

# Chapter 5

## Intraspecific Competition

### 5.1 Introduction

Organisms grow, reproduce and die (Chapter 4). They are affected by the conditions in which they live (Chapter 2), and by the resources that they obtain (Chapter 3). But no organism lives in isolation. Each, for at least part of its life, is a member of a population composed of individuals of its own species.

#### a definition of competition

Individuals of the same species have very similar requirements for survival, growth and reproduction; but their combined demand for a resource may exceed the immediate supply. The individuals then compete for the resource and, not surprisingly, at least some of them become deprived. This chapter is concerned with the nature of such intraspecific competition, its effects on the competing individuals and on populations of competing individuals. We begin with a working definition: 'competition is an interaction between individuals, brought about by a shared requirement for a resource, and leading to a reduction in the survivorship, growth and/or reproduction of at least some of the competing individuals concerned'. We can now look more closely at competition.

Consider, initially, a simple hypothetical community: a thriving population of grasshoppers (all of one species) feeding on a field of grass (also of one species). To provide themselves with energy and material for growth and reproduction, grasshoppers eat grass; but in order to find and consume that grass they must use energy. Any grasshopper might find itself at a spot where there is no grass because some other grasshopper has eaten it. The grasshopper must then move on and expend more energy before it takes in food. The more grasshoppers there are, the more often this will happen. An increased energy expenditure and a decreased rate of food intake may all decrease a grasshopper's chances of survival, and also leave less energy available for development and reproduction. Survival and reproduction determine a grasshopper's contribution to the next generation. Hence, the

more intraspecific competitors for food a grasshopper has, the less its likely contribution will be.

As far as the grass itself is concerned, an isolated seedling in fertile soil may have a very high chance of surviving to reproductive maturity. It will probably exhibit an extensive amount of modular growth, and will probably therefore eventually produce a large number of seeds. However, a seedling that is closely surrounded by neighbors (shading it with their leaves and depleting the water and nutrients of its soil with their roots) will be very unlikely to survive, and if it does, will almost certainly form few modules and set few seeds.

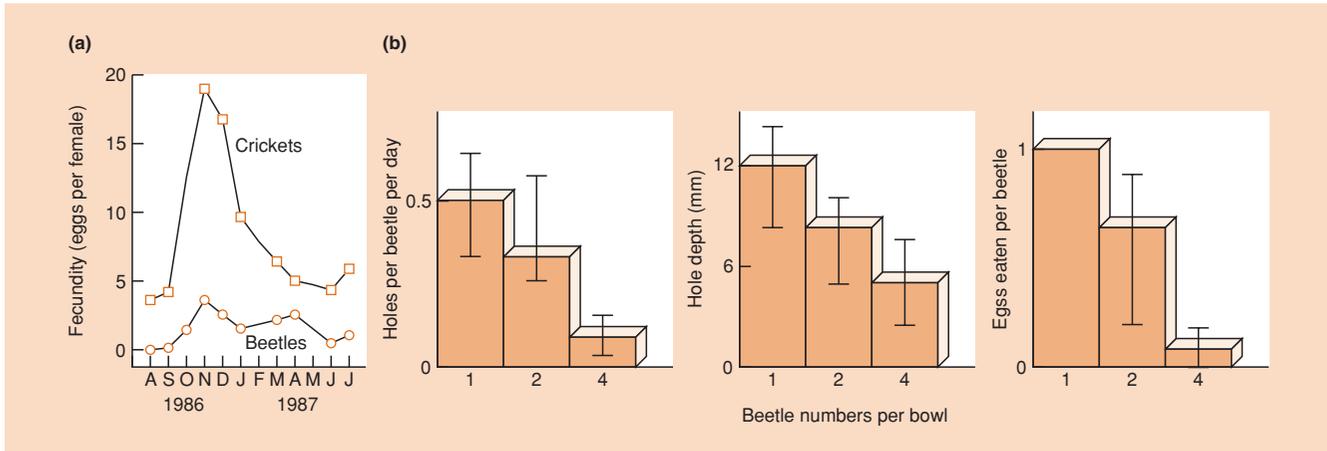
We can see immediately that the ultimate effect of competition on an individual is a decreased contribution to the next generation compared with what would have happened had there been no competitors. Intraspecific competition typically leads to decreased rates of resource intake per individual, and thus to decreased rates of individual growth or development, or perhaps to decreases in the amounts of stored reserves or to increased risks of predation. These may lead, in turn, to decreases in survivorship and/or decreases in fecundity, which together determine an individual's reproductive output.

#### 5.1.1 Exploitation and interference

In many cases, competing individuals do not interact with one another directly.

#### exploitation

Instead, individuals respond to the level of a resource, which has been depressed by the presence and activity of other individuals. The grasshoppers were one example. Similarly, a competing grass plant is adversely affected by the presence of close neighbors, because the zone from which it extracts resources (light, water, nutrients) has been overlapped by the 'resource depletion zones' of these neighbors, making it more difficult to extract those resources. In such cases, competition may be described as



**Figure 5.1** Intraspecific competition amongst cave beetles (*Neapheanops tellkampfi*). (a) Exploitation. Beetle fecundity is significantly correlated ( $r = 0.86$ ) with cricket fecundity (itself a good measure of the availability of cricket eggs – the beetles' food). The beetles themselves reduce the density of cricket eggs. (b) Interference. As beetle density in experimental arenas with 10 cricket eggs increased from 1 to 2 to 4, individual beetles dug fewer and shallower holes in search of their food, and ultimately ate much less ( $P < 0.001$  in each case), in spite of the fact that 10 cricket eggs was sufficient to satiate them all. Means and standard deviations are given in each case. (After Griffith & Poulson, 1993.)

*exploitation*, in that each individual is affected by the amount of resource that remains after that resource has been exploited by others. Exploitation can only occur, therefore, if the resource in question is in limited supply.

#### interference

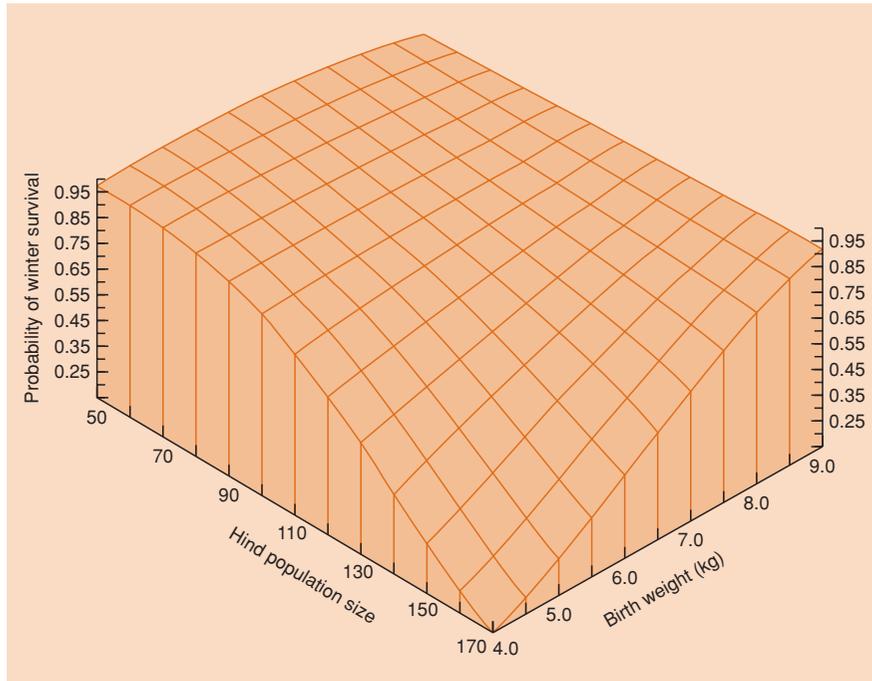
In many other cases, competition takes the form of *interference*. Here individuals interact directly with each other, and one individual will actually prevent another from exploiting the resources within a portion of the habitat. For instance, this is seen amongst animals that defend territories (see Section 5.11) and amongst the sessile animals and plants that live on rocky shores. The presence of a barnacle on a rock prevents any other barnacle from occupying that same position, even though the supply of food at that position may exceed the requirements of several barnacles. In such cases, space can be seen as a resource in limited supply. Another type of interference competition occurs when, for instance, two red deer stags fight for access to a harem of hinds. Either stag, alone, could readily mate with all the hinds, but they cannot both do so since matings are limited to the 'owner' of the harem.

Thus, interference competition may occur for a resource of real value (e.g. space on a rocky shore for a barnacle), in which case the interference is accompanied by a degree of exploitation, or for a surrogate resource (a territory, or ownership of a harem), which is only valuable because of the access it provides to a real resource (food, or females). With exploitation, the intensity of competition is closely linked to the level of resource present and the level required, but with interference, intensity may be high even when the level of the real resource is not limiting.

In practice, many examples of competition probably include elements of both exploitation and interference. For instance, adult cave beetles, *Neapheanops tellkampfi*, in Great Onyx Cave, Kentucky, compete amongst themselves but with no other species and have only one type of food – cricket eggs, which they obtain by digging holes in the sandy floor of the cave. On the one hand, they suffer indirectly from exploitation: beetles reduce the density of their resource (cricket eggs) and then have markedly lower fecundity when food availability is low (Figure 5.1a). But they also suffer directly from interference: at higher beetle densities they fight more, forage less, dig fewer and shallower holes and eat far fewer eggs than could be accounted for by food depletion alone (Figure 5.1b).

#### 5.1.2 One-sided competition

Whether they compete through exploitation or interference, individuals within a species have many fundamental features in common, using similar resources and reacting in much the same way to conditions. None the less, intraspecific competition may be very one sided: a strong, early seedling will shade a stunted, late one; an older and larger bryozoan on the shore will grow over a smaller and younger one. One example is shown in Figure 5.2. The overwinter survival of red deer calves in the resource-limited population on the island of Rhum, Scotland (see Chapter 4) declined sharply as the population became more crowded, but those that were smallest at birth were by far the most likely to die. Hence, the ultimate effect of competition is



**Figure 5.2** Those red deer that are smallest when born are the least likely to survive over winter when, at higher densities, survival declines. (After Clutton-Brock *et al.*, 1987.)

far from being the same for every individual. Weak competitors may make only a small contribution to the next generation, or no contribution at all. Strong competitors may have their contribution only negligibly affected.

Finally, note that the likely effect of intraspecific competition on any individual is greater the more competitors there are. The effects of intraspecific competition are thus said to be density dependent. We turn next to a more detailed look at the density-dependent effects of intraspecific competition on death, birth and growth.

## 5.2 Intraspecific competition, and density-dependent mortality and fecundity

Figure 5.3 shows the pattern of mortality in the flour beetle *Tribolium confusum* when cohorts were reared at a range of densities. Known numbers of eggs were placed in glass tubes with 0.5 g of a flour–yeast mixture, and the number of individuals that survived to become adults in each tube was noted. The same data have been expressed in three ways, and in each case the resultant curve has been divided into three regions. Figure 5.3a describes the relationship between density and the *per capita* mortality rate – literally, the mortality rate ‘per head’, i.e. the probability of an individual dying or the proportion that died between the egg and adult stages. Figure 5.3b describes how the number that died prior to the adult stage changed with density; and Figure 5.3c describes the relationship between density and the numbers that survived.

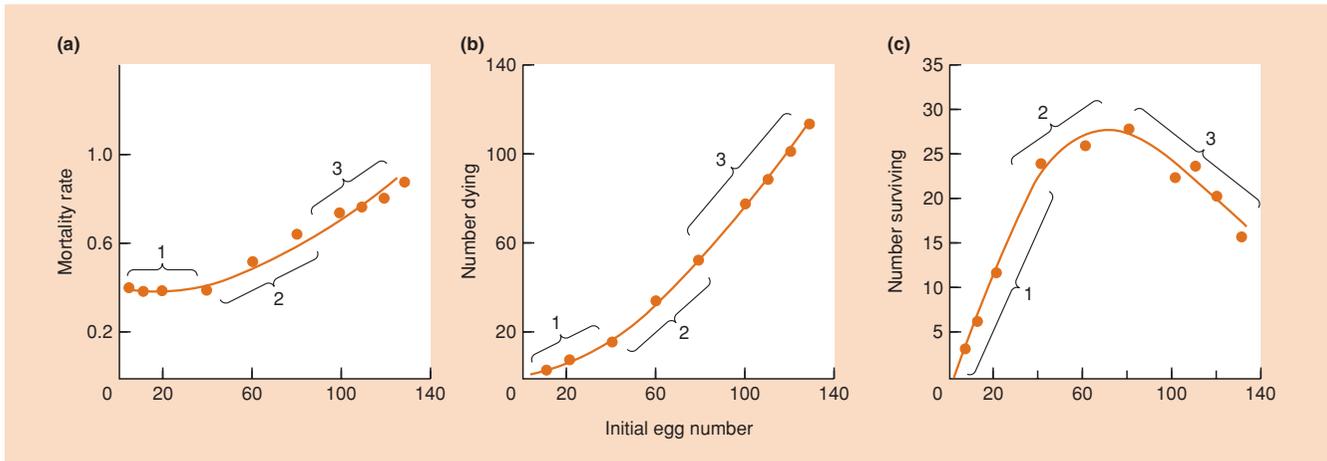
Throughout region 1 (low density) the mortality rate remained constant as density was increased (Figure 5.3a). The numbers dying and the numbers surviving both rose (Figure 5.3b, c) (not surprising, given that the numbers ‘available’ to die and survive increased), but the proportion dying remained the same, which accounts for the straight lines in region 1 of these figures. Mortality in this region is said to be density independent. Individuals died, but the chance of an individual surviving to become an adult was not changed by the initial density. Judged by this, there was no intraspecific competition between the beetles at these densities. Such density-independent deaths affect the population at all densities. They represent a baseline, which any density-dependent mortality will exceed.

In region 2, the mortality rate increased with density (Figure 5.3a): there was density-dependent mortality. The numbers dying continued to rise with density, but unlike region 1 they did so more than proportionately (Figure 5.3b). The numbers surviving also continued to rise, but this time less than proportionately (Figure 5.3c). Thus, over this range, increases in egg density continued to lead to increases in the total number of surviving adults. The mortality rate had increased, but it ‘undercompensated’ for increases in density.

undercompensating  
density dependence

In region 3, intraspecific competition was even more intense. The increasing mortality rate ‘overcompensated’ for any increase in density, i.e. over this range, the more eggs there were present, the fewer adults survived: an increase in the initial number of eggs led to an even

overcompensating  
density dependence



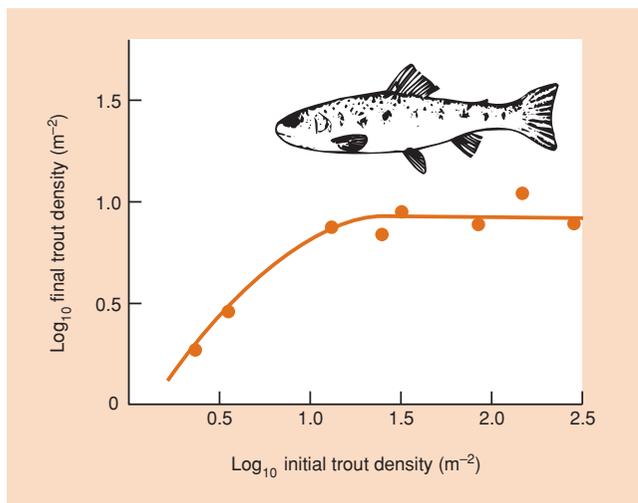
**Figure 5.3** Density-dependent mortality in the flour beetle *Tribolium confusum*: (a) as it affects mortality rate, (b) as it affects the numbers dying, and (c) as it affects the numbers surviving. In region 1 mortality is density independent; in region 2 there is undercompensating density-dependent mortality; in region 3 there is overcompensating density-dependent mortality. (After Bellows, 1981.)

greater proportional increase in the mortality rate. Indeed, if the range of densities had been extended, there would have been tubes with no survivors: the developing beetles would have eaten all the available food before any of them reached the adult stage.

**exactly compensating density dependence**

A slightly different situation is shown in Figure 5.4. This illustrates the relationship between density and mortality in young trout.

At the lower densities there was undercompensating density dependence, but at higher densities mortality never overcompensated. Rather, it compensated exactly for any increase in density: any rise in the number of fry was matched by an exactly equivalent rise in the



**Figure 5.4** An exactly compensating density-dependent effect on mortality: the number of surviving trout fry is independent of initial density at higher densities. (After Le Cren, 1973.)

mortality rate. The number of survivors therefore approached and maintained a constant level, irrespective of initial density.

The patterns of density-dependent fecundity that result from intraspecific competition are, in a sense, a mirror-image of those for mortality (Figure 5.5).

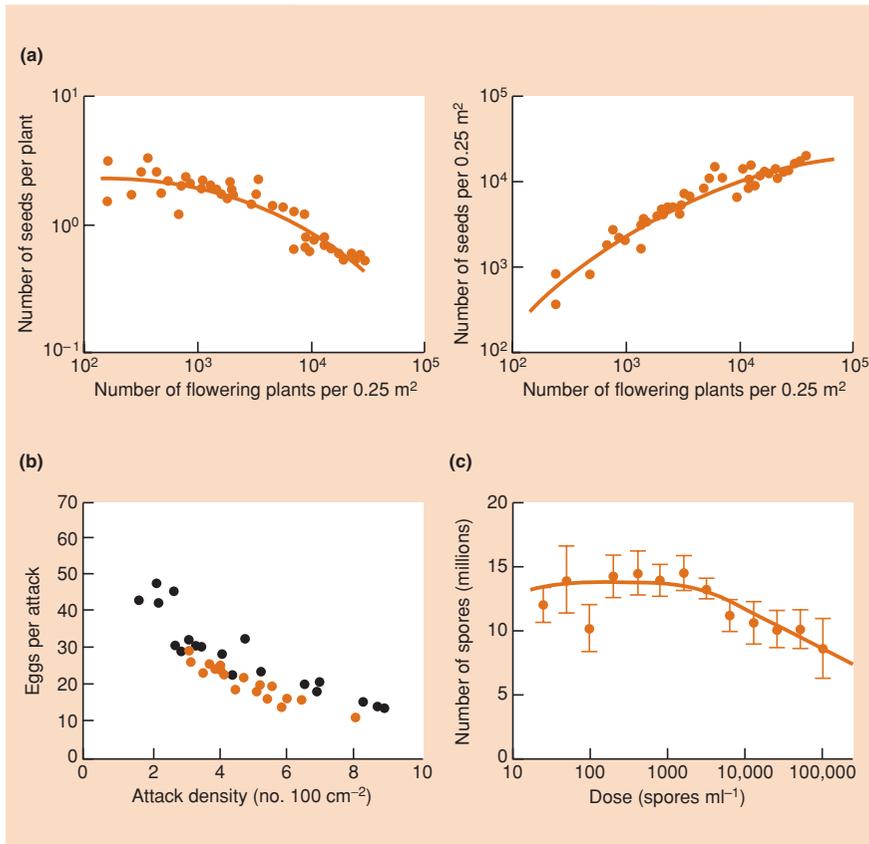
**intraspecific competition and fecundity**

Here, though, the per capita birth rate falls as intraspecific competition intensifies. At low enough densities, the birth rate may be density independent (Figure 5.5a, lower densities). But as density increases, and the effects of intraspecific competition become apparent, birth rate initially shows undercompensating density dependence (Figure 5.5a, higher densities), and may then show exactly compensating density dependence (Figure 5.5b, throughout; Figure 5.5c, lower densities) or overcompensating density dependence (Figure 5.5c, higher densities).

Thus, to summarize, irrespective of variations in over- and undercompensation, the essential point is a simple one: at appropriate densities, intraspecific competition can lead to density-dependent mortality and/or fecundity, which means that the death rate increases and/or the birth rate decreases as density increases. Thus, whenever there is intraspecific competition, its effect, whether on survival, fecundity or a combination of the two, is density dependent. However, as subsequent chapters will show, there are processes other than intraspecific competition that also have density-dependent effects.

### 5.3 Density or crowding?

Of course, the intensity of intraspecific competition experienced by an individual is not really determined by the density of the population as a whole. The effect on an individual is determined,



**Figure 5.5** (a) The fecundity (seeds per plant) of the annual dune plant *Vulpia fasciculata* is constant at the lowest densities (density independence, left). However, at higher densities, fecundity declines but in an undercompensating fashion, such that the total number of seeds continues to rise (right). (After Watkinson & Harper, 1978.) (b) Fecundity (eggs per attack) in the southern pine beetle, *Dendroctonus frontalis*, in East Texas declines with increasing attack density in a way that compensates more or less exactly for the density increases: the total number of eggs produced was roughly 100 per 100 cm<sup>2</sup>, irrespective of attack density over the range observed (●, 1992; ●, 1993). (After Reeve *et al.*, 1998.) (c) When the planktonic crustacean *Daphnia magna* was infected with varying numbers of spores of the bacterium *Pasteuria ramosa*, the total number of spores produced per host in the next generation was independent of density (exactly compensating) at the lower densities, but declined with increasing density (overcompensating) at the higher densities. Standard errors are shown. (After Ebert *et al.*, 2000.)

rather, by the extent to which it is crowded or inhibited by its immediate neighbors.

One way of emphasizing this is by noting that there are actually at least three different meanings of ‘density’ (see Lewontin & Levins, 1989, where details of calculations and terms can be found). Consider a population of insects, distributed over a population of plants on which they feed. This is a typical example of a very general phenomenon – a population (the insects in this case) being distributed amongst different patches of a resource (the plants). The density would usually be calculated as the number of insects (let us say 1000) divided by the number of plants (say 100), i.e. 10 insects per plant. This, which we would normally call simply the ‘density’, is actually the ‘resource-weighted density’. However, it gives an accurate measure of the intensity of competition suffered by the insects (the extent to which they are crowded) only if there are exactly 10 insects on every plant and every plant is the same size.

#### three meanings of density

Suppose, instead, that 10 of the plants support 91 insects each, and the remaining 90 support just one insect.

The resource-weighted density would still be 10 insects per plant. But the average density experienced by the insects would be 82.9 insects per plant. That is, one adds

up the densities experienced by each of the insects ( $91 + 91 + 91 \dots + 1 + 1$ ) and divides by the total number of insects. This is the ‘organism-weighted density’, and it clearly gives a much more satisfactory measure of the intensity of competition the insects are likely to suffer.

However, there remains the further question of the average density of insects experienced by the plants. This, which may be referred to as the ‘exploitation pressure’, comes out at 1.1 insects per plant, reflecting the fact that most of the plants support only one insect.

What, then, is the density of the insect? Clearly, it depends on whether you answer from the perspective of the insect or the plant – but whichever way you look at it, the normal practice of calculating the resource-weighted density and calling it the ‘density’ looks highly suspect. The difference between resource- and organism-weighted densities is illustrated for the human population of a number of US states in Table 5.1 (where the ‘resource’ is simply land area). The organism-weighted densities are so much larger than the usual, but rather unhelpful, resource-weighted densities essentially because most people live, crowded, in cities (Lewontin & Levins, 1989).

The difficulties of relying on density to characterize the potential intensity of intraspecific competition are particularly

**Table 5.1** A comparison of the resource- and organism-weighted densities of five states, based on the 1960 USA census, where the ‘resource patches’ are the counties within each state. (After Lewontin & Levins, 1989.)

State	Resource-weighted density (km <sup>-2</sup> )	Organism-weighted density (km <sup>-2</sup> )
Colorado	44	6,252
Missouri	159	6,525
New York	896	48,714
Utah	28	684
Virginia	207	13,824

acute with sessile, modular organisms, because, being sessile, they compete almost entirely only with their immediate neighbors, and being modular, competition is directed most at the modules that are closest to those neighbors. Thus, for instance, when silver birch

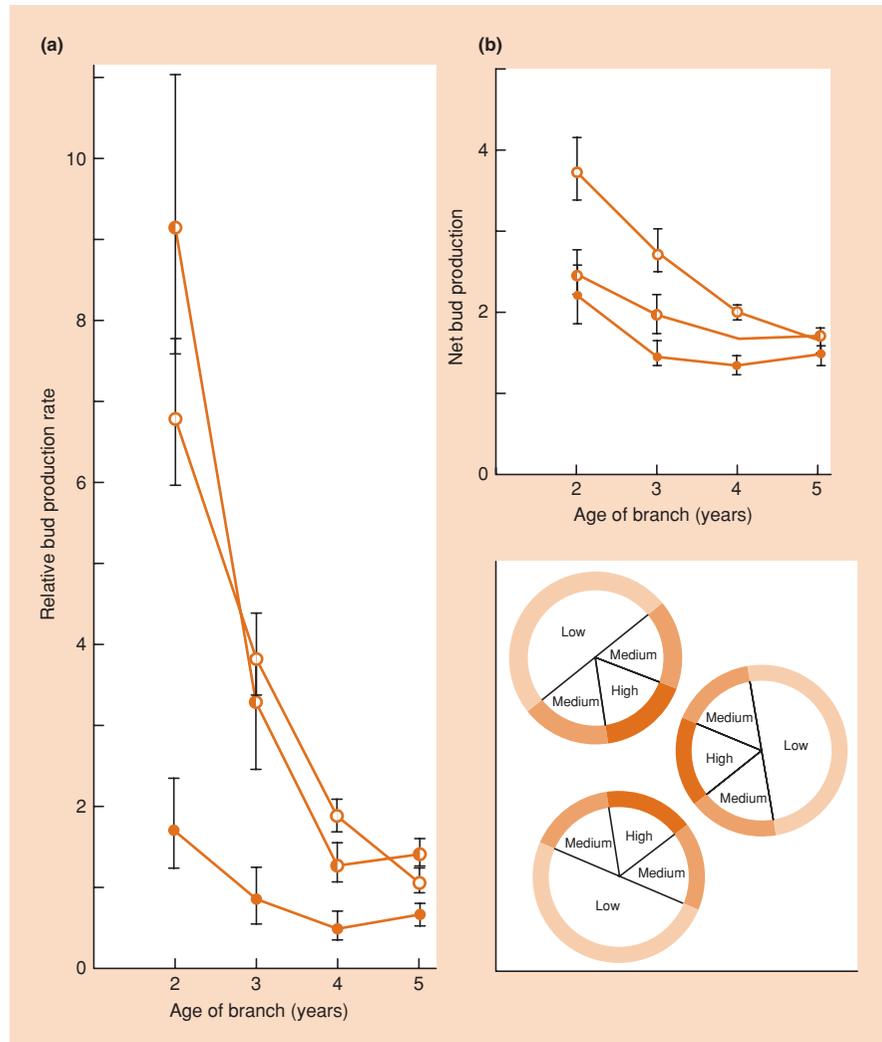
trees (*Betula pendula*) were grown in small groups, the sides of individual trees that interfaced with neighbors typically had a lower ‘birth’ and higher death rate of buds (see Section 4.2); whereas on sides of the same trees with no interference, bud birth rate was higher, death rate lower, branches were longer and the form approached that of an open-grown individual (Figure 5.6). Different modules experience different intensities of competition, and quoting the density at which an individual was growing would be all but pointless.

Thus, whether mobile or sessile, different individuals meet or suffer from different numbers of competitors.

density: a convenient expression of crowding

Density, especially resource-weighted density, is an abstraction that applies to the population as a whole but need not apply to any of the individuals within it. None the less, density may often be the most convenient way of expressing the degree to which individuals are crowded – and it is certainly the way it has usually been expressed.

**Figure 5.6** Mean relative bud production (new buds per existing bud) for silver birch trees (*Betula pendula*), expressed (a) as gross bud production and (b) as net bud production (birth minus death), in different interference zones. These zones are themselves explained in the inset. ●, high interference; ○, medium; ○, low. Bars represent standard errors. (After Jones & Harper, 1987.)

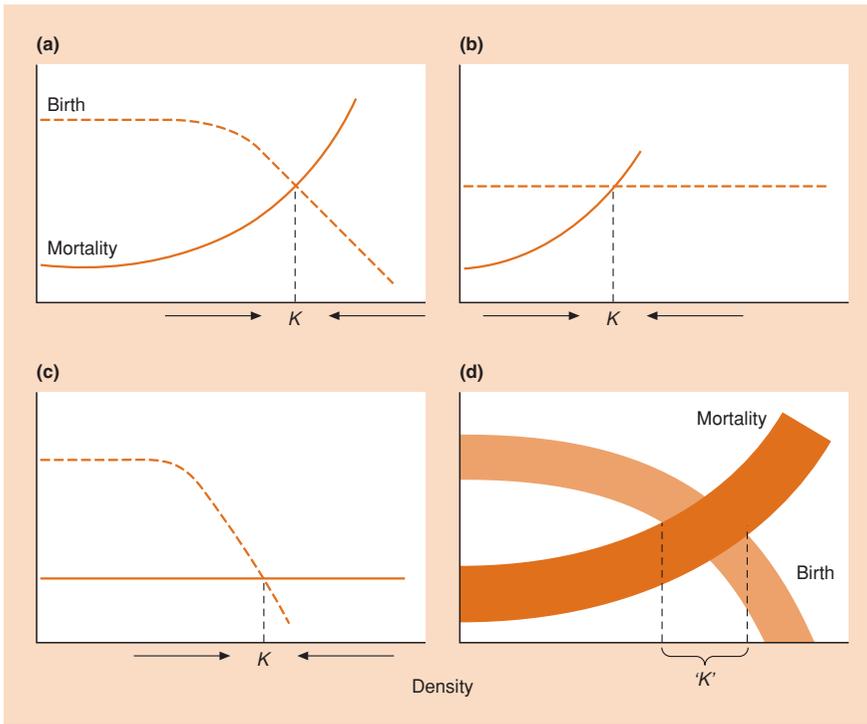


**5.4 Intraspecific competition and the regulation of population size**

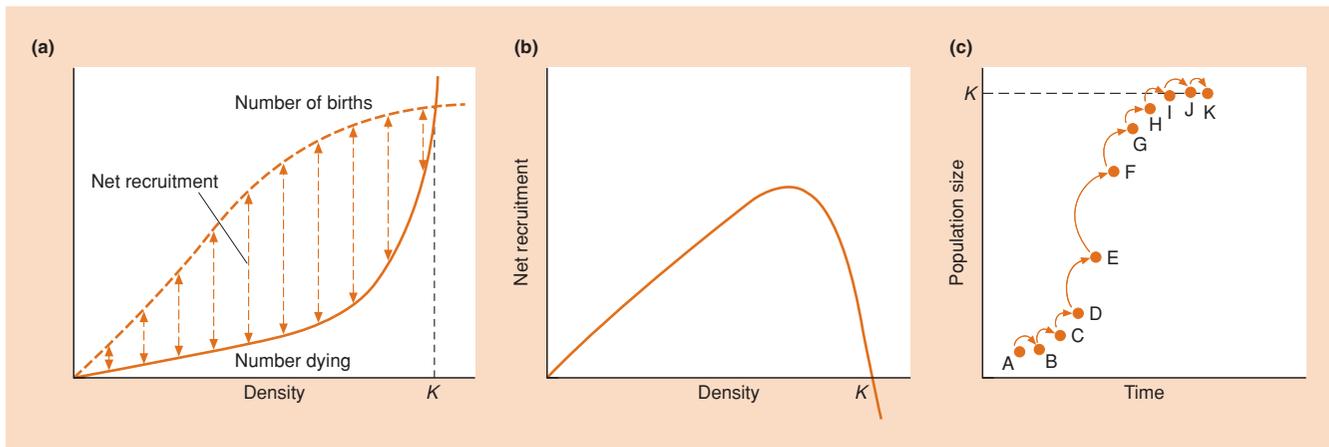
There are, then, typical patterns in the effects of intraspecific competition on birth and death (see Figures 5.3–5.5). These generalized patterns are summarized in Figures 5.7 and 5.8.

**5.4.1 Carrying capacities**

Figure 5.7a–c reiterates the fact that as density increases, the per capita birth rate eventually falls and the per capita death rate eventually rises. There must, therefore, be a density at which these curves cross. At densities below this point, the birth rate exceeds



**Figure 5.7** Density-dependent birth and mortality rates lead to the regulation of population size. When both are density dependent (a), or when either of them is (b, c), their two curves cross. The density at which they do so is called the carrying capacity ( $K$ ). Below this the population increases, above it the population decreases:  $K$  is a stable equilibrium. However, these figures are the grossest of caricatures. The situation is closer to that shown in (d), where mortality rate broadly increases, and birth rate broadly decreases, with density. It is possible, therefore, for the two rates to balance not at just one density, but over a broad range of densities, and it is towards this broad range that other densities tend to move.



**Figure 5.8** Some general aspects of intraspecific competition. (a) Density-dependent effects on the numbers dying and the number of births in a population: net recruitment is ‘births minus deaths’. Hence, as shown in (b), the density-dependent effect of intraspecific competition on net recruitment is a domed or ‘n’-shaped curve. (c) A population increasing in size under the influence of the relationships in (a) and (b). Each arrow represents the change in size of the population over one interval of time. Change (i.e. net recruitment) is small when density is low (i.e. at small population sizes: A to B, B to C) and is small close to the carrying capacity (I to J, J to K), but is large at intermediate densities (E to F). The result is an ‘S’-shaped or sigmoidal pattern of population increase, approaching the carrying capacity.

the death rate and the population increases in size. At densities above the crossover point, the death rate exceeds the birth rate and the population declines. At the crossover density itself, the two rates are equal and there is no net change in population size. This density therefore represents a stable equilibrium, in that all other densities will tend to approach it. In other words, intraspecific competition, by acting on birth rates and death rates, can regulate populations at a stable density at which the birth rate equals the death rate. This density is known as the *carrying capacity* of the population and is usually denoted by  $K$  (Figure 5.7). It is called a carrying capacity because it represents the population size that the resources of the environment can just maintain ('carry') without a tendency to either increase or decrease.

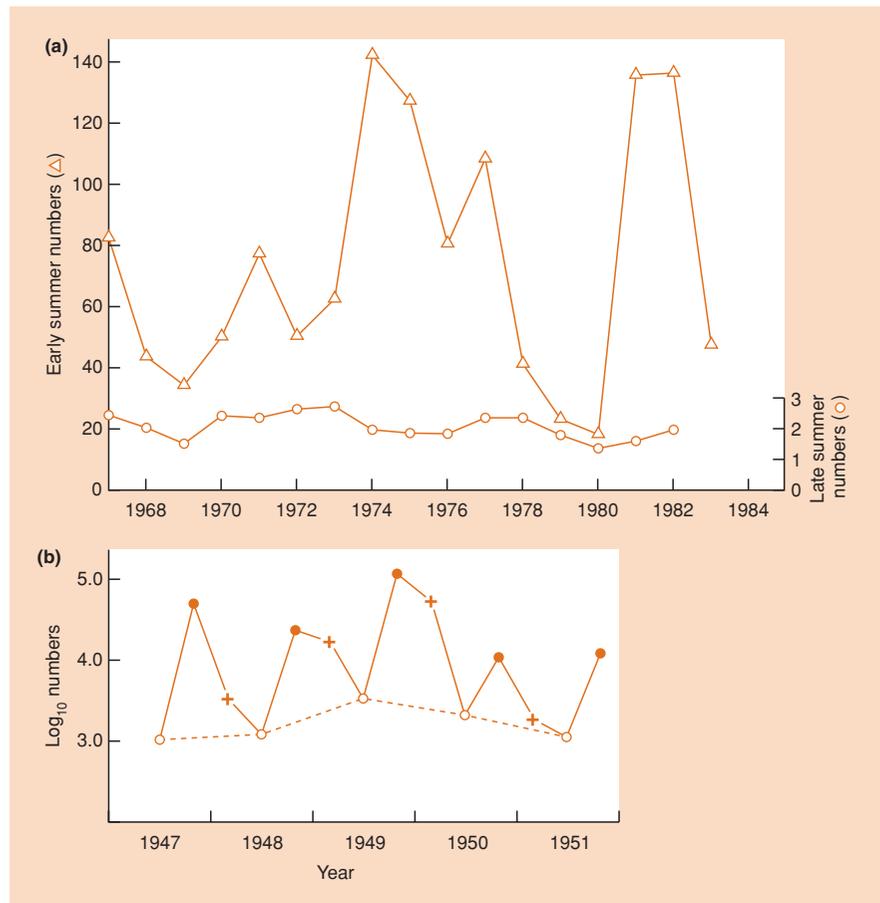
real populations lack simple carrying capacities

However, whilst hypothetical populations caricatured by line drawings like Figures 5.7a–c can be characterized by a simple carrying capacity, this is not true of any natural population. There are unpredictable environmental fluctuations; individuals are affected by a whole wealth of factors of which intraspecific

competition is only one; and resources not only affect density but respond to density as well. Hence, the situation is likely to be closer to that depicted in Figure 5.7d. Intraspecific competition does not hold natural populations to a predictable and unchanging level (the carrying capacity), but it may act upon a very wide range of starting densities and bring them to a much narrower range of final densities, and it therefore tends to keep density within certain limits. It is in this sense that intraspecific competition may be said typically to be capable of regulating population size. For instance, Figure 5.9 shows the fluctuations within and between years in populations of the brown trout (*Salmo trutta*) and the grasshopper, *Chorthippus brunneus*. There are no simple carrying capacities in these examples, but there are clear tendencies for the 'final' density each year ('late summer numbers' in the first case, 'adults' in the second) to be relatively constant, despite the large fluctuations in density within each year and the obvious potential for increase that both populations possess.

In fact, the concept of a population settling at a stable carrying capacity, even in caricatured populations, is relevant only to situations in which density dependence is not strongly overcompensating. Where there is overcompensation, cycles or even

**Figure 5.9** Population regulation in practice. (a) Brown trout (*Salmo trutta*) in an English Lake District stream.  $\Delta$ , numbers in early summer, including those newly hatched from eggs;  $\circ$ , numbers in late summer. Note the difference in vertical scales. (After Elliott, 1984.) (b) The grasshopper, *Chorthippus brunneus*, in southern England.  $\bullet$ , eggs;  $+$ , nymphs;  $\circ$ , adults. Note the logarithmic scale. (After Richards & Waloff, 1954.) There are no definitive carrying capacities, but the 'final' densities each year ('late summer' and 'adults') are relatively constant despite large fluctuations within years.



chaotic changes in population size may be the result. We return to this point later (see Section 5.8).

### 5.4.2 Net recruitment curves

An alternative general view of intraspecific competition is shown in Figure 5.8a, which deals with numbers rather than rates. The difference there between the two curves ('births minus deaths' or 'net recruitment') is the net number of additions expected in the population during the appropriate stage or over one interval of time. Because of the shapes of the birth and death curves, the net number of additions is small at the lowest densities, increases as density rises, declines again as the carrying capacity is approached and is then negative (deaths exceed births) when the initial density exceeds  $K$  (Figure 5.8b). Thus, total recruitment into a population is small when there are few individuals available to give birth, and small when intraspecific competition is intense. It reaches a peak, i.e. the population increases in size most rapidly, at some intermediate density.

peak recruitment occurs at intermediate densities

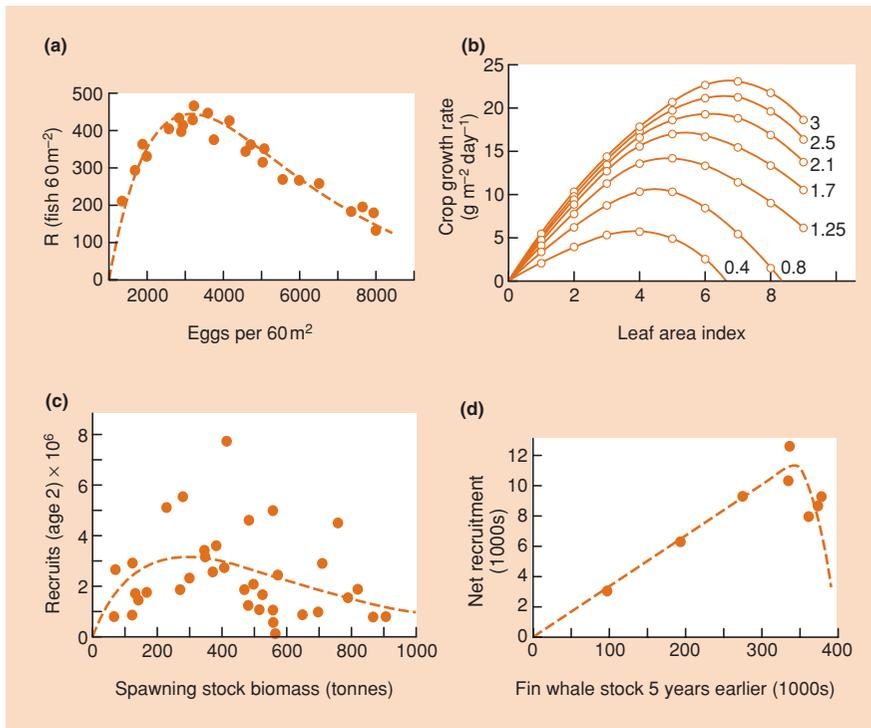
The precise nature of the relationship between a population's net rate of recruitment and its density varies with the detailed biology of the species concerned (e.g. the trout, clover plants, herring and whales in Figure 5.10a–d).

Moreover, because recruitment is affected by a whole multiplicity of factors, the data points rarely fall exactly on any single curve. Yet,

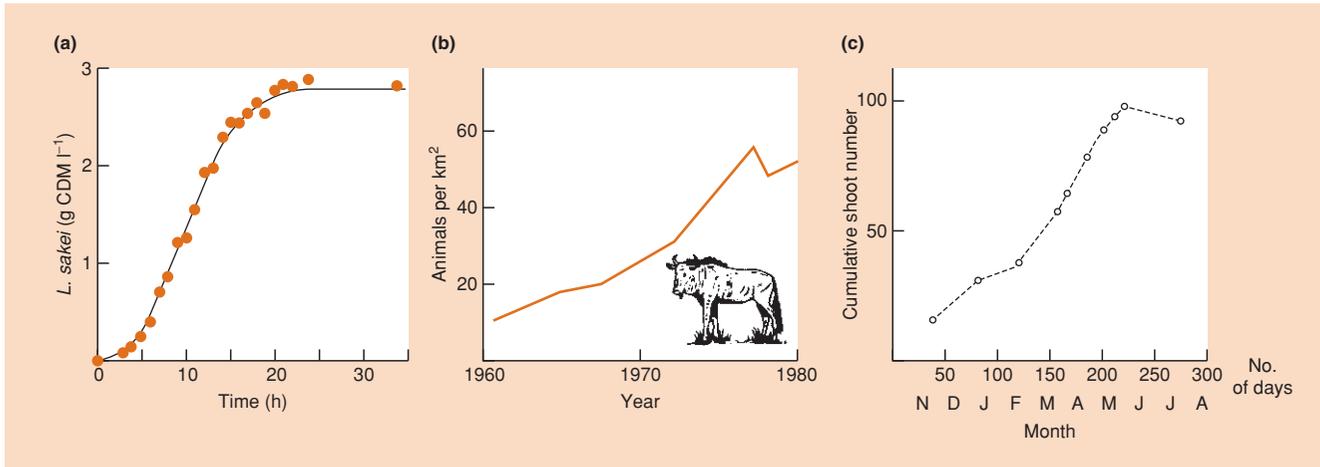
in each case in Figure 5.10, a domed curve is apparent. This reflects the general nature of density-dependent birth and death whenever there is intraspecific competition. Note also that one of these (Figure 5.10b) is modular: it describes the relationship between the leaf area index (LAI) of a plant population (the total leaf area being borne per unit area of ground) and the population's growth rate (modular birth minus modular death). The growth rate is low when there are few leaves, peaks at an intermediate LAI, and is then low again at a high LAI, where there is much mutual shading and competition and many leaves may be consuming more in respiration than they contribute through photosynthesis.

### 5.4.3 Sigmoidal growth curves

In addition, curves of the type shown in Figure 5.8a and b may be used to suggest the pattern by which a population might increase from an initially very small size (e.g. when a species colonizes a previously unoccupied area). This is illustrated in Figure 5.8c. Imagine a small population, well below the carrying capacity of its environment (point A). Because the population is small, it increases in size only slightly during one time interval, and only reaches point B. Now, however, being larger, it increases in size more rapidly during the next time interval (to point C), and even more during the next (to point D). This process continues until the population passes beyond the peak of its net recruitment curve (Figure 5.8b). Thereafter, the population increases in size less and less with each time interval until the population reaches its



**Figure 5.10** Some dome-shaped net-recruitment curves. (a) Six-month old brown trout, *Salmo trutta*, in Black Brows Beck, UK, between 1967 and 1989. (After Myers, 2001; following Elliott, 1994.) (b) The relationship between crop growth rate of subterranean clover, *Trifolium subterraneum*, and leaf area index at various intensities of radiation (kJ cm<sup>-2</sup> day<sup>-1</sup>). (After Black, 1963.) (c) 'Blackwater' herring, *Clupea harengus*, from the Thames estuary between 1962 and 1997. (After Fox, 2001.) (d) Estimates for the stock of Antarctic fin whales. (After Allen, 1972.)



**Figure 5.11** Real examples of S-shaped population increase. (a) The bacterium *Lactobacillus sakei* (measured as grams of ‘cell dry mass’ (CDM) per liter) grown in nutrient broth. (After Leroy & de Vuyst, 2001.) (b) The population of wildebeest *Connochaetes taurinus*, of the Serengeti region of Tanzania and Kenya seems to be leveling off after rising from a low density caused by the disease rinderpest. (After Sinclair & Norton-Griffiths, 1982; Deshmukh, 1986.) (c) The population of shoots of the annual *Juncus gerardi* in a salt marsh habitat on the west coast of France. (After Bouzille *et al.*, 1997.)

carrying capacity ( $K$ ) and ceases completely to increase in size. The population might therefore be expected to follow an S-shaped or ‘sigmoidal’ curve as it rises from a low density to its carrying capacity. This is a consequence of the hump in its recruitment rate curve, which is itself a consequence of intraspecific competition.

Of course, Figure 5.8c, like the rest of Figure 5.8, is a gross simplification. It assumes, apart from anything else, that changes in population size are affected only by intraspecific competition. Nevertheless, something akin to sigmoidal population growth can be perceived in many natural and experimental situations (Figure 5.11).

Intraspecific competition will be obvious in certain cases (such as overgrowth competition between sessile organisms on a rocky shore), but this will not be true of every population examined. Individuals are also affected by predators, parasites and prey, competitors from other species, and the many facets of their physical and chemical environment. Any of these may outweigh or obscure the effects of intraspecific competition; or the effect of these other factors at one stage may reduce the density to well below the carrying capacity for all subsequent stages. Nevertheless, intraspecific competition probably affects most populations at least sometimes during at least one stage of their life cycle.

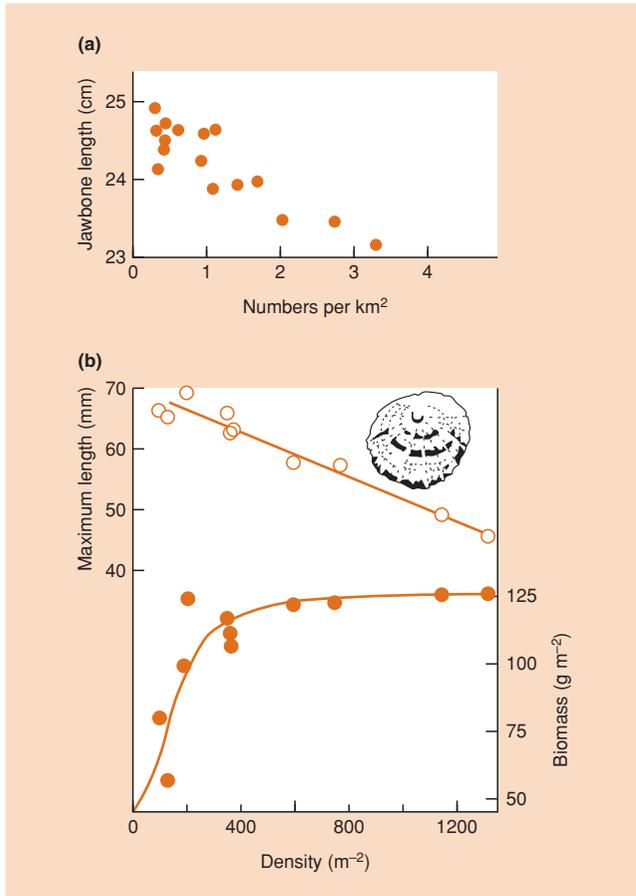
## 5.5 Intraspecific competition and density-dependent growth

Intraspecific competition, then, can have a profound effect on the number of individuals in a population; but it can have an equally

profound effect on the individuals themselves. In populations of unitary organisms, rates of growth and rates of development are commonly influenced by intraspecific competition. This necessarily leads to density-dependent effects on the composition of a population. For instance, Figure 5.12a and b shows two examples in which individuals were typically smaller at higher densities. This, in turn, often means that although the numerical size of a population is regulated only approximately by intraspecific competition, the total biomass is regulated much more precisely. This, too, is illustrated by the limpets in Figure 5.12b.

### 5.5.1 The law of constant final yield

Such effects are particularly marked in modular organisms. For example, when carrot seeds (*Daucus carota*) were sown at a range of densities, the yield per pot at the first harvest (29 days) increased with the density of seeds sown (Figure 5.13). After 62 days, however, and even more after 76 and 90 days, yield no longer reflected the numbers sown. Rather it was the same over a wide range of initial densities, especially at higher densities where competition was most intense. This pattern has frequently been noted by plant ecologists and has been called the ‘law of constant final yield’ (Kira *et al.*, 1953). Individuals suffer density-dependent reductions in growth rate, and thus in individual plant size, which tend to compensate exactly for increases in density (hence the constant final yield). This suggests, of course, that there are limited resources available for plant growth, especially at high densities, which is borne out in Figure 5.13 by the higher (constant) yields at higher nutrient levels.



**Figure 5.12** (a) Jawbone length indicates that reindeer grow to a larger size at lower densities. (After Skogland, 1983.) (b) In populations of the limpet *Patella cochlear*, individual size declines with density leading to an exact regulation of the population’s biomass. (After Branch, 1975.)

Yield is density ( $d$ ) multiplied by mean weight per plant ( $\bar{w}$ ). Thus, if yield is constant ( $c$ ):

$$d\bar{w} = c, \tag{5.1}$$

and so:

$$\log d + \log \bar{w} = \log c \tag{5.2}$$

and:

$$\log \bar{w} = \log c - 1 \cdot \log d \tag{5.3}$$

and thus, a plot of log mean weight against log density should have a slope of  $-1$ .

Data on the effects of density on the growth of the grass *Vulpia fasciculata* are shown in Figure 5.14, and the slope of the curve

towards the end of the experiment does indeed approach a value of  $-1$ . Here too, as with the carrot plants, individual plant weight at the first harvest was reduced only at very high densities – but as the plants became larger, they interfered with each other at successively lower densities.

constant yield and modularity

The constancy of the final yield is a result, to a large extent, of the modularity of plants. This was clear when perennial rye grass (*Lolium perenne*) was sown at a 30-fold range of densities (Figure 5.15). After 180 days some genets had died; but the range of final tiller (module) densities was far narrower than that of genets (individuals). The regulatory powers of intraspecific competition were operating largely by affecting the number of modules per genet rather than the number of genets themselves.

### 5.6 Quantifying intraspecific competition

Every population is unique. Nevertheless, we have already seen that there are general patterns in the action of intraspecific competition. In this section we take such generalizations a stage further. A method will be described, utilizing  $k$  values (see Chapter 4) to summarize the effects of intraspecific competition on mortality, fecundity and growth. Mortality will be dealt with first. The method will then be extended for use with fecundity and growth.

A  $k$  value was defined by the use of  $k$  values formula:

$$k = \log(\text{initial density}) - \log(\text{final density}), \tag{5.4}$$

or, equivalently:

$$k = \log(\text{initial density}/\text{final density}). \tag{5.5}$$

For present purposes, ‘initial density’ may be denoted by  $B$ , standing for ‘numbers before the action of intraspecific competition’, whilst ‘final density’ may be denoted by  $A$ , standing for ‘numbers after the action of intraspecific competition’. Thus:

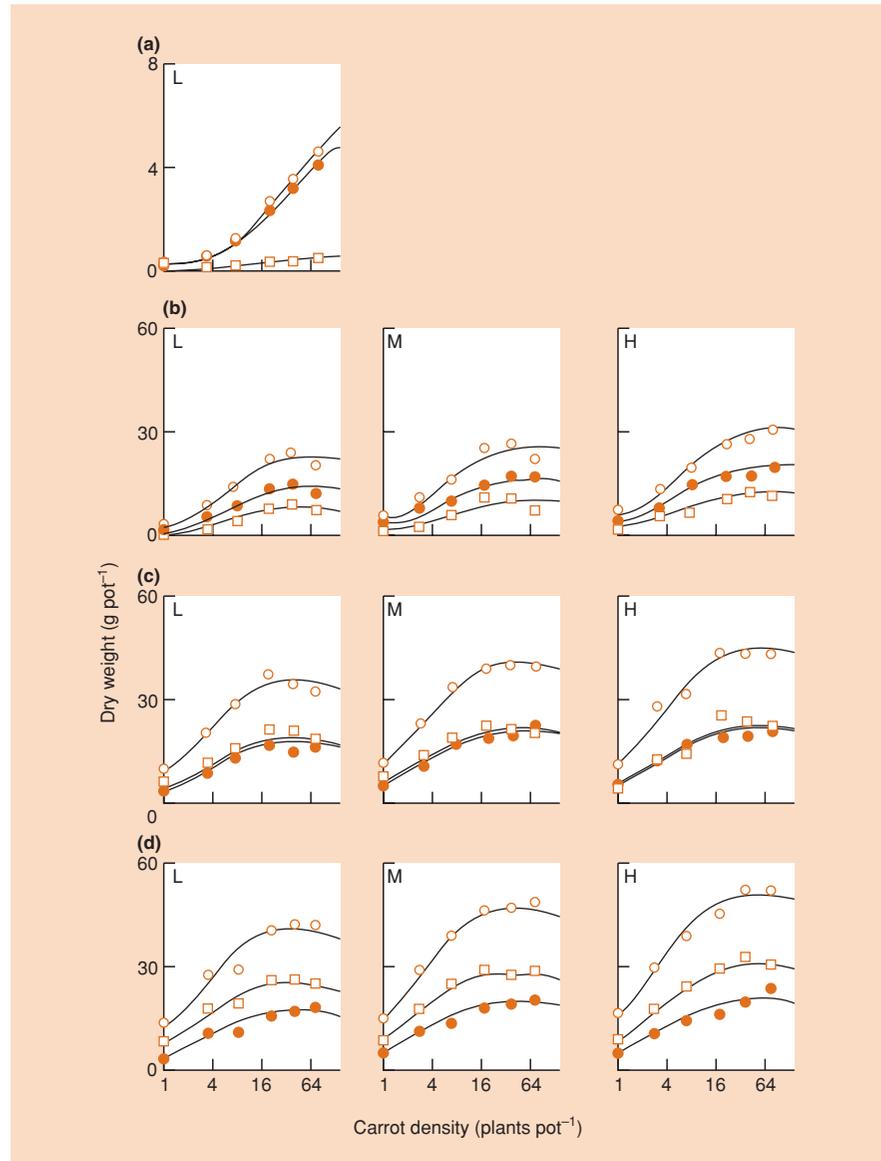
$$k = \log(B/A). \tag{5.6}$$

Note that  $k$  increases as mortality rate increases.

Some examples of the effects of intraspecific competition on mortality are shown in Figure 5.16, in which  $k$  is plotted against  $\log B$ . In several cases,  $k$  is constant at the lowest densities. This is an indication of density independence: the proportion surviving is not correlated with initial density. At higher densities,  $k$  increases with initial density; this indicates density dependence. Most importantly,

plots of  $k$  against log density

**Figure 5.13** The relationship between yield per pot and sowing density in carrots (*Daucus carota*) at four harvests ((a) 29 days after sowing, (b) 62 days, (c) 76 days, and (d) 90 days) and at three nutrient levels (low, medium and high: L, M and H), given to pots weekly after the first harvest. Points are means of three replicates, with the exception of the lowest density (9) and the first harvest (9). □, root weight, ●, shoot weight, ○, total weight. The curves were fitted in line with theoretical yield–density relationships, the details of which are unimportant in this context. (After Li *et al.*, 1996.)



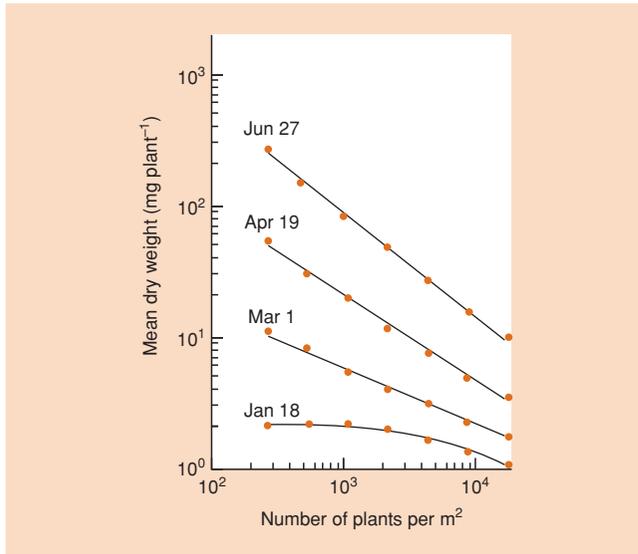
however, the way in which  $k$  varies with the logarithm of density indicates the precise nature of the density dependence. For example, Figure 5.16a and b describes, respectively, situations in which there is under- and exact compensation at higher densities. The exact compensation in Figure 5.16b is indicated by the slope of the curve (denoted by  $b$ ) taking a constant value of 1 (the mathematically inclined will see that this follows from the fact that with exact compensation  $A$  is constant). The undercompensation that preceded this at lower densities, and which is seen in Figure 5.16a even at higher densities, is indicated by the fact that  $b$  is less than 1.

#### scramble and contest

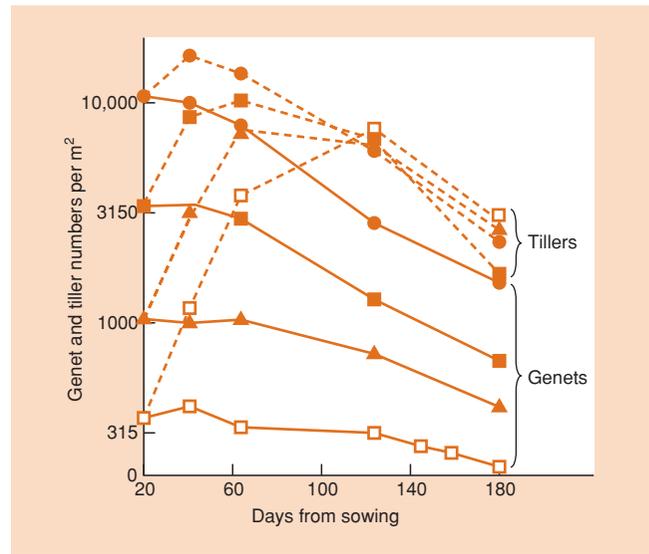
Exact compensation ( $b = 1$ ) is often referred to as pure contest competition, because there are a constant number of

winners (survivors) in the competitive process. The term was initially proposed by Nicholson (1954), who contrasted it with what he called pure scramble competition. Pure scramble is the most extreme form of overcompensating density dependence, in which all competing individuals are so adversely affected that none of them survive, i.e.  $A = 0$ . This would be indicated in Figure 5.16 by a  $b$  value of infinity (a vertical line), and Figure 5.16c is an example in which this is the case. More common, however, are examples in which competition is scramble-like, i.e. there is considerable but not total overcompensation ( $b \gg 1$ ). This is shown, for instance, in Figure 5.16d.

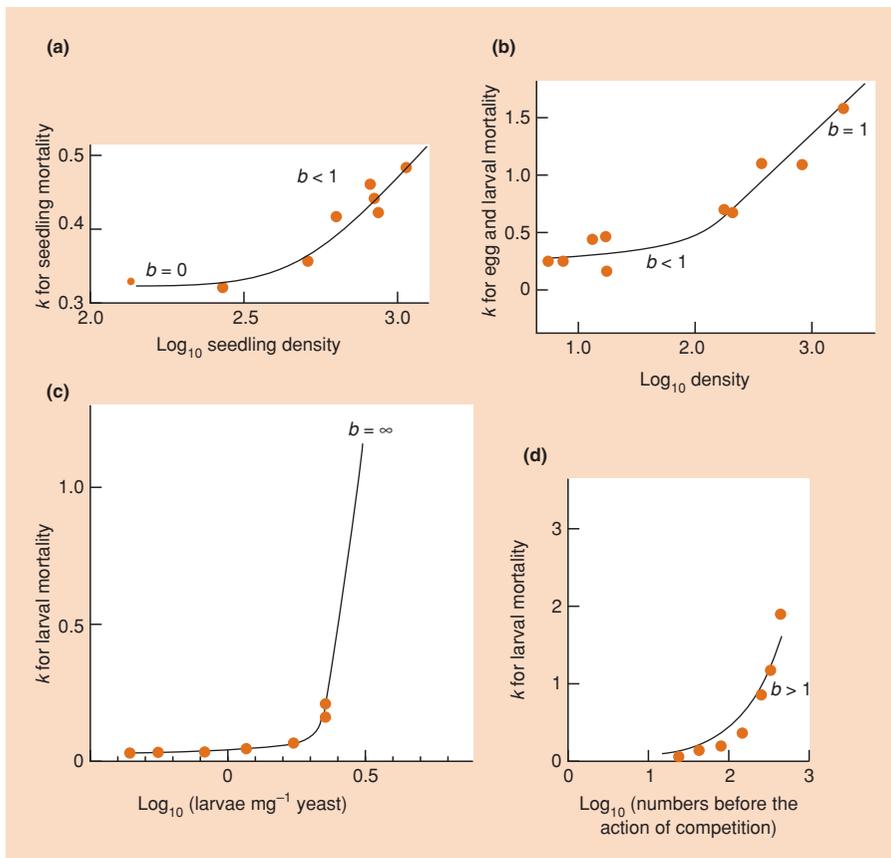
Plotting  $k$  against  $\log B$  is thus an informative way of depicting the effects of intraspecific competition on mortality. Variations in the slope of the curve ( $b$ ) give a clear indication



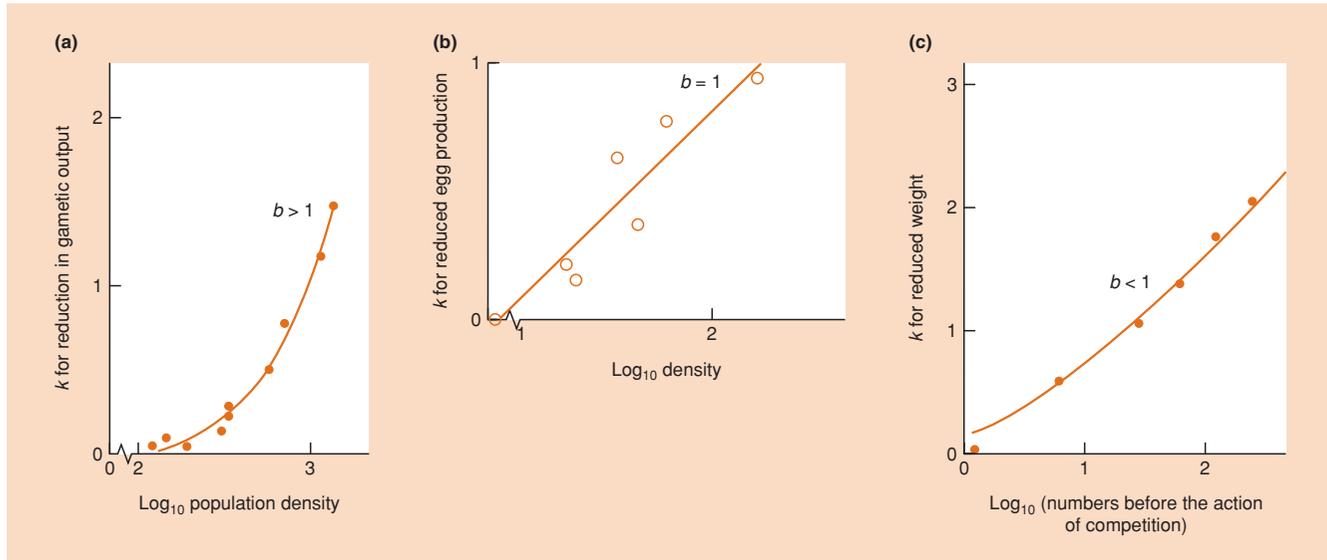
**Figure 5.14** The ‘constant final yield’ of plants illustrated by a line of slope  $-1$  when log mean weight is plotted against log density in the dune annual, *Vulpia fasciculata*. On January 18, particularly at low densities, growth and hence mean dry weight were roughly independent of density. But by June 27, density-dependent reductions in growth compensated exactly for variations in density, leading to a constant yield. (After Watkinson, 1984.)



**Figure 5.15** Intraspecific competition in plants often regulates the number of modules. When populations of rye grass (*Lolium perenne*) were sown at a range of densities, the range of final tiller (i.e. module) densities was far narrower than that of genets. (After Kays & Harper, 1974.)



**Figure 5.16** The use of  $k$  values for describing patterns of density-dependent mortality. (a) Seedling mortality in the dune annual, *Androsace septentrionalis*, in Poland. (After Symonides, 1979.) (b) Egg mortality and larval competition in the almond moth, *Ephestia cautella*. (After Benson, 1973a.) (c) Larval competition in the fruit-fly, *Drosophila melanogaster*. (After Bakker, 1961.) (d) Larval mortality in the moth, *Plodia interpunctella*. (After Snyman, 1949.)



**Figure 5.17** The use of  $k$  values for describing density-dependent reductions in fecundity and growth. (a) Fecundity in the limpet *Patella cochlear* in South Africa. (After Branch, 1975.) (b) Fecundity in the cabbage root fly, *Eriosichia brassicae*. (After Benson, 1973b.) (c) Growth in the shepherd's purse plant, *Capsella bursa-pastoris*. (After Palmblad, 1968.)

of the manner in which density dependence changes with density. The method can also be extended to fecundity and growth.

For fecundity, it is necessary to think of  $B$  as the 'total number of offspring that would have been produced had there been no intraspecific competition', i.e. if each reproducing individual had produced as many offspring as it would have done in a competition-free environment.  $A$  is then the total number of offspring actually produced. (In practice,  $B$  is usually estimated from the population experiencing the least competition – not necessarily competition-free.) For growth,  $B$  must be thought of as the total biomass, or total number of modules, that would have been produced had all individuals grown as if they were in a competition-free situation.  $A$  is then the total biomass or total number of modules actually produced.

Figure 5.17 provides examples in which  $k$  values are used to describe the effects of intraspecific competition on fecundity and growth. The patterns are essentially similar to those in Figure 5.16. Each falls somewhere on the continuum ranging between density independence and pure scramble, and their position along that continuum is immediately apparent. Using  $k$  values, all examples of intraspecific competition can be quantified in the same terms. With fecundity and growth, however, the terms 'scramble' and especially 'contest' are less appropriate. It is better simply to talk in terms of exact, over- and undercompensation.

## 5.7 Mathematical models: introduction

The desire to formulate general rules in ecology often finds its expression in the construction of mathematical or graphical

models. It may seem surprising that those interested in the natural living world should spend time reconstructing it in an artificial mathematical form; but there are several good reasons why this should be done. The first is that models can crystallize, or at least bring together in terms of a few parameters, the important, shared properties of a wealth of unique examples. This simply makes it easier for ecologists to think about the problem or process under consideration, by forcing us to try to extract the essentials from complex systems. Thus, a model can provide a 'common language' in which each unique example can be expressed; and if each can be expressed in a common language, then their properties relative to one another, and relative perhaps to some ideal standard, will be more apparent.

These ideas are more familiar, perhaps, in other contexts. Newton never laid hands on a perfectly frictionless body, and Boyle never saw an ideal gas – other than in their imaginations – but Newton's Laws of Motion and Boyle's Law have been of immeasurable value to us for centuries.

Perhaps more importantly, however, models can actually shed light on the real world that they mimic. Specific examples below will make this apparent. Models can, as we shall see, exhibit properties that the system being modeled had not previously been known to possess. More commonly, models make it clear how the behavior of a population, for example, depends on the properties of the individuals that comprise it. That is, models allow us to see the likely consequences of any assumptions that we choose to make – 'If it were the case that only juveniles migrate, what would this do to the dynamics of their populations?' – and so on. Models can do this because mathematical methods are designed precisely to allow a set of assumptions to be followed through

to their natural conclusions. As a consequence, models often suggest what would be the most profitable experiments to carry out or observations to make – ‘Since juvenile migration rates appear to be so important, these should be measured in each of our study populations’.

These reasons for constructing models are also criteria by which any model should be judged. Indeed, a model is only useful (i.e. worth constructing) if it does perform one or more of these functions. Of course, in order to perform them a model must adequately describe real situations and real sets of data, and this ‘ability to describe’ or ‘ability to mimic’ is itself a further criterion by which a model can be judged. However, the crucial word is ‘adequate’. The only perfect description of the real world is the real world itself. A model is an adequate description, ultimately, as long as it performs a useful function.

In the present case, some simple models of intraspecific competition will be described. They will be built up from a very elementary starting point, and their properties (i.e. their ability to satisfy the criteria described above) will then be examined. Initially, a model will be constructed for a population with discrete breeding seasons.

### 5.8 A model with discrete breeding seasons

#### 5.8.1 Basic equations

In Section 4.7 we developed a simple model for species with discrete breeding seasons, in which the population size at time  $t$ ,  $N_t$ , altered in size under the influence of a fundamental net reproductive rate,  $R$ . This model can be summarized in two equations:

$$N_{t+1} = N_t R \tag{5.7}$$

and:

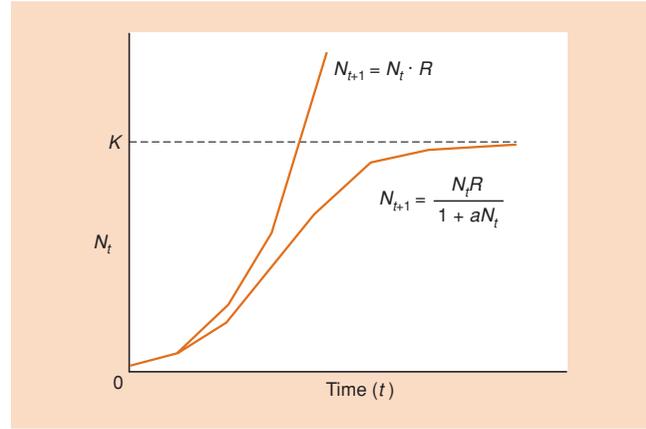
$$N_t = N_0 R^t \tag{5.8}$$

**no competition:  
exponential growth**

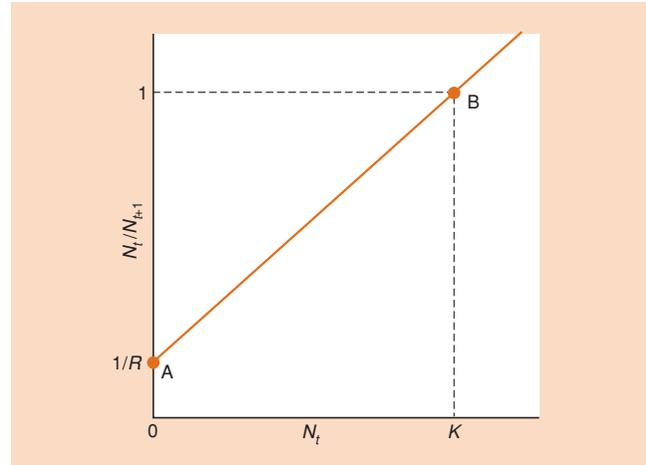
The model, however, describes a population in which there is no competition.  $R$  is constant, and if  $R > 1$ , the population will continue to increase in size indefinitely (‘exponential growth’, shown in Figure 5.18). The first step is therefore to modify the equations by making the net reproductive rate subject to intraspecific competition. This is done in Figure 5.19, which has three components.

At point A, the population size is very small ( $N_t$  is virtually zero). Competition is therefore negligible, and the actual net reproductive rate is adequately defined by an unmodified  $R$ . Thus, Equation 5.7 is still appropriate, or, rearranging the equation:

$$N_t/N_{t+1} = 1/R. \tag{5.9}$$



**Figure 5.18** Mathematical models of population increase with time, in populations with discrete generations: exponential increase (left) and sigmoidal increase (right).



**Figure 5.19** The simplest, straight-line way in which the inverse of generation increase ( $N_t/N_{t+1}$ ) might rise with density ( $N_t$ ). For further explanation, see text.

At point B, by contrast, the population size ( $N_t$ ) is very much larger and there is a significant amount of intraspecific competition, such that the net reproductive rate has been so modified by competition that the population can collectively do no better than replace itself each generation, because ‘births’ equal ‘deaths’. In other words,  $N_{t+1}$  is simply the same as  $N_t$ , and  $N_t/N_{t+1}$  equals 1. The population size at which this occurs is, by definition, the carrying capacity,  $K$  (see Figure 5.7).

The third component of Figure 5.19 is the straight line joining point A to point B and extending beyond it. This describes the progressive modification of the actual net reproductive rate as population size increases; but its straightness is simply an

**incorporating  
competition**

assumption made for the sake of expediency, since all straight lines are of the simple form:  $y = (\text{slope})x + (\text{intercept})$ . In Figure 5.19,  $N_t/N_{t+1}$  is measured on the  $y$ -axis,  $N_t$  on the  $x$ -axis, the intercept is  $1/R$  and the slope, based on the segment between points A and B, is  $(1 - 1/R)/K$ . Thus:

$$\frac{N_t}{N_{t+1}} = \frac{1 - \frac{1}{R}}{K} \cdot N_t + \frac{1}{R} \quad (5.10)$$

or, rearranging:

$$N_{t+1} = \frac{N_t R}{1 + \frac{(R-1)N_t}{K}} \quad (5.11)$$

a simple model of intraspecific competition

For further simplicity,  $(R-1)/K$  may be denoted by  $a$  giving:

$$N_{t+1} = \frac{N_t R}{(1 + aN_t)} \quad (5.12)$$

This is a model of population increase limited by intraspecific competition. Its essence lies in the fact that the unrealistically constant  $R$  in Equation 5.7 has been replaced by an actual net reproductive rate,  $R/(1 + aN_t)$ , which decreases as population size ( $N_t$ ) increases.

which comes first –  $a$  or  $K$ ?

We, like many others, derived Equation 5.12 as if the behavior of a population is jointly determined by  $R$  and  $K$ , the per capita rate of increase and the

population's carrying capacity –  $a$  is then simply a particular combination of these. An alternative point of view is that  $a$  is meaningful in its own right, measuring the per capita susceptibility to crowding: the larger the value of  $a$ , the greater the effect of density on the actual rate of increase in the population (Kuno, 1991). Now the behavior of a population is seen as being jointly determined by two properties of the individuals within it – their intrinsic per capita rate of increase and their susceptibility to crowding,  $R$  and  $a$ . The carrying capacity of the population ( $K = (R-1)/a$ ) is then simply an outcome of these properties. The great advantage of this viewpoint is that it places individuals and populations in a more realistic biological perspective. Individuals come first: individual birth rates, death rates and susceptibilities to crowding are subject to natural selection and evolve. Populations simply follow: a population's carrying capacity is just one of many features that reflect the values these individual properties take.

properties of the simplest model

The properties of the model in Equation 5.12 may be seen in Figure 5.19 (from which the model was derived) and Figure 5.18 (which shows

a hypothetical population increasing in size over time in conformity with the model). The population in Figure 5.18 describes an S-shaped curve over time. As we saw earlier, this is a desirable quality of a model of intraspecific competition. Note, however, that there are many other models that would also generate such a curve. The advantage of Equation 5.12 is its simplicity.

The behavior of the model in the vicinity of the carrying capacity can best be seen by reference to Figure 5.19. At population sizes that are less than  $K$  the population will increase in size; at population sizes that are greater than  $K$  the population size will decline; and at  $K$  itself the population neither increases nor decreases. The carrying capacity is therefore a stable equilibrium for the population, and the model exhibits the regulatory properties classically characteristic of intraspecific competition.

## 5.8.2 What type of competition?

It is not yet clear, however, just exactly what type or range of competition this model is able to describe. This can be explored by tracing the relationship between  $k$  values and  $\log N$  (as in Section 5.6). Each generation, the potential number of individuals produced (i.e. the number that would be produced if there were no competition) is  $N_t R$ . The actual number produced (i.e. the number that survive the effects of competition) is  $N_t R/(1 + aN_t)$ .

Section 5.6 established that:

$$k = \log(\text{number produced}) - \log(\text{number surviving}). \quad (5.13)$$

Thus, in the present case:

$$k = \log N_t R - \log N_t R/(1 + aN_t), \quad (5.14)$$

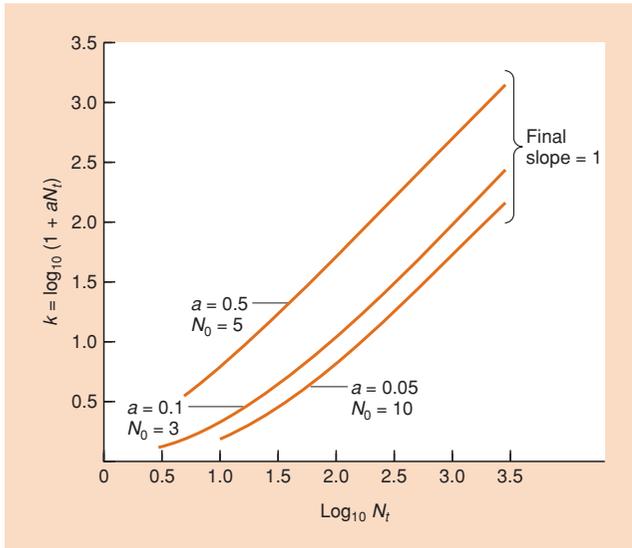
or, simplifying:

$$k = \log(1 + aN_t). \quad (5.15)$$

Figure 5.20 shows a number of plots of  $k$  against  $\log_{10} N_t$  with a variety of values of  $a$  inserted into the model. In every case, the slope of the graph approaches and then attains a value of 1. In other words, the density dependence always begins by under-compensating and then compensates perfectly at higher values of  $N_t$ . The model is therefore limited in the type of competition that it can produce, and all we have been able to say so far is that *this type* of competition leads to very tightly controlled regulation of populations.

## 5.8.3 Time lags

One simple modification that we can make is to relax the assumption that populations respond instantaneously to changes



**Figure 5.20** The intraspecific competition inherent in Equation 5.13. The final slope of  $k$  against  $\log_{10} N_t$  is unity (exact compensation), irrespective of the starting density  $N_0$  or the constant  $a (= (R - 1)/K)$ .

in their own density, i.e. that present density determines the amount of resource available to a population and this in turn determines the net reproductive rate within the population. Suppose instead that the amount of resource available is determined by the density one time interval previously. To take a specific example, the amount of grass in a field in spring (the resource available to cattle) might be determined by the level of grazing (and hence, the density of cattle) in the previous year. In such a case, the reproductive rate itself will be dependent on the density one time interval ago. Thus, since in Equations 5.7 and 5.12:

$$N_{t+1} = N_t \times \text{reproductive rate}, \quad (5.16)$$

Equation 5.12 may be modified to:

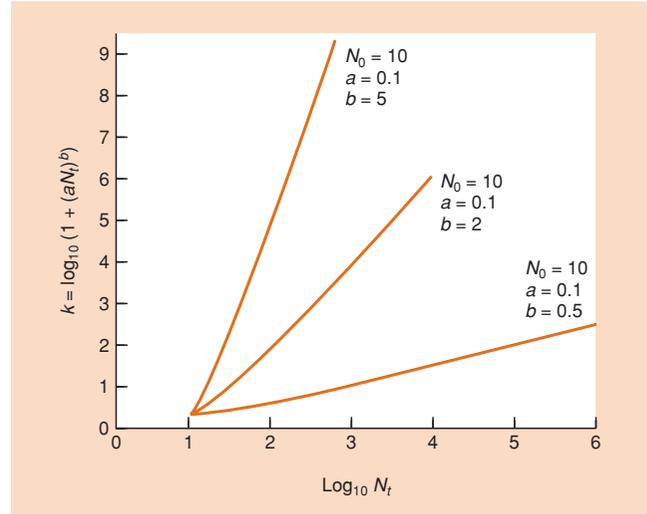
$$N_{t+1} = \frac{N_t R}{1 + aN_{t-1}}. \quad (5.17)$$

time lags provoke population fluctuations

There is a time lag in the population's response to its own density, caused by a time lag in the response of its resources. The behavior of the modified model is as follows:

- $R < 1.33$ : direct approach to a stable equilibrium
- $R > 1.33$ : damped oscillations towards that equilibrium.

In comparison, the original Equation 5.12, without a time lag, gave rise to a direct approach to its equilibrium for all values of  $R$ . The



**Figure 5.21** The intraspecific competition inherent in Equation 5.19. The final slope is equal to the value of  $b$  in the equation.

time lag has provoked the fluctuations in the model, and it can be assumed to have similar, destabilizing effects on real populations.

### 5.8.4 Incorporating a range of competition

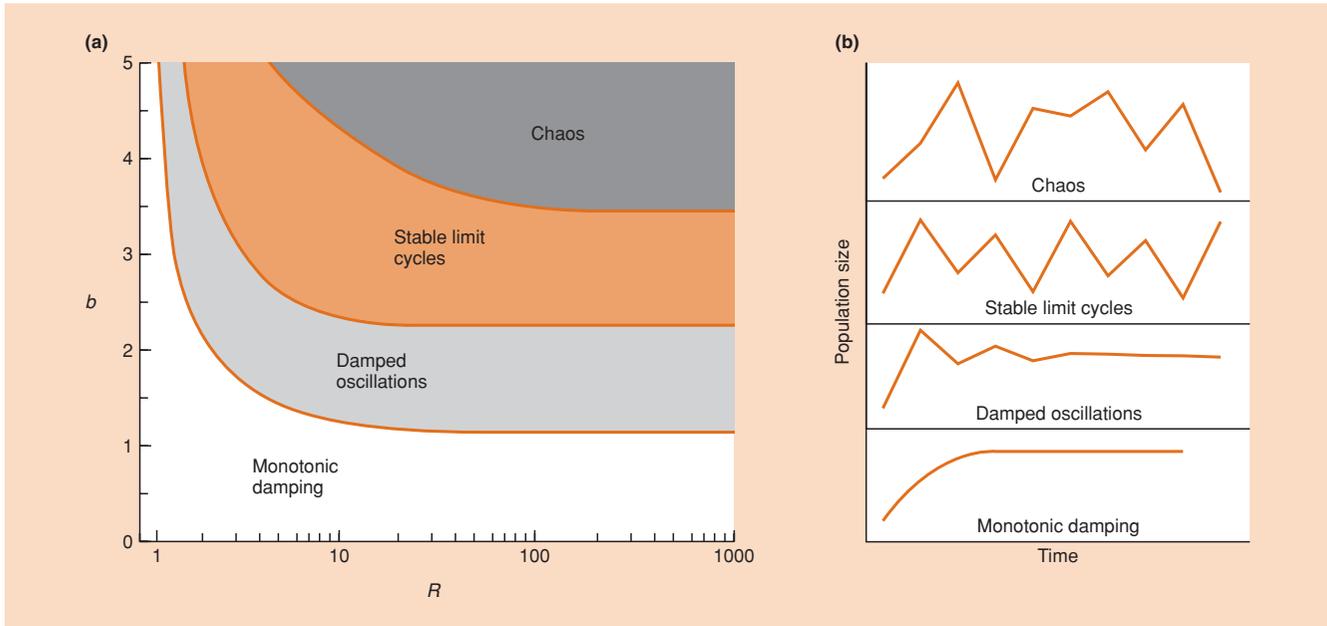
A simple modification of Equation 5.12 of far more general importance was originally suggested by Maynard Smith and Slatkin (1973) and was discussed in detail by Bellows (1981). It alters the equation to:

$$N_{t+1} = \frac{N_t R}{1 + (aN_t)^b}. \quad (5.18)$$

The justification for this modification may be seen by examining some of the properties of the revised model. For example, Figure 5.21 shows plots of  $k$  against  $\log N_t$ , analogous to those in Figure 5.20:  $k$  is now  $\log_{10}[1 + (aN_t)^b]$ . The slope of the curve, instead of approaching 1 as it did previously, now approaches the value taken by  $b$  in Equation 5.18. Thus, by the choice of appropriate values, the model can portray undercompensation ( $b < 1$ ), perfect compensation ( $b = 1$ ), scramble-like overcompensation ( $b > 1$ ) or even density independence ( $b = 0$ ). This model has the generality that Equation 5.12 lacks, with the value of  $b$  determining the type of density dependence that is being incorporated.

Another desirable quality that Equation 5.18 shares with other good models is an ability to throw fresh light on the real world. By sensible analysis of the population dynamics generated by the equation,

the dynamic pattern? it's  $R$  and  $b$



**Figure 5.22** (a) The range of population fluctuations (themselves shown in (b)) generated by Equation 5.19 with various combinations of  $b$  and  $R$  inserted. (After May, 1975a; Bellows, 1981.)

it is possible to draw guarded conclusions about the dynamics of natural populations. The mathematical method by which this and similar equations may be examined is set out and discussed by May (1975a), but the results of the analysis (Figure 5.22) can be appreciated without dwelling on the analysis itself. Figure 5.22b shows the various patterns of population growth and dynamics that Equation 5.18 can generate. Figure 5.22a sets out the conditions under which each of these patterns occurs. Note first that the pattern of dynamics depends on two things: (i)  $b$ , the precise type of competition or density dependence; and (ii)  $R$ , the effective net reproductive rate (taking density-independent mortality into account). By contrast,  $a$  determines not the type of pattern, but only the level about which any fluctuations occur.

As Figure 5.22a shows, low values of  $b$  and/or  $R$  lead to populations that approach their equilibrium size without fluctuating at all ('monotonic damping'). This has already been hinted at in Figure 5.18. There, a population behaving in conformity with Equation 5.12 approached equilibrium directly, irrespective of the value of  $R$ . Equation 5.12 is a special case of Equation 5.18 in which  $b = 1$  (perfect compensation); Figure 5.22a confirms that for  $b = 1$ , monotonic damping is the rule whatever the effective net reproductive rate.

As the values of  $b$  and/or  $R$  increase, the behavior of the population changes first to damped oscillations gradually approaching equilibrium, and then to 'stable limit cycles' in which the population fluctuates around an equilibrium level, revisiting the same two, four or even more points time and time again. Finally, with

large values of  $b$  and  $R$ , the population fluctuates in an apparently irregular and chaotic fashion.

### 5.8.5 Chaos

Thus, a model built around a density-dependent, supposedly regulatory process (intraspecific competition) can lead to a very wide range of population dynamics. If a model population has even a moderate fundamental net reproductive rate (and the ability to leave 100 (=  $R$ ) offspring in the next generation in a competition-free environment is not unreasonable), and if it has a density-dependent reaction which even moderately overcompensates, then far from being stable, it may fluctuate widely in numbers without the action of any extrinsic factor. The biological significance of this is the strong suggestion that even in an environment that is wholly constant and predictable, the intrinsic qualities of a population and the individuals within it may, by themselves, give rise to population dynamics with large and perhaps even chaotic fluctuations. The consequences of intraspecific competition are clearly not limited to 'tightly controlled regulation'.

This leads us to two important conclusions. First, time lags, high reproductive rates and overcompensating density dependence are capable (either alone or in combination) of producing all types of fluctuations in population density, without invoking any extrinsic cause. Second, and equally important, this has been made apparent by the analysis of mathematical models.

**key characteristics of chaotic dynamics**

In fact, the recognition that even simple ecological systems may contain the seeds of chaos has led to chaos itself becoming a topic of interest amongst ecologists (Schaffer & Kot, 1986; Hastings *et al.*, 1993; Perry *et al.*, 2000). A detailed exposition of the nature of chaos is not appropriate here, but a few key points should be understood.

- 1 The term ‘chaos’ may itself be misleading if it is taken to imply a fluctuation with absolutely no discernable pattern. Chaotic dynamics do not consist of a sequence of random numbers. On the contrary, there are tests (although they are not always easy to put into practice) designed to distinguish chaotic from random and other types of fluctuations.
- 2 Fluctuations in chaotic ecological systems occur between definable upper and lower densities. Thus, in the model of intraspecific competition that we have discussed, the idea of ‘regulation’ has not been lost altogether, even in the chaotic region.
- 3 Unlike the behavior of truly regulated systems, however, two similar population trajectories in a chaotic system will not tend to converge on (‘be attracted to’) the same equilibrium density or the same limit cycle (both of them ‘simple’ attractors). Rather, the behavior of a chaotic system is governed by a ‘strange attractor’. Initially, very similar trajectories will diverge from one another, exponentially, over time: chaotic systems exhibit ‘extreme sensitivity to initial conditions’.
- 4 Hence, the long-term future behavior of a chaotic system is effectively impossible to predict, and prediction becomes increasingly inaccurate as one moves further into the future. Even if we appear to have seen the system in a particular state before – and know precisely what happened subsequently last time – tiny (perhaps immeasurable) initial differences will be magnified progressively, and past experience will become of increasingly little value.

Ecology must aim to become a predictive science. Chaotic systems set us some of the sternest challenges in prediction. There has been an understandable interest, therefore, in the question ‘How often, if ever, are ecological systems chaotic?’ Attempts to answer this question, however, whilst illuminating, have certainly not been definitive.

**Takens’ theorem: reconstructing the attractor**

Most recent attempts to detect chaos in ecological systems have been based on a mathematical advance known as *Takens’ theorem*. This says, in the context of ecology, that even when a system comprises a number of interacting elements, its characteristics (whether it is chaotic, etc.) may be deduced from a time series of abundances of just one of those elements (e.g. one species). This is called ‘reconstructing the attractor’. To be more specific: suppose, for example, that a system’s behavior is

determined by interactions between four elements (for simplicity, four species). First, one expresses the abundance of just one of those species at time  $t$ ,  $N_t$ , as a function of the sequence of abundances at *four* successive previous time points:  $N_{t-1}$ ,  $N_{t-2}$ ,  $N_{t-3}$ ,  $N_{t-4}$  (the same number of ‘lags’ as there are elements in the original system). Then, the attractor of this lagged system of abundances is an accurate reconstruction of the attractor of the original system, which determines its characteristics.

In practice, this means taking a series of abundances of, say, one species and finding the ‘best’ model, in statistical terms, for predicting  $N_t$  as a function of lagged abundances, and then investigating this reconstructed attractor as a means of investigating the nature of the dynamics of the underlying system. Unfortunately, ecological time series (compared, say, to those of physics) are particularly short and particularly noisy. Thus, methods for identifying a ‘best’ model and applying Takens’ theorem, and for identifying chaos in ecology generally, have been ‘the focus of continuous methodological debate and refinement’ (Bjørnstad & Grenfell, 2001), one consequence of which is that any suggestion of a suitable method in a textbook such as this is almost certainly doomed to be outmoded by the time it is first read.

Notwithstanding these technical difficulties, however, and in spite of occasional demonstrations of apparent chaos in artificial laboratory environments (Costantino *et al.*, 1997), a consensus view has grown that chaos is not a dominant pattern of dynamics in natural ecological systems. One trend, therefore, has been to seek to understand why chaos might *not* occur in nature, despite its being generated readily by ecological models. For example, Fussmann and Heber (2002) examined model populations embedded in food webs and found that as the webs took on more of the characteristics observed in nature (see Chapter 20) chaos became less likely.

Thus, the potential importance of chaos in ecological systems is clear.

**how common – or important – is chaos?**

From a fundamental point of view, we need to appreciate that if we have a relatively simple system, it may nevertheless generate complex, chaotic dynamics; and that if we observe complex dynamics, the underlying explanation may nevertheless be simple. From an applied point of view, if ecology is to become a predictive and manipulative science, then we need to know the extent to which long-term prediction is threatened by one of the hallmarks of chaos – extreme sensitivity to initial conditions. The key practical question, however – ‘how common is chaos?’ – remains largely unanswered.

## 5.9 Continuous breeding: the logistic equation

The model derived and discussed in Section 5.8 was appropriate for populations that have discrete breeding seasons and can therefore be described by equations growing in discrete steps, i.e. by ‘difference’ equations. Such models are not appropriate,

however, for those populations in which birth and death are continuous. These are best described by models of continuous growth, or ‘differential’ equations, which will be considered next.

***r*, the intrinsic rate of natural increase**

The net rate of increase of such a population will be denoted by  $dN/dt$  (referred to in speech as ‘ $dN$  by  $dt$ ’). This represents the ‘speed’ at which a population increases in size,  $N$ , as time,  $t$ , progresses. The increase in size of the whole population is the sum of the contributions of the various individuals within it. Thus, the average rate of increase per individual, or the ‘per capita rate of increase’ is given by  $dN/dt(1/N)$ . But we have already seen in Section 4.7 that in the absence of competition, this is the definition of the ‘intrinsic rate of natural increase’,  $r$ . Thus:

$$\frac{dN}{dt} \left( \frac{1}{N} \right) = r \quad (5.19)$$

and:

$$\frac{dN}{dt} = rN. \quad (5.20)$$

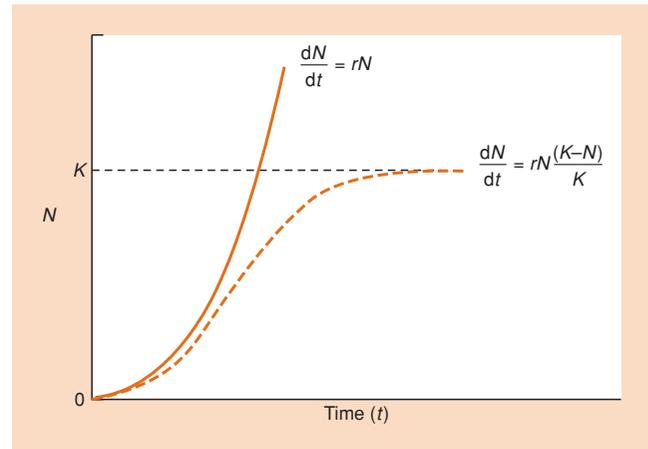
A population increasing in size under the influence of Equation 5.20, with  $r > 0$ , is shown in Figure 5.23. Not surprisingly, there is unlimited, ‘exponential’ increase. In fact, Equation 5.20 is the continuous form of the exponential difference Equation 5.8, and as discussed in Section 4.7,  $r$  is simply  $\log_e R$ . (Mathematically adept readers will see that Equation 5.20 can be obtained by differentiating Equation 5.8.)  $R$  and  $r$  are clearly measures of the same commodity: ‘birth plus survival’ or ‘birth minus death’; the difference between  $R$  and  $r$  is merely a change of currency.

For the sake of realism, intraspecific competition must obviously be added to Equation 5.20. This can be achieved most simply by a method exactly equivalent to the one used in Figure 5.19, giving rise to:

$$\frac{dN}{dt} = rN \left( \frac{K - N}{K} \right). \quad (5.21)$$

This is known as the logistic equation (coined by Verhulst, 1838), and a population increasing in size under its influence is shown in Figure 5.23.

The logistic equation is the continuous equivalent of Equation 5.12, and it therefore has all the essential characteristics of Equation 5.12, and all of its shortcomings. It describes a sigmoidal growth curve approaching a stable carrying capacity, but it is only one of many reasonable equations that do this. Its major advantage is its simplicity. Moreover, whilst it was possible to incorporate a range of competitive intensities into



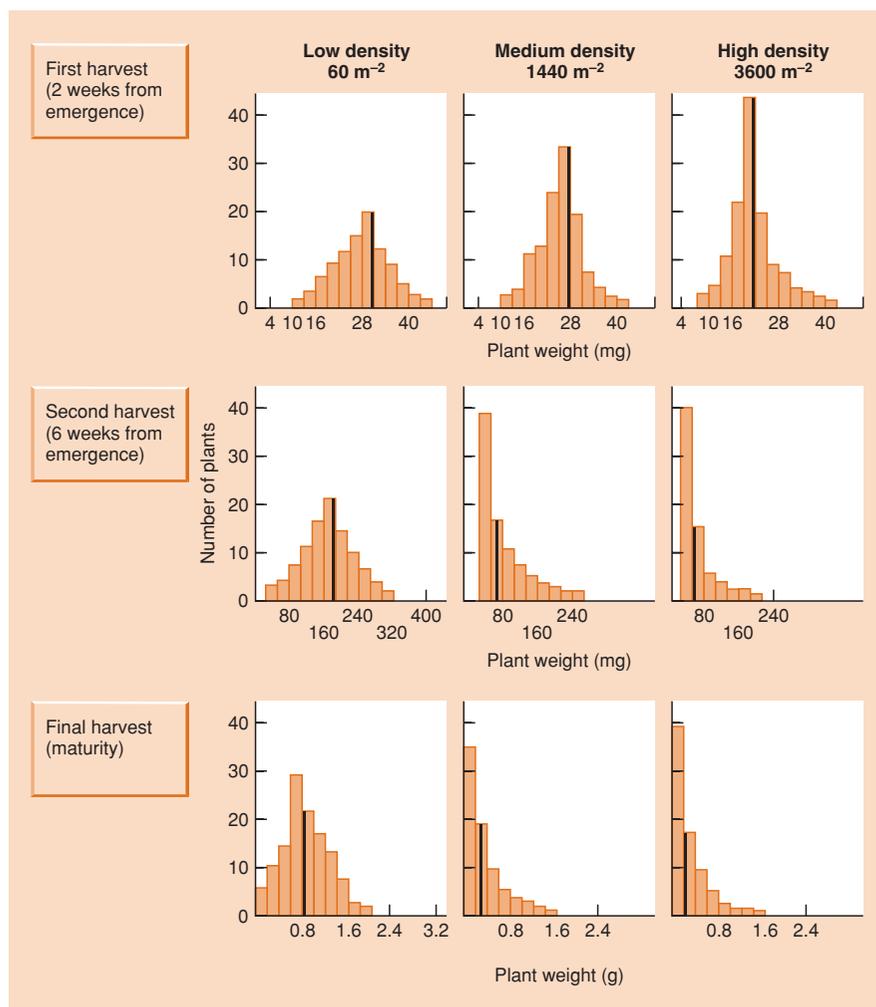
**Figure 5.23** Exponential (—) and sigmoidal (---) increase in density ( $N$ ) with time for models of continuous breeding. The equation giving sigmoidal increase is the logistic equation.

Equation 5.12, this is by no means easy with the logistic equation. The logistic is therefore doomed to be a model of perfectly compensating density dependence. Nevertheless, in spite of these limitations, the equation will be an integral component of models in Chapters 8 and 10, and it has played a central role in the development of ecology.

## 5.10 Individual differences: asymmetric competition

### 5.10.1 Size inequalities

Until now, we have focused on what happens to the whole population or the average individual within it. Different individuals, however, may respond to intraspecific competition in very different ways. Figure 5.24 shows the results of an experiment in which flax (*Linum usitatissimum*) was sown at three densities, and harvested at three stages of development, recording the weight of each plant individually. This made it possible to monitor the effects of increasing amounts of competition not only as a result of variations in sowing density, but also as a result of plant growth (between the first and the last harvests). When intraspecific competition was at its least intense (at the lowest sowing density after only 2 weeks’ growth) the individual plant weights were distributed symmetrically about the mean. When competition was at its most intense, however, the distribution was strongly skewed to the left: there were many very small individuals and a few large ones. As the intensity of competition gradually increased, the degree of skewness increased as well. Decreased size – but increased skewness in size – is also seen to



**Figure 5.24** Competition and a skewed distribution of plant weights. Frequency distributions of individual plant weights in populations of flax (*Linum usitatissimum*), sown at three densities and harvested at three ages. The black bar is the mean weight. (After Obeid *et al.*, 1967.)

be associated with increased density (and presumably competition) in cod (*Gadus morhua*) living off the coast of Norway (Figure 5.25).

the inadequacy of  
the average

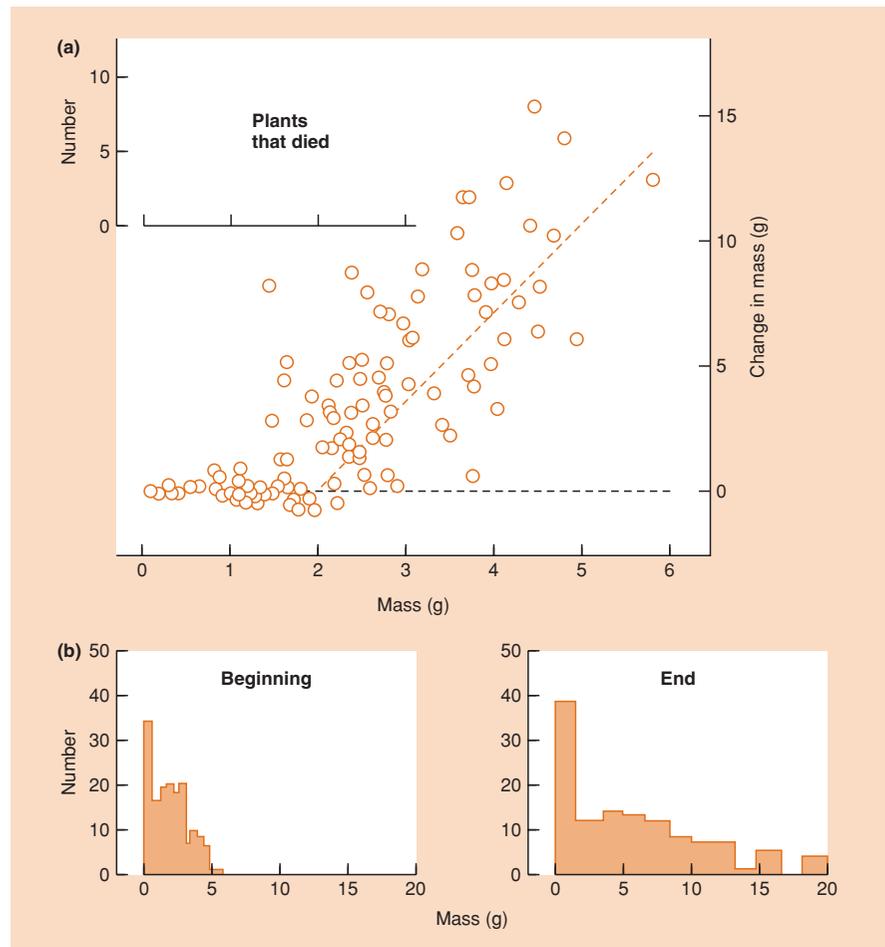
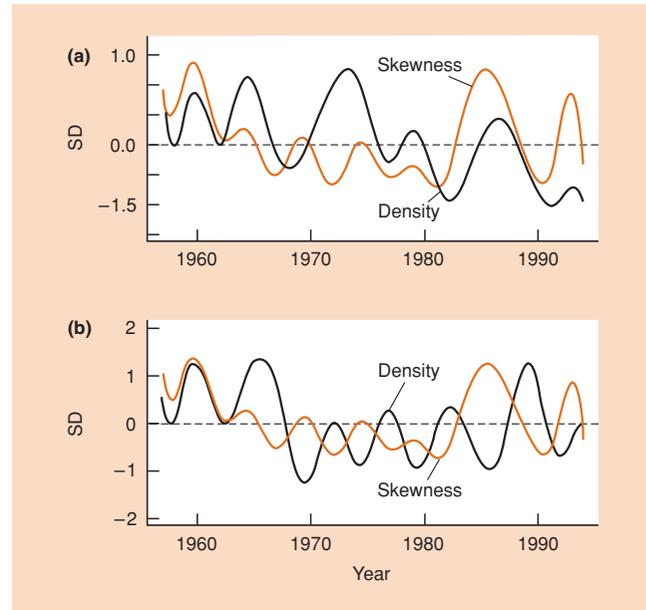
More generally, we may also say that increased competition increased the degree of size inequality within the population, i.e. the extent to which total biomass was unevenly distributed amongst the different individuals (Weiner, 1990). Rather similar results have been obtained from a number of other populations of animals (Uchmanski, 1985) and plants (Uchmanski, 1985; Weiner & Thomas, 1986). Typically, populations experiencing the most intense competition have the greatest size inequality and often have a size distribution in which there are many small and a few large individuals. Characterizing a population by an arbitrary ‘average’ individual can obviously be very misleading under such circumstances, and can divert attention from the fact that intraspecific competition is a force affecting individuals, even though its effects may often be detected in whole populations.

### 5.10.2 Preempting resources

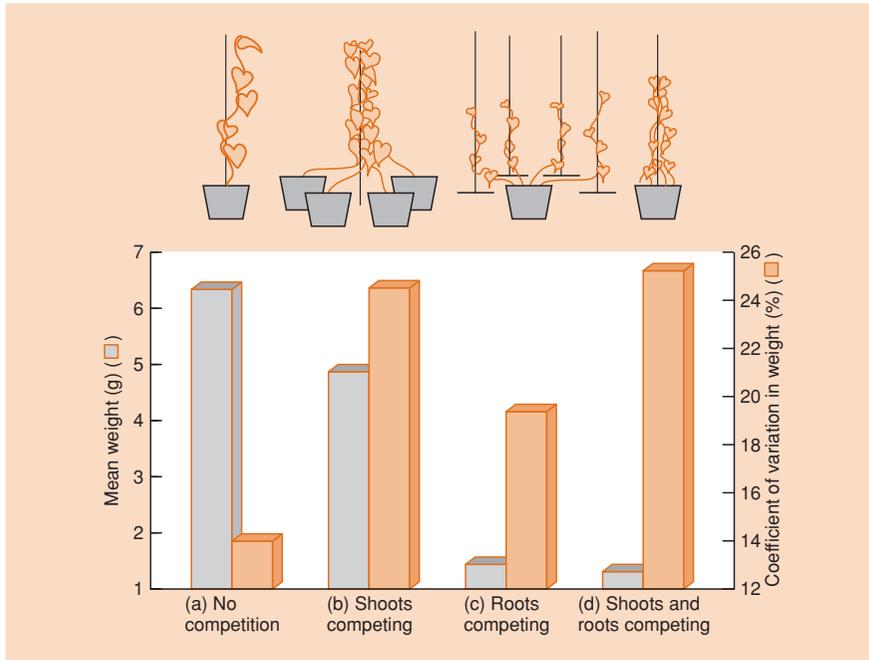
An indication of the way in which competition can exaggerate underlying inequalities in a population comes from observations on a natural, crowded population of the woodland annual *Impatiens pallida* in southeastern Pennsylvania. Over an 8-week period, growth was very much faster in large than in small plants – in fact, small plants did not grow at all (Figure 5.26a). This increased significantly the size inequality within the population (Figure 5.26b). Thus, the smaller a plant was initially, the more it was affected by neighbors. Plants that established early preempted or ‘captured’ space, and subsequently were little affected by intraspecific competition. Plants that emerged later entered a universe in which most of the available space had already been preempted; they were therefore greatly affected by intraspecific competition. Competition was asymmetric: there was a hierarchy. Some individuals were affected far more than others, and small initial differences were transformed by competition into much larger differences 8 weeks later.

If competition is asymmetric because superior competitors preempt resources, then competition is most likely to be asymmetric when it occurs for resources that are most liable to be preempted. Specifically, competition amongst plants for light, in which a superior competitor can overtop and shade an inferior, might be expected to lend itself far more readily to preemptive resource capture than competition for soil nutrients or water, where the roots of even a very inferior competitor will have more immediate access to at least some of the available resources than

**Figure 5.25** (right) Values of skewness (in the frequency distribution of lengths) and density (a) and of skewness and mean length (b) are expressed as standard deviations from mean values for the years 1957–94 for cod (*Gadus morhua*) from the Skagerrak, off the coast of Norway. Despite marked fluctuations from year to year, much of it the result of variations in weather, skewness was clearly greatest at high densities ( $r = 0.58$ ,  $P < 0.01$ ) when lengths were smallest ( $r = -0.45$ ,  $P < 0.05$ ), that is, when competition was most intense. (After Lekve *et al.*, 2002.)



**Figure 5.26** Asymmetric competition in a natural population of *Impatiens pallida*. (a) The increase in mass of survivors of different sizes over an 8-week period, and the distribution of initial sizes of those individuals that died over the same period. The horizontal axis is the same in each case. (b) The distribution of individual weights at the beginning (Gini coefficient, a measure of inequality, 0.39) and the end of this period (Gini coefficient, 0.48). (After Thomas & Weiner, 1989.)



**Figure 5.27** When morning glory vines competed, root competition was most effective in reducing mean plant weight (treatments significantly different,  $P < 0.01$ , for all comparisons except (c) with (d)), but shoot competition was most effective in increasing the degree of size inequality, as measured by the coefficient of variation in weight (significant differences between treatments (a) and (b),  $P < 0.05$ , and (a) and (d),  $P < 0.01$ ). (After Weiner, 1986.)

the roots of its superiors. This expectation is borne out by the results of an experiment in which morning glory vines (*Ipomoea tricolor*) were grown as single plants in pots ('no competition'), as several plants rooted in their own pots but with their stems intertwined on a single stake ('shoots competing'), as several plants rooted in the same pot, but with their stems growing up their own stakes ('roots competing') and as several plants rooted in the same pot with their stems intertwined on one stake ('shoots and roots competing') (Figure 5.27). Despite the fact that root competition was more intense than shoot competition, in the sense that it led to a far greater decrease in the mean weight of individual plants, it was shoot competition for light that led to a much greater increase in size inequality.

skews and other hierarchies

Skewed distributions are one possible manifestation of hierarchical, asymmetric competition, but there are many others. For instance, Ziemba and

Collins (1999) studied competition amongst larval salamanders (*Ambystoma tigrinum nebulosum*) that were either isolated or grouped together with competitors. The size of the largest surviving larvae was unaffected by competition ( $P = 0.42$ ) but the smallest larvae were much smaller ( $P < 0.0001$ ). This emphasizes that intraspecific competition is not only capable of exaggerating individual differences, it is also greatly affected by individual differences.

Asymmetric competition was observed on a much longer timescale in a population of the herbaceous perennial *Anemone hepatica* in Sweden (Figure 5.28) (Tamm, 1956). Despite the crops of seedlings that entered the population between 1943 and 1952, it is quite clear that the most important factor determining which individuals survived to 1956 was whether or not they were established in 1943. Of the 30 individuals that had reached

large or intermediate size by 1943, 28 survived until 1956, and some of these had branched. By contrast, of the 112 plants that were either small in 1943 or appeared as seedlings subsequently, only 26 survived to 1956, and not one of these was sufficiently well established to have flowered. Similar patterns can be observed in tree populations. The survival rates, the birth rates and thus the fitnesses of the few established adults are high; those of the many seedlings and saplings are comparatively low.

These considerations illustrate a final, important general point: asymmetries tend to reinforce the regulatory powers of intraspecific competition. Tamm's established plants were successful competitors year after year, but his small plants and seedlings were repeatedly unsuccessful. This guaranteed a near constancy in the number of established plants between 1943 and 1956. Each year there was a near-constant number of 'winners', accompanied by a variable number of 'losers' that not only failed to grow, but usually, in due course, died.

asymmetry enhances regulation

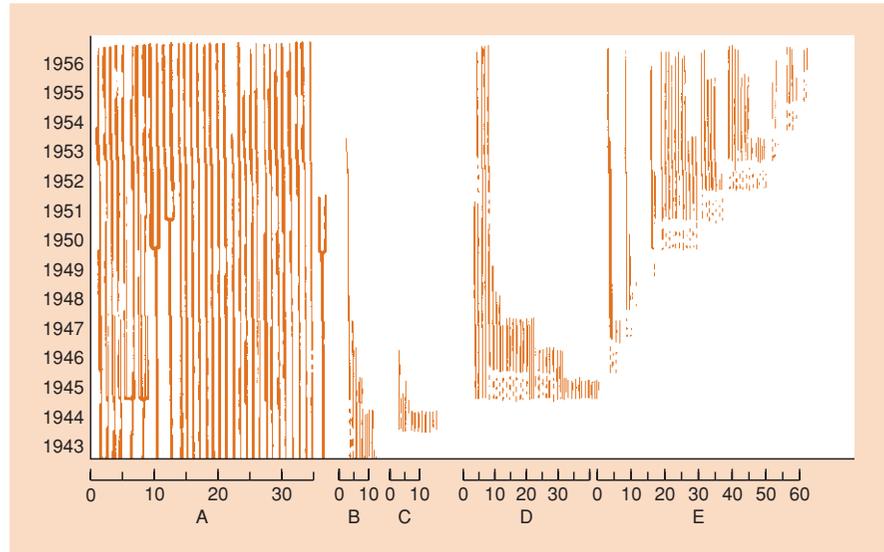
## 5.11 Territoriality

Territoriality is one particularly important and widespread phenomenon that results in asymmetric intraspecific competition. It occurs when there is active interference between individuals, such that a more or less exclusive area, the territory, is defended against intruders by a recognizable pattern of behavior.

Individuals of a territorial species that fail to obtain a territory often make no contribution whatsoever to future generations. Territoriality, then,

territoriality is a contest

**Figure 5.28** Space preemption in a perennial, *Anemone hepatica*, in a Swedish forest. Each line represents one individual: straight for unramified ones, branched where the plant has ramified, bold where the plant flowered and broken where the plant was not seen that year. Group A were alive and large in 1943, group B alive and small in 1943, group C appeared first in 1944, group D in 1945 and group E thereafter, presumably from seedlings. (After Tamm, 1956.)



is a 'contest'. There are winners (those that come to hold a territory) and losers (those that do not), and at any one time there can be only a limited number of winners. The exact number of territories (winners) is usually somewhat indeterminate in any one year, and certainly varies from year to year, depending on environmental conditions. Nevertheless, the contest nature of territoriality ensures, like asymmetric competition generally, a comparative constancy in the number of surviving, reproducing individuals. One important consequence of territoriality, therefore, is population regulation, or more particularly, the regulation of the number of territory holders. Thus, when territory owners die, or are experimentally removed, their places are often rapidly taken by newcomers. For instance, in great tit (*Parus major*) populations, vacated woodland territories are reoccupied by birds coming from hedgerows where reproductive success is noticeably lower (Krebs, 1971).

Some have felt that the regulatory consequences of territoriality must themselves be the root cause underlying the evolution of territorial behavior – territoriality being favored because the population as a whole benefitted from the rationing effects, which guaranteed that the population did not overexploit its resources (e.g. Wynne-Edwards, 1962). However, there are powerful and fundamental reasons for rejecting this 'group selectionist' explanation (essentially, it stretches evolutionary theory beyond reasonable limits): the ultimate cause of territoriality must be sought within the realms of natural selection, in some advantage accruing to the individual.

#### benefits and costs of territoriality

Any benefit that an individual does gain from territoriality, of course, must be set against the costs of defending the territory. In some animals this defense involves fierce combat between competitors, whilst in

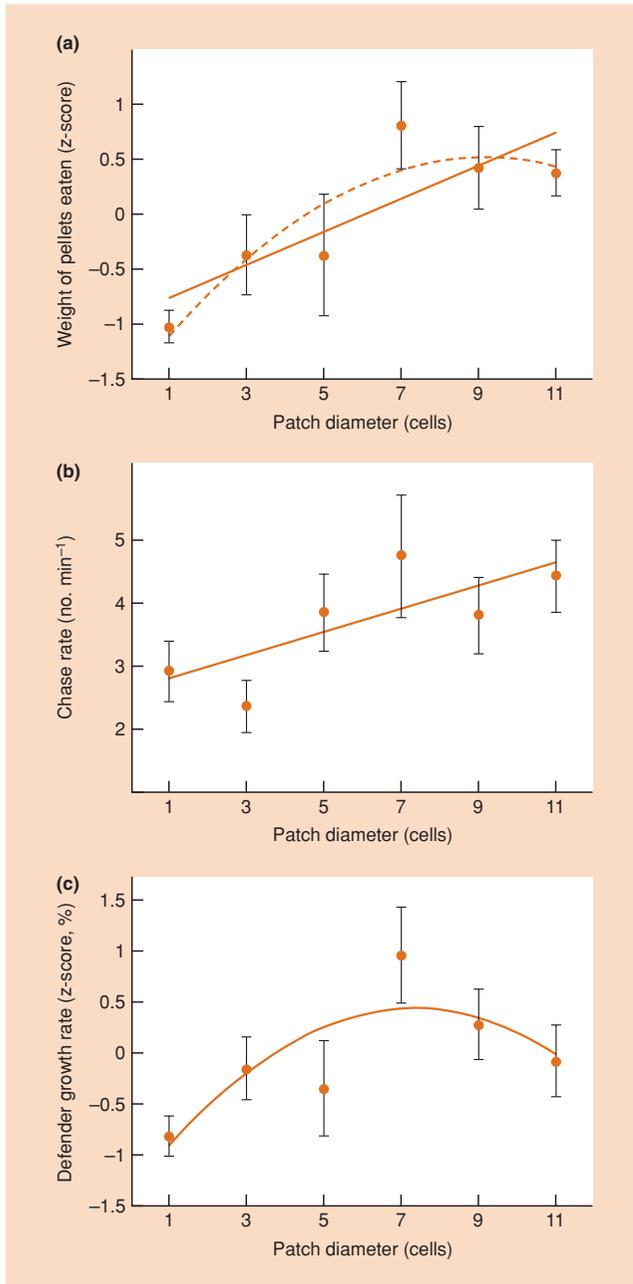
others there is a more subtle mutual recognition by competitors of one another's keep-out signals (e.g. song or scent). Yet, even when the chances of physical injury are minimal, territorial animals typically expend energy in patrolling and advertizing their territories, and these energetic costs must be exceeded by any benefits if territoriality is to be favored by natural selection (Davies & Houston, 1984; Adams, 2001).

Praw and Grant (1999), for example, investigated the costs and benefits to convict cichlid fish (*Archocentrus nigrofasciatus*) of defending food patches of different sizes. As patch size increased, the amount of food eaten by a patch defender increased (the benefit; Figure 5.29a), but the frequency of chasing intruders (the cost; Figure 5.29b) also increased. Evolution should favor an intermediate patch (territory) size at which the trade-off between costs and benefits is optimized, and indeed, the growth rate of defenders was greatest in intermediate-sized patches (Figure 5.29c).

On the other hand, explaining territoriality only in terms of a net benefit to the territory owner is rather like history always being written by the victors. There is another, possibly trickier question, which seems not to have been answered – could those individuals without a territory not do better by challenging the territory owners more often and with greater determination?

Of course, describing territoriality in terms of just 'winners' and 'losers' is an oversimplification. Generally, there are first, second and a range of consolation prizes – not all territories are equally valuable. This has been demonstrated in an unusually striking way in a study of oystercatchers (*Haematopus ostralegus*) on the Dutch coast, where pairs of birds defend both nesting territories on the salt marsh and feeding territories on the mudflats (Ens *et al.*, 1992). For some birds (the 'residents'), the feeding territory is simply an extension of the

not simply winners and losers



**Figure 5.29** Optimal territory size in the convict cichlid fish, *Archocentrus nigrofasciatus*. (a) As patch (territory) size increased, the amount of food eaten by a territory defender (standardized z score) increased but leveled off at the largest sizes (solid line, linear regression:  $r^2 = 0.27$ ,  $P = 0.002$ ; dashed line, quadratic regression:  $r^2 = 0.33$ ,  $P = 0.003$ ). (b) As patch (territory) size increased, the chase rate of territory defenders increased (linear regression:  $r^2 = 0.68$ ,  $P < 0.0001$ ). (c) As patch (territory) size increased, the growth rate of territory defenders (standardized z score) was highest at intermediate-sized territories (quadratic regression:  $r^2 = 0.22$ ,  $P = 0.028$ ). (After Praw & Grant, 1999.)

nesting territory: they form one spatial unit. For other pairs, however (the 'leapfrogs'), the nesting territory is further inland and hence separated spatially from the feeding territory (Figure 5.30a). Residents fledge many more offspring than do leapfrogs (Figure 5.30b), because they deliver far more food to them (Figure 5.30c). From an early age, resident chicks follow their parents onto the mudflats, taking each prey item as soon as it is captured. Leapfrog chicks, however, are imprisoned on their nesting territory prior to fledging; all their food has to be flown in. It is far better to have a resident than a leapfrog territory.

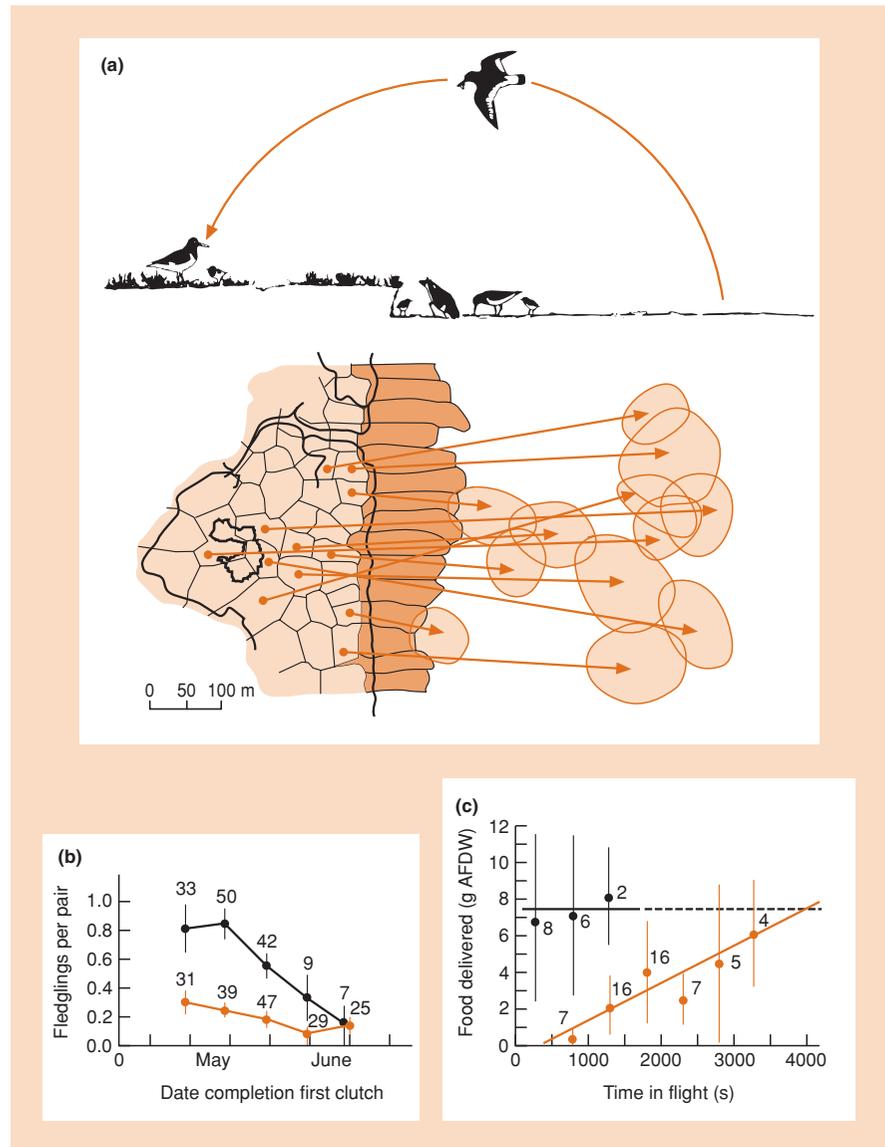
## 5.12 Self-thinning

We have seen throughout this chapter that intraspecific competition can influence the number of deaths, the number of births and the amount of growth within a population. We have illustrated this largely by looking at the end results of competition. But in practice, the effects are often progressive. As a cohort ages, the individuals grow in size, their requirements increase and they therefore compete at a greater and greater intensity. This in turn tends gradually to increase their risk of dying. But if some individuals die, then the density and the intensity of competition are decreased – which affects growth, which affects competition, which affects survival, which affects density, and so on.

### 5.12.1 Dynamic thinning lines

The patterns that emerge in growing, crowded cohorts of individuals were originally the focus of particular attention in plant populations. For example, perennial rye grass (*Lolium perenne*) was sown at a range of densities, and samples from each density were harvested after 14, 35, 76, 104 and 146 days (Figure 5.31a). Figure 5.31a has the same logarithmic axes – density and mean plant weight – as Figure 5.14. It is most important to appreciate the difference between the two. In Figure 5.14, each line represented a separate yield–density relationship at different ages of a cohort. Successive points along a line represent different initial sowing densities. In Figure 5.31, each line itself represents a different sowing density, and successive points along a line represent populations of this initial sowing density at different ages. The lines are therefore trajectories that follow a cohort through time. This is indicated by arrows, pointing from many small, young individuals (bottom right) to fewer, larger, older individuals (top left).

Mean plant weight (at a given age) was always greatest in the lowest density populations (Figure 5.31a). It is also clear that the highest density populations were the first to suffer substantial mortality. What is most noticeable, however, is that eventually, in all cohorts, density declined and mean plant weight increased in unison: populations progressed along roughly the same straight



**Figure 5.30** (a) A coastal area in the Netherlands providing both nesting and feeding territories for oystercatchers. In 'resident' territories (dark shading), nesting and feeding areas are adjacent and chicks can be taken from one to the other at an early age. 'Leapfrogs', however, have separate nesting and feeding territories (light shading) and food has to be flown in until the chicks fledge. (b) Residents (●) fledge more chicks than leapfrogs (○). (c) Residents (●) deliver more food per tide (grams of ash-free dry weight (g AFDW)), with standard deviations than leapfrogs (○). The latter deliver more, the more effort (in flying) they expend, but still cannot match the residents. (After Ens *et al.*, 1992.)

line. The populations are said to have experienced *self-thinning* (i.e. a progressive decline in density in a population of growing individuals), and the line that they approached and then followed is known as a *dynamic thinning line* (Weller, 1990).

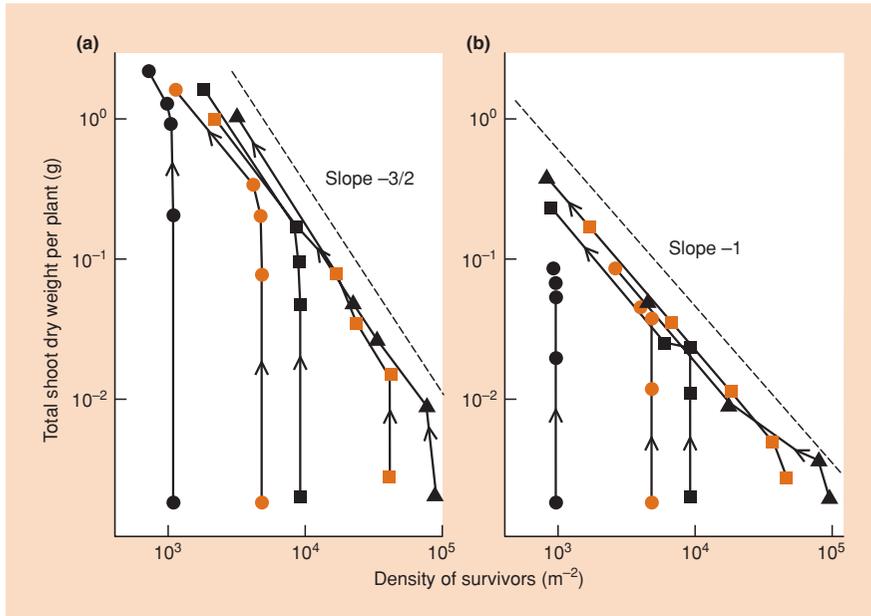
The lower the sowing density, the later was the onset of self-thinning. In all cases, though, the populations initially followed a trajectory that was almost vertical, i.e. there was little mortality. Then, as they neared the thinning line, the populations suffered increasing amounts of mortality, so that the slopes of all the self-thinning trajectories gradually approached the dynamic thinning line and then progressed along it. Note also that Figure 5.31 has been drawn, following convention, with log density on the *x*-axis and log mean weight on the *y*-axis. This is not meant to imply that density is the independent variable on

which mean weight depends. Indeed, it can be argued that mean weight increases naturally during plant growth, and this determines the decrease in density. The most satisfactory view is that density and mean weight are wholly interdependent.

Plant populations (if sown at sufficiently high densities) have repeatedly been found to approach and then follow a dynamic thinning line. For many years, all such lines were widely perceived as having a slope of roughly  $-3/2$ , and the relationship was often referred to as the ' $-3/2$  power law' (Yoda *et al.*, 1963; Hutchings, 1983), since density ( $N$ ) was seen as related to mean weight ( $\bar{w}$ ) by the equation:

$$\log \bar{w} = \log c - 3/2 \log N \quad (5.22)$$

the  $-3/2$  power law



**Figure 5.31** Self-thinning in *Lolium perenne* sown at five densities: 1000 (●), 5000 (○), 10,000 (■), 50,000 (□) and 100,000 (▲) ‘seeds’ m<sup>-2</sup>, in: (a) 0% shade and (b) 83% shade. The lines join populations of the five sowing densities harvested on five successive occasions. They therefore indicate the trajectories, over time, that these populations would have followed. The arrows indicate the directions of the trajectories, i.e. the direction of self-thinning. For further discussion, see text. (After Lonsdale & Watkinson, 1983.)

or:

$$\bar{w} = c N^{-3/2} \tag{5.23}$$

where c is constant.

Note, however, that there are statistical problems in using Equations 5.22 and 5.23 to estimate the slope of the relationship (Weller, 1987). In particular, since  $\bar{w}$  is usually estimated as  $B/N$ , where B is the total biomass per unit area,  $\bar{w}$  and N are inevitably correlated, and any relationship between them is, to a degree, spurious. It is therefore preferable to use the equivalent relationships, lacking autocorrelation:

$$\log B = \log c - 1/2 \log N \tag{5.24}$$

or:

$$B = c N^{-1/2}. \tag{5.25}$$

### 5.12.2 Species and population boundary lines

In fact, in many cases where biomass–density relationships have been documented, it is not a single cohort that has been followed over time, but a series of crowded populations at different densities (and possibly different ages) that have been compared. In such cases, it is more correct to speak of a *species boundary line* – a line beyond which combinations of density and mean weight appear not to be possible for that species (Weller, 1990). Indeed, since what is possible for a species will vary with the environment in

which it is living, the species boundary line will itself subsume a whole series of *population* boundary lines, each of which defines the limits of a particular population of that species in a particular environment (Sackville Hamilton *et al.*, 1995).

Thus, a self-thinning population should approach and then track its population boundary line, which, as a trajectory, we would call its dynamic thinning line – but this need not also be its species boundary line. For example, the light regime, soil fertility, spatial arrangement of seedlings, and no doubt other factors may all alter the boundary line (and hence the dynamic thinning line) for a particular population (Weller, 1990; Sackville Hamilton *et al.*, 1995). Soil fertility, for example, has been found in different studies to alter the slope of the thinning line, the intercept, neither, or both (Morris, 2002).

The influence of light is also worth considering in more detail, since it highlights a key feature of thinning and boundary lines. A slope of roughly  $-3/2$  means that mean plant weight is increasing faster than density is decreasing, and hence that total biomass is increasing (a slope of  $-1/2$  on a total biomass–density graph). But eventually this must stop: total biomass cannot increase indefinitely. Instead, the thinning line might be expected to change to a slope of  $-1$ : that is, loss through mortality is exactly balanced by the growth of survivors, such that the total biomass remains constant (a horizontal line on a total biomass–density graph). This can be seen when populations of *Lolium perenne* (Figure 5.31b) were grown at low light intensities. A boundary (and thinning line) with a slope of  $-1$  was apparent

dynamic thinning and boundary lines need not be the same

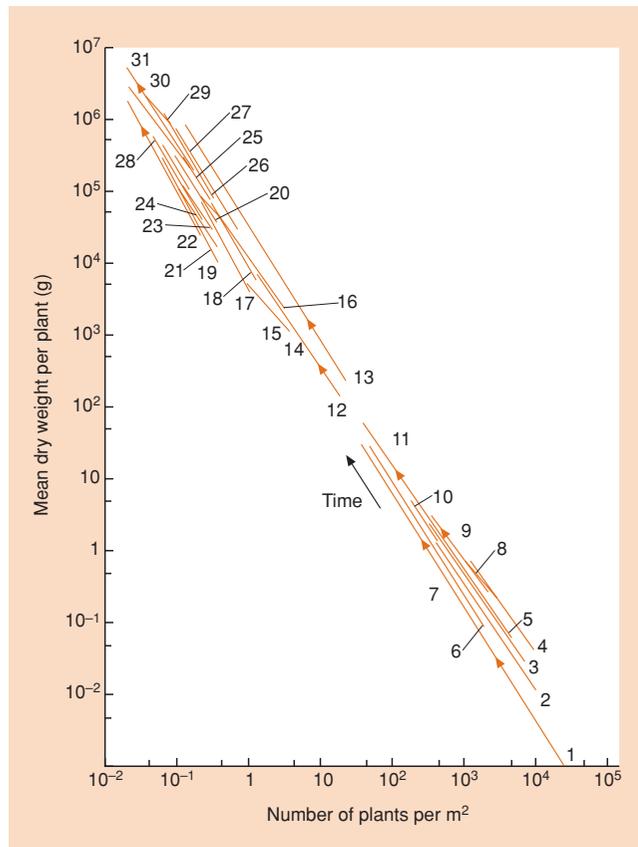
thinning slopes of  $-1$

at much lower densities than it would otherwise be. Clearly, the light regime can alter the population boundary line. This also emphasizes, however, that boundary lines with negative slopes steeper than  $-1$  (whether or not they are exactly  $-3/2$ ) imply limits to the allowable combinations of plant densities and mean weights that set in *before* the maximum biomass from an area of land has been reached. Possible reasons are discussed below.

### 5.12.3 A single boundary line for all species?

Intriguingly, when the thinning and boundary lines of all sorts of plants are plotted on the same figure, they all appear to have approximately the same slope and also to have intercepts (i.e. values of  $c$  in Equation 5.24) falling within a narrow range (Figure 5.32). To the lower right of the figure are high-density populations of small plants (annual herbs and perennials with short-lived

shoots), whilst to the upper left are sparse populations of very large plants, including coastal redwoods (*Sequoia sempervirens*), the tallest known trees. Fashions change in science as in everything else. At one time, ecologists looked at Figure 5.32 and saw uniformity – all plants marching in  $-3/2$  time (e.g. White, 1980), with variations from the norm seen as either ‘noise’ or as only of minor interest. Subsequently, serious doubt was cast on the conformity of individual slopes to  $-3/2$ , and on the whole idea of a single, ideal thinning line (Weller, 1987, 1990; Zeide, 1987; Lonsdale, 1990). There really is no contradiction, though. On the one hand, the lines in Figure 5.32 occupy a very much smaller portion of the graph than one would expect by chance alone. There is apparently some fundamental phenomenon linking this whole spectrum of plant types: not an invariable ‘rule’ but an underlying trend. On the other hand, the variations between the lines are real and important and in as much need of explanation as the general trend.



**Figure 5.32** Self-thinning in a wide variety of herbs and trees. Each line is a different species, and the line itself indicates the range over which observations were made. The arrows, drawn on representative lines only, indicate the direction of self-thinning over time. The figure is based on Figure 2.9 of White (1980), which also gives the original sources and the species names for the 31 data sets.

### 5.12.4 A geometric basis for self-thinning

We proceed, therefore, by examining possible bases for the general trend, and then enquiring why different species or populations might display their own variations on this common theme. Two broad types of explanation for the trend have been proposed. The first (and for many years the only one) is geometric; the second is based on resource allocation in plants of different sizes.

The geometric argument runs as follows. In a growing cohort of plants, as the mass of the population increases, the leaf area index ( $L$ , the leaf area per unit area of land) does not keep on increasing. Instead, beyond a certain point, it remains constant irrespective of plant density ( $N$ ). It is, in fact, precisely beyond this point that the population follows the dynamic thinning line. We can express this by writing:

$$L = \lambda N = \text{constant} \quad (5.26)$$

where  $\lambda$  is the mean leaf area per surviving plant. However, the leaf area of individual plants increases as they grow, and so too therefore does their mean,  $\lambda$ . It is reasonable to expect  $\lambda$ , because it is an area, to be related to linear measurements of a plant, such as stem diameter,  $D$ , by a formula of the following type:

$$\lambda = aD^2 \quad (5.27)$$

where  $a$  is a constant. Similarly, it is reasonable to expect mean plant weight,  $\bar{w}$ , to be related to  $D$  by:

$$\bar{w} = bD^3 \quad (5.28)$$

where  $b$  is also a constant. Putting Equations 5.26–5.28 together, we obtain:

$$\bar{w} = b(L/a)^{3/2} \cdot N^{-3/2} \quad (5.29)$$

This is structurally equivalent to the  $-3/2$  power law in Equation 5.23, with the intercept constant,  $c$ , given by  $b(L/a)^{3/2}$ .

It is apparent, therefore, why thinning lines might generally be expected to have slopes of approximately  $-3/2$ . Moreover, if the relationships in Equations 5.27 and 5.28 were roughly the same for all plant species, and if all plants supported roughly the same leaf area per unit area of ground ( $L$ ), then the constant  $c$  would be approximately the same for all species. On the other hand, suppose that  $L$  is not quite constant for some species (see Equation 5.26), or that the powers in Equations 5.27 and 5.28 are not exactly 2 or 3, or that the constants in these equations ( $a$  and  $b$ ) either vary between species or are not actually constants at all. Thinning lines will then have slopes that depart from  $-3/2$ , and slopes and intercepts that vary from species to species. It is easy to see why, according to the geometric argument, there is a broad similarity in the behavior of different species, but also why, on closer examination, there are variations between species and no such thing as a single, 'ideal' thinning line.

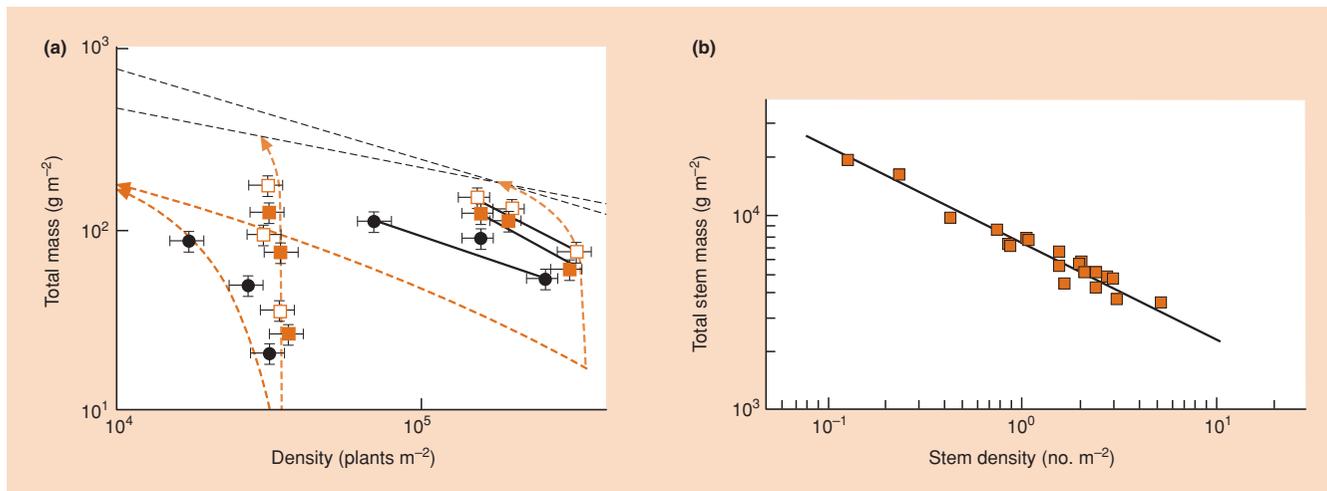
#### complications of the geometric argument

Furthermore, contrary to the simple geometric argument, the yield–density relationship in a growing cohort need not depend only on the numbers that die and the way the survivors grow. We have seen (see Section 5.10) that competition is frequently highly asymmetric. If those

Furthermore, contrary to the simple geometric argument, the yield–density relationship in a growing cohort need not depend only on the numbers that die and the way the survivors grow. We have seen (see Section 5.10) that competition is frequently highly asymmetric. If those

that die in a cohort are predominantly the very smallest individuals, then density (individuals per unit area) will decline more rapidly as the cohort grows than it would otherwise do, and the slope will be shallower, especially in the early stages of self-thinning. This idea is supported by a comparison of self-thinning in normal *Arabidopsis thaliana* plants with self-thinning in mutants that overexpress phytochrome A, greatly reducing their shade tolerance, and making competition amongst them more asymmetric (Figure 5.33a).

It seems possible, too, to use departures from the assumptions built into Equations 5.26–5.29 to explain at least some of the variations from a 'general'  $-3/2$  rule. Osawa and Allen (1993) estimated a number of the parameters in these equations from data on the growth of individual plants of mountain beech (*Nothofagus solandri*) and red pine (*Pinus densiflora*). They estimated, for instance, that the exponents in Equations 5.27 and 5.28 were not 2 and 3, but 2.08 and 2.19 for mountain beech, and 1.63 and 2.41 for red pine. These suggest thinning slopes of  $-1.05$  in the first case and  $-1.48$  in the second, which compare quite remarkably well with the observed slopes of  $-1.06$  and  $-1.48$  (Figure 5.33b). The similarities between the estimates and observations for the intercept constants were equally impressive. These results show, therefore, that thinning lines with slopes other than  $-3/2$  can occur, but can be explicable in terms of the detailed biology of the species concerned – and that even when slopes of  $-3/2$  do occur, they may do so, as with red pine, for the 'wrong' reason ( $-2.41/1.63$  rather than  $-3/2$ ).



**Figure 5.33** (a) The relationship between total biomass and density in two wild-type strains of *Arabidopsis thaliana* plants (□ and ■) and a phytochrome A overexpressing mutant strain (●) 15, 22 and 33 days after sowing (bottom to top). Data points give means ( $\pm 1$  SE,  $n = 3$ ). In each case, the strains were sown at two initial densities; solid black regression lines are shown in each case for the higher density. The steeper dotted black line has a slope of  $-1/2$  (indicative of  $-3/2$  self-thinning) and the shallow line a slope of  $-1/3$  (indicative of  $-4/3$  self-thinning). Model trajectories for asymmetric (—) and symmetric (---) competition are also shown. The mutant strain exhibited shallower thinning lines, indicative of more asymmetric competition. (After Stoll *et al.*, 2002.) (b) The species boundary line for populations of red pine, *Pinus densiflora* (slope =  $-1.48$ ) from northern Japan. (After Osawa & Allen, 1993.)

### 5.12.5 A resource-allocation basis for thinning boundaries

The increasing recognition that a variety of slope values might be expected, even on the geometric argument, along with the statistical difficulties of estimating slopes, has left the way open for alternative explanations for the underlying trend itself. Enquist *et al.* (1998) made use of the much more general model of West *et al.* (1997), which considered the most effective architectural designs of organisms (not just plants) for distributing acquired resources throughout those organisms. This suggested that the rate of resource use per individual,  $u$ , should be related to mean plant weight,  $\bar{w}$ , according to the equation:

$$u = a\bar{w}^{3/4} \quad (5.30)$$

where  $a$  is a constant. Indeed, Enquist *et al.* (1998) were also able to find empirical support for this relationship.

They then argued that plants have evolved to make full use of the resources available, and so if  $S$  is the rate of resource supply per unit area and  $N_{\max}$  the maximum allowable density of plants, then:

$$S = N_{\max}u \quad (5.31)$$

or, from Equation 5.30:

$$S = aN_{\max}\bar{w}^{3/4}. \quad (5.32)$$

But when the plants have arrived at an equilibrium with the rate of resource supply,  $S$  should itself be constant. Hence:

$$\bar{w} = bN_{\max}^{-4/3}, \quad (5.33)$$

where  $b$  is another constant. In short, the expected slope of a population boundary on this argument is  $-4/3$  rather than  $-3/2$ .

Enquist and colleagues themselves considered the available data to be more supportive of their prediction of a slope of  $-4/3$  than the more conventional  $-3/2$ . This has not, however, been the conclusion drawn either from previous data surveys or from the analysis of subsequent experiments (e.g. Figure 5.33a; Stoll *et al.*, 2002). In part, the discrepancy may have arisen because the geometric argument is focused on light acquisition, and the data collected to test it have likewise been focused on above-ground plant parts (photosynthetic or support tissue); whereas Enquist *et al.*'s is a much more general resource-acquisition argument, and at least some of their data were based on overall plant weights (leaves, shoots and roots). Related to this, Enquist *et al.*'s data sets were focused on maximum densities of large numbers of species, whereas other analyses have focused on the self-thinning process,

which occurs largely before the overall resource-determined limit has been reached. Again, therefore, there may be no contradiction between the two approaches.

### 5.12.6 Self-thinning in animal populations

Animals, whether they are sessile or mobile, must also 'self-thin', insofar as growing individuals within a cohort increasingly compete with one another and reduce their own density. There is nothing linking all animals quite like the shared need for light interception that links all plants, so there is even less likelihood of a general self-thinning 'law' for animals. On the other hand, crowded sessile animals can, like plants, be seen as needing to pack 'volumes' beneath an approximately constant area, and mussels, for example, have been found to follow a thinning line with a slope of  $-1.4$ , and barnacles a line with a slope of  $-1.6$  (Hughes & Griffiths, 1988). Moreover, self-thinning in the gregarious tunicate, *Pyura praeputialis*, on the coast of Chile was found to follow a slope of only  $-1.2$ ; but when the analysis was modified to acknowledge that rocky shore invertebrates are more 'three-dimensional' than plants, and may fit more than one layer into a fully occupied area (as opposed to the constant leaf area index of plants), then the estimated slope was  $-1.5$  (Figure 5.34a).

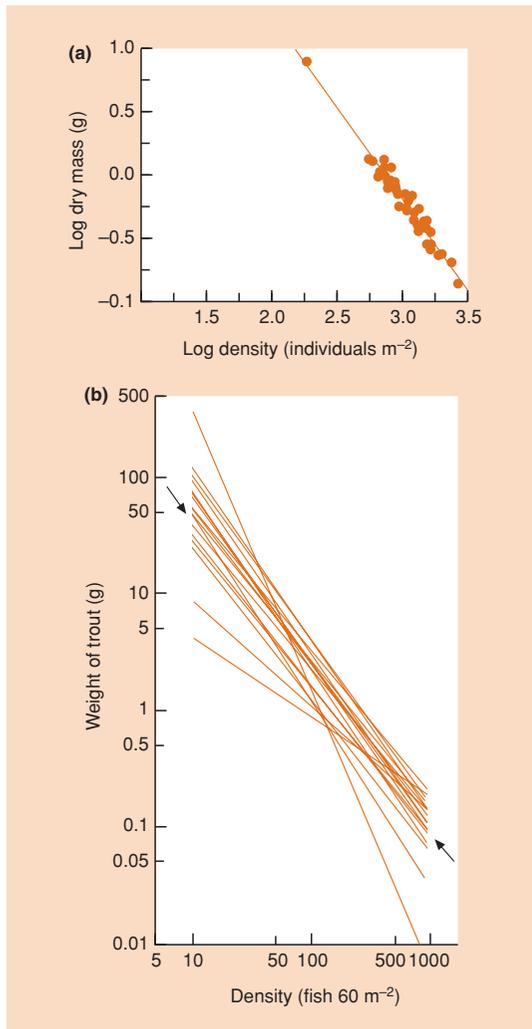
For mobile animals, it has been suggested that the relationship between metabolic rate and body size could generate thinning lines with slopes of  $-4/3$  (Begon *et al.*, 1986). However, the generality of this is probably even more questionable than the 'rules' in plants, given variations in resource supply, variations in the coefficients in the underlying relationships, and the possibilities of self-thinning depending on, say, territorial behavior rather than simply food availability (Steingrímsson & Grant, 1999). Nonetheless, evidence of self-thinning in animals is increasingly reported, especially in fish, even if the basis for it remains uncertain (e.g. Figure 5.34b).

Plants are not so consistent in their pattern of self-thinning as was once thought. It may be that animals are not much less bound than plants by 'general' self-thinning rules.

## Summary

Intraspecific competition is defined and explained. Exploitation and interference are distinguished, and the commonly one-sided nature of competition is emphasized.

We describe the effects of intraspecific competition on rates of mortality and fecundity, distinguishing under-, over- and exactly compensating density dependence. We explain, however, that density itself is usually just a convenient expression of crowding or shortage of resources.



**Figure 5.34** (a) Self-thinning in the gregarious tunicate, *Pyura praeputialis*, where density has been modified to include an 'effective area' which incorporates the number of layers in the tunicate colonies. The estimated slope is  $-1.49$  (95% CI  $-1.59$  to  $-1.39$ ,  $P < 0.001$ ). (After Guíñez & Castilla, 2001.) (b) Dynamic thinning lines for 23 year-classes of sea trout, *Salmo trutta*, from an English Lake District stream, with the position of the mean regression line (slope =  $-1.35$ ) indicated by the arrows (After Elliott, 1993.)

These effects at the individual level lead in turn to patterns, and regulatory tendencies, at the population level. The carrying capacity is defined and its limitations are explained, along with the domed nature of net recruitment curves and the sigmoidal nature of population growth curves.

We describe the effects of intraspecific competition on rates of growth, explaining the 'law of constant final yield', especially in modular organisms.

The use of  $k$  values in quantifying intraspecific competition is described, and scramble and contest competition are distinguished.

We introduce the use of mathematical models in ecology generally, then go on to develop a model of a population with discrete breeding seasons subject to intraspecific competition. The model illustrates the tendency of time lags to provoke population fluctuations and that different types of competition may lead to different types of population dynamics, including patterns of deterministic chaos – the nature and importance of which are themselves explained. A model with continuous breeding is also developed, leading to the logistic equation.

The importance of individual differences in generating asymmetries in competition is explained, as is the importance of competition in generating individual differences. Asymmetries tend to enhance regulation; territoriality is a particularly important example of this.

The progressive effects of competition on growth and mortality may often be interlinked in the process of self-thinning, which has been a particular focus in plant populations. We explain the nature of dynamic thinning lines and the  $-3/2$  power law when single cohorts are followed, and also species and population boundary lines when a series of crowded populations is observed at different densities. We address the question of whether there is a single boundary line for all species.

We explain how two broad types of explanation for the consistent trend amongst species have been proposed: those based on geometry and those based on resource allocation in plants of different sizes.

Finally we examine self-thinning in animal populations and conclude that plants are not so consistent in their pattern of self-thinning as was once thought, while animals are not much less bound than plants by 'general' self-thinning rules.