

Figure 1.8. Total catch of Blue Whales in the Antarctic, 1920–1963, and an index of abundance of Blue Whales in the Antarctic (estimated as the number of whales caught per catcher-ton-day), 1945–1963 (after Gulland 1971).

Blue Whale populations were already very depleted by the time quotas were introduced in 1945. The stocks of the species continued to decline, and a shorter open season for the species was introduced in 1953. However, the difference between the catch and the productive potential of the whale population continued to widen because the quotas were more or less fixed and

the population did not reproduce quickly enough to replace the numbers removed. The imposition of quotas, and the allocation of the catch among countries, were topics of intense political and scientific argument from the 1950s through 1967. In 1960 and 1961, the International Whaling Commission failed to set quotas at all because of disagreements among its member nations. As late as 1955 there was no agreement on the extent, or even the existence, of a decline in Antarctic whale stocks. Fin Whales were the mainstay of the industry at this time, and their abundance did not begin to decline dramatically until 1955, even though the abundances of other whale species were obviously falling. Throughout the period of the early 1960s, Blue Whale stocks continued to decline. The population abundance data for the Blue Whale from the period 1945–1963 fit a straight line quite well, suggesting that the decline in the population size was approximately exponential (Figure 1.9).

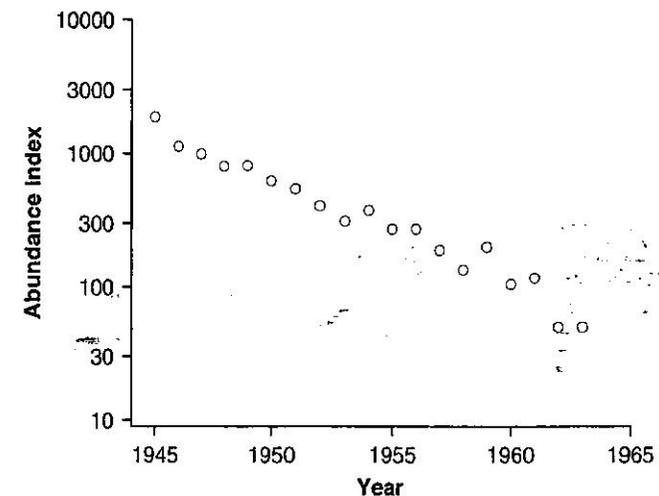


Figure 1.9. The abundance index for Blue Whale in Figure 1.8 plotted on a logarithmic scale.

In 1963, evidence was presented to the whaling industry that its quota was three times higher than the level at which further depletion of the stock could be avoided. The industry reduced its harvest to these levels by 1967. One critical failure in the process of regulation of the industry was that scientists failed to provide clear advice to the industry after 1955, when a

reduction in the quota was clearly necessary and would have been much less drastic than the reduction that eventually was necessary. The Blue Whale population was reduced from about 20 to 50 thousand individuals in the 1930s to between 9 and 14 thousand in the mid 1950s. It remained approximately constant at about 14,000 individuals between 1965 and 1975.

## 1.5 Additional topic

### 1.5.1 Population Growth in Continuous Time

Most examples in this book involve populations of species living in temperate regions, which have distinct reproductive seasons tied to the seasonality of the environment. This property, together with the way most field studies estimate demographic parameters (by periodically observing a population), make it easy and natural to use the discrete-time formulations of population models. However, some natural populations reproduce and die continuously, as does the human population. The basic model for population growth in discrete time was

$$N(t+1) = N(t) + B - D$$

This could be rewritten as

$$\begin{aligned} \Delta N &= N(t+1) - N(t) \\ &= B - D \end{aligned}$$

The symbol  $\Delta N$  is the difference in population size. If the time interval represented by  $\Delta N$  is small, we can approximate it by the derivative  $dN/dt$ . Rather than express births and deaths as numbers of individuals, they may be expressed as instantaneous rates, giving

$$\begin{aligned} dN/dt &= bN - dN \\ &= (b - d)N \\ &= rN \end{aligned}$$

The difference between the birth rate and the death rate in continuous time is called the instantaneous growth rate ( $r$ ). The equation above may be solved, giving

$$N(t) = N(0) \cdot e^{rt}$$

This equation says that the population size at time  $t$  in the future is given by the current population size, multiplied by  $e^{rt}$ . In this equation,  $e$  is a constant (about 2.7); sometimes  $e^{rt}$  is written as  $\exp(rt)$ . By analogy with the equivalent discrete time equation, you can see that

$$R = e^r$$

because  $R^t = (e^r)^t = e^{rt}$ . The equation for exponential population growth in continuous time is equivalent to the model in discrete time, in which the time interval is made arbitrarily small. Frequently, models for population growth are written in continuous time because they are analytically tractable, i.e., one can find solutions to the equations using calculus. Equations in discrete time, although more plausible for many biological scenarios, are generally less tractable. However, this is not a big disadvantage when numerical solutions can be obtained using computer simulations. We will ignore models in continuous time in this book because discrete-time models are more applicable to most of our examples, and they are easier to explain and understand. While we shall mention analytical solutions where they exist, we will use computer simulations to solve most of the problems.

## 1.6 Exercises

### Exercise 1.1: Blue Whale Recovery

This exercise is based on the Blue Whale example of Section 1.4.3. The population dynamics of the Blue Whale population and predictions of harvest levels have been made using exponential models. The growth rate ( $R$ ) of the population during the period represented in Figure 1.9 was 0.82, i.e., the population declined by 18% per year. The fecundity of Blue Whale has been estimated to be between 0.06 to 0.14 and natural mortality to be around 0.04. In the absence of harvest, the growth rate of the population would be between 1.02 and 1.10. We want to estimate the time it will take for the Blue Whale population to recover its 1930s level. Assuming a population size in 1963 of 10,000 and a target population size of 50,000, calculate how many years it will take the population to recover:

(a) if its growth rate is 1.10

(b) if its growth rate is 1.02

Hint: Use the method for calculating doubling time, but with a factor different from 2.

### Exercise 1.2: Human Population, 1800–1995

In this exercise, we will investigate the data on human population growth given in Section 1.4.1. Before you begin the exercise, look at your watch and record the time.

**Step 1.** Calculate the growth rate of the human population for each interval in Table 1.1. Note that each interval is a different number of years: initially 50, then 20, later 5 years. It is important to convert all these into annual growth rates, so that we can compare them. Use the method described in Section 1.4.1 to calculate the annual growth rate from 1800 to 1850, from 1850 to 1870, so on, and finally from 1990 to 1995. Enter the results in Table 1.3 below (in the table, the first growth rate is already calculated as an example).

Table 1.3. Calculating the annual growth rate of the human population.

Year	Population (billions)	Time interval (years)	Population in previous census	Growth rate in $T$ years ( $R^T$ )	Annual growth rate ( $R$ )
$t$	$N(t)$	$T$	$N(t-T)$	$N(t)/N(t-T)$	$[N(t)/N(t-T)]^{(1/T)}$
1800	0.91	—	—	—	—
1850	1.13	50	0.91	1.24176	1.00434
1870	1.30		1.13		
1890	1.49		1.30		
1910	1.70		1.49		
1930	2.02		1.70		
1950	2.51		2.02		
1970	3.62		2.51		
1975	3.97		3.62		
1980	4.41		3.97		
1985	4.84		4.41		
1990	5.29		4.84		
1995	5.75		5.29		

**Step 2.** Plot the growth rate against year and comment on any pattern.

**Step 3.** It is important to know the difference between relative and absolute growth. Even though the annual growth rate (a relative measure of growth) declines, the number of individuals added to the population each year (an absolute measure of growth) may increase. The number added to the population in one year is equal to  $N(R-1)$ , where  $N$  is the population size and  $R$  is the annual growth rate. For example, in 1850,

$$1.13 \text{ billion} \cdot 0.00434 = 4.9 \text{ million}$$

people were added to the population. (Strictly speaking this is not correct, because the two numbers refer to different times: 1.00434 is the average growth from 1800 to 1850, whereas 1.13 billion is the population size in 1850. However, for the purpose of this exercise, it is a reasonable approximation.)

Calculate the number of people added to the human population each year, for 1975, 1985, and 1995, using Table 1.4 below. Compare the change in annual growth rate with the absolute increase in the population size per year.

Table 1.4. Calculating the number of individuals added to the human population.

Year	Population size	Annual growth rate	Annual number of people added to the population
1975	3.97 billion		
1985	4.84 billion		
1995	5.75 billion		

**Step 4.** Using the estimated number of people added to the human population in 1995, calculate the approximate number of people added to the human population:

- per day
- per hour
- per minute
- during the time you completed the exercise

### Exercise 1.3: Human Population, 1995–2035

In this exercise you will investigate one rather optimistic scenario of the slow-down and stabilization of human population. Specifically, you will calculate the population size in 2035, assuming that by that time the growth rate has reached 1.00 (no growth). For this exercise, assume that (i) the fecundity in 1995 is 0.0273, (ii) the survival rate will not change in the future, and (iii) in the 40 years after 1995, the fecundity will decrease so as to make the annual growth rate in 2035,  $R(2035) = 1.0$ .

**Step 1.** Using the annual growth rate for 1995 you calculated above, estimate the annual decrease in fecundity necessary to make  $R(2035) = 1.0$ . Assume a linear decrease, i.e., an equal amount of decrease in fecundity for each year.

**Step 2.** Calculate the fecundity and the annual growth rate for years 2005, 2015, 2025, and 2035, and enter them in Table 1.5 below.

**Step 3.** Calculate the 10-year growth rates for the periods 1995–2005, 2005–2015, 2015–2025, and 2025–2035, by multiplying each annual growth rate by itself 10 times. For example the 10-year growth rate for 1995–2005 is  $R(1995)^{10}$ . Enter these in the table below (enter the 10-year growth rate for period 1995–2005 in the line for 1995.)

Table 1.5. Projecting human population growth.

Year	Fecundity ( $f$ )	Annual growth rate ( $R$ )	10-year growth rate ( $R^{10}$ )	Population at the beginning of the 10-year interval	Population at the end of the 10-year interval
1995	0.0273			5.75 billion	
2005					
2015					
2025					
2035		1.0000	1.0000		

**Step 4.** Estimate the population size at the end of each 10-year period by multiplying the 10-year growth rate you calculated in the previous step with the population size at the beginning of the time period.

How much did the population increase while the fecundity was decreasing for 40 years? If the fecundity decreased to the same level in 80 years instead of 40, would the final population size be larger or smaller?

### 1.7 Further reading

- Ehrlich, P. R. and A. H. Ehrlich. 1990. *The population explosion*. Simon and Schuster, New York.
- Elton, C. S. 1958. *The ecology of invasions by animals and plants*. Methuen, London.
- Hardin, G. 1993. *Living within limits: ecology, economics and population taboos*. Oxford University Press, New York.
- Holdren, J.P. 1991. Population and the energy problem. *Population and Environment* 12:231-255.
- Vitousek, P. M., P. R. Ehrlich, A. H. Ehrlich and P. M. Matson. 1986. Human appropriation of the products of photosynthesis. *BioScience* 36:368–373.