physiological connection to their parent plant, and in the same pot, so that parent and daughter might compete (unsevered,

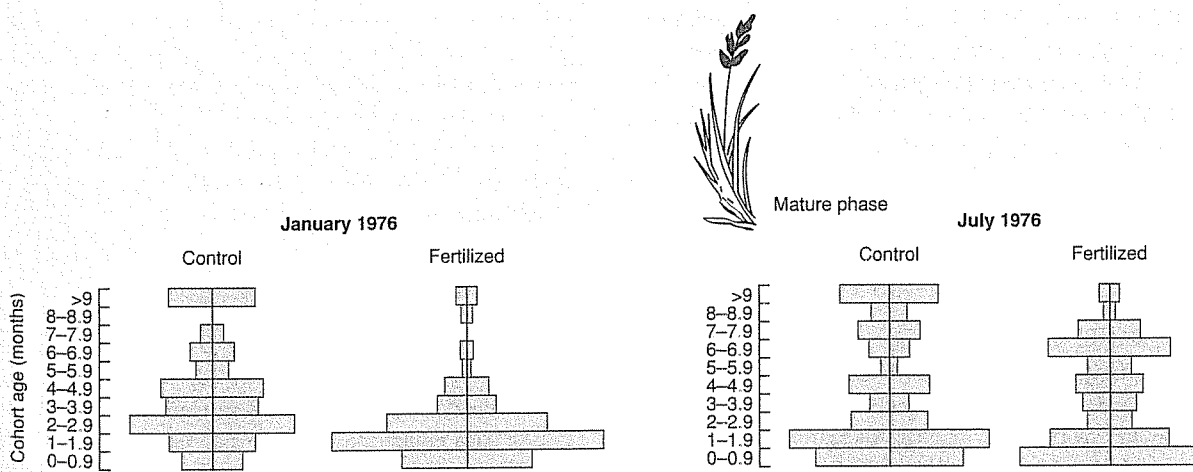
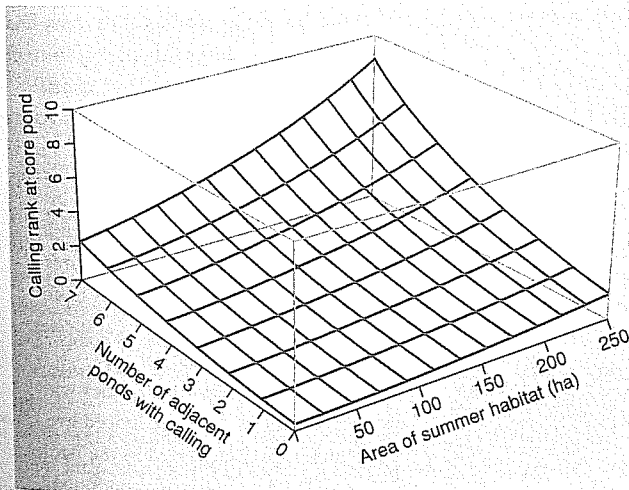


Figure 4.3 The age structure of shoots in clones of the sand sedge *Carex arenaria* growing on sand dunes in North Wales, UK. Clones are composed of shoots of different ages. The effect of applying fertilizer is to change this age structure. The clones become dominated by young shoots and the older shoots die. (After Noble *et al.*, 1979.)

square or rectangular device used to demarcate the boundaries of the area on the ground). For soil-dwelling organisms the unit is usually a volume of soil; for lake dwellers a volume of water; for many herbivorous insects the unit is one typical plant or leaf, and so on. Further details of sampling methods, and of methods for counting individuals generally, can be found in one of many texts devoted to ecological methodology (e.g. Brower *et al.*, 1998; Krebs, 1999; Southwood & Henderson, 2000).

For animals, especially, there are two further methods of estimating population size. The first is known as capture–recapture. At its simplest, this involves catching a random sample of a population, marking individuals so that they can be recognized subsequently, releasing them so that they remix with the rest of the population and then catching a further random sample. Population size can be estimated from the proportion of this second sample that bear a mark. Roughly speaking, the proportion of marked animals in the second sample will be high when the population is relatively small, and low when the population is relatively large. Data sets become much more complex – and methods of analysis become both more complex and much more powerful – when there are a whole sequence of capture–recapture samples (see Schwarz & Seber, 1999, for a review).

The final method is to use an index of abundance. This can provide information on the relative size of a population, but by itself usually gives little indication of absolute size. As an example, Figure 4.5 shows the effect on the abundance of leopard frogs (*Rana*



**Figure 4.5** The abundance (calling rank) of leopard frogs in ponds increases significantly with both the number of adjacent ponds that are occupied and the area of summer habitat within 1 km of the pond. Calling rank is the sum of an index measured on four occasions, namely: 0, no individuals calling; 1, individuals can be counted, calls not overlapping; 2, calls of < 15 individuals can be distinguished with some overlapping; 3, calls of  $\geq 15$  individuals. (After Pope *et al.*, 2000.)

*pipiens*) in ponds near Ottawa, Canada, of the number of occupied ponds and the amount of summer (terrestrial) habitat in the vicinity of the pond. Here, frog abundance was estimated from the 'calling rank': essentially compounded from whether there were no frogs, 'few', 'many' or 'very many' frogs calling on each of four occasions. Despite their shortcomings, even indices of abundance can provide valuable information.

Counting births can be more difficult even than counting individuals. The formation of the zygote is often regarded as the starting point in the life of an individual. But it is a stage that is often hidden and extremely hard to study. We simply do not know, for most animals and plants, how many embryos die before 'birth', though in the rabbit at least 50% of embryos are thought to die in the womb, and in many higher plants it seems that about 50% of embryos abort before the seed is fully grown and mature. Hence, it is almost always impossible in practice to treat the formation of a zygote as the time of birth. In birds we may use the moment that an egg hatches; in mammals when an individual ceases to be supported within the mother on her placenta and starts to be supported outside her as a suckling; and in plants we may use the germination of a seed as the birth of a seedling, although it is really only the moment at which a developed embryo restarts into growth after a period of dormancy. We need to remember that half or more of a population will often have died before they can be recorded as born!

Counting deaths poses as many problems. Dead bodies do not linger long in nature. Only the skeletons of large animals persist long after death. Seedlings may be counted and mapped one day and gone without trace the next. Mice, voles and soft-bodied animals such as caterpillars and worms are digested by predators or rapidly removed by scavengers or decomposers. They leave no carcasses to be counted and no evidence of the cause of death. Capture–recapture methods can go a long way towards estimating deaths from the loss of marked individuals from a population (they are probably used as often to measure survival as abundance), but even here it is often impossible to distinguish loss through death and loss through emigration.

#### 4.4 Life cycles

To understand the forces determining the abundance of a population, we need to know the phases of the constituent organisms' lives when these forces act most significantly. For this, we need to understand the sequences of events that occur in those organisms' life cycles. A highly simplified, generalized life history (Figure 4.6a) comprises birth, followed by a prereproductive period, a period of reproduction, perhaps a postreproductive period, and then death as a result of senescence (though of course other forms of mortality may intervene at any time). The variety of life cycles is also

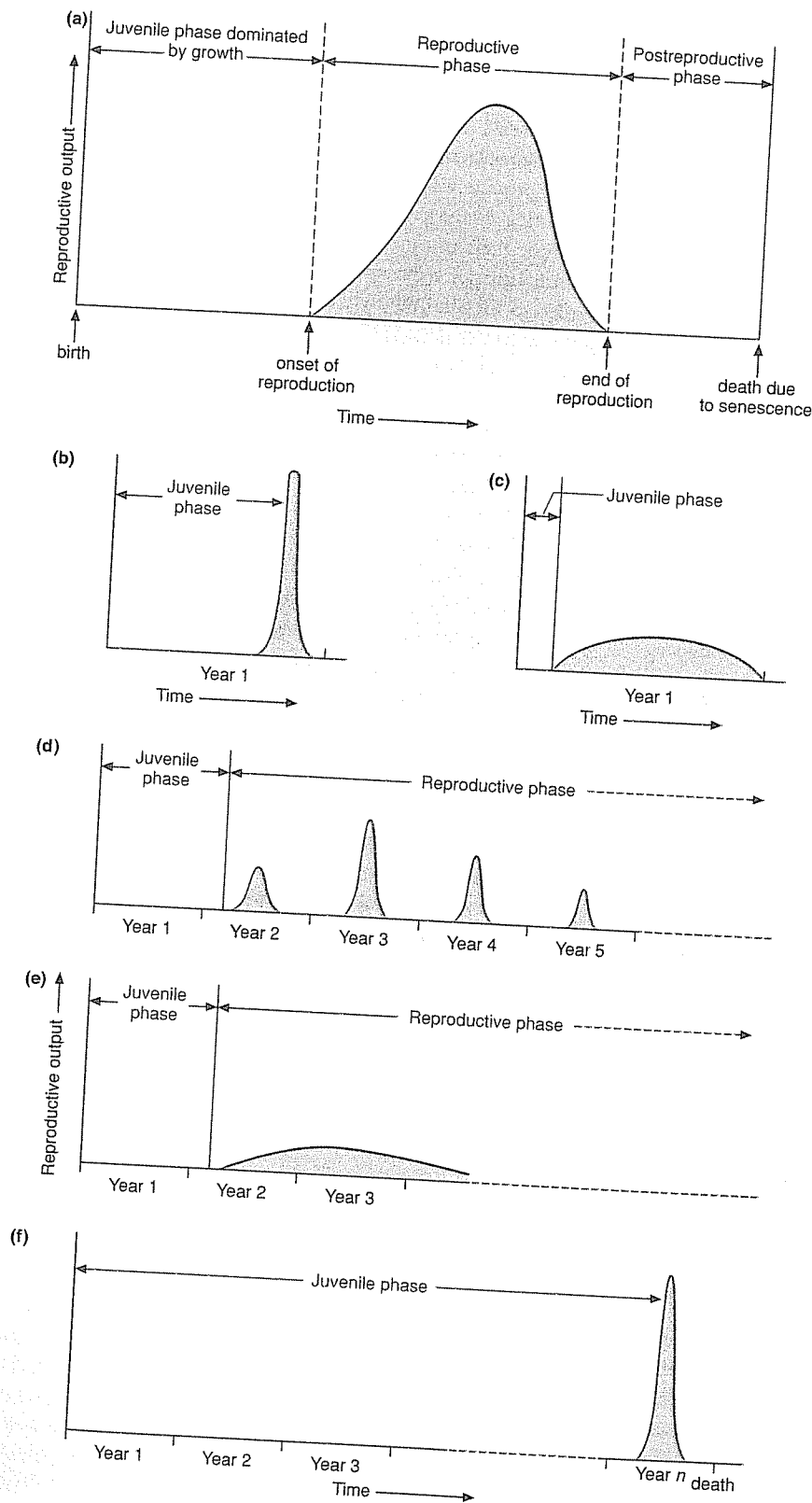


Figure 4.6 (a) An outline life history for a unitary organism. Time passes along the horizontal axis, which is divided into different phases. Reproductive output is plotted on the vertical axis. The figures below (b-f) are variations on this basic theme. (b) A semelparous annual species. (c) An iteroparous annual species. (d) A long-lived iteroparous species with seasonal breeding (that may indeed live much longer than suggested in the figure). (e) A long-lived species with continuous breeding (that may again live much longer than suggested in the figure). (f) A semelparous species living longer than a year. The pre-reproductive phase may be a little over 1 year (a biennial species, breeding in its second year) or longer, often much longer, than this (as shown).

summarized diagrammatically in Figure 4.6, although there are many life cycles that defy this simple classification. Some organisms fit several or many generations within a single year, some have just one generation each year (annuals), and others have a life cycle extended over several or many years. For all organisms, though, a period of growth occurs before there is any reproduction, and growth usually slows down (and in some cases stops altogether) when reproduction starts.

Whatever the length of their life cycle, species may, broadly, be either *semelparous* or *iteroparous* (often referred to by plant scientists as monocarpic and polycarpic). In semelparous species, individuals have only a single, distinct period of reproductive output in their lives, prior to which they have largely ceased to grow, during which they invest little or nothing in survival to future reproductive events, and after which they die. In iteroparous species, an individual normally experiences several or many such reproductive events, which may in fact merge into a single extended period of reproductive activity. During each period of reproductive activity the individual continues to invest in future survival and possibly growth, and beyond each it therefore has a reasonable chance of surviving to reproduce again.

For example, many annual plants are semelparous (Figure 4.6b): they have a sudden burst of flowering and seed set, and then they die. This is commonly the case among the weeds of arable crops. Others, such as groundsel (*Senecio vulgaris*), are iteroparous (Figure 4.6c): they continue to grow and produce new flowers and seeds through the season until they are killed by the first lethal frost of winter. They die with their buds on.

There is also a marked seasonal rhythm in the lives of many long-lived iteroparous plants and animals, especially in their reproductive activity: a period of reproduction once per year (Figure 4.6d). Mating (or the flowering of plants) is commonly triggered by the length of the photoperiod (see Section 2.3.7) and usually makes sure that young are born, eggs hatch or seeds are ripened when seasonal resources are likely to be abundant. Here, though, unlike annual species, the generations overlap and individuals of a range of ages breed side by side. The population is maintained in part by survival of adults and in part by new births.

In wet equatorial regions, on the other hand, where there is very little seasonal variation in temperature and rainfall and scarcely any variation in photoperiod, we find species of plants that are in flower and fruit throughout the year – and continuously breeding species of animal that subsist on this resource (Figure 4.6e). There are several species of fig (*Ficus*), for instance, that bear fruit continuously and form a reliable year-round food supply for birds and primates. In more seasonal climates, humans are unusual in also breeding continuously throughout the year,

though numbers of other species, cockroaches, for example, do so in the stable environments that humans have created.

Amongst long-lived (i.e. longer than annual) semelparous plants the variety of life cycles (Figure 4.6f), some are strictly biennial – each individual takes two summers and the intervening winter to develop, but has only a single reproductive phase, in its second summer. An example is the white sweet clover, *Melilotus alba*. In New York State, this has relatively high mortality during the first growing season (whilst seedlings were developing into established plants), followed by much lower mortality until the end of the second summer, when the plants flowered and survivorship decreased rapidly. No plants survive to a third summer. Thus, there is an overlap of two generations at most (Klemow & Raynal, 1981). A more typical example of a semelparous species with overlapping generations is the composite *Grindelia lanceolata*, which may flower in its third, fourth or fifth years. But whenever an individual does flower, it dies soon after.

A well-known example of a semelparous animal with overlapping generations (Figure 4.6f) is the Pacific salmon *Oncorhynchus nerka*. Salmon are spawned in rivers. They spend the first phase of their juvenile life in fresh water and then migrate to the sea, often traveling thousands of miles. At maturity they return to the stream in which they were hatched. Some mature and return to reproduce after only 2 years at sea; others mature more slowly and return after 3, 4 or 5 years. At the time of reproduction the population of salmon is composed of overlapping generations of individuals. But all are semelparous: they lay their eggs and then die; their bout of reproduction is terminal.

There are even more dramatic examples of species that have a long life but reproduce just once. Many species of bamboo form dense clones of shoots that remain vegetative for many years: up to 100 years in some species. The whole population of shoots, from the same and sometimes different clones, then flowers simultaneously in a mass suicidal orgy. Even when shoots have become physically separated from each other, the parts still flower synchronously.

In the following sections we look at the patterns of birth and death in some of these life cycles in more detail, and at how these patterns are quantified. Often, in order to monitor and examine changing patterns of mortality with age or stage, a *life table* is used. This allows a *survivorship curve* to be constructed, which traces the decline in numbers, over time, of a group of newly born or newly emerged individuals or modules – or it can be thought of as a plot of the probability, for a representative newly born individual, of surviving to various ages. Patterns of birth amongst individuals of different ages are often monitored at the same time as life tables are constructed. These patterns are displayed in *fecundity schedules*.



4.5 Annual species

Annual life cycles take approximately 12 months or rather less to complete (Figure 4.6b, c). Usually, every individual in a population breeds during one particular season of the year, but then dies before the same season in the next year. Generations are therefore said to be discrete, in that each generation is distinguishable from every other; the only overlap of generations is between breeding adults and their offspring during and immediately after the breeding season. Species with discrete generations need not be annual, since generation lengths other than 1 year are conceivable. In practice, however, most are: the regular annual cycle of seasonal climates provides the major pressure in favor of synchrony.

4.5.1 Simple annuals: cohort life tables

A life table and fecundity schedule are set out in Table 4.1 for the annual plant *Phlox drummondii* in Nixon, Texas (Leverich & Levin, 1979). The life table is known as a cohort life table, because a single cohort of individuals (i.e. a group of individuals born within the same short interval of time) was followed from birth to the death of the last survivor. With an annual species like *Phlox*, there is no other way of constructing a life table. The life cycle of *Phlox* was divided into a number of age classes. In other cases, it is more appropriate to divide it into stages (e.g. insects with eggs, larvae, pupae, etc.) or into size classes. The number

in the *Phlox* population was recorded on various occasions before germination (i.e. when the plants were seeds), and then again at regular intervals until all individuals had flowered and died. The advantage of using age classes is that it allows an observer to look in detail at the patterns of birth and mortality within stages (e.g. the seedling stage). The disadvantage is an individual's age is not necessarily the best, nor even a satisfactory, measure of its biological 'status'. In many long-lived plants, for instance, individuals of the same age may be reproducing actively, or growing vegetatively but not reproducing, or doing neither. In such cases, a classification based on developmental stages (as opposed to ages) is clearly appropriate. The decision to use age classes in *Phlox* was based on the small number of stages, the demographic variation within each and the synchronous development of the whole population.

The first column of Table 4.1 sets out the columns of the various classes (in this case, age a life table classes). The second column,  $a_x$ , then lists the major part of the raw data: it gives the total number of individuals surviving to the start of each class ( $a_0$  individuals in the initial class,  $a_{63}$  in the following one (which started on day 63), and so on). The problem with any  $a_x$  column is that its information is specific to one population in 1 year, making comparisons with other populations and other years very difficult. The data have therefore been standardized, next, in a column of  $l_x$  values. This is headed by an  $l_0$  value of 1.000, and all succeeding figures have been brought into line accordingly (e.g.  $l_{124} = 1.000 \times 295/$

Table 4.1 A cohort life table for *Phlox drummondii*. The columns are explained in the text. (After Leverich & Levin, 1979.)

Age interval (days) $x - x'$	Number surviving to day $x$ $a_x$	Proportion of original cohort surviving to day $x$ $l_x$	Proportion of original cohort dying during interval $d_x$	Mortality rate per day $q_x$	$\log_{10} l_x$	Daily killing power $k_x$	$F_x$	$m_x$	$l_x m_x$
0-63	996	1.000	-	-	-	-	-	-	-
63-124	668	0.671	0.329	0.006	0.00	0.003	-	-	-
124-184	295	0.296	0.375	0.013	-0.17	0.006	-	-	-
184-215	190	0.191	0.105	0.007	-0.53	0.003	-	-	-
215-264	176	0.177	0.014	0.003	-0.72	0.001	-	-	-
264-278	172	0.173	0.004	0.002	-0.75	0.001	-	-	-
278-292	167	0.168	0.005	0.002	-0.76	0.001	-	-	-
292-306	159	0.160	0.008	0.004	-0.78	0.002	-	-	-
306-320	154	0.155	0.005	0.002	-0.80	0.001	53.0	0.33	0.05
320-334	147	0.148	0.007	0.003	-0.81	0.001	485.0	3.13	0.49
334-348	105	0.105	0.043	0.025	-0.83	0.011	802.7	5.42	0.80
348-362	22	0.022	0.083	0.106	-0.98	0.049	972.7	9.26	0.97
362--	0	0.000	0.022	1.000	-1.66	-	94.8	4.31	0.10
							2408.2		2.41

$$R_0 = \sum l_x m_x = \frac{\sum F_x}{a_0} = 2.41.$$

996 = 0.296). Thus, whilst the  $a_0$  value of 996 is peculiar to this set of data, all studies have an  $l_0$  value of 1.000, making all studies comparable. The  $l_x$  values are best thought of as the proportion of the original cohort surviving to the start of a stage or age class.

To consider mortality more explicitly, the proportion of the original cohort dying during each stage ( $d_x$ ) is computed in the next column, being simply the difference between successive values of  $l_x$ ; for example  $d_{124} = 0.296 - 0.191 = 0.105$ . The stage-specific mortality rate,  $q_x$ , is then computed. This considers  $d_x$  as a fraction of  $l_x$ . Furthermore, the variable length of the age classes makes it sensible to convert the  $q_x$  values to 'daily' rates. Thus, for instance, the fraction dying between days 124 and 184 is  $0.105/0.296 = 0.355$ , which translates, on the basis of compound 'interest', into a daily rate or fraction,  $q_{124}$ , of 0.007.  $q_x$  may also be thought of as the average 'chance' or probability of an individual dying during an interval. It is therefore equivalent to  $(1 - p_x)$  where  $p$  refers to the probability of survival.

The advantage of the  $d_x$  values is that they can be summed: thus, the proportion of the cohort dying in the first 292 days (essentially the prereproductive stage) was  $d_0 + d_{63} + d_{124} + \dots + d_{278} (= 0.840)$ . The disadvantage is that the individual values give no real idea of the intensity or importance of mortality during a particular stage. This is because the  $d_x$  values are larger the more individuals there are, and hence the more there are available to die. The  $q_x$  values, on the other hand, are an excellent measure of the intensity of mortality. For instance, in the present example it is clear from the  $q_x$  column that the mortality rate increased markedly in the second period; this is not clear from the  $d_x$  column. The  $q_x$  values, however, have the disadvantage that, for example, summing the values over the first 292 days gives no idea of the mortality rate over that period.

The advantages are combined, however, in the next column of the life table, which contains  $k_x$  values (Haldane, 1949; Varley & Gradwell, 1970).  $k_x$  is defined simply as the difference between successive values of  $\log_{10} a_x$  or successive values of  $\log_{10} l_x$  (they amount to the same thing), and is sometimes referred to as a 'killing power'. Like  $q_x$  values,  $k_x$  values reflect the intensity or rate of mortality (as Table 4.1 shows); but unlike summing the  $q_x$  values, summing  $k_x$  values is a legitimate procedure. Thus, the killing power or  $k$  value for the final 28 days is  $(0.011 \times 14) + (0.049 \times 14) = 0.84$ , which is also the difference between  $-0.83$  and  $-1.66$  (allowing for rounding errors). Note too that like  $l_x$  values,  $k_x$  values are standardized, and are therefore appropriate for comparing quite separate studies. In this and later chapters,  $k_x$  values will be used repeatedly.

#### 4.5.2 Fecundity schedules and basic reproductive rates

The fecundity schedule in Table 4.1 (the final three columns) begins with a column of raw data,  $F_x$ : the total number of seeds produced

during each period. This is followed in the next column by  $m_x$ : the individual fecundity or birth rate, i.e. the mean number of seeds produced per surviving individual. Although the reproductive season for the *Phlox* population lasts for 56 days, each individual plant is semelparous. It has a single reproductive phase during which all of its seeds develop synchronously (or nearly so). The extended reproductive season occurs because different individuals enter this phase at different times.

Perhaps the most important summary term that can be extracted from a life table and fecundity schedule is the basic reproductive rate, denoted by  $R_0$ . This is the mean number of offspring (of the first stage in the life cycle - in this case seeds) produced per original individual by the end of the cohort. It therefore indicates, in annual species, the overall extent by which the population has increased or decreased over that time. (As we shall see below, the situation becomes more complicated when generations overlap or species breed continuously.)

There are two ways in which  $R_0$  can be computed. The first is from the formula:

$$R_0 = \sum F_x/a_0, \quad (4.2)$$

i.e. the total number of seeds produced during one generation divided by the original number of seeds ( $\sum F_x$  means the sum of the values in the  $F_x$  column). The more usual way of calculating  $R_0$ , however, is from the formula:

$$R_0 = \sum l_x m_x, \quad (4.3)$$

i.e. the sum of the number of seeds produced per original individual during each of the stages (the final column of the fecundity schedule). As Table 4.1 shows, the basic reproductive rate is the same, whichever formula is used.

The age-specific fecundity,  $m_x$  (the fecundity per surviving individual), demonstrates the existence of a preproductive period, a gradual rise to a peak and then a rapid decline. The reproductive output of the whole population,  $F_x$ , parallels this pattern to a large extent, but also takes into account the fact that whilst the age-specific fecundity was changing, the size of the population was gradually declining. This combination of fecundity and survivorship is an important property of  $F_x$  values, shared by the basic reproductive rate ( $R_0$ ). It makes the point that actual reproduction depends both on reproductive potential ( $m_x$ ) and on survivorship ( $l_x$ ).

In the case of the *Phlox* population,  $R_0$  was 2.41. This means that there was a 2.41-fold increase in the size of the population over one generation. If such a value were maintained from generation to generation, the *Phlox* population would grow ever larger and soon cover the globe. Thus, a balanced and realistic picture of the life and death of *Phlox*, or any other species, can only emerge from several or many years' data.

## 4.5.3 Survivorship curves

The pattern of mortality in the *Phlox* population is illustrated in Figure 4.7a using both  $q_x$  and  $k_x$  values. The mortality rate was fairly high at the beginning of the seed stage but became very low towards the end. Then, amongst the adults, there was a period where the mortality rate fluctuated about a moderate level, followed finally by a sharp increase to very high levels during the last weeks of the generation. The same pattern is shown in a different form in Figure 4.7b. This is a survivorship curve, and follows the decline of  $\log_{10} l_x$  with age. When the mortality rate is roughly constant, the survivorship curve is more or less straight; when the rate increases, the curve is convex; and when the rate decreases, the curve is concave. Thus, the curve is concave towards the end of the seed stage, and convex towards the end of the generation. Survivorship curves are the most widely used way of depicting patterns of mortality.

the logarithmic scale  
in survivorship curves

The y-axis in Figure 4.7b is logarithmic. The importance of using logarithms in survivorship curves can be seen by imagining two investigations of the same population. In the first, the whole population is censused: there is a decline in one time interval from 1000 to 500 individuals. In the second, samples are taken, and over the same time interval this index of density declines from 100 to 50. The two cases are biologically identical, i.e. the rate or probability of death per individual over the time interval (the *per capita* rate) is the same. The slopes of the two logarithmic survivorship curves reflect this: both would be  $-0.301$ . But on simple linear scales the slopes

would differ. Logarithmic survivorship curves therefore have the advantage of being standardized from study to study, just like the 'rates'  $q_x$ ,  $k_x$  and  $m_x$ . Plotting numbers on a logarithmic scale will also indicate when per capita rates of increase are identical. 'Log numbers' will therefore often be used in preference to 'numbers' when numerical change is being plotted.

## 4.5.4 A classification of survivorship curves

Life tables provide a great deal of data on specific organisms. But ecologists search for generalities: patterns of life and death that we can see repeated in the lives of many species. A useful set of survivorship curves was developed long ago by Pearl (1928) whose three types generalize what we know about the way in which the risks of death are distributed through the lives of different organisms (Figure 4.8). Type I describes the situation in which mortality is concentrated toward the end of the maximum lifespan. It is perhaps most typical of humans in developed countries and their carefully tended zoo animals and pets. Type II is a straight line that describes a constant mortality rate from birth to maximum age. It describes, for instance, the survival of seeds buried in the soil. Type III indicates extensive early mortality, but a high rate of subsequent survival. This is typical of species that produce many offspring. Few survive initially, but once individuals reach a critical size, their risk of death remains low and more or less constant. This appears to be the most common survivorship curve among animals and plants in nature.

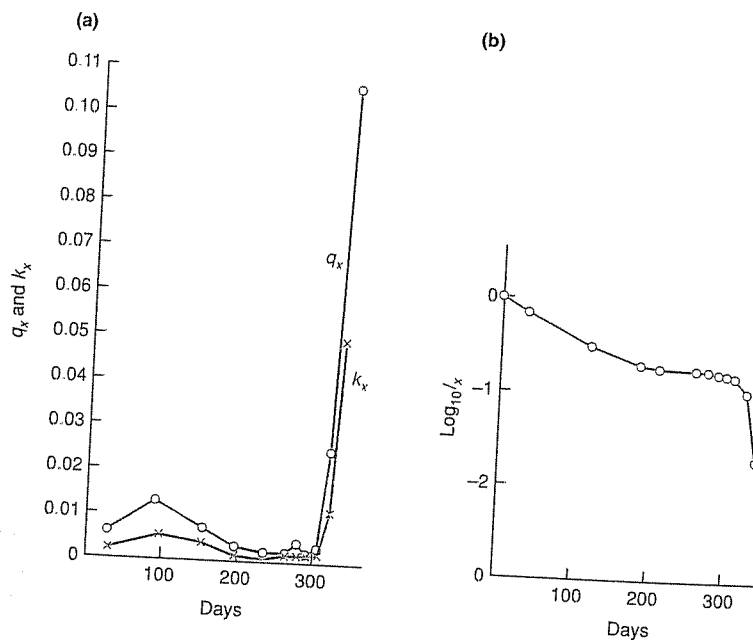
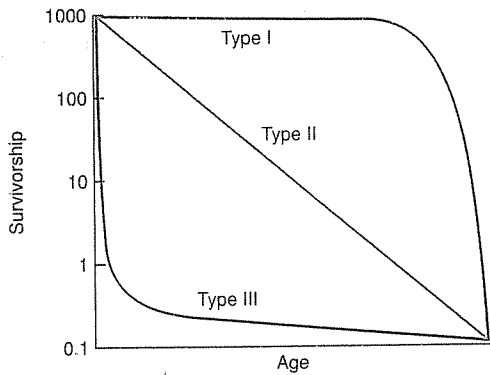


Figure 4.7 Mortality and survivorship in the life cycle of *Phlox drummondii*. (a) The age-specific daily mortality rate ( $q_x$ ) and daily killing power ( $k_x$ ). (b) The survivorship curve:  $\log_{10} l_x$  plotted against age. (After Leverich & Levin, 1979.)

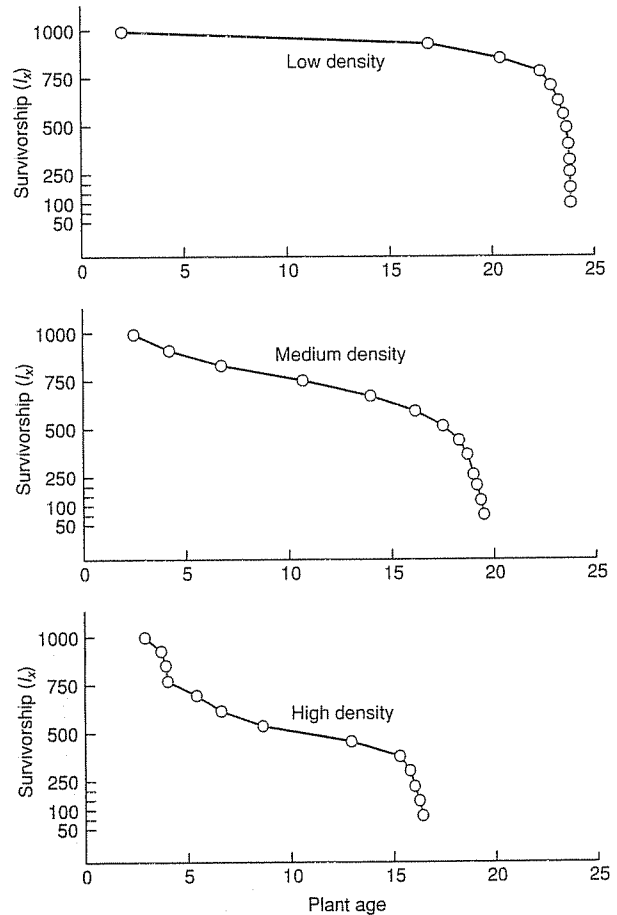


**Figure 4.8** A classification of survivorship curves. Type I (convex) – epitomized perhaps by humans in rich countries, cosseted animals in a zoo or leaves on a plant – describes the situation in which mortality is concentrated at the end of the maximum lifespan. Type II (straight) indicates that the probability of death remains constant with age, and may well apply to the buried seed banks of many plant populations. Type III (concave) indicates extensive early mortality, with those that remain having a high rate of survival subsequently. This is true, for example, of many marine fish, which produce millions of eggs of which very few survive to become adults. (After Pearl, 1928; Deevey, 1947.)

These types of survivorship curve are useful generalizations, but in practice, patterns of survival are usually more complex. Thus, in a population of *Erophila verna*, a very short-lived annual plant inhabiting sand dunes, survival can follow a type I curve when the plants grow at low densities; a type II curve, at least until the end of the lifespan, at medium densities; and a type III curve in the early stages of life at the highest densities (Figure 4.9).

#### 4.5.5 Seed banks, ephemerals and other not-quite-annuals

Using *Phlox* as an example of an annual plant has, to a certain extent, been misleading, because the group of seedlings developing in 1 year is a true cohort: it derives entirely from seed set by adults in the previous year. Seeds that do not germinate in 1 year will not survive till the next. In most 'annual' plants this is not the case. Instead, seeds accumulate in the soil in a buried *seed bank*. At any one time, therefore, seeds of a variety of ages are likely to occur together in the seed bank, and when they germinate the seedlings will also be of varying ages (age being the length of time since the seed was first produced). The formation of something comparable to a seed bank is rarer amongst animals, but there are



**Figure 4.9** Survivorship curves ( $l_x$ , where  $l_0 = 1000$ ) for the sand-dune annual plant *Erophila verna* monitored at three densities: high (initially 55 or more seedlings per 0.01 m<sup>2</sup> plot); medium (15–30 seedlings per plot); and low (1–2 seedlings per plot). The horizontal scale (plant age) is standardized to take account of the fact that each curve is the average of several cohorts, which lasted different lengths of time (around 70 days on average). (After Symonides, 1983.)

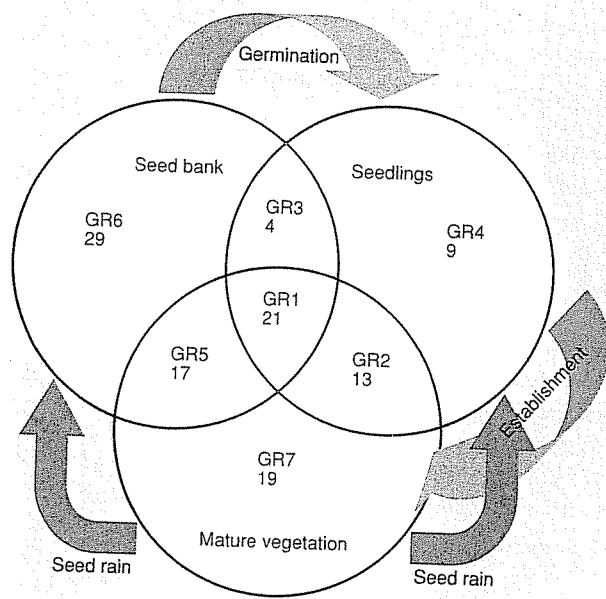
examples to be seen amongst the eggs of nematodes, mosquitoes and fairy shrimps, the gemmules of sponges and the statocysts of bryozoans.

Note that species commonly referred to as 'annual', but with a seed bank (or animal equivalent), are not strictly annual species at all, even if they progress from germination to reproduction within 1 year, since some of the seeds destined to germinate each year will already be more than 12 months old. All we can do, though, is bear this fact in mind, and note that it is just one example of real organisms spoiling our attempts to fit them neatly into clear-cut categories.

the species  
composition of seed  
banks

As a general rule, dormant seeds, which enter and make a significant contribution to seed banks, are more common in annuals and other short-lived plant species than they are in longer lived species, such that short-lived species tend to predominate in buried seed banks, even when most of the established plants above them belong to much longer lived species. Certainly, the species composition of seed banks and the mature vegetation above may be very different (Figure 4.10).

Annual species with seed banks are not the only ones for which the term annual is, strictly speaking, inappropriate. For example, there are many annual plant species living in deserts that are far from seasonal in their appearance. They have a substantial buried seed bank, with germination occurring on rare occasions after substantial rainfall. Subsequent development is usually rapid, so that the period from germination to seed production is short. Such plants are best described as semelparous *ephemerals*.



**Figure 4.10** Species recovered from the seed bank, from seedlings and from mature vegetation in a coastal grassland site on the western coast of Finland. Seven species groups (GR1–GR7) are defined on the basis of whether they were found in only one, two, or all three stages. GR3 (seed bank and seedlings only) is an unreliable group of species that are mostly incompletely identified; in GR5 there are many species difficult to identify as seedlings that may more properly belong to GR1. None the less, the marked difference in composition, especially between the seed bank and the mature vegetation, is readily apparent. (After Jutila, 2003.)

A simple annual label also fails to fit species where the majority of individuals in each generation are annual, but where a small number postpone reproduction until their second summer. This applies, for example, to the terrestrial isopod *Philoscia muscorum* living in northeast England (Sunderland *et al.*, 1976). Approximately 90% of females bred only in the first summer after they were born; the other 10% bred only in their second summer. In some other species, the difference in numbers between those that reproduce in their first or second years is so slight that the description *annual–biennial* is most appropriate.

In short, it is clear that annual life cycles merge into more complex ones without any sharp discontinuity.

#### 4.6 Individuals with repeated breeding seasons

Many species breed repeatedly (assuming they survive long enough), but nevertheless have a specific breeding season. Thus, they have overlapping generations (see Figure 4.6d). Amongst the more obvious examples are temperate-region birds living for more than 1 year, some corals, most trees and other iteroparous perennial plants. In these, individuals of a range of ages breed side by side. None the less, some species in this category, some grasses for example, and many birds, live for relatively short periods.

##### 4.6.1 Cohort life tables

Constructing a cohort life table for species that breed repeatedly is more difficult than constructing one for an annual species. A cohort must be recognized and followed (often for many years), even though the organisms within it are coexisting and intermingling with organisms from many other cohorts, older and younger. This was possible, though, as part of an extensive study of red deer (*Cervus elaphus*) on the small island of Rhum, Scotland (Lowe, 1969). The deer live for up to 16 years, and the females (hinds) are capable of breeding each year from their fourth summer onwards. In 1957, Lowe and his coworkers made a very careful count of the total number of deer on the island, including the total number of calves (less than 1 year old). Lowe's cohort consisted of the deer that were calves in 1957. Thus, each year from 1957 to 1966, every one of the deer that was discovered that had died from natural causes, or had been shot under the rigorously controlled conditions of this Nature Conservancy Council reserve, was examined and aged reliably by examining tooth replacement, eruption and wear. It was therefore possible to identify those dead deer that had been calves in 1957; and by 1966, 92% of this cohort had been observed dead and their age at death therefore determined. The life table for this cohort of hinds (or the 92% sample of it) is presented in Table 4.2; the survivorship curve is shown in Figure 4.11. There appears to be a fairly consistent increase in the risk of mortality with age (the curve is convex).

Table 4.2 Cohort life table for red deer hinds on the island of Rhum that were calves in 1957 (After Lowe, 1969.)

Age (years) $x$	Proportion of original cohort surviving to the beginning of age-class $x$ $l_x$	Proportion of original cohort dying during age-class $x$ $d_x$	Mortality rate $q_x$
1	1.000	0	0
2	1.000	0.061	0.061
3	0.939	0.185	0.197
4	0.754	0.249	0.330
5	0.505	0.200	0.396
6	0.305	0.119	0.390
7	0.186	0.054	0.290
8	0.132	0.107	0.810
9	0.025	0.025	1.000

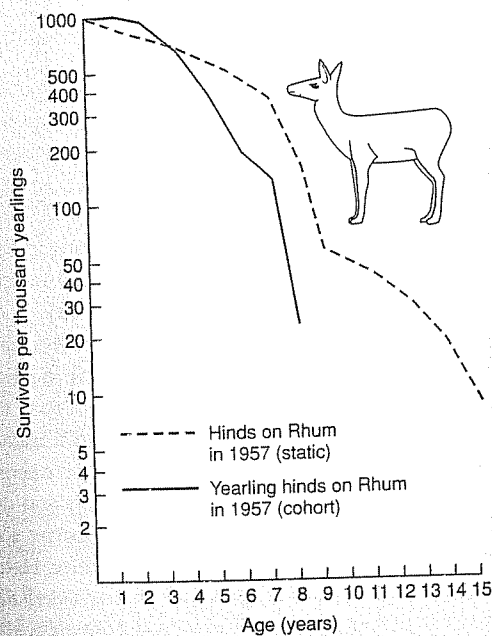


Figure 4.11 Two survivorship curves for red deer hinds on the island of Rhum. As explained in the text, one is based on the cohort life table for the 1957 calves and therefore applies to the post-1957 period; the other is based on the static life table of the 1957 population and therefore applies to the pre-1957 period. (After Lowe, 1969.)

#### 4.6.2 Static life tables

The difficulties of constructing a cohort life table for an organism with overlapping generations are eased somewhat when the organism is sessile. In such a case, newly arrived or newly emerged

individuals can be mapped, photographed or even marked in some way, so that they (or their exact location) can be recognized whenever the site is revisited subsequently. Taken overall, however, practical problems have tended to deter ecologists from constructing cohort life tables for long-lived iteroparous organisms with overlapping generations, even when the individuals are sessile. But there is an alternative: the construction of a static life table. As will become clear, this alternative is seriously flawed – but it is often better than nothing at all.

An interesting example emerges from Lowe's study of red deer on Rhum. As has already been explained, a large proportion of the deer that died from 1957 to 1966 could be aged reliably. Thus, if, for example, a fresh corpse was examined in 1961 and was found to be 6 years old, it was known that in 1957 the deer was alive and 2 years old. Lowe was therefore eventually able to reconstruct the age structure of the 1957 population: age structures are the basis for static life tables. Of course, the age structure of the 1957 population could have been ascertained by shooting and examining large numbers of deer in 1957; but since the ultimate aim of the project was the enlightened conservation of the deer, this method would have been somewhat inappropriate. (Note that Lowe's results did not represent the total numbers alive in 1957, because a few carcasses must have decomposed or been eaten before they could be discovered and examined.) Lowe's raw data for red deer hinds are presented in column 2 of Table 4.3.

Remember that the data in Table 4.3 refer to ages in 1957. They can be used as a basis for a life table, but only if it is assumed that there had been no year-to-year variation prior to 1957 in either the total number of births or the age-specific survival rates. In other words, it must be assumed that the 59 6-year-old deer alive in 1957 were the survivors of 78 5-year-old deer alive in 1956, who were themselves the survivors of 81 4-year olds in 1955, and so on. Or, in short, that the data in Table 4.3 are the same as would have been obtained if a single cohort had been followed.

Age (years) $x$	Number of individuals observed of age $x$			Smoothed			
	$a_x$	$l_x$	$d_x$	$q_x$	$l_x$	$d_x$	$q_x$
1	129	1.000	0.116	0.116	1.000	0.137	0.137
2	114	0.884	0.008	0.009	0.863	0.085	0.097
3	113	0.876	0.251	0.287	0.778	0.084	0.108
4	81	0.625	0.020	0.032	0.694	0.084	0.121
5	78	0.605	0.148	0.245	0.610	0.084	0.137
6	59	0.457	0.047	—	0.526	0.084	0.159
7	65	0.504	0.078	0.155	0.442	0.085	0.190
8	55	0.426	0.232	0.545	0.357	0.176	0.502
9	25	0.194	0.124	0.639	0.181	0.122	0.672
10	9	0.070	0.008	0.114	0.059	0.008	0.141
11	8	0.062	0.008	0.129	0.051	0.009	0.165
12	7	0.054	0.038	0.704	0.042	0.008	0.198
13	2	0.016	0.008	0.500	0.034	0.009	0.247
14	1	0.080	-0.023	—	0.025	0.008	0.329
15	4	0.031	0.015	0.484	0.017	0.008	0.492
16	2	0.016	—	—	0.009	0.009	1.000

Table 4.3 A static life table for red deer hinds on the island of Rhum, based on the reconstructed age structure of the population in 1957. (After Lowe, 1969.)

static life tables: flawed but sometimes useful, none the less

Having made these assumptions, the  $l_x$ ,  $d_x$  and  $q_x$  columns were constructed. It is clear, however, that the assumptions are false. There were actually more animals in their seventh year than in their sixth year, and more in their 15th year than in their 14th year. There were therefore 'negative' deaths and meaningless mortality rates. The pitfalls of constructing such static life tables (and equating age structures with survivorship curves) are amply illustrated.

Nevertheless, the data can be useful. Lowe's aim was to provide a general idea of the population's age-specific survival rate prior to 1957 (when culling of the population began). He could then compare this with the situation after 1957, as illustrated by the cohort life table previously discussed. He was more concerned with general trends than with the particular changes occurring from 1 year to the next. He therefore 'smoothed out' the variations in numbers between ages 2–8 and 10–16 years to give a steady decline during both of these periods. The results of this process are shown in the final three columns of Table 4.3, and the survivorship curve is plotted in Figure 4.11. A general picture does indeed emerge: the introduction of culling on the island appears to have decreased overall survivorship significantly, overcoming any possible compensatory decreases in natural mortality.

Notwithstanding this successful use of a static life table, the interpretation of static life tables generally, and the age structures from which they stem, is fraught with difficulty: usually, age structures offer no easy short cuts to understanding the dynamics of populations.

#### 4.6.3 Fecundity schedules

Static fecundity schedules, i.e. age-specific variations in fecundity within a particular season, can also provide useful information, especially if they are available from successive breeding seasons. We can see this for a population of great tits (*Parus major*) in Wytham Wood, near Oxford, UK (Table 4.4), where the data could be obtained only because the individual birds could be aged (in this case, because they had been marked with individually recognizable leg-rings soon after hatching). The table shows that mean fecundity rose to a peak in 2-year-old birds and declined gradually thereafter. Indeed, most iteroparous species show an age- or stage-related pattern of fecundity. For instance, Figure 4.12 shows the size-dependent fecundity of moose (*Alces alces*) in Sweden.

#### 4.6.4 The importance of modularity

The sedge *Carex bigelowii*, growing in a lichen heath in Norway, illustrates the difficulties of constructing any sort of life table for organisms that are not only iteroparous with overlapping generations but are also modular (Figure 4.13). *Carex bigelowii* has an extensive underground rhizome system that produces tillers (aerial shoots) at intervals along its length as it grows. It grows by producing a lateral meristem in the axil of a leaf belonging to a 'parent' tiller. This lateral is completely dependent on the parent tiller at first, but is potentially capable of developing into a vegetative parent tiller itself, and also of flowering, which it does

Table 4.4 Mean clutch size and age of great tits in Wytham Wood, near Oxford, UK. (After Perrins, 1965.)

Age (years)	1961		1962		1963	
	Number of birds	Mean clutch size	Number of birds	Mean clutch size	Number of birds	Mean clutch size
Yearlings	128	7.7	54	8.5	54	9.4
2	18	8.5	43	9.0	33	10.0
3	14	8.3	12	8.8	29	9.7
4			5	8.2	9	9.7
5			1	8.0	2	9.5
6					1	9.0

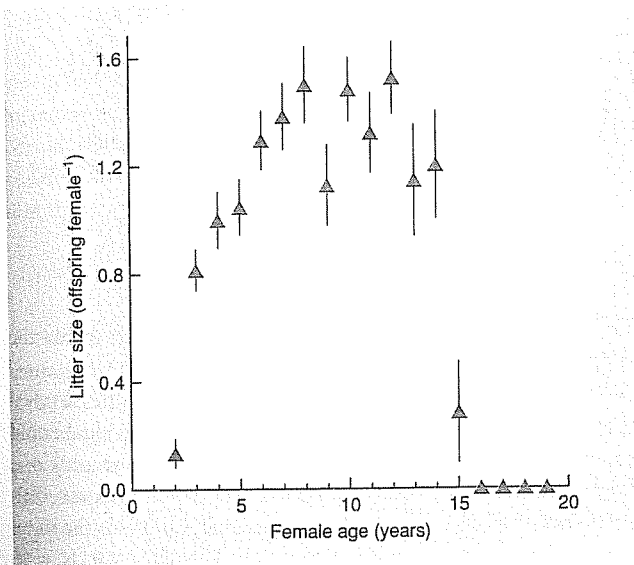


Figure 4.12 Age-dependent reproduction (average litter size) in a population of moose (*Alces alces*) in Sweden (means with standard errors). (After Ericsson *et al.*, 2001.)

when it has produced a total of 16 or more leaves. Flowering, however, is always followed by tiller death, i.e. the tillers are semelparous although the genets are iteroparous.

Callaghan (1976) took a number of well-separated young tillers, and excavated their rhizome systems through progressively older generations of parent tillers. This was made possible by the persistence of dead tillers. He excavated 23 such systems containing a total of 360 tillers, and was able to construct a type of static life table (and fecundity schedule) based on the growth stages (Figure 4.13). There were, for example, 1.04 dead vegetative tillers (per m<sup>2</sup>) with 31–35 leaves. Thus, since there were also 0.26 tillers in the next (36–40 leaves) stage, it can be assumed that a total of 1.30 (i.e. 1.04 + 0.26) living vegetative tillers entered the 31–35 leaf stage. As there were 1.30 vegetative tillers and 1.56 flowering tillers in the 31–35 leaf stage, 2.86 tillers must have survived from the 26–30 stage. It is in this way that the

life table – applicable not to individual genets but to tillers (i.e. modules) – was constructed.

There appeared to be no new establishment from seed in this particular population (no new genets); tiller numbers were being maintained by modular growth alone. However, a ‘modular growth schedule’ (*laterals*), analogous to a fecundity schedule, has been constructed.

Note finally that stages rather than age classes have been used here – something that is almost always necessary when dealing with modular iteroparous organisms, because variability stemming from modular growth accumulates year upon year, making age a particularly poor measure of an individual’s chances of death, reproduction or further modular growth.

## 4.7 Reproductive rates, generation lengths and rates of increase

### 4.7.1 Relationships between the variables

In the previous section we saw that the life tables and fecundity schedules drawn up for species with overlapping generations are at least superficially similar to those constructed for species with discrete generations. With discrete generations, we were able to compute the basic reproductive rate ( $R_0$ ) as a summary term describing the overall outcome of the patterns of survivorship and fecundity. Can a comparable summary term be computed when generations overlap?

Note immediately that previously, for species with discrete generations,  $R_0$  described two separate population parameters. It was the number of offspring produced on average by an individual over the course of its life; but it was also the multiplication factor that converted an original population size into a new population size, one generation hence. With overlapping generations, when a cohort life table is available, the basic reproductive rate can be calculated using the same formula:

$$R_0 = \sum l_x m_x \quad (4.4)$$



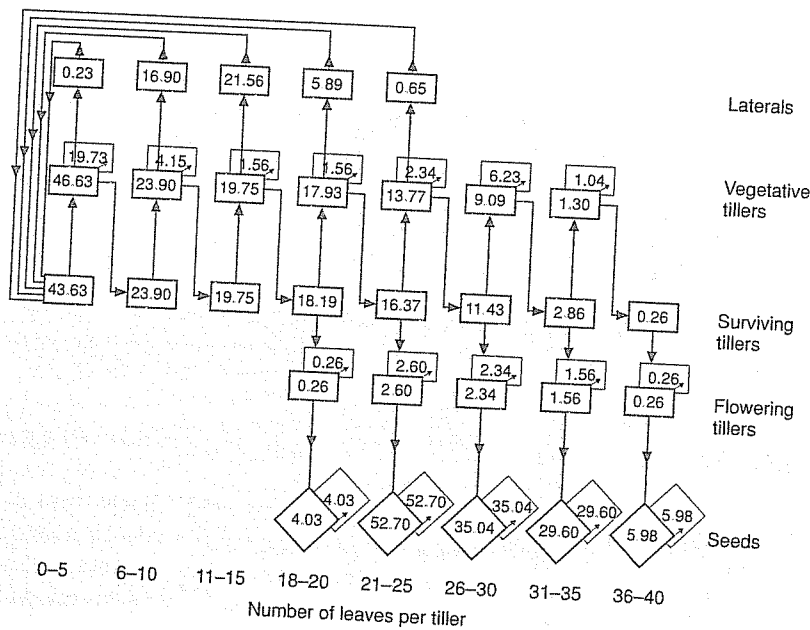


Figure 4.13 A reconstructed static life table for the modules (tillers) of a *Carex bigelowii* population. The densities per m<sup>2</sup> of tillers are shown in rectangular boxes, and those of seeds in diamond-shaped boxes. Rows represent tiller types, whilst columns depict size classes of tillers. Thin-walled boxes represent dead tiller (or seed) compartments, and arrows denote pathways between size classes, death or reproduction (After Callaghan, 1976)

and it still refers to the average number of offspring produced by an individual. But further manipulations of the data are necessary before we can talk about the rate at which a population increases or decreases in size – or, for that matter, about the length of a generation. The difficulties are much greater still when only a static life table (i.e. an age structure) is available (see below).

We begin by deriving a general relationship that links population size, the rate of population increase, and time – but which is not limited to measuring time in terms of generations. Imagine a population that starts with 10 individuals, and which, after successive intervals of time, rises to 20, 40, 80, 160 individuals and so on. We refer to the initial population size as  $N_0$  (meaning the population size when no time has elapsed). The population size after one time interval is  $N_1$ , after two time intervals it is  $N_2$ , and in general after  $t$  time intervals it is  $N_t$ . In the present case,  $N_0 = 10$ ,  $N_1 = 20$ , and we can say that:

$$N_1 = N_0 R, \tag{4.5}$$

the fundamental net reproductive rate,  $R$

where  $R$ , which is 2 in the present case, is known as the *fundamental net reproductive rate* or the *fundamental net per capita rate of increase*. Clearly, popula-

tions will increase when  $R > 1$ , and decrease when  $R < 1$ . (Unfortunately, the ecological literature is somewhat divided between those who use 'R' and those who use the symbol  $\lambda$  for the same parameter. Here we stick with  $R$ , but we sometimes

use  $\lambda$  in later chapters to conform to standard usage within the topic concerned.)

$R$  combines the birth of new individuals with the survival of existing individuals. Thus, when  $R = 2$ , each individual could give rise to two offspring but die itself, or give rise to only one offspring and remain alive: in either case,  $R$  (birth plus survival) would be 2. Note too that in the present case  $R$  remains the same over the successive intervals of time, i.e.  $N_2 = 40 = N_1 R$ ,  $N_3 = 80 = N_2 R$ , and so on. Thus:

$$N_3 = N_1 R \times R = N_0 R \times R \times R = N_0 R^3, \tag{4.6}$$

and in general terms:

$$N_{t+1} = N_t R, \tag{4.7}$$

and:

$$N_t = N_0 R^t \tag{4.8}$$

Equations 4.7 and 4.8 link together population size, rate of increase and  $R$ ,  $R_0$  and  $T$  time; and we can now link these in turn with  $R_0$ , the basic reproductive rate, and with the generation length (defined as lasting  $T$  intervals of time). In Section 4.5.2, we saw that  $R_0$  is the multiplication factor that converts one population size to another population size, one generation later, i.e.  $T$  time intervals later. Thus:

$$N_T = N_0 R_0^T \quad (4.9)$$

But we can see from Equation 4.8 that:

$$N_T = N_0 R^T \quad (4.10)$$

Therefore:

$$R_0 = R^T \quad (4.11)$$

or, if we take natural logarithms of both sides:

$$\ln R_0 = T \ln R \quad (4.12)$$

$r$ , the intrinsic rate of natural increase

The term  $\ln R$  is usually denoted by  $r$ , the *intrinsic rate of natural increase*. It is the rate at which the population increases in size, i.e. the change in population size per individual per unit time. Clearly, populations will increase in size for  $r > 0$ , and decrease for  $r < 0$ ; and we can note from the preceding equation that:

$$r = \ln R_0 / T \quad (4.13)$$

Summarizing so far, we have a relationship between the average number of offspring produced by an individual in its lifetime,  $R_0$ , the increase in population size per unit time,  $r (= \ln R)$ , and the generation time,  $T$ . Previously, with discrete generations (see Section 4.5.2), the unit of time was a generation. It was for this reason that  $R_0$  was the same as  $R$ .

#### 4.7.2 Estimating the variables from life tables and fecundity schedules

In populations with overlapping generations (or continuous breeding),  $r$  is the intrinsic rate of natural increase that the population has the *potential* to achieve; but it will only actually achieve this rate of increase if the survivorship and fecundity schedules remain steady over a long period of time. If they do,  $r$  will be approached gradually (and thereafter maintained), and over the same period the population will gradually approach a stable age structure (i.e. one in which the proportion of the population in each age class remains constant over time; see below). If, on the other hand, the fecundity and survivorship schedules alter over time – as they almost always do – then the rate of increase will continually change, and it will be impossible to characterize in a single figure. Nevertheless, it can often be useful to characterize a population in terms of its potential, especially when the aim is to make a comparison, for instance comparing various populations of the same species in different environments, to see which environment appears to be the most favorable for the species.

The most precise way to calculate  $r$  is from the equation:

$$\sum e^{-rx} l_x m_x = 1, \quad (4.14)$$

where the  $l_x$  and  $m_x$  values are taken from a cohort life table, and  $e$  is the base of natural logarithms. However, this is a so-called 'implicit' equation, which cannot be solved directly (only by iteration, usually on a computer), and it is an equation without any clear biological meaning. It is therefore customary to use instead an approximation to Equation 4.13, namely:

$$r \approx \ln R_0 / T_c \quad (4.15)$$

where  $T_c$  is the *cohort generation time* (see below). This equation shares with Equation 4.13 the advantage of making explicit the dependence of  $r$  on the reproductive output of individuals ( $R_0$ ) and the length of a generation ( $T$ ). Equation 4.15 is a good approximation when  $R_0 \approx 1$  (i.e. population size stays approximately constant), or when there is little variation in generation length, or for some combination of these two things (May, 1976).

We can estimate  $r$  from Equation 4.15 if we know the value of the cohort generation time  $T_c$ , which is the average length of time between the birth of an individual and the birth of one of its own offspring. This, being an average, is the sum of all these birth-to-birth times, divided by the total number of offspring, i.e.:

$$T_c = \sum x l_x m_x / \sum l_x m_x$$

or

$$T_c = \sum x l_x m_x / R_0 \quad (4.16)$$

This is only approximately equal to the true generation time  $T$ , because it takes no account of the fact that some offspring may themselves develop and give birth during the reproductive life of the parent.

Thus Equations 4.15 and 4.16 allow us to calculate  $T_c$ , and thus an approximate value for  $r$ , from a cohort life table of a population with either overlapping generations or continuous breeding. In short, they give us the summary terms we require. A worked example is set out in Table 4.5, using data for the barnacle *Balanus glandula*. Note that the precise value of  $r$ , from Equation 4.14, is 0.085, compared to the approximation 0.080; whilst  $T$ , calculated from Equation 4.13, is 2.9 years compared to  $T_c = 3.1$  years. The simpler and biologically transparent approximations are clearly satisfactory in this case. They show that since  $r$  was somewhat greater than zero, the population would have increased in size, albeit rather slowly, if the schedules had remained steady. Alternatively, we may say that, as judged by this cohort life table, the barnacle population had a good chance of continued existence.

**Table 4.5** A cohort life table and a fecundity schedule for the barnacle *Balanus glandula* at Pile Point, San Juan Island, Washington (Connell, 1970). The computations for  $R_0$ ,  $T_c$  and the approximate value of  $r$  are explained in the text. Numbers marked with an asterisk were interpolated from the survivorship curve.

Age (years) $x$	$a_x$	$l_x$	$m_x$	$l_x m_x$	$x l_x m_x$
0	1,000,000	1.000	0	0	
1	62	0.0000620	4,600	0.285	0.285
2	34	0.0000340	8,700	0.296	0.592
3	20	0.0000200	11,600	0.232	0.696
4	15.5*	0.0000155	12,700	0.197	0.788
5	11	0.0000110	12,700	0.140	0.700
6	6.5*	0.0000065	12,700	0.082	0.492
7	2	0.0000020	12,700	0.025	0.175
8	2	0.0000020	12,700	0.025	0.200
				1.282	3.928

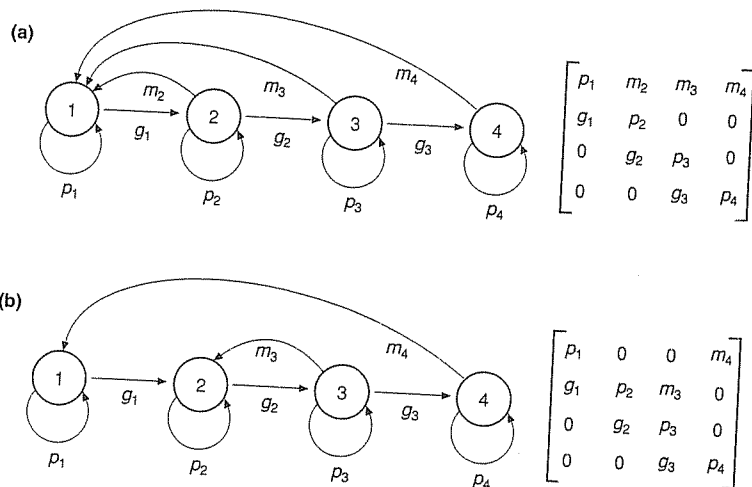
$$R_0 = 1.282; \quad T_c = \frac{3.928}{1.282} = 3.1; \quad r = \frac{\ln R_0}{T_c} = 0.08014.$$

### 4.7.3 The population projection matrix

A more general, more powerful, and therefore more useful method of analyzing and interpreting the fecundity and survival schedules of a population with overlapping generations makes use of the population projection matrix (see Caswell, 2001, for a full exposition). The word 'projection' in its title is important. Just like the simpler methods above, the idea is not to take the cur-

rent state of a population and forecast what *will* happen to the population in the future, but to project forward to what *would* happen if the schedules remained the same. Caswell uses the analogy of the speedometer in a car: it provides us with an invaluable piece of information about the car's current state, but a reading of, say, 80 km h<sup>-1</sup> is simply a projection, not a serious forecast that we will actually have traveled 80 km in 1 hour's time.

The population projection matrix acknowledges that most life cycles comprise a sequence of distinct classes with different rates of fecundity and survival: life cycle stages, perhaps, or size classes, rather than simply different ages. The resultant patterns can be summarized in a 'life cycle graph', though this is not a graph in the everyday sense but a flow diagram depicting the transitions from class to class over each step in time. Two examples are shown in Figure 4.14 (see also Caswell, 2001). The first (Figure 4.14a) indicates a straightforward sequence of classes where, over each time step, individuals in class  $i$  may: (i) survive and remain in that class (with probability  $p_i$ ); (ii) survive and grow and/or develop into the next class (with probability  $g_i$ ); and (iii) give birth to  $m_i$  newborn individuals into the youngest/smallest class. Moreover, as Figure 4.14b shows, a life cycle graph can also depict a more complex life cycle, for example with both sexual reproduction (here, from reproductive class 4 into 'seed' class 1) and vegetative growth of new modules (here, from 'mature module' class 3 to 'new module' class 2). Note that the notation here is slightly different from that in life tables like Table 4.1 above. There the focus was on age classes, and the passage of time inevitably meant the passing of individuals from one age class to the next:  $p$  values therefore referred to survival from one age class to the next. Here, by contrast, an individual



**Figure 4.14** Life cycle graphs and population projection matrices for two different life cycles. The connection between the graphs and the matrices is explained in the text. (a) A life cycle with four successive classes. Over one time step, individuals may survive within the same class (with probability  $p_i$ ), survive and pass to the next class (with probability  $g_i$ ) or die, and individuals in classes 2, 3 and 4 may give birth to individuals in class 1 (with per capita fecundity  $m_i$ ). (b) Another life cycle with four classes, but in this case only reproductive class 4 individuals can give birth to class 1 individuals, but class 3 individuals can 'give birth' (perhaps by vegetative growth) to further class 2 individuals.

need not pass from one class to the next over a time step, and it is therefore necessary to distinguish survival within a class (*p* values here) from passage and survival into the next class (*g* values).

The information in a life cycle graph can be summarized in a population projection matrix. Such matrices are shown alongside the graphs in elements of the matrix

Figure 4.14. The convention is to contain the elements of a matrix within square brackets. In fact, a projection matrix is itself always 'square': it has the same number of columns as rows. The rows refer to the class number at the endpoint of a transition: the columns refer to the class number at the start. Thus, for instance, the matrix element in the third row of the second column describes the flow of individuals from the second class into the third class. More specifically, then, and using the life cycle in Figure 4.14a as an example, the elements in the main diagonal from top left to bottom right represent the probabilities of surviving and remaining in the same class (the *ps*), the elements in the remainder of the first row represent the fecundities of each subsequent class into the youngest class (the *ms*), while the *gs*, the probabilities of surviving and moving to the next class, appear in the subdiagonal below the main diagonal (from 1 to 2, from 2 to 3, etc).

Summarizing the information in this way is useful because, using standard rules of matrix manipulation, we can take the numbers in the different classes ( $n_1, n_2, \text{etc.}$ ) at one point in time ( $t_1$ ), expressed as a 'column vector' (simply a matrix comprising just one column), *pre*-multiply this vector by the projection matrix, and generate the numbers in the different classes one time step later ( $t_2$ ). The mechanics of this – that is, where each element of the new column vector comes from – are as follows:

$$\begin{bmatrix} p_1 & m_2 & m_3 & m_4 \\ g_1 & p_2 & 0 & 0 \\ 0 & g_2 & p_3 & 0 \\ 0 & 0 & g_3 & p_4 \end{bmatrix} \times \begin{bmatrix} n_{1,t1} \\ n_{2,t1} \\ n_{3,t1} \\ n_{4,t1} \end{bmatrix} = \begin{bmatrix} n_{1,t2} \\ n_{2,t2} \\ n_{3,t2} \\ n_{4,t2} \end{bmatrix}$$

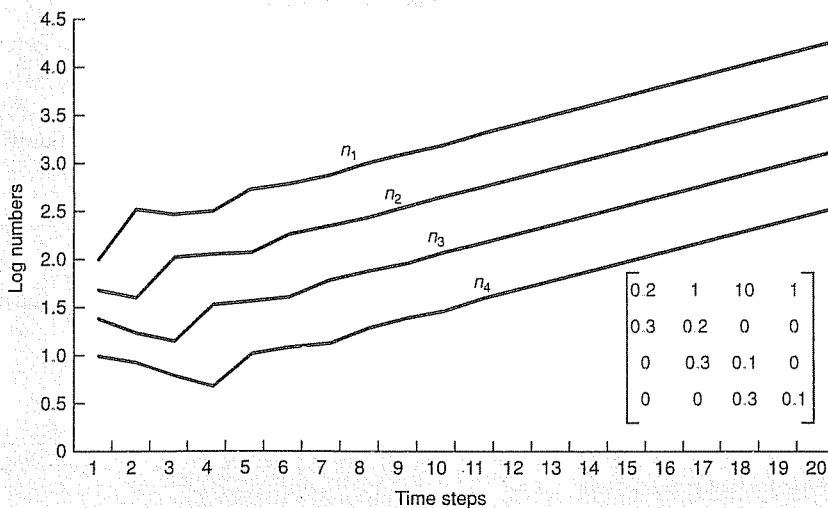
$$= \begin{bmatrix} (n_{1,t1} \times p_1) + (n_{2,t1} \times m_2) + (n_{3,t1} \times m_3) + (n_{4,t1} \times m_4) \\ (n_{1,t1} \times g_1) + (n_{2,t1} \times p_2) + (n_{3,t1} \times 0) + (n_{4,t1} \times 0) \\ (n_{1,t1} \times 0) + (n_{2,t1} \times g_2) + (n_{3,t1} \times p_3) + (n_{4,t1} \times 0) \\ (n_{1,t1} \times 0) + (n_{2,t1} \times 0) + (n_{3,t1} \times g_3) + (n_{4,t1} \times p_4) \end{bmatrix}$$

Thus, the numbers in the first class,  $n_1$ , are the survivors from that class one time step previously plus those

born into it from the other classes, and so on. Figure 4.15 shows this process repeated 20 times (i.e. for 20 time steps) with some hypothetical values in the projection matrix shown as an inset in the figure. It is apparent that there is an initial (transient) period in which the proportions in the different classes alter, some increasing and others decreasing, but that after about nine time steps, all classes grow at the same exponential rate (a straight line on a logarithmic scale), and so therefore does the whole population. The *R* value is 1.25. Also, the proportions in the different classes are constant: the population has achieved a stable class structure with numbers in the ratios 51.5 : 14.7 : 3.8 : 1.

Hence, a population projection matrix allows us to summarize a potentially complex array of survival, growth and reproductive processes, and characterize that population succinctly by determining the per capita rate of increase, *R*, implied by the matrix. But crucially, this 'asymptotic' *R* can be determined directly, without the need for a simulation, by application of the methods of matrix algebra, though these are quite beyond our scope here

Figure 4.15 A population growing according to the life cycle graph shown in Figure 4.14a, with parameter values as shown in the insert here. The starting conditions were 100 individuals in class 1 ( $n_1 = 100$ ), 50 in class 2, 25 in class 4 and 10 in class 4. On a logarithmic (vertical) scale, exponential growth appears as a straight line. Thus, after about 10 time steps, the parallel lines show that all classes were growing at the same rate ( $R = 1.25$ ) and that a stable class structure had been achieved.



### Box 4.1 Reproductive value

The reproductive value of an individual of age  $x$  ( $RV_x$ ) is the currency by which the worth of a life history in the hands of natural selection may be judged. It is defined in terms of the life-table statistics discussed earlier. Specifically:

$$RV_x = \sum_{y=x}^{y=y_{\max}} \left( \frac{l_y}{l_x} \cdot m_y \cdot R^{x-y} \right)$$

where  $m_x$  is the birth rate of the individual in age-class  $x$ ;  $l_x$  is the probability that the individual will survive to age  $x$ ;  $R$  is the net reproductive rate of the whole population per unit time (the time unit here being the age interval); and  $\Sigma$  means 'the sum of'.

To understand this equation, it is easiest to split  $RV_x$  into its two components:

$$RV_x = m_x + \sum_{y=x+1}^{y=y_{\max}} \left( \frac{l_y}{l_x} \cdot m_y \cdot R^{x-y} \right)$$

Here,  $m_x$ , the individual's birth rate at its current age, can be thought of as its *contemporary reproductive output*. What remains is then the *residual reproductive value* (Williams, 1966): the sum of the 'expectations of reproduction' at all subsequent ages, modified in each case by  $R^{x-y}$  for reasons described below. The 'expectation of reproduction' for age class  $y$  is  $(l_y/l_x \cdot m_y)$ , i.e. it is the birth rate of the individual should it reach that age ( $m_y$ ), discounted by the probability of it doing so given that it has already reached stage  $x$  ( $l_y/l_x$ ).

Reproductive value takes on its simplest form where the overall population size remains approximately constant. In

such cases,  $R = 1$  and can be ignored. The reproductive value of an individual is then simply its total lifetime expectation of reproductive output (from its current age class and from all subsequent age classes).

However, when the population consistently increases or decreases, this must be taken into account. If the population increases, then  $R > 1$  and  $R^{x-y} < 1$  (because  $x < y$ ). Hence, the terms in the equation are reduced by  $R^{x-y}$  the larger the value of  $y$  (the further into the future we go), signifying that future (i.e. 'residual') reproduction adds relatively little to  $RV_x$ , because the proportionate contribution to a growing population made by a given reproductive output in the future is relatively small – whereas the offspring from present or early reproduction themselves have an early opportunity to contribute to the growing population. Conversely, if the population decreases, then  $R < 1$  and  $R^{x-y} > 1$ , and the terms in the equation are successively increased, reflecting the greater proportionate contribution of future reproduction.

In any life history, the reproductive values at different ages are intimately connected, in the sense that when natural selection acts to maximize reproductive value at one age, it constrains the values of the life table parameters – and thus reproductive value itself – for subsequent ages. Hence, strictly speaking, natural selection acts ultimately to maximize reproductive value *at birth*,  $RV_0$  (Kozłowski, 1993). (Note that there is no contradiction between this and the fact that reproductive value is typically low at birth (Figure 4.18). Natural selection can discriminate only between those options available at that stage.)

survival and expected future fecundity; (iii) this is done in a way that takes account of the contribution of an individual to future generations, relative to the contributions of others; and (iv) the life history favored by natural selection from amongst those available in the population will be the one for which the sum of contemporary output and RRV is highest.

The way in which reproductive value changes with age in two contrasting populations is illustrated in Figure 4.18. It is low for young individuals when each of them has only a low probability of surviving to reproductive maturity; but for those that do survive, it then increases steadily as the age of first reproduction is approached, as it becomes more and more certain that surviving individuals will reach reproductive maturity. Reproductive value is then low again for old individuals, since their reproductive output is likely to have declined, and their expectation of future

reproduction is even lower. The detailed rise and fall, of course, varies with the detailed age- or stage-specific birth or mortality schedules of the species concerned.

#### 4.8.3 Trade-offs

Any organism's life history must, of necessity, be a compromise allocation of the resources that are available to it. Resources devoted to one trait are unavailable to others. A 'trade-off' is a negative relationship between two life history characteristics in which increases in one are associated with decreases in the other as a result of such compromises. For instance, Douglas fir trees (*Pseudotsuga menziesii*) benefit both from reproducing and from growing (since, amongst other things, this enhances future