CHAPTER 2

Logistic Population Growth

Model Presentation and Predictions

In Chapter 1, we assumed (unrealistically) that resources for population growth were unlimited. Consequently, the per capita birth and death rates, b and d, remained constant. We did explore some models in which b and d fluctuated through time (environmental stochasticity), but those fluctuations were **density-independent**; in other words, birth and death rates did not depend on the size of the population. In this chapter, we assume that resources for growth and reproduction are limited. As a consequence, birth and death rates depend on population size. To derive this more complex **logistic growth model**, we will start with the familiar growth equation:

$$\frac{dN}{dt} = (b' - d')N \qquad \text{Expression 2.1}$$

but now we will modify b' and d' so they are density-dependent and reflect crowding.

DENSITY DEPENDENCE

In the face of increased crowding, we expect the per capita birth rate to *decrease* because less food and fewer resources are available for organisms to use for reproduction. The simplest formula for a decreasing birth rate is a straight line (see Figure 2.1):

$$b' = b - aN \qquad \text{Expression 2.2}$$

In this expression, N is population size, b' is the per capita birth rate, and b and a are constants. From Expression 2.2, the larger N is, the lower the birth rate. On the other hand, if N is close to zero, the birth rate is close to b. The constant b is the birth rate that would be achieved under ideal (uncrowded) conditions, whereas b' is the actual birth rate, which is reduced by crowding. Thus, b has the same interpretation as in the original exponential growth model: it is the instantaneous per capita birth rate when resources are unlimited. The constant a measures the strength of density dependence. The larger a is, the more sharply the birth rate drops with each individual added to the population. If there is no density dependence, then $a = 0$, and the birth rate equals b, regardless of population size. Thus, the exponential growth model is a special case of the logistic model in which there are no crowding effects on the birth rate ($a = 0$) or on the death rate ($c = 0$).

Using similar reasoning, we can modify the death rate to reflect density dependence. In this case, we expect the death rate to *increase* as the population grows:

$$d' = d + cN \qquad \text{Expression 2.3}$$

Again, the constant d is the death rate when the population size is close to zero, and the population is growing (almost) exponentially. The constant c measures the increase in the death rate from density dependence.

Expressions 2.2 and 2.3 are the simplest mathematical descriptions of the effects of crowding on birth and death rates. In real populations, the functions may be more complex. For example, b' and d' may not decline in a linear fashion; instead, there may be no change in b' or d' until a critical threshold density is reached. Some animals can reproduce, hunt, care for their offspring, or avoid predators more efficiently in groups than they can by themselves. For these populations, b' may actually increase and d' decrease as the population grows. This **Allee effect** (Allee et al. 1949) is usually important when the population is small, and may generate a critical minimum population size, below which extinction occurs (see Problem 2.3). But as the population grows, we expect negative density effects to appear as resources are depleted.

Note that *both* birth and death rates are density-dependent in this model. But it might be that only the death rate is affected by population size, and the birth rate remains density-independent, or vice versa. Fortunately, the algebra of this case works out exactly the same (see Problem 2.5). As long as either the birth rate *or* the death rate shows a density-dependent effect, we arrive at the logistic model.

Now we substitute Expressions 2.2 and 2.3 back into 2.1:

$$\frac{dN}{dt} = [(b - aN) - (d + cN)]N \qquad \text{Expression 2.4}$$

After rearranging the terms:

$$\frac{dN}{dt} = [(b - d) - (a + c)N]N \qquad \text{Expression 2.5}$$

Next, we multiply Expression 2.5 by $[(b - d)/(b - d)]$. This term equals 1.0, so it does not change the results, but allows us to simplify further:

$$\frac{dN}{dt} = \left[\frac{(b-d)}{(b-d)}\right][(b - d) - (a + c)N]N \qquad \text{Expression 2.6}$$

$$\frac{dN}{dt} = [(b-d)]\left[\frac{(b-d)}{(b-d)} - \frac{(a+c)}{(b-d)}N\right]N \qquad \text{Expression 2.7}$$

Treating $(b - d)$ as r, we have:

$$\frac{dN}{dt} = rN\left[1 - \frac{(a+c)}{(b-d)}N\right] \qquad \text{Expression 2.8}$$

CARRYING CAPACITY

Because a, c, b, and d are all constants in Expression 2.8, we can define a new constant K:

$$K = \frac{(b-d)}{(a+c)} \qquad \text{Expression 2.9}$$

The constant K is used for more than just mathematical convenience. It has a ready biological interpretation as the **carrying capacity** of the environment. K represents the maximum population size that can be supported; it encompasses many potentially limiting resources, including the availability of space, food, and shelter. In our model, these resources are depleted incrementally as crowding increases. Because K represents maximum sustainable population size, its units are numbers of individuals. Substituting K back into Expression 2.8 gives:

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right) \qquad \text{Equation 2.1}$$

Equation 2.1 is the logistic growth equation, which was introduced to ecology in 1838 by P.-F. Verhulst (1804–1849). It is the simplest equation describing population growth in a resource-limited environment, and it forms the basis for many models in ecology.

The logistic growth equation looks like the equation for exponential growth (rN) multiplied by an additional term in parentheses ($1 - N/K$). The term in parentheses represents the **unused portion of the carrying capacity**. As an analogy, think of the carrying capacity as a square frame that will hold a limited number of flat tiles, which are the individuals. If the population should ever exceed the carrying capacity, there would be more tiles than could fit in the frame. The unused portion of the carrying capacity is the percentage of the area of the frame that is empty (Krebs 1985).

For example, suppose $K = 100$ and $N = 7$. The unused portion of the carrying capacity is $[1 - (7/100)] = 0.93$. The population is relatively uncrowded and is growing at 93% of the growth rate of an exponentially increasing population $[rN(0.93)]$. In contrast, if the population is close to K ($N = 98$), the unused carrying capacity of the environment is small: $[1 - (98/100)] = 0.02$. Consequently, the population grows very slowly, at 2% of the exponential growth rate $[rN(0.02)]$. Finally, if the population should ever exceed carrying capacity ($N > K$), the term in parentheses becomes negative, which means that the growth rate is less than zero, and the population declines towards K. Thus, density-dependent birth and death rates provide an effective brake on exponential population growth.

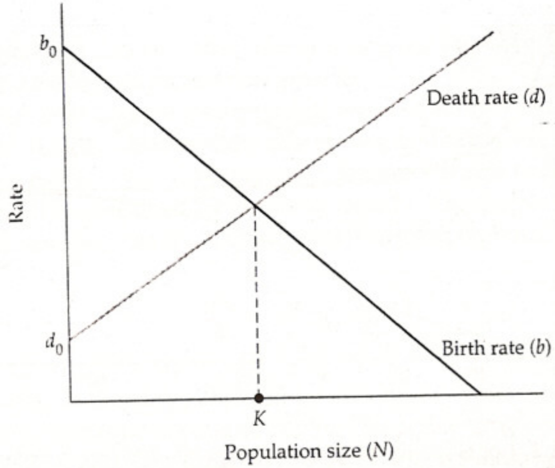


Figure 2.1 Density-dependent birth and death rates in the logistic model. The graph illustrates how the per capita rates of birth and death change as a function of crowding. The population reaches a stable equilibrium ($N = K$) at the intersection of the curves, where birth and death rates are equal.

When will the population stop growing? As in the exponential model, the rate of population growth (dN/dt) is zero when either r or N equals zero. But in the logistic model, the population will also stop growing when $N = K$. This is illustrated in Figure 2.1, which shows the density-dependent birth and death functions in the same graph. The two curves intersect at the point $N = K$ and form a **stable equilibrium**. The equilibrium is stable because no matter what the starting size of the population, it will move towards K. If N is less than K, we are at a point to the left of the intersection of the birth and death curves. In this region of the graph, the birth rate exceeds the death rate, so the population will increase. If we are to the right of the intersection point, the death rate is higher than the birth rate, and the population will decline (see Appendix).

As with the exponential growth model, we can use the rules of calculus to integrate the growth equation and express population size as a function of time:

$$N_t = \frac{K}{1 + \left[(K - N_0)/N_0\right]e^{-rt}} \qquad \text{Equation 2.2}$$

From Equation 2.2, the graph of N versus time for logistic growth is a characteristic S-shaped curve (Figure 2.2). When the population is small, it

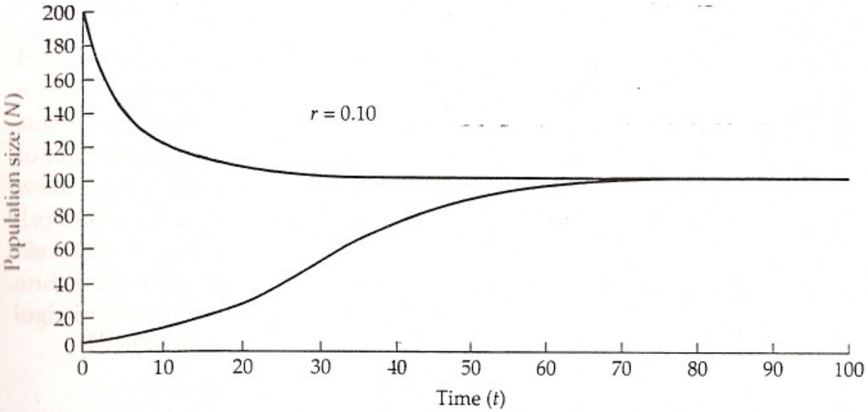


Figure 2.2 Logistic growth curve. The graph of N versus time increases in a characteristic S-shaped fashion when the population begins below carrying capacity. Above carrying capacity, the curve drops rapidly to the equilibrium point. In this example, $K = 100$, and the starting population size is 5 or 200.

increases rapidly, at a rate slightly less than that predicted by the exponential model. The population grows at its highest rate when $N = K/2$ (the steepest point on the curve), and then growth decreases as the population approaches K (Figure 2.3a). This is in contrast to the exponential model, in which the population growth rate increases linearly with population size (Figure 2.3b). In the logistic model, if the population should begin above K, Equation 2.1 takes on a negative value, and N will decline towards carrying capacity.

Regardless of the initial number of individuals (N_0), a population growing according to the logistic model will quickly reach a fixed carrying capacity, which is determined solely by K. However, the time it takes to reach that equilibrium is proportional to r; faster-growing populations reach K more quickly.

Model Assumptions

Because the logistic model is derived from the exponential model, it shares the assumptions of no time lags, migration, genetic variation, or age structure in the population. But resources are limited in the logistic model, so we make two additional assumptions:

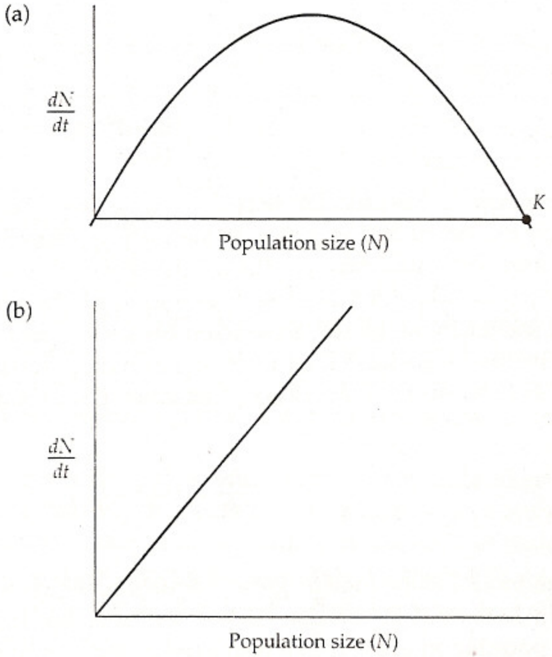


Figure 2.3 Population growth rate (dN/dt) as a function of population size. (a) Logistic growth. (b) Exponential growth.

- ✓ ***Constant carrying capacity.*** In order to achieve the S-shaped logistic growth curve, we must assume that K is a constant: resource availability does not vary through time. Later in this chapter, we will relax this assumption.

- ✓ ***Linear density dependence.*** The logistic model assumes that each individual added to the population causes an incremental decrease in the per capita rate of population growth. This is illustrated in Figure 2.4a, which shows the **per capita population growth rate** $(1/N)(dN/dt)$ as a function of population size. This per capita rate is at its maximum value of $(b - d) = r$ when N is close to zero, then declines linearly to zero when N reaches K. If N exceeds K, the per capita growth rate becomes negative. Although b and d are constants, the actual birth and death rates (b' and d') now change as a function of population size (Expressions 2.2 and 2.3). In contrast, the corresponding graph for the exponential growth model is a horizontal line because the per capita growth rate is independent of population size (Figure 2.4b).

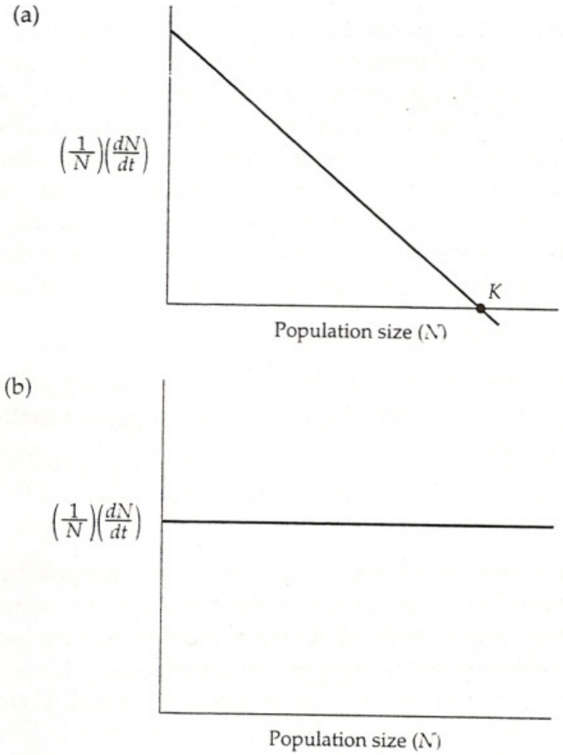


Figure 2.4 Per capita growth rates $(1/N)(dN/dt)$ as a function of population size. (a) Logistic growth. (b) Exponential growth.

Model Variations

TIME LAGS

The logistic growth model assumes that when another individual is added to the population, the per capita growth rate decreases immediately. But in many populations there may be **time lags** in the density-dependent response. For example, if a population of gulls increases in size in the fall, density dependence may not be expressed until the following spring, when females lay eggs. In a tropical rain forest, density-dependent mortality of mahogany trees (*Swietenia mahogani*) may occur in the seedling stage, but density-dependent reproduction may not occur until 50 years later, when the trees first begin to flower. Individuals do not immediately adjust their growth and reproduction when resources change, and these delays can affect population dynamics. Seasonal availability of resources, growth responses of prey populations, and age and size structure of consumer populations can introduce important time lags in population growth.

How can time lags be incorporated into our model? Suppose there is a time lag of length τ between the change in population size and its effect on population growth rate. Consequently, the growth rate of the population at time t (dN/dt) is controlled by its size at time $t - \tau$ in the past $(N_{t-\tau})$. Incorporating this time lag into the logistic growth equation gives:

$$\frac{dN}{dt} = rN\left(1 - \frac{N_{t-\tau}}{K}\right) \qquad \text{Equation 2.3}$$

The behavior of this **delay differential equation** depends on two factors: (1) the length of the time lag τ, and (2) the "response time" of the population, which is inversely proportional to r (May 1976). Populations with fast growth rates have short response times $(1/r)$.

The ratio of the time lag τ to the response time $(1/r)$, or $r\tau$, controls population growth. If $r\tau$ is "small" $(0 < r\tau < 0.368)$, the population increases smoothly to carrying capacity (Figure 2.5a). If $r\tau$ is "medium" $(0.368 < r\tau < 1.570)$, the population first overshoots, then undershoots the carrying capacity; these **damped oscillations** diminish with time until K is reached (Figure 2.5b). The exact numerical values for these trajectories are not important. What is important is to understand how the behavior of the model changes as $r\tau$ is increased.

If $r\tau$ is "large" $(r\tau > 1.570)$ the population enters into a **stable limit cycle**, periodically rising and falling about K, but never settling on a single equilibrium point (Figure 2.5c). The carrying capacity is the midpoint between the high and low points in the cycle. The cycle is stable because if the population is perturbed, it will return to these characteristic oscillations. When $r\tau$ is large, the time lag is so much longer than the response time that the population repeatedly overshoots and then undershoots K. The population resembles a heating system with a faulty thermostat that constantly overheats and then overcools, never achieving an equilibrium temperature.

Cyclic populations are characterized by their **amplitude** and **period** (Figure 2.5c). The amplitude is the difference between the maximum and the average population size. It is measured on the y axis of the graph of N vs. t, and its units are number of individuals. The larger the amplitude, the greater the population fluctuations. If the amplitude is too large, the population may hit the "floor" of zero and go extinct. The period is the amount of time it takes for one complete population cycle to occur. It is measured on the x axis, in units of time. The longer the period, the greater the amount of time between population peaks.

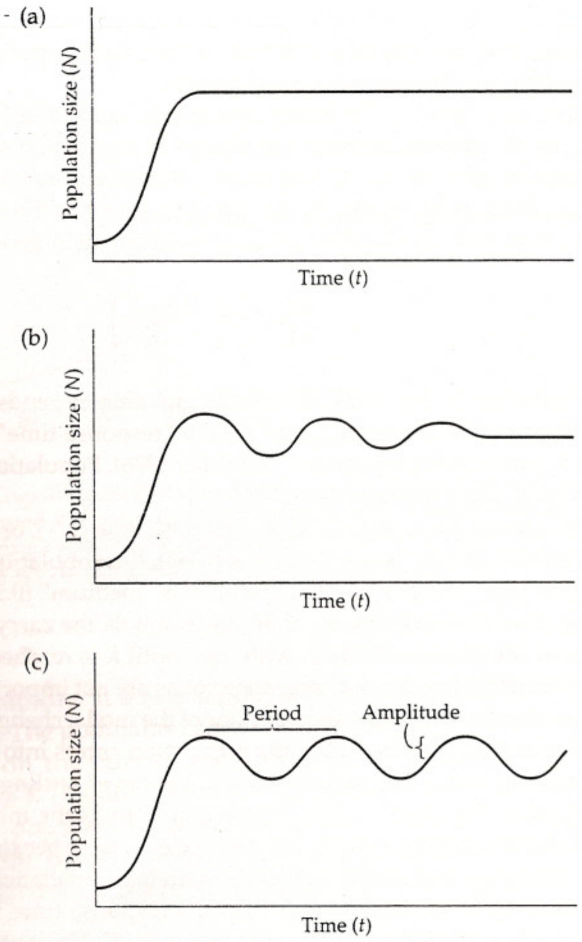


Figure 2.5 Logistic growth curves with a time lag. The behavior of the model depends on $r\tau$, the product of the intrinsic rate of increase and the time lag. (a) "Small" $r\tau$ behaves like the model with no time lag. (b) "Medium" $r\tau$ generates dampened oscillations and convergence on carrying capacity. (c) "Large" $r\tau$ generates a stable limit cycle and does not converge on the carrying capacity.

In a logistic model with a time lag, the amplitude of the cycle increases with increasing values of $r\tau$. This makes intuitive sense—if the population is growing very rapidly, or if the time lag is very long, the population will greatly overshoot K before it begins a phase of decline.

The period of the cycle is always about 4τ, regardless of the intrinsic rate of increase. Thus, a population with a time lag of one year can be expected to reach a peak density every four years. Why should the period of the cycle be four times as long as the lag? When the population reaches K, it will continue to increase for a length of time τ before starting to decrease. The distance from K to the population peak is about one-quarter of the cycle, so the length of the entire cycle is approximately 4τ. This result may explain the observation that many populations of mammals in seasonal, high-latitude environments cycle with peaks every three or four years (May 1976; see Chapter 6).

DISCRETE POPULATION GROWTH

We will now explore a model in which population growth is discrete rather than continuous. A discrete version of the logistic equation is:

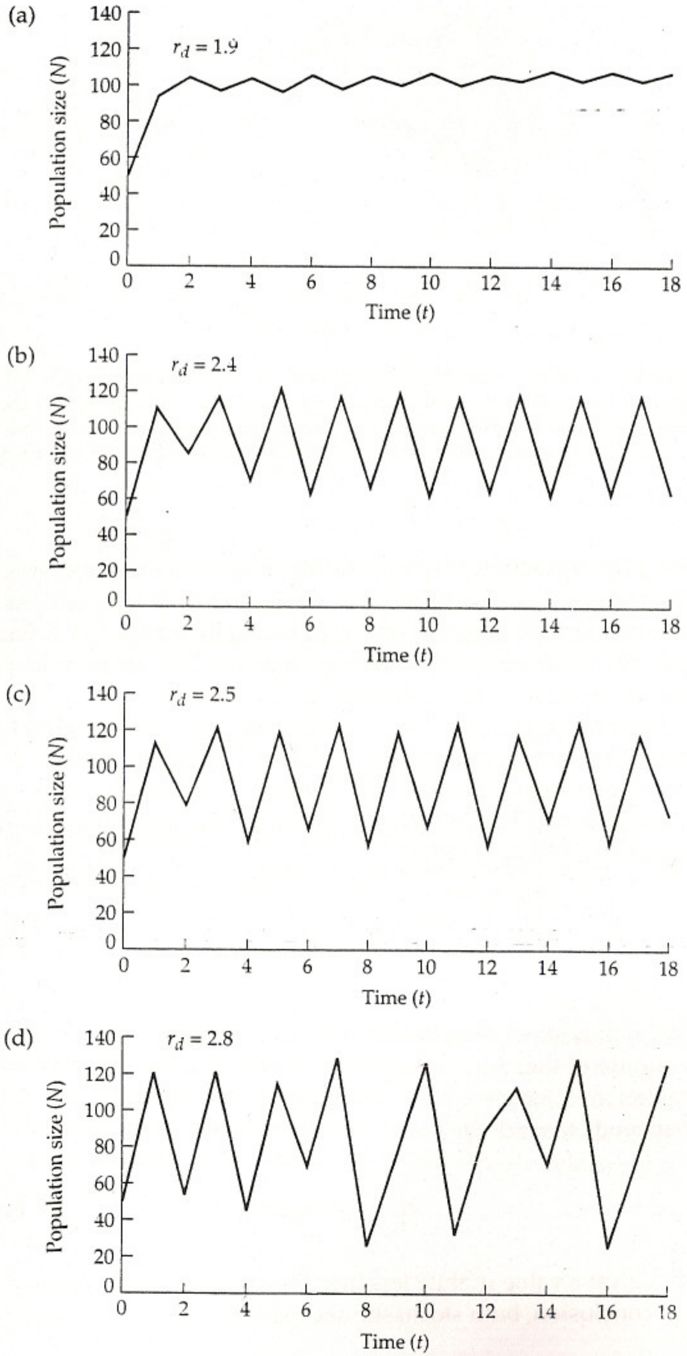
$$N_{t+1} = N_t + r_d N_t\left(1 - \frac{N_t}{K}\right) \qquad \text{Equation 2.4}$$

This discrete growth logistic equation is analogous to the continuous model (Equation 2.1) in the same way that Equation 1.4 was analogous to the original exponential model (Equation 1.2). Note that the growth rate is the discrete growth factor r_d, described in Chapter 1.

A discrete population growth model has a built-in time lag of length 1.0. The population size at one time step in the future (N_{t+1}) depends on the current population size (N_t). In the last section, we saw that the product $r\tau$ controls the dynamics when a time lag is present. For the discrete model, the lag is of length 1.0, so the dynamics depend solely on r_d.

If r_d is not large, the behavior of this discrete equation is similar to that of its continuous cousin. At "small" r_d ($r_d < 2.000$), the population approaches K with damped oscillations (Figure 2.6a). At "less small" r_d ($2.000 < r_d < 2.449$), the population enters into a stable two-point limit cycle. This is similar to the continuous model, except that the population rises and falls to sharp "points," rather than following a smooth curve. The points in the discrete model correspond to peaks and valleys of the cycle (Figure 2.6b). Between an r_d of 2.449 and an r_d of 2.570, the population grows with more complex limit cycles. For example, a four-point limit cycle has two distinct peaks and two distinct valleys before it starts to repeat. The number of points in the limit cycle increases geometrically (2, 4, 8, 16, 32, 64, etc.) as the value of r_d is increased in this interval (Figure 2.6c).

But if r_d is larger than 2.570, the limit cycles break down, and the population grows in a complex, nonrepeating pattern known as **chaos** (Figure 2.6d). Mathematical models of chaos are important in many areas of science, from the description of turbulent flow to the prediction of major weather patterns.



◀ **Figure 2.6** The behavior of the discrete logistic growth curve is determined by the size of r_d. (a) "Small" r_d generates damped oscillations ($r_d = 1.9$). (b) "Less small" r_d generates a stable two-point limit cycle ($r_d = 2.4$). (c) "Medium" r_d generates a more complex four-point limit cycle ($r_d = 2.5$). (d) "Large" r_d generates a chaotic pattern of fluctuations that appears random ($r_d = 2.8$).

Population biologists were among the first to appreciate that simple discrete equations may generate complex patterns (May 1974b). What is interesting about chaos is that seemingly random fluctuations in population size can emerge from a model that is entirely deterministic. Indeed, the track of a chaotic population may be so complex that it is difficult to distinguish from the track of a stochastic population.

However, chaos does not mean stochastic, or random, change. The fluctuations in a chaotic population have nothing to do with chance or randomness. Once the parameters of the model are specified (K, r_d, and N_0), the same erratic population track will be produced each time we run the model. The source of these erratic fluctuations is the density-dependent feedback of the logistic equation, combined with the built-in time lag of the discrete model. A characteristic of a chaotic population is sensitivity to initial conditions. If we alter the starting conditions, say, by changing the initial population size (N_0), the populations will diverge more and more as time goes on (Figure 2.7).

In contrast, a truly stochastic population fluctuates because one or more of its parameters (r_d or K) changes with each time step. In a stochastic model, if we alter the starting population slightly, but retain the same pattern of variation in r_d or K, the two population tracks will be slightly different, but they will not diverge as in Figure 2.7. In the next section we explore stochastic models in which the carrying capacity varies with time.

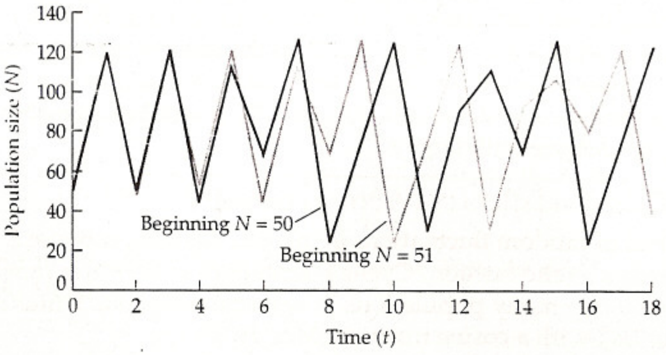


Figure 2.7 Divergence of population tracks with chaos. Both populations followed the same logistic equation, but the starting N for one of the populations was 50 and the other was 51. Note that, as more time passes, the two populations begin to diverge from one another.

RANDOM VARIATION IN CARRYING CAPACITY

In our analysis of environmental stochasticity (Chapter 1), we assumed that resources were unlimited, but that r varied randomly with time. For the logistic model, we will now assume that r is fixed, but that the carrying capacity varies randomly with time. Random variation in K means that the maximum population size that the environment can support changes unpredictably with time. How does this variation in resources affect the behavior of the logistic model? There are several mathematical approaches to the problem (May 1973; Roughgarden 1979), none of which yields a simple answer.

When r varied randomly in our exponential model, we found that the average population size was the same as in the deterministic model ($\bar{N}_t = N_0e^{rt}$). So, you might reason that the average population size in the logistic model should approximate the average carrying capacity ($\bar{K}$). But this is not the case. Instead, $\bar{N}$ will always be *less* than $\bar{K}$. Why should this be so? When a population is above K, it declines faster than a population that is increasing from a corresponding level below K (see Problem 2.4). This asymmetry is reflected in Figure 2.2, which shows that the population tracks above and below carrying capacity are not mirror images of one another. If the carrying capacity is described by its mean ($\bar{K}$) and variance ($\sigma^2_{\bar{K}}$), a rough approximation to the average population size is (May 1974a):

$$\bar{N} \approx \bar{K} - \frac{\sigma^2_{\bar{K}}}{2} \qquad \text{Equation 2.5}$$

Thus, the more variable the environment, the smaller the average population size. The pattern of population fluctuations also depends on r (Levins 1969). Populations with large r are very sensitive to changes in K, and they will tend to track these fluctuations quite closely. Consequently, the average population size will be only slightly less than the average carrying capacity. In contrast, populations with small r are relatively sluggish and will not exhibit large increases or decreases (Figure 2.8); $\bar{N}$ will be somewhat smaller than for populations with large r.

PERIODIC VARIATION IN CARRYING CAPACITY

Instead of random fluctuations in carrying capacity, suppose K varies repeatedly, in a cyclic fashion. Cyclic fluctuations in carrying capacity probably characterize many populations in seasonal temperate latitudes, and can be described with a cosine function (May 1976):

$$K_t = k_0 + k_1[\cos(2\pi t / c)] \qquad \text{Equation 2.6}$$

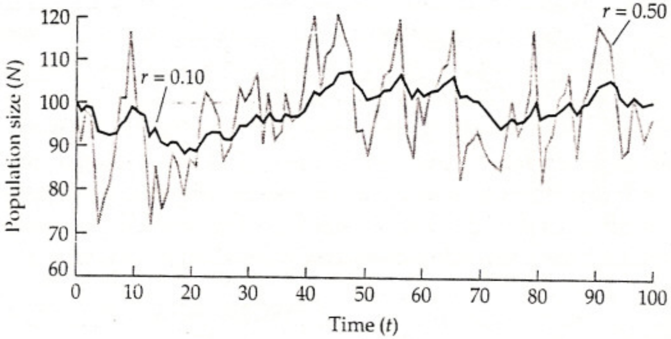


Figure 2.8 Logistic population growth with random variation in carrying capacity. Note that the population with the larger growth rate ($r = 0.50$) tracks the fluctuations in carrying capacity, whereas the population with the small growth rate ($r = 0.10$) is less variable and does not respond as quickly to fluctuations in resources.

Here, K_t is the carrying capacity at time t, k_0 is the mean carrying capacity, k_1 is the amplitude of the cycle, and c is the length of the cycle. As t increases, the cosine term in parentheses varies cyclically from −1 to 1. Thus, during a single cycle of length c, the carrying capacity of the environment varies from a minimum of $k_0 - k_1$ to a maximum of $k_0 + k_1$.

How does this cyclic variation in carrying capacity affect population growth? The length of the carrying capacity cycle functions as a kind of time lag, so once again, the behavior of the model depends on rc. If rc is small ($<< 1.0$), the population tends to "average" the fluctuations in the environment and persists at roughly:

$$\bar{N} \approx \sqrt{k_0^2 - k_1^2} \qquad \text{Equation 2.7}$$

Thus, if rc is small, $\bar{N}$ is less than $\bar{K}$, and the reduction is greater when the amplitude of the cycle is large; both patterns are similar to the results for a population in which K varies stochastically. If rc is large ($>> 1.0$), the population tends to track the fluctuations in the environment:

$$N_t \approx k_0 + k_1 \cos(2\pi t / c) \qquad \text{Equation 2.8}$$

although at a value slightly less than the actual carrying capacity (Figure 2.9).

In conclusion, both stochastic and periodic variation in carrying capacity

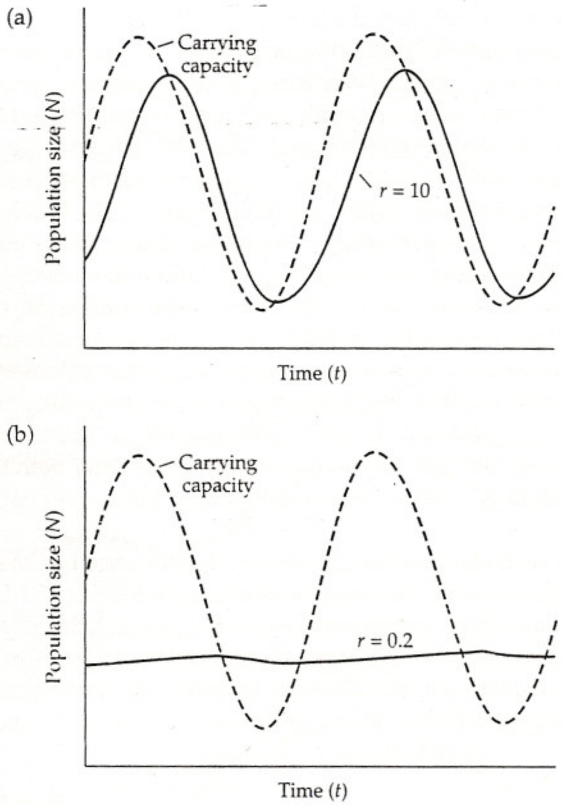


Figure 2.9 Logistic growth with periodic variation in the carrying capacity. The carrying capacity of the environment varies according to a cosine function. As with random variation, the population with the large growth rate ($r = 10$) tends to track the variation (a), and the population with the small growth rate ($r = 0.2$) tends to average it (b). The dashed line indicates K. (From May 1976.)

reduce populations, and the more variable the environment, the lower the average population size. In a variable environment, populations with large r, such as most insects, may be expected to track variation in carrying capacity, whereas populations with small r, such as large mammals, may be expected to average the environmental variation and remain relatively constant.

Empirical Examples

SONG SPARROWS OF MANDARTE ISLAND

Mandarte Island is a rocky, 6-hectare island off the coast of British Columbia. The island is home to a population of song sparrows (*Melospiza melodia*) that has been studied for many decades (Smith et al. 1991). On average, only one new female migrant joins this population each year, so most of the changes in population size are due to local births and deaths. Over the past 30 years, the population has varied between 4 and 72 breeding females and between 9 and 100 breeding males. The sparrow population of Mandarte Island does not conform to a simple logistic growth model; population size is variable and there have been periods of increase followed by rapid declines (Figure 2.10). Some of these, such as the crash in 1988, were caused by an unusually cold winter and an increased death rate. Other declines were not correlated with any obvious change in the environment.

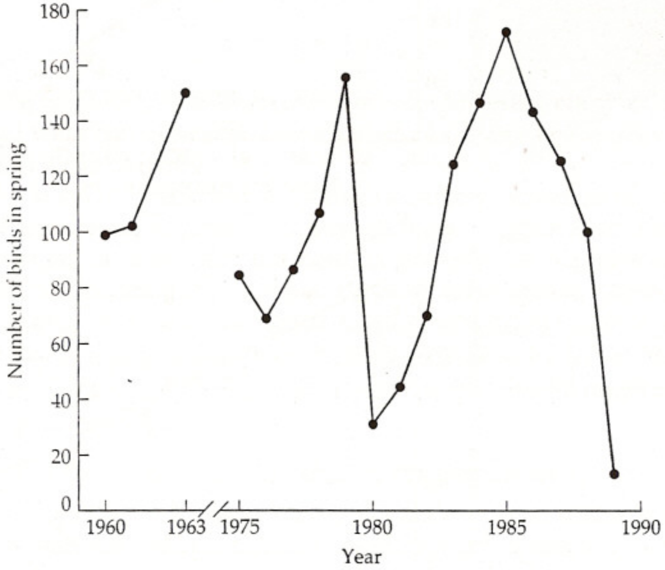


Figure 2.10 Population size of the song sparrow (*Melospiza melodia*) on Mandarte Island. (After Smith et al. 1991.)

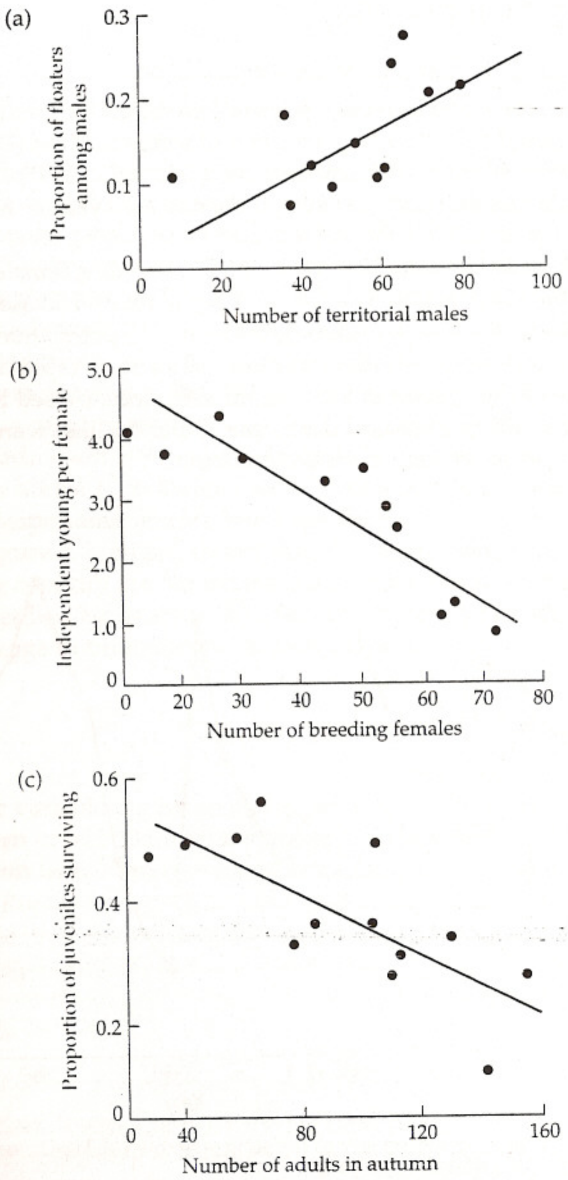


Figure 2.11 Density dependence in the Mandarte Island song sparrow (*Melospiza melodia*) population. As the population becomes more crowded (a) the proportion of nonterritorial "floater" males increases; (b) the number of surviving young produced per female decreases; (c) juvenile survival decreases. (After Arcese and Smith 1988 and Smith et al. 1991.)

Although this population is clearly buffeted by density-independent changes, there is good evidence of underlying density dependence. Male song sparrows defend territories that determine their breeding success, but limited food resources and space prevent many males from ever establishing territories. These nonterritorial "floaters" are behaviorally submissive individuals. Their proportion increased in a density-dependent fashion as the population became more crowded (Figure 2.11a). When the resident territory holders were experimentally removed, floater males quickly took over their territories, so the total breeding population size remained relatively constant.

Density dependence is also seen in the number of surviving young produced per female (Figure 2.11b), and in the survival of juveniles (Figure 2.11c), both of which decreased as the population size increased. Experimental studies confirmed that food limitation was the controlling factor: when food levels for sparrows were artificially enhanced, female reproductive output increased fourfold (Arcese and Smith 1988). Thus, both territoriality and food limitation generated density-dependent birth and death rates in song sparrows.

Nevertheless, although density dependence has the potential to control population sizes, the risk of extinction for Mandarte Island sparrows probably comes from unpredictable environmental catastrophes and other density-independent forces. Somewhat paradoxically, it is these density-independent fluctuations that allow us to detect density dependence, because they push the population above or below its equilibrium and reveal the underlying dynamics of birth and death rates.

POPULATION DYNAMICS OF SUBTIDAL ASCIDIANS

Ascidians, or "sea squirts," are filter-feeding invertebrates that live attached to pier pilings and rock walls. These animals are important components of subtidal "fouling" communities throughout the world. Ascidians are actually primitive chordates that disperse with a sexually produced tadpole larva. The perennial ascidian *Ascidia mentula* has been the subject of a long-term study of population dynamics on vertical rock walls off the Swedish west coast (Svane 1984).

Six populations were monitored continually for 12 years with photographs of permanent plots. At sheltered sites within a fjord, density was highest in shallow plots; at exposed stations, density was highest in deep-water plots. At all sites, populations fluctuated considerably (Figure 2.12), in contrast to the predictions of the basic logistic model. Mortality was primarily due to "bulldozing" by sea urchins and temperature fluctuations. These factors seemed to operate in a density-independent fashion, because there was no relationship between mortality rate and population size (Figure 2.13a). In

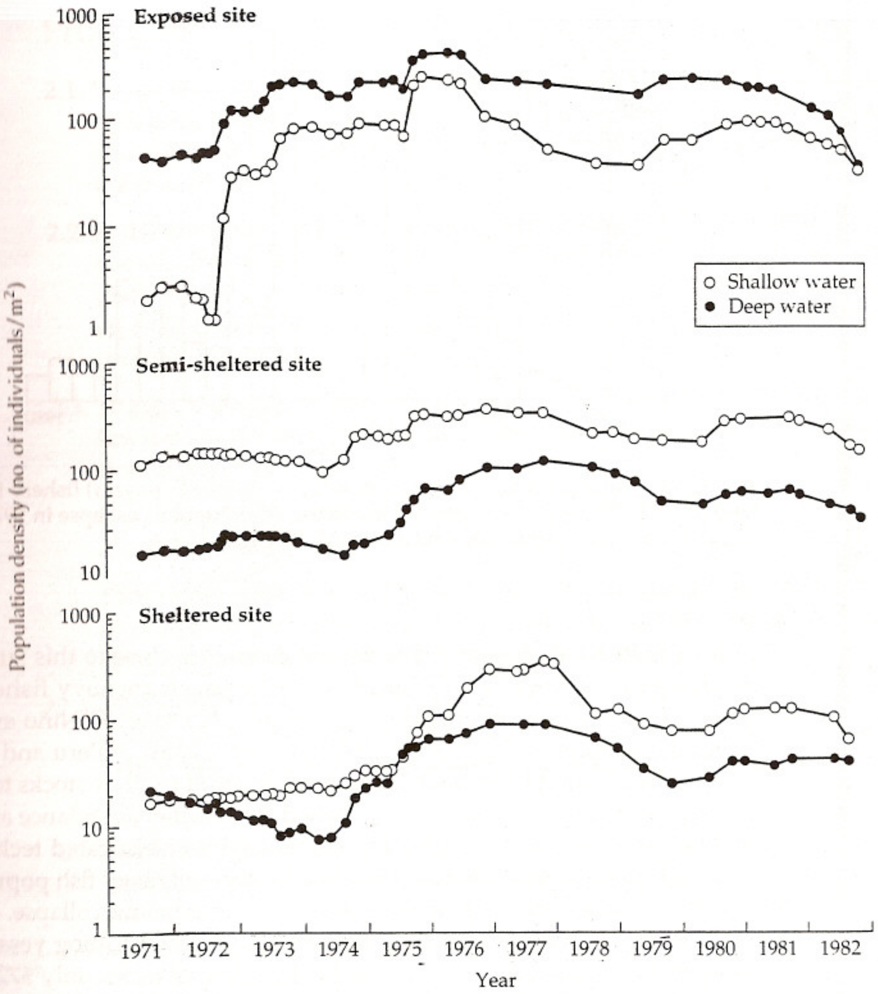


Figure 2.12 Population density of ascidians (*Ascidia mentula*) at six subtidal sites off the coast of Sweden. Population densities are greater in shallow water than in deep, except at the exposed site. Note the use of a logarithmic scale for the y axis, which diminishes the appearance of population fluctuations. (After Svane 1984.)

contrast, reproduction (as measured by larval recruitment) was density-dependent and decreased at high densities. At low densities, there was evidence of an Allee effect: recruitment actually increased with population density until a density of approximately 100 animals per square meter was reached (Figure 2.13b). Possible explanations for this Allee effect include the behavioral attraction of larvae to established adults and entrapment of larvae by local water currents.

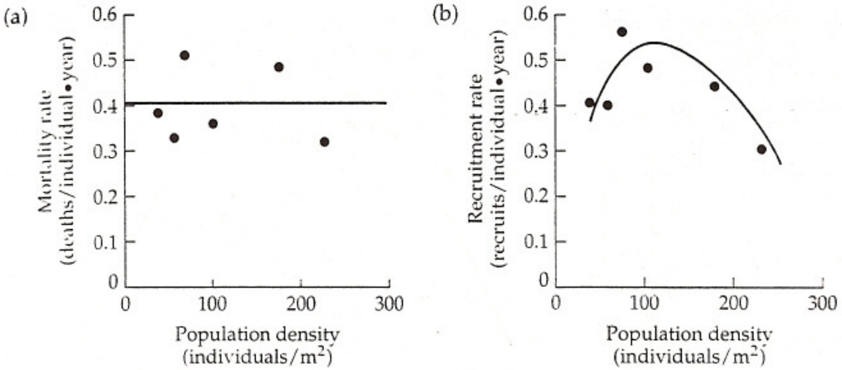


Figure 2.13 (a) Density-independent mortality rates. The mortality rate of ascidians (*Ascidia mentula*) at the six population sites appears to be independent of population size. (b) Density-dependent recruitment rates. The rate of recruitment of new juveniles into ascidian populations is density-dependent and is lower in more dense populations. Note the appearance of a possible Allee effect, as recruitment is also decreased at sites with very low abundance. (After Svane 1984.)

Like the Mandarte Island sparrows, these ascidians showed some evidence of underlying density dependence, although the population never reached a steady carrying capacity. Both the ascidian and sparrow populations were affected by temperature fluctuations, although these effects seemed more subtle and long-term for the ascidians. Unlike the isolated sparrow population, the ascidian populations were potentially linked by larval dispersal between sites, so that a realistic model of population dynamics might be especially complex (see Chapter 4).

LOGISTIC GROWTH AND THE COLLAPSE OF FISHERIES POPULATIONS

How many tons of fish should be harvested each year to maximize long-term yield? This **optimal yield** problem has been very important to commercial fisheries because of the huge amounts of money involved and because overfishing has been a problem since at least the 1920s, when commercial stocks of many species started to decline. The logistic growth curve provides a simple, though often unpopular, prescription for optimal fishing strategies.

The optimal strategy is the one that maximizes the population growth rate, because this rate determines how quickly fish can be removed from the pop-

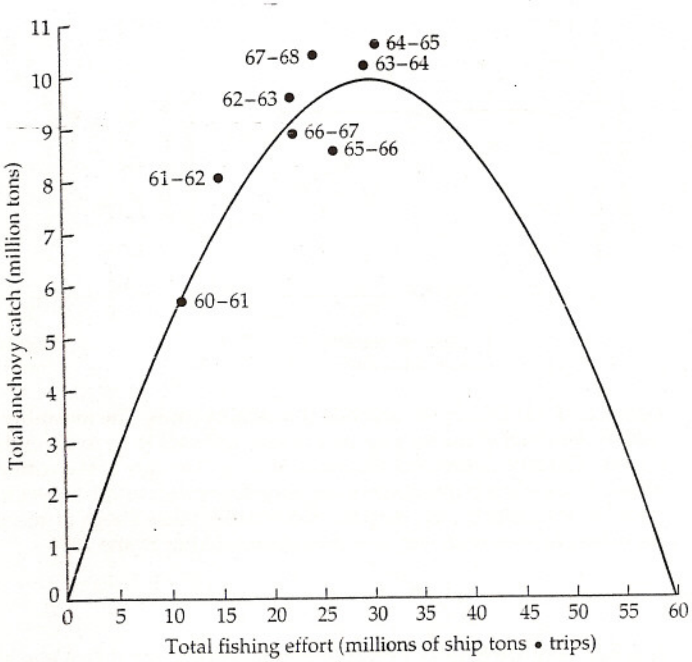


Figure 2.14 Relationship between fishing effort and total catch for the Peruvian anchovy (*Engraulis ringens*) fishery. Each point represents the fishing catch and effort for a particular year. The data include fishing effort by humans and fish catches by seabird populations. The parabola is drawn by fitting the logistic model to data from Boerema and Gulland (1973). (After Krebs 1985.)

ulation while still maintaining a constant stock for future production. If a population is growing according to the logistic equation, maximum population growth rate occurs if the population is held at $K/2$, half the carrying capacity (Figure 2.3a). Two other strategies are guaranteed to produce low yields. The first is to be extremely conservative and remove very few animals at each harvest. This keeps the standing stock large, but the yield is low because the population is close to carrying capacity and grows slowly. The other strategy is to harvest the population down to a very small size. This also produces low yield because there are so few individuals left to reproduce.

Unfortunately, this latter strategy of overdepletion has been followed by all the world's fisheries. Figure 2.14 shows the yearly catch of Peruvian anchovy (*Engraulis ringens*) fitted to the predictions of a simple logistic model. The model predicts a maximum sustained yield of approximately 10 to 11 million metric tons per year. The annual catch was close to this sustained maximum from 1964 to 1971. In 1972, the Peruvian anchovy fishery collapsed, in part due to overfishing, and in part due to an El Niño event, in which a warm tropical water mass moved off the coast of Peru and greatly reduced productivity. Although fishing was reduced to allow stocks to recover, anchovy populations have never reached their former abundance and fishing yields remain low (Figure 2.15). Increasingly sophisticated technology and large factory-ships have depleted world stocks of many fish populations to the point where the industry itself is doomed to economic collapse. In 1989, for example, the cost of operating the world's 3 million fishing vessels was estimated at $92 billion, whereas the total catch was worth only $72 billion (Pitt 1993). The disappearance of human societies that depend on fishing is also inevitable.

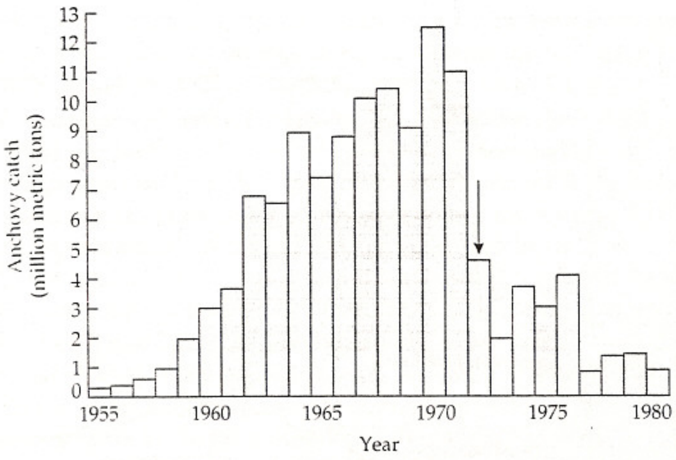


Figure 2.15 Total catch for the Peruvian anchovy (*Engraulis ringens*) fishery from 1955 to 1981. This was the largest fishery in the world until its collapse in 1972. (After Krebs 1985; unpublished data from M. H. Glanz.).

The situation can only be remedied by worldwide restrictions on fishing and short-term reductions in catch. Unfortunately, this will not be easy because each individual fishing vessel tries to maximize its short-term yield by intensive fishing. Migratory fish populations do not obey political boundaries, making international policies difficult to enforce. The problem of short-term versus long-term profits in the exploitation of natural resources is known as "the tragedy of the commons" (Hardin 1968).