Crew members sort fish on a trawler. As the large predators, such as cod, have been exhausted, we turn our attention to smaller prey. Some call this fishing down the food chain.

CHAPTER

6 Population Biology

Nature teaches more than she preaches.

—John Burroughs—

LEARNING OUTCOMES

After studying this chapter, you should be able to:

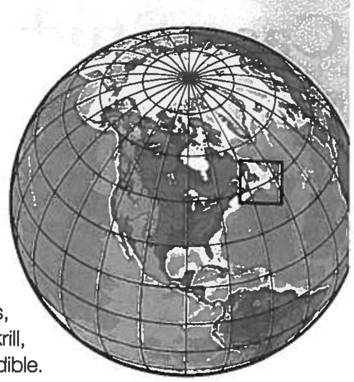
6.1 Describe the dynamics of population growth.

6.2 Summarize the factors that increase or decrease populations.

6.3 Compare and contrast the factors that regulate population growth.

6.4 Identify some applications of population dynamics in conservation biology.

Case Study How Many Fish in the Sea?



When John Cabot discovered Newfoundland in 1497, cod (*Gadus morhua*) were so abundant that sailors could simply scoop them up in baskets. Growing up to 2 meters (6 feet) long, weighing as much as 100 kg (220 lbs) and living up to 25 years, cod have been a major food resource for Europeans for more than 500 years. Because the firm, white flesh of the cod has little fat, it can be salted and dried to produce a long-lasting food that can be stored or shipped to distant markets.

No one knows how many cod there may have once been in the ocean. Coastal people recognized centuries ago that huge schools would gather to spawn on shoals and rocky reefs from Massachusetts around the North Atlantic to the British Isles. In 1990, Canadian researchers watched on sonar as a school estimated to contain several hundred million fish spawned on the Gorges Bank off Newfoundland. Because a single mature female cod can lay up to 10 million eggs in a spawning, a school like this—only one of many in the ocean—might have produced a quadrillion eggs.

It seems that such an abundant and fecund an animal could never be threatened by humans. In 1883, Thomas Huxley, the eminent biologist and friend of Charles Darwin, said, "I believe that the cod fishery . . . and probably all the great sea fisheries are inexhaustible . . . Nothing we do seriously affects the number of fish." But in Huxley's time, most cod were caught on handlines by fishermen in small wooden dories. He couldn't have imagined the size and efficiency of modern fishing fleets. Following World War II, fishing boats grew larger, more powerful, and more numerous, while their fish-finding and harvesting technology grew tremendously more effective.

Modern trawlers now pull nets with mouths large enough to engulf a dozen jumbo jets at a time. Heavy metal doors, connected by a thick metal chain, hold the net down on the ocean floor, where it crushes bottom-dwelling organisms and reduces habitat to rubble. A single pass of the trawler not only can scoop up millions of fish, it leaves a devastated community that may take decades to repair. Some environmental groups have called for a complete ban on trawling everywhere in the world.

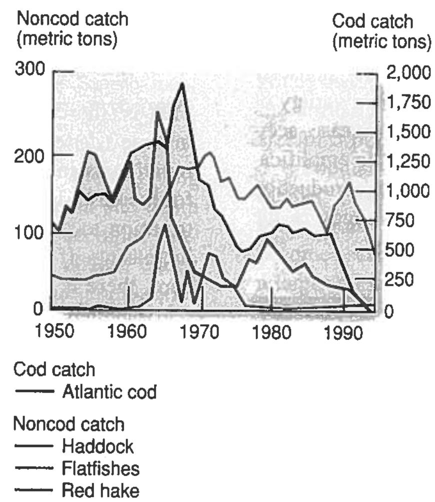


FIGURE 6.1 Commercial harvests in the Northwest Atlantic of some important ground (bottom) fish, 1950–1995.
Source: World Resources Institute, 2000.

It's difficult to know how many fish are in the ocean. We can't see them easily, and often we don't even know where they are. Our estimates of population size often are based on the harvest brought in by fishing boats. Biologists warn that many marine species are overfished and in danger of catastrophic population crashes. Research shows that 90 percent of large predators such as tuna, marlin, swordfish, sharks, cod, and halibut are gone from the ocean.

Fish and seafood (including freshwater species) contribute more than 140 million metric tons of highly valued food every year, and are the main animal protein source for about one-quarter of the world population. Marine biologists note, however, that we're "fishing down the food chain." First we pursued the top predators and ground fish until they were commercially extinct, then we went after smaller fish, such as pilchard, capelin, pollock, and eels. When they became scarce, we turned to squid, skates, and other species once discarded as unwanted by-catch. Finally, we've begun harvesting invertebrates, such as sea cucumbers and krill, that many people regard as inedible.

In 2006, an international team of researchers predicted that all the world's major fish and seafood populations will collapse by 2048 if current trends in overfishing and habitat destruction continue. Marine biodiversity, they found, has declined dramatically, particularly since the 1950s. Three-fourths of all major marine fisheries are reported to be fully exploited, overfished, or severely depleted. About one-third of those species are already in collapse—defined as having catches decline 90 percent from the maximum catch. Nevertheless, scientists say, it's not too late to turn this situation around. Many fish stocks can recover quickly if we change destructive fishing practices.

Some governments already have heeded warnings about declining marine fisheries. In 1972, Iceland unilaterally declared a 200 nautical mile (370 km) exclusive economic zone that excluded all foreign fishing boats. In 2003 the Canadian government, in response to declining populations of prized ground fish (fig. 6.1) banned all trawling in the Gulf of St. Lawrence and in the Atlantic Ocean northeast of Newfoundland and Labrador. More than 40,000 Canadians lost their jobs, and many fishing towns were decimated. Marine scientists have called for similar bans in European portions of the North Atlantic, but governments there have been reluctant to impose draconian regulations. They've closed specific fisheries, such as anchovy harvest in the Bay of Biscay and sand eel fishing off Scotland, but they've only gradually reduced quotas for fisheries, such as cod, despite growing evidence of population declines.

Industry trade groups deny that there's a problem with marine fish populations. If restrictions were lifted, they argue, they could catch plenty of fish. It's true that some cod stocks, including the Barents Sea and the Atlantic around Iceland, are stable or even increasing. Establishing marine preserves, like the one around Apo Island in the Philippines, described in chapter 5, can quickly replenish many species if enough fish are available for breeding.

It's questionable, however, if some areas will ever recover their former productivity. It appears that overharvesting may have irreversibly disrupted marine ecosystems and food webs. On the Gorges Bank off the coast of Newfoundland, trillions of tiny tentacled organisms called hydroids now prey on both the organisms that once fed young cod as well as the juvenile cod themselves. Although hydroids have probably always been present, they once were held in check by adult fish.

Case Study *continued*

Now not enough fish survive to regulate hydroid populations. Is this a shift to a permanent new state, or just a temporary situation?

This case study illustrates some of the complexities and importance of population biology. How can we predict the impacts of human actions and environmental change on different kinds organisms? What are acceptable harvest limits and minimum viable population sizes? In this chapter, we'll look at some of the factors that affect population dynamics of biological organisms.

For more information, see

Worm, B., et al. 2006. Impacts of biodiversity loss on ocean ecosystem services. *Science* 314 (5800):787–90.

6.1 Dynamics of Population Growth

Many biological organisms can produce unbelievable numbers of offspring if environmental conditions are right. Consider the common housefly (*Musca domestica*). Each female fly lays 120 eggs (assume half female) in a generation. In 56 days those eggs become mature adults, able to reproduce. In one year, with seven generations of flies being born and reproducing, that original fly would be the proud parent of 5.6 trillion offspring. If this rate of reproduction continued for ten years, the entire earth would be covered in several meters of housefly bodies. Luckily housefly reproduction, as for most organisms, is constrained in a variety of ways—scarcity of resources, competition, predation, disease, accident. The housefly merely demonstrates the remarkable amplification—the **biotic potential**—of unrestrained biological reproduction (fig. 6.2). Population dynamics describes these changes in the number of organisms in a population over time.

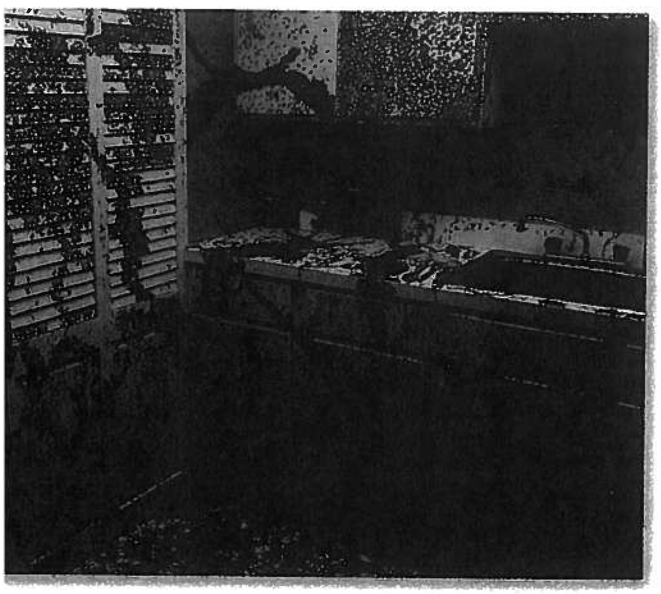


FIGURE 6.2 Reproduction gives many organisms the potential to expand populations explosively. The cockroaches in this kitchen could have been produced in only a few generations. A single female cockroach can produce up to 80 eggs every six months. This exhibit is in the Smithsonian Institute's National Museum of Natural History.

Growth without limits is exponential

As you learned in chapter 3, a population consists of all the members of a single species living in a specific area at the same time. The growth of the housefly population just described is **exponential,** having no limit and possessing a distinctive shape when graphed over time. An exponential growth rate (increase in numbers per unit of time) is expressed as a constant fraction, or exponent, which is used as a multiplier of the existing population. The mathematical formula for exponential growth is:

$$\frac{dN}{dt} = rN$$

That is, the change in numbers of individuals (dN) per change in time (dt) equals the rate of growth (r) times the number of individuals in the population (N). The r term (intrinsic capacity for increase) is a fraction representing the average individual contribution to population growth. If r is positive, the population is increasing. If r is negative, the population is shrinking. If r is zero, there is no change, and $dN/dt = 0$.

A graph of exponential population growth is described as a **J curve** (fig. 6.3) because of its shape. As you can see, the number of individuals added to a population at the beginning of an exponential growth curve can be rather small. But within a very short time, the numbers begin to increase quickly because a fixed percentage leads to a much larger increase as the population size grows.

The exponential growth equation is a very simple model; it is an idealized, simple description of the real world. The same equation is used to calculate growth in your bank account due to compounded interest rates; achieving the potential of your savings depends on you never making a withdrawal. Just as species populations lose individuals and experience reduced biotic potential, not all of your dollars will survive to a ripe old age and contribute fully to your future cash position.

Carrying capacity relates growth to its limits

In the real world there are limits to growth. Around 1970, ecologists developed the concept of **carrying capacity** to mean the number or biomass of animals that can be supported (without harvest) in a certain area of habitat. The concept is now used more generally to suggest a limit of sustainability that an environment has in relation to the size of a species population. Carrying capacity is helpful in understanding the population dynamics of some species, perhaps even humans.

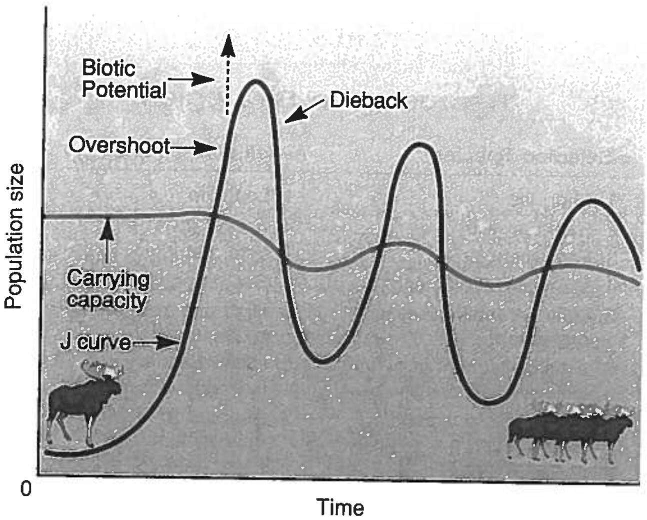


FIGURE 6.3 J curve, or exponential growth curve, with overshoot of carrying capacity. Exponential growth in an unrestrained population (*left side of curve*) leads to a population crash and oscillations below former levels. After the overshoot, carrying capacity may be reduced because of damage to the resources of the habitat. Moose on Isle Royale in Lake Superior may be exhibiting this growth pattern in response to their changing environment.

When a population **overshoots** or exceeds the carrying capacity of its environment, resources become limited and death rates rise. If deaths exceed births, the growth rate becomes negative and the population may suddenly decrease, a change called a **population crash** or dieback. (see fig. 6.3). Some populations can go through repeated **boom-and-bust cycles** in which they repeatedly overshoot the carrying capacity of their habitat and then crash catastrophically. This oscillation can eventually lower the environmental carrying capacity for an entire food web.

Moose and other browsers or grazers sometimes overgraze their food plants, for example, such that future populations of herbivores in the same habitat find less preferred food to sustain them, at least until the habitat recovers. Some species go through predictable cycles if simple factors are involved, such as the seasonal light- and temperature-dependent bloom of algae in a lake. Cycles can be irregular if complex environmental and biotic relationships exist. Irregular cycles include migratory locust outbreaks in the Sahara, or tent caterpillars in temperate forests—these represent irruptive population growth. Population dynamics are also affected by the emigration of organisms from an overcrowded habitat, or immigration of individuals into new habitat, as occurred in 2005 when owls suddenly invaded the northern United States due to a food shortage in their Canadian habitat.

Feedback produces logistic growth

Not all biological populations cycle through exponential overshoot and catastrophic dieback. Many species are regulated by both internal and external factors and come into equilibrium with their environmental resources while maintaining relatively stable population sizes. When resources are unlimited, they may even grow exponentially, but this growth slows as the carrying capacity of the environment is approached. This population dynamic is called **logistic growth** because of its constantly changing rate.

Mathematically, this growth pattern is described by the following equation, which adds a feedback term for carrying capacity (K) to the exponential growth equation:

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

The logistic growth equation says that the change in numbers over time (dN/dt) equals the exponential growth rate (rN) times the portion of the carrying capacity (K) not already taken by the current population size (N). The term ($1 - N/K$) establishes the relationship between population size at any given time step and the number of individuals the environment can support. Depending on whether N is less than or greater than K, the rate of growth will be positive or negative.

The logistic growth curve has a different shape than the exponential growth curve. It is a sigmoidal-shaped, or **S curve** (fig. 6.4). It describes a population that decreases if its numbers exceed the carrying capacity of the environment. In the Data Analysis exercise at the end of this chapter, you will learn how the terms in the exponential and logistic equations influence the size of a population at any time.

Population growth rates are affected by external and internal factors. External factors are habitat quality, food availability, and interactions with other organisms. As populations grow, food becomes scarcer and competition for resources more intense. With a larger population, there is an increased risk that disease or para-

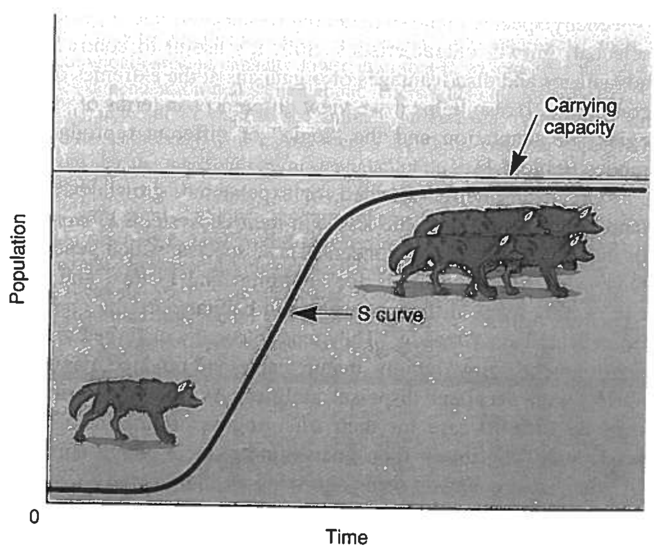


FIGURE 6.4 S curve, or logistic growth curve, describes a population's changing numbers over time in response to feedback from the environment or its own population density. Over the long run, a conservative and predictable population dynamic may win the race over an exponential population dynamic. Species with this growth pattern tend to be *K*-selected.

sites will spread, or that predators will be attracted to the area. Some organisms become physiologically stressed when conditions are crowded, but other internal factors of maturity, body size, and hormonal status may cause them to reduce their reproductive output. Overcrowded house mice ($>1{,}600/m^3$), for instance, average 5.1 baby mice per litter, while uncrowded house mice ($<34/m^3$) produce 6.2 babies per litter. All these factors are **density-dependent,** meaning as population size increases, the effect intensifies. With density-independent factors, a population is affected no matter what its size. Drought, an early killing frost, flooding, landslide, or habitat destruction by people—all increase mortality rates regardless of the population size. Density-independent limits to population are often nonbiological, capricious acts of nature.

Species respond to limits differently: *r*- and *K*-selected species

The story of the race between the hare and the tortoise has parallels to the way that species deal with limiting factors in their environment. Some organisms, such as dandelions and barnacles, depend on a high rate of reproduction and growth (rN) to secure a place in the environment. These organisms are called ***r*-selected species** because they employ a high reproductive rate (r) to overcome the high mortality of virtually ignored offspring. Without predators or diseases to control their population, those species can overshoot carrying capacity and experience population crashes, but as long as vast quantities of young are produced, a few will survive. Other organisms that reproduce more conservatively—longer generation times, late sexual maturity, fewer young—are referred to as ***K*-selected species,** because their growth slows as the carrying capacity (K) of their environment is approached.

Many species blend exponential (*r*-selected) and logistic (*K*-selected) growth characteristics. Still, it's useful to contrast the advantages and disadvantages of organisms at the extremes of the continuum. It also helps if we view differences in terms of "strategies" of adaptation and the "logic" of different reproductive modes (table 6.1).

Organisms with *r*-selected, or exponential, growth patterns tend to occupy low trophic levels in their ecosystems (chapter 3) or they are successional pioneers. These species, which generally have wide tolerance limits for environmental factors, and thus can occupy many different niches and habitats, are the ones we often describe as "weedy." They tend to occupy disturbed or new environments, grow rapidly, mature early, and produce many offspring with excellent dispersal abilities. As individual parents, they do little to care for their offspring or protect them from predation. They invest their energy in producing huge numbers of young and count on some surviving to adulthood.

A female clam, for example, can release up to 1 million eggs in her lifetime. The vast majority of young clams die before reaching maturity, but if even a few survive, the species will continue. Many marine invertebrates, parasites, insects, rodents, and annual plants follow this reproductive strategy. Also included in this group are most invasive and pioneer organisms, weeds, pests, and nuisance species.

TABLE 6.1

Reproductive Strategies

r-Selected Species	*K*-Selected Species
1. Short life	1. Long life
2. Rapid growth	2. Slower growth
3. Early maturity	3. Late maturity
4. Many, small offspring	4. Few, large offspring
5. Little parental care and protection	5. High parental care or protection
6. Little investment in individual offspring	6. High investment in individual offspring
7. Adapted to unstable environment	7. Adapted to stable environment
8. Pioneers, colonizers	8. Later stages of succession
9. Niche generalists	9. Niche specialists
10. Prey	10. Predators
11. Regulated mainly by intrinsic factors	11. Regulated mainly by extrinsic factors
12. Low trophic level	12. High trophic level

So-called *K*-selected organisms are usually larger, live long lives, mature slowly, produce few offspring in each generation, and have few natural predators. Elephants, for example, are not reproductively mature until they are 18 to 20 years old. In youth and adolescence, a young elephant belongs to an extended family that cares for it, protects it, and teaches it how to behave. A female elephant normally conceives only once every 4 or 5 years. The gestation period is about 18 months; thus, an elephant herd doesn't produce many babies in any year. Since elephants have few enemies and live a long life (60 or 70 years), this low reproductive rate produces enough elephants to keep the population stable, given good environmental conditions and no poachers.

When you consider the species you recognize from around the world, can you pigeonhole them into categories of *r*- or *K*-selected species? What strategies seem to be operating for ants, bald eagles, cheetahs, clams, dandelions, giraffes, or sharks?

Think About It

Which of the following strategies do humans follow: Do we more closely resemble wolves and elephants in our population growth, or does our population growth pattern more closely resemble that of moose and rabbits? Will we overshoot our environment's carrying capacity (or are we already doing so), or will our population growth come into balance with our resources?

6.2 Factors that Increase or Decrease Populations

Now that you have seen population dynamics in action, let's focus on what happens *within* populations, which are, after all, made up of individuals. In this section, we will discuss how new members

What Do You Think?

Too Many Deer?

A century ago, few Americans had ever seen a wild deer. Uncontrolled hunting and habitat destruction had reduced the deer population to about 500,000 animals nationwide. Some states had no deer at all. To protect the remaining deer, laws were passed in the 1920s and 1930s to restrict hunting, and the main deer predators—wolves and mountain lions—were exterminated throughout most of their former range.

As Americans have moved from rural areas to urban centers, forests have regrown, and deer populations have undergone explosive growth. Maturing at age two, a female deer can give birth to twin fawns every year for a decade or more. Increasing more than 20 percent annually, a deer population can double in just three years, an excellent example of irruptive, exponential growth.

Wildlife biologists estimate that the contiguous 48 states now have a population of more than 30 million white-tailed deer (*Odocoileus virginianus*), probably triple the number present in pre-Columbian tim Some areas have as many as 200 deer per square mile (77/km^2). At t density, woodland plant diversity is generally reduced to a few species tl deer won't eat. Most deer, in such conditions, suffer from malnourishme and many die every year of disease and starvation. Other species are dim ished as well. Many small mammals and ground-dwelling birds begin disappear when deer populations reach 25 animals per square mile. 50 deer per square mile, most ecosystems are seriously impoverished.

A white-tailed deer (*Odocoileus virginianus*)

The social costs of large deer populations are high. In Pennsylvar alone, where deer numbers are now about 500 times greater than a centu ago, deer destroy about $70 million worth of crops and $75 million woı of trees annually. Every year some 40,000 collisions with motor vehicl cause $80 million in property damage. Deer help spread Lyme disease, an in many states, chronic wasting disease is found in wild deer herds. Son of the most heated criticisms of current deer management policies are the suburbs. Deer love to browse on the flowers, young trees, and ornament bushes in suburban yards. Heated disputes often arise between those wł love to watch deer and their neighbors who want to exterminate them al

In remote forest areas, many states have extended hunting season increased the bag limit to four or more animals, and encouraged hunteı to shoot does (females) as well as bucks (males). Some hunters criticiz these changes because they believe that fewer deer will make it harde to hunt successfully and less likely that they'll find a trophy buck. Otł ers, however, argue that a healthier herd and a more diverse ecosysteı is better for all concerned.

In urban areas, increased sport hunting usually isn't acceptable Wildlife biologists argue that the only practical way to reduce deer herd is culling by professional sharpshooters. Animal rights activists protes lethal control methods as cruel and inhumane. They call instead for fertilit controls, reintroduction of predators, such as wolves and mountain lions or trap and transfer programs. Birth control works in captive population but is expensive and impractical with wild animals. Trapping, also, i expensive, and there's rarely anyplace willing to take surplus animals Predators may kill domestic animals or even humans.

This case study shows that carrying capacity can be more comple› than the maximum number of organisms an ecosystem can support While it may be possible for 200 deer to survive in a square mile, there's an ecological carrying capacity lower than that if we consider the otheı species dependent on that same habitat. There's also an ethical carrying capacity if we don't want to see animals suffer from malnutrition and starve to death every winter. And there's a cultural carrying capacity if we consider the tolerable rate of depredation on crops and lawns or an acceptable number of motor vehicle collisions.

If you were a wildlife biologist charged with managing the deer herd in your state, how would you reconcile the different interests in this issue? How would you define the optimum deer population, and what methods would you suggest to reach this level? What social or ecological indicators would you look for to gauge whether deer populations are excessive or have reached an appropriate level?

are added to and old members removed from populations. We also will examine the composition of populations in terms of age classes and introduce terminology that will apply in subsequent chapters.

Natality, fecundity, and fertility are measures of birth rates

Natality is the production of new individuals by birth, hatching, germination, or cloning, and is the main source of addition to most biological populations. Natality is usually sensitive to environmental conditions so that successful reproduction is tied strongly to nutritional levels, climate, soil or water conditions, and—in some species—social interactions between members of the species. The maximum rate of reproduction under ideal conditions varies widely among organisms and is a species-specific characteristic. We already have mentioned, for instance, the differences in natality between several different species.

Fecundity is the physical ability to reproduce, while **fertility** is a measure of the actual number of offspring produced. Because of lack of opportunity to mate and successfully produce offspring, many fecund individuals may not contribute to population growth. Human fertility often is determined by personal choice of fecund individuals.

Immigration adds to populations

Organisms are introduced into new ecosystems by a variety of methods. Seeds, spores, and small animals may be floated on winds or water currents over long distances. This is a major route of colonization for islands, mountain lakes, and other remote locations. Sometimes organisms are carried as hitchhikers in the fur, feathers, or intestines of animals traveling from one place to another. They also may ride on a raft of drifting vegetation. Some animals travel as adults—flying, swimming, or walking. In some ecosystems, a population is maintained only by a constant influx of immigrants. Salmon, for instance, must be important predators in some parts of the ocean, but their numbers are maintained only by recruitment from mountain streams thousands of kilometers away.

Mortality and survivorship measure longevity

An organism is born and eventually it dies; it is mortal. **Mortality,** or death rate, is determined by dividing the number of organisms that die in a certain time period by the number alive at the beginning of the period.

Since the number of survivors is more important to a population than is the number that died, mortality is often better expressed in terms of **survivorship** (the percentage of a cohort that survives to a certain age) or **life expectancy** (the probable number of years of survival for an individual of a given age). Aging has an interesting effect on life expectancy. For each year you survive, your life expectancy increases. If you were one year old in 2000, for example, you could expect to live, on average, 76.7 years more. But if you had already reached age 75 that year, rather than having only 1.7 more years to live, you could expect to survive another 11.2 years, on average. How could this be? At age 1, many in your cohort were likely to die early for one reason or another. By age 75, most of those individuals are already dead, giving the rest of you a longer average life probability. Even at age 100, long past your starting life expectancy, you would still have 2.7 more years to live, on average.

Human life expectancies have risen dramatically nearly everywhere in the world over the past century. In 1900 the world average life expectancy was only about 30 years, which was not much higher than the average lifespan in the Roman Empire 2,000 years earlier. By 2006, the average was 64.3 years (fig. 6.5). Improved nutrition, sanitation, and medical care were responsible for most of that increase. Demographers wonder how much more life expectancies can increase. Notice the great discrepancy in life expectancies between rich and poor countries. Currently, microstates Andorra, San Marino, and Singapore have the world's highest life expectancies (83.5, 82.1, and 81.6 years, respectively). Japan is nearly as high with a countrywide average of 81.5 years. The lowest national life expectancies are in Africa, where diseases, warfare, poverty, and famine cause many early deaths. In Swaziland, Botswana, and Lesotho, for example, the average person lives only 32.6, 33.7, and 34.4 years, respectively. In many African countries AIDS has reduced life expectancies by about 25 percent in the past two decades. This can be seen in the lag in progress in life expectancies between 1980 and 2000 in these countries in fig. 6.5.

Large discrepancies also exist in the United States. While the nation-wide average life expectancy is 77.5 years, Asian American women in Bergen County, New Jersey, live 91 years on average, while Native American men on the Pine Ridge Reservation in South Dakota are reported to typically live only 48 years. Two-thirds of African countries have life expectancies greater than Pine Ridge. Women almost always have higher life expectancies than men. Worldwide, the average difference between sexes is 3 years, but in Russia the difference between men and women is 13 years. Is this because women are biologically superior to men, and thus live longer? Or is it simply that men are generally employed in more hazardous occupations and often engage in more dangerous behaviors (drinking, smoking, reckless driving)?

Life span is the longest period of life reached by a given type of organism. The process of living entails wear and tear that eventually overwhelm every organism, but maximum age is dictated

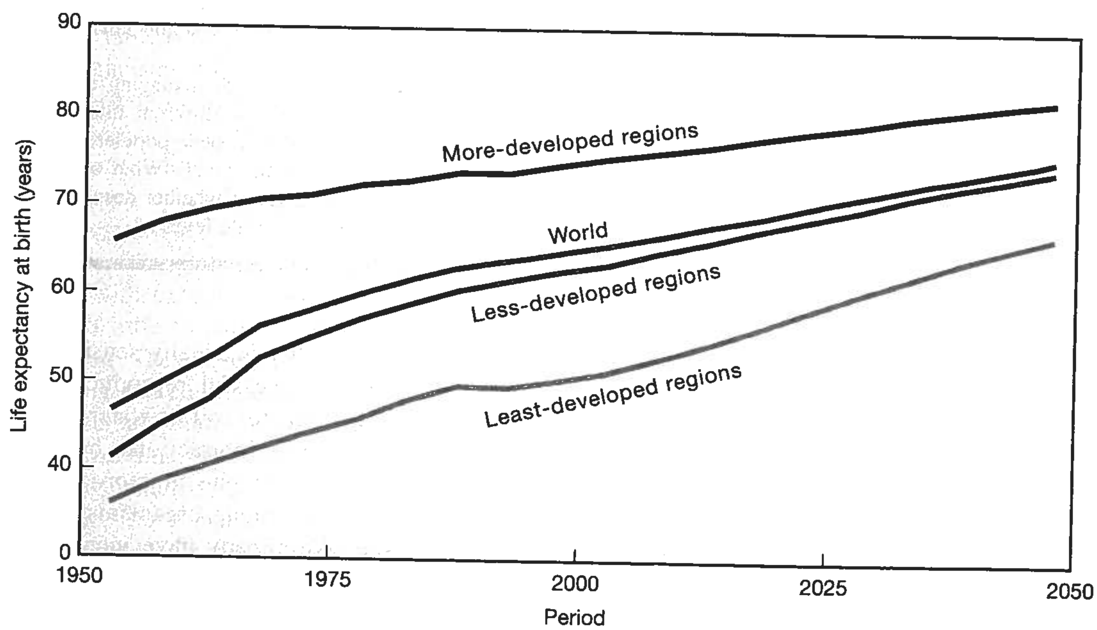


FIGURE 6.5 Life expectancy has increased nearly everywhere in the world, but the increase has lagged in the least-developed countries.
Data from the Population Division of the United Nations, 2006.

primarily by physiological aspects of the organism itself. There is an enormous difference in life span between different species. Some microorganisms live their whole life cycles in a matter of hours or minutes. Bristlecone pine trees in the mountains of California, on the other hand, have life spans up to 4,600 years. The maximum life span for humans appears to be about 120 years.

Most organisms do not live anywhere near the maximum life span for their species. The major factors in early mortality are predation, parasitism, disease, accidents, fighting, and environmental influences, such as climate and nutrition. Important differences in relative longevity among different species are reflected in the survivorship curves shown in figure 6.6.

Four general patterns of survivorship can be seen in this idealized figure. Curve (*a*) is the pattern of organisms that tend to live their full physiological life span if they reach maturity and then have a high mortality rate when they reach old age. This pattern is typical of many large mammals, such as whales, bears, and elephants (when not hunted by humans), as well as humans in developed countries. Interestingly, some very small organisms, including predatory protozoa and rotifers (small, multicellular, freshwater animals), have similar survivorship curves even though their maximum life spans may be hundreds or thousands of times shorter than those of large mammals. In general, curve (*a*) is the pattern for top consumers in an ecosystem, although many annual plants have a similar survivorship pattern.

Curve (*b*) represents the survivorship pattern for organisms for which the probability of death is generally unrelated to age. Sea gulls, for instance, die from accidents, poisoning, and other fac that act more or less randomly. Their mortality rate is gene constant with age, and their survivorship curve is a straight li

Curve (*c*) is characteristic of many songbirds, rabbits, m bers of the deer family, and humans in less-developed count (see chapter 7). They have a high mortality early in life w they are more susceptible to external factors, such as predat disease, starvation, or accidents. Adults in the reproductive ph have a high level of survival. Once past reproductive age, t become susceptible again to external factors and the numbe survivors falls quite rapidly.

Curve (*d*) is typical of organisms at the base of a f chain or those especially susceptible to mortality early in l Many tree species, fish, clams, crabs, and other invertebr species produce a very large number of highly vulnerable c spring, few of which survive to maturity. Those individuals t do survive to adulthood, however, have a very high chance living most of the maximum life span for the species. Figure shows some examples of organisms with each of these sur vorship patterns.

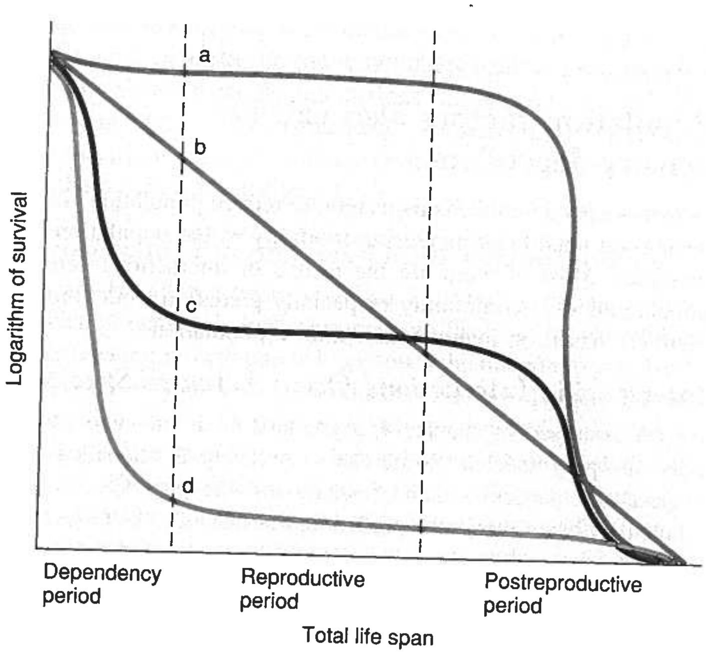


FIGURE 6.6 Four basic types of survivorship curves for organisms with different life histories. Curve (a) represents organisms such as humans or whales, which tend to live out the full physiological life span if they survive early growth. Curve (b) represents organisms such as sea gulls, which have a fairly constant mortality at all age levels. Curve (c) represents such organisms as white-tailed deer, which have high mortality rates in early and late life. Curve (d) represents such organisms as clams and redwood trees, which have a high mortality rate early in life but live a full life if they reach adulthood.

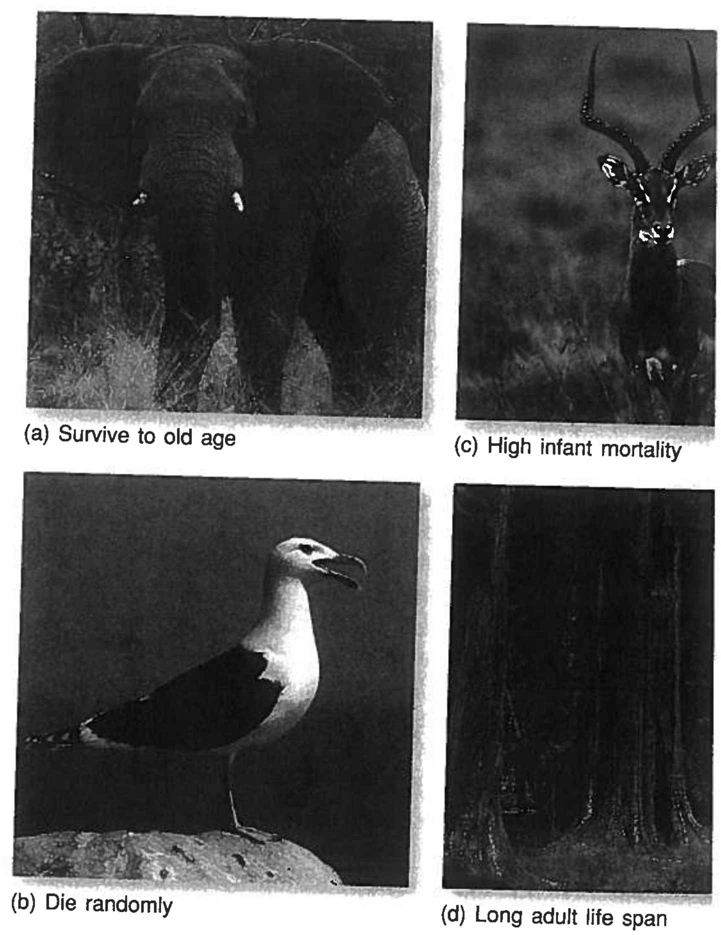


FIGURE 6.7 Different survivorship patterns. (a) Most elephants survive to old age. (b) Seagulls die randomly at all ages from accidents. (c) Antelope have high infant mortality, but adults survive well. (d) Redwood trees have very high seedling losses, but mature trees live thousands of years.

Think About It

Which of these survivorship patterns best describes humans? Are we more like elephants or deer? Do wealth and modernity have something to do with it? Might people in Bangladesh have different survivorship prospects than you do?

Emigration removes members of a population

Emigration, the movement of members out of a population, is the second major factor that reduces population size. The dispersal factors that allow organisms to migrate into new areas are important in removing surplus members from the source population. Emigration can even help protect a species. For instance, if the original population is destroyed by some catastrophic change in their environment, their genes still are carried by descendants in other places. Many organisms have very specific mechanisms to facilitate migration of one or more of each generation of offspring.

6.3 Factors that Regulate Population Growth

So far, we have seen that differing patterns of natality, mortality, life span, and longevity can produce quite different rates of population growth. The patterns of survivorship and age structure created by these interacting factors not only show us how a population is growing but also can indicate what general role that species plays in its ecosystem. They also reveal a good deal about how that species is likely to respond to disasters or resource bonanzas in its environment. But what factors *regulate* natality, mortality, and the other components of population growth? In this section, we will look at some of the mechanisms that determine how a population grows.

Various factors regulate population growth, primarily by affecting natality or mortality, and can be classified in different ways. They can be *intrinsic* (operating within individual organisms or between organisms in the same species) or *extrinsic* (imposed from outside the population). Factors can also be either **biotic** (caused by living organisms) or **abiotic** (caused by nonliving components of the environment). Finally, the regulatory factors can act in a *density-dependent* manner (effects are stronger or a higher proportion of the population is affected as population density increases) or *density-independent* manner (the effect is the same or a constant proportion of the population is affected regardless of population density).

In general, biotic regulatory factors tend to be density-dependent, while abiotic factors tend to be density-independent. There has been much discussion about which of these factors is most important in regulating population dynamics. In fact, it probably depends on the particular species involved, its tolerance levels, the stage of growth and development of the organisms involved, the specific ecosystem in which they live, and the way combinations of factors interact. In most cases, density-dependent and density-independent factors probably exert simultaneous influences. Depending on whether regulatory factors are regular and predictable or irregular and unpredictable, species will develop different strategies for coping with them.

Population factors can be density-independent

In general, the factors that affect natality or mortality independently of population density tend to be abiotic components of the ecosystem. Often weather (conditions at a particular time) or climate (average weather conditions over a longer period) are among the most important of these factors. Extreme cold or even moderate cold at the wrong time of year, high heat, drought, excess rain, severe storms, and geologic hazards—such as volcanic eruptions, landslides, and floods—can have devastating impacts on particular populations.

Abiotic factors can have beneficial effects as well, as anyone who has seen the desert bloom after a rainfall can attest. Fire is a powerful shaper of many biomes. Grasslands, savannas, and some montane and boreal forests often are dominated—even created—by periodic fires. Some species, such as jack pine and Kirtland's warblers, are so adapted to periodic disturbances in the environment that they cannot survive without them.

In a sense, these density-independent factors don't really regulate population *per se,* since regulation implies a homeostatic feedback that increases or decreases as density fluctuates. By definition, these factors operate without regard to the number of organisms involved. They may have such a strong impact on a population, however, that they completely overwhelm the influence of any other factor and determine how many individuals make up a particular population at any given time.

Population factors also can be density-dependent

Density-dependent mechanisms tend to reduce population size by decreasing natality or increasing mortality as the population size increases. Most of them are the results of interactions *between* populations of a community (especially predation), but some of them are based on interactions *within* a population.

Interspecific Interactions Occur between Species

As we discussed in chapter 4, a predator feeds on—and usually kills—its prey species. While the relationship is one-sided with respect to a particular pair of organisms, the prey species as a whole may benefit from the predation. For instance, the moose that gets eaten by wolves doesn't benefit individually, but the moose *population* is strengthened because the wolves tend to kill old or sick members of the herd. Their predation helps prevent population overshoot, so the remaining moose are stronger and healthier.

Sometimes predator and prey populations oscillate in a sort of synchrony with each other as is shown in figure 6.8, which shows the number of furs brought into Hudson Bay Company trading posts in Canada between 1840 and 1930. As you can see, the numbers of Canada lynx fluctuate on about a ten-year cycle that is similar to, but slightly out of phase with, the population peaks of snowshoe hares. Although there are some doubts now about

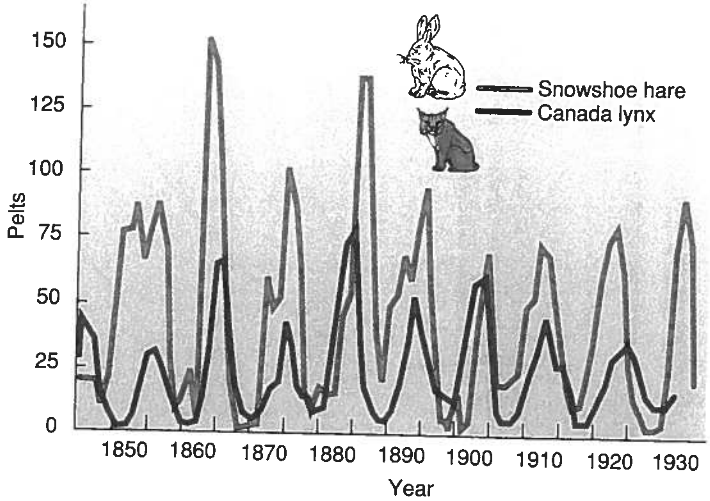


FIGURE 6.8 Ten-year oscillations in the populations of snowshoe hare and lynx in Canada suggest a close linkage of predator and prey, but may not tell the whole story. These data are based on the number of pelts received by the Hudson Bay Company each year, meaning fur-traders were unwitting accomplices in later scientific research.
Source: Data from D. A. MacLulich, *Fluctuations in the Numbers of the Varying Hare* (Lepus americus).Toronto: University of Toronto Press, 1937, reprinted 1974.

how and where these data were collected, this remains a classic example of population dynamics. When prey populations (hares) are abundant, predators (lynx) reproduce more successfully and their population grows. When hare populations crash, so do the lynx. This predator-prey oscillation is known as the Lotka-Volterra model after the scientists who first described it mathematically.

Not all interspecific interactions are harmful to one of the species involved. Mutualism and commensalism, for instance, are interspecific interactions that are beneficial or neutral in terms of population growth (chapter 4).

Intraspecific Interactions Occur within Species

Individuals within a population also compete for resources. When population density is low, resources are likely to be plentiful and the population growth rate will approach the maximum possible for the species, assuming that individuals are not so dispersed that they cannot find mates. As population density approaches the carrying capacity of the environment, however, one or more of the vital resources becomes limiting. The stronger, quicker, more aggressive, more clever, or luckier members get a larger share, while others get less and then are unable to reproduce successfully or survive.

Territoriality is one principal way many animal species control access to environmental resources. The individual, pair, or group that holds the territory will drive off rivals if possible, either by threats, displays of superior features (colors, size, dancing ability), or fighting equipment (teeth, claws, horns, antlers). Members of the opposite sex are attracted to individuals that are able to seize and defend the largest share of the resources. From a selective point of view, these successful individuals presumably represent superior members of the population and the ones best able to produce offspring that will survive.

FIGURE 6.9 Animals often battle over resources. This conflict ca induce stress and affect reproductive success.

Stress and Crowding Can Affect Reproduction

Stress and crowding also are density-dependent population cont factors. When population densities get very high, organisms oft exhibit symptoms of what is called stress shock or **stress-relat diseases.** These terms describe a loose set of physical, psycholo cal, and/or behavioral changes that are thought to result from t stress of too much competition and too close proximity to oth members of the same species. There is a considerable controver about what causes such changes and how important they are regulating natural populations. The strange behavior and high mc tality of arctic lemmings or hares during periods of high populati density may be a manifestation of stress shock (fig. 6.9). On tl other hand, they could simply be the result of malnutrition, infe tious disease, or some other more mundane mechanism at work.

Some of the best evidence for the existence of stress-relate disease comes from experiments in which laboratory animal usually rats or mice, are grown in very high densities with plent of food and water but very little living space. A variety of sym toms are reported, including reduced fertility, low resistance t infectious diseases, and pathological behavior. Dominant animal seem to be affected least by crowding, while subordinate an mals—the ones presumably subjected to the most stress in intr specific interactions—seem to be the most severely affected.

Case Study A Plague of Locusts *Schistocerca gregariu* the desert locust, has been called the world's most destruc tive insect. Throughout recorded human history, locus plagues have periodically swarmed out of deserts and into settle areas. Their impact on human lives has often been so disruptiv that records of plagues have taken on religious significance an made their way into sacred and historical texts.

Locusts usually are solitary creatures resembling ordinar grasshoppers. Every few decades, however, when rain comes to th desert and vegetation flourishes, locusts reproduce rapidly until th ground is literally crawling with bugs. High population densitie and stress bring ominous changes in these normally innocuou insects. They stop reproducing, grow longer wings, group togethe in enormous swarms, and begin to move across the desert. Dense clouds of insects darken the sky, moving as much as 100 km per day. Locusts may be small, but they can eat their own body weight of vegetation every day. A single swarm can cover 1,200 km^2 and contain 50 to 100 billion individuals. The swarm can strip pastures, denude trees, and destroy crops in a matter of hours, consuming as much food in a day as 500,000 people would need for a year. Eventually, having exhausted their food supply and migrated far from the desert where conditions favor reproduction, the locusts die and aren't seen again for decades.

Huge areas of crops and rangeland in northern Africa, the Middle East, and Asia are within the reach of the desert locust. This small insect, with its voracious appetite, can affect the livelihood of at least one-tenth of the world's population. During quiet periods, called recessions, African locusts are confined to the Sahara Desert, but when conditions are right, swarms invade countries as far away as Spain, Russia, and India. Swarms are even reported to have crossed the Atlantic Ocean from Africa to the Caribbean.

Unusually heavy rains in the Sahara in 2004 created the conditions for a locust explosion. Four generations bred in rapid succession, and swarms of insects moved out of the desert. Twenty-eight countries in Africa and the Mediterranean area were afflicted. Crop losses reached 100 percent in some places, and food supplies for millions of people were threatened. Officials at the United Nations warned that we could be headed toward another great plague. Hundreds of thousands of hectares of land were treated with pesticides, but millions of dollars of crop damage were reported anyway.

This case study illustrates the power of exponential growth and the disruptive potential of a boom-and-bust life cycle. Stress, population density, migration, and intraspecific interactions all play a role in this story. Although desert conditions usually keep locust numbers under control, their biotic potential for reproduction is a serious worry for residents of many countries.

6.4 Conservation Biology

Small, isolated populations can undergo catastrophic declines due to environmental change, genetic problems, or stochastic (random or unpredictable) events. A critical question in conservation biology is the minimum population size of a rare and endangered species required for long-term viability. In this section, we'll look at some factors that limit species and genetic diversity. We'll also consider the interaction of collections of subpopulations of species in fragmented habitats.

Island biogeography describes isolated populations

In a classic 1967 study, R. H. MacArthur and E. O. Wilson asked why it is that small islands far from the mainland generally have far fewer species than larger or nearer islands. Their theory of **island biogeography** explains that diversity in isolated habitats is a balance between colonization and extinction rates. An island far from a population source has a lower colonization rate for terrestrial species because it is harder for organisms to reach (fig. 6.10). At

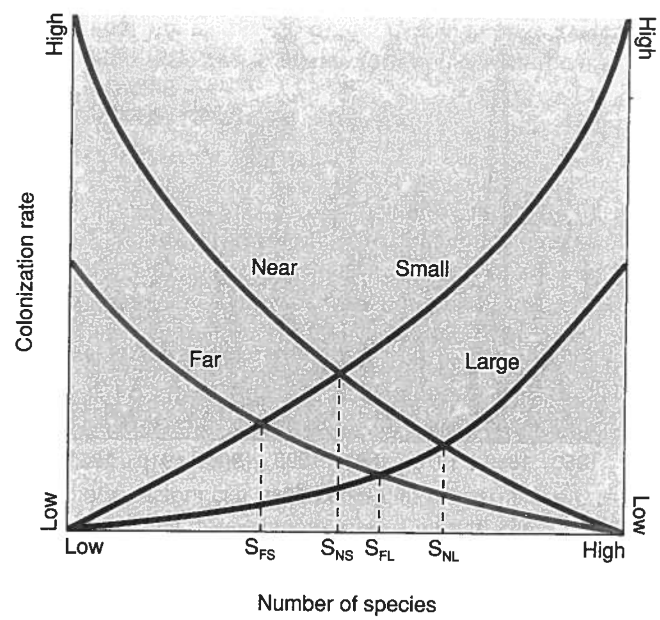


FIGURE 6.10 Predicted species richness on an island resulting from a balance between colonization (immigration) and extinction by natural causes. This island biogeography theory of MacArthur and Wilson (1967) is used to explain why large islands near a mainland (S_{NL}) tend to have more species than small, far islands (S_{FS}).
Source: Based on MacArthur and Wilson, *The Theory of Island Biogeography,* 1967, Princeton University Press.

the same time, the limited habitat on a small island can support fewer individuals of any given species. This creates a greater probability that a species could go extinct due to natural disasters, diseases, or demographic factors such as imbalance between sexes in a particular generation. Larger islands, or those closer to the mainland, on the other hand, are more likely to be colonized or to retain those species already successfully established. Thus they tend to have greater diversity than smaller, more remote places.

Island biogeographical effects have been observed in many places. Cuba, for instance, is 100 times as large and has about 10 times as many amphibian species as its Caribbean neighbor, Monserrat. Similarly, in a study of bird species on the California Channel Islands, Jared Diamond observed that on islands with fewer than 10 breeding pairs, 39 percent of the populations went extinct over an 80-year period. In contrast, only 10 percent of populations numbering between 10 and 100 pairs went extinct, and no species with over 1,000 pairs disappeared over this time (fig. 6.11). This theory of a balance between colonization and extinction is now seen to explain species dynamics in many small, isolated habitat fragments whether on islands or not.

Conservation genetics is important in survival of endangered species

Genetics plays an important role in the survival or extinction of small, isolated populations. In large populations, genetic variation

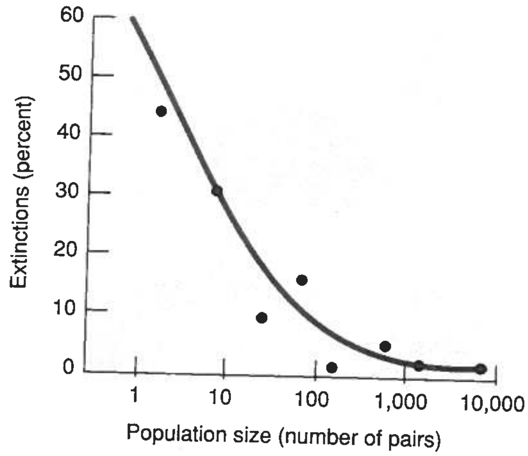


FIGURE 6.11 Extinction rates of bird species on the California Channel Islands as a function of population size over 80 years.
Source: H. L. Jones and J. Diamond, "Short-term-base studies of turnover in breeding bird populations on the California coast island," in *Condor,* vol. 78:526–49, 1976.

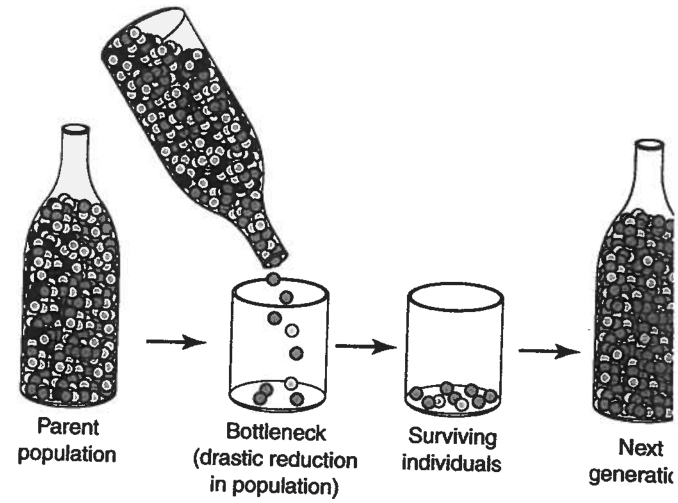


FIGURE 6.12 Genetic drift: the bottleneck effect. The parent population contains roughly equal numbers of blue and yellow individuals. By chance, the few remaining individuals that comprise the next generatic are mostly blue. The bottleneck occurs because so few individuals form t next generation, as might happen after an epidemic or catastrophic storr

tends to persist in what is called a Hardy-Weinberg equilibrium, named after the scientists who first described why this occurs. If mating is random, no mutations (changes in genetic material) occur, and there is no gene in-flow or selective pressure for or against particular traits, random distribution of gene types (alleles) will occur during gamete formation and sexual reproduction. That is, different alleles will be distributed in the offspring in the same ratio they occur in the parents, and genetic diversity is preserved.

In a large population, these conditions for maintaining genetic equilibrium are generally operative. The addition or loss of a few individuals or appearance of new genotypes makes little difference in the total gene pool, and genetic diversity is relatively constant. In small, isolated populations, however, immigration, mortality, mutations, or chance mating events involving only a few individuals can greatly alter the genetic makeup of the whole population. We call the gradual changes in gene frequencies due to random events **genetic drift.**

For many species, loss of genetic diversity causes a number of harmful effects that limit adaptability, reproduction, and species survival. A **founder effect** or **demographic bottleneck** occurs when just a few members of a species survive a catastrophic event or colonize new habitat geographically isolated from other members of the same species. Any deleterious genes present in the founders will be overrepresented in subsequent generations (fig. 6.12). Inbreeding, mating of closely related individuals, also makes expression of rare or recessive genes more likely.

Some species seem not to be harmed by inbreeding or lack of genetic diversity. The northern elephant seal, for example, was reduced by overharvesting a century ago, to fewer than 100 individuals. Today there are more than 150,000 of these enormous animals along the Pacific coast of Mexico and California. No marine mammal is known to have come closer to extinction and then made such a remarkable recovery. All northern elephant seals today appear to be essentially genetically identical and yet they seem to have no apparent problems. Although interpretatic of their situation are controversial, in highly selected populatio where only the most fit individuals reproduce, or in which th are few deleterious genes, inbreeding and a high degree of gene identity may not be such a negative factor.

Cheetahs, also appear to have undergone a demographic b tleneck sometime in the not-too-distant past. All the male cheeta throughout the world appear to be nearly genetically identic

FIGURE 6.13 Sometime in the past, cheetahs underwent a severe population crash. Now all male cheetahs in the world are nearly geneticall identical, and deformed sperm, low fertility levels, and low infant survival are common in the species.

suggesting that they all share a single male ancestor (fig. 6.13). This lack of diversity is thought to be responsible for an extremely low fertility rate, a high abundance of abnormal sperm, and low survival rate for offspring, all of which threatens the survival of the species.

Population viability analysis calculates chances of survival

Conservation biologists use the concepts of island biogeography, genetic drift, and founder effects to determine **minimum viable population size,** or number of individuals needed for long-term survival of rare and endangered species. A classic example is that of the grizzly bear (*Ursus arctos horribilis*) in North America. Before European settlement, grizzlies roamed from the Great Plains west to California and north to Alaska. Hunting and habitat destruction reduced the number of grizzlies from an estimated 100,000 in 1800 to less than 1,200 animals in six separate subpopulations that now occupy less than 1 percent of the historic range. Recovery target sizes—based on estimated environmental carrying capacities—call for fewer than 100 bears for some subpopulations. Conservation genetics predicts that a completely isolated population of 100 bears cannot be maintained for more than a few generations. Even the 600 bears now in Yellowstone National Park will be susceptible to genetic problems if completely isolated. Interestingly, computer models suggest that translocating only two unrelated bears into small populations every generation (about ten years) could greatly increase population viability.

Metapopulations are important interconnections

For mobile organisms, separated populations can have gene exchange if suitable corridors or migration routes exist. A **metapopulation** is a collection of populations that have regular or intermittent gene flow between geographically separate units (fig. 6.14). For example, the Bay checkerspot butterfly (*Euphydrays editha bayensis*) in California exists in several distinct habitat patches. Individuals occasionally move among these patches, mating with existing animals or recolonizing empty habitats. Thus, the apparently separate groups form a functional metapopulation.

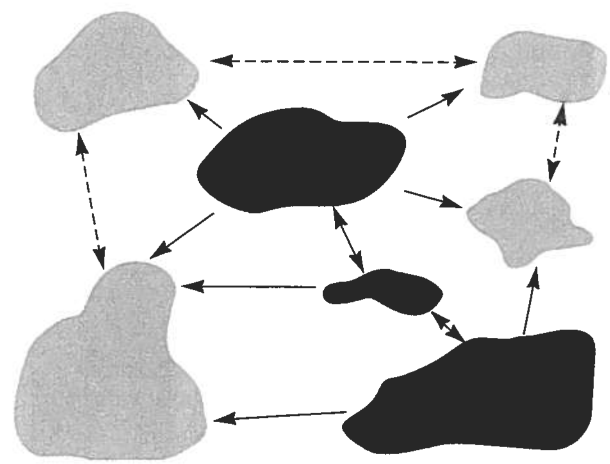


FIGURE 6.14 A metapopulation is composed of several local populations linked by regular (*solid arrows*) or occasional (*dashed lines*) gene flows. Source populations (*dark*) provide excess individuals, which emigrate to and colonize sink habitats (*light*).

A "source" habitat, where birth rates are higher than death rates, produces surplus individuals that can migrate to new locations within a metapopulation. "Sink" habitats, on the other hand, are places where mortality exceeds birth rates. Sinks may be spatially larger than sources but because of unfavorable conditions, the species would disappear in the sink habitat if it were not periodically replenished from a source population. In general, the larger a reserve is, the better it is for endangered species. Sometimes, however, adding to a reserve can be negative if the extra area is largely sink habitat. Individuals dispersing within the reserve may settle in unproductive areas if better habitat is hard to find. Recent studies using a metapopulation model for spotted owls predict just such a problem for this species in the Pacific Northwest.

Some conservation biologists argue that we ought to try to save every geographically distinct population or "evolutionarily significant unit (ESU)" possible in order to preserve maximum genetic diversity. Paul Ehrlich and Gretchen Daily estimate there may be an average of 220 ESU for every one of the 10 to 50 billion species in the world. Saving all of them would be a gargantuan task.

CONCLUSION

Given optimum conditions, populations of many organisms can grow exponentially; that is, they can expand at a constant *rate* per unit of time. This biotic potential can produce enormous populations that far surpass the carrying capacity of the environment if left unchecked. Obviously, no population grows at this rate forever. Sooner or later, predation, disease, starvation, or some other factor will cause the population to crash. Not all species follow this boom-and-bust pattern, however. Most top predators have intrinsic factors that limit their reproduction and prevent overpopulation.

Overharvesting of species, habitat destruction, predator elimination, introduction of exotic species, and other forms of human disruption can also drive populations to boom and/or crash. Population dynamics are an important part of conservation biology. Principles, such as island biogeography, genetic drift, demographic bottlenecks, and metapopulation interactions are critical in endangered species protection.

Reviewing Learning Outcomes

By now you should be able to explain the following points:

6.1 Describe the dynamics of population growth.

- Growth without limits is exponential.
- Carrying capacity relates growth to its limits.
- Feedback produces logistic growth.
- Species respond to limits differently: *r*- and *K*-selected species.

6.2 Summarize the factors that increase or decrease populations.

- Natality, fecundity, and fertility are measures of birth rates.
- Immigration adds to populations.
- Mortality and survivorship measure longevity.
- Emigration removes members of a population.

6.3 Compare and contrast the factors that regulate populatic growth.

- Population factors can be density-independent.
- Population factors also can be density-dependent.

6.4 Identify some applications of population dynamics in conse vation biology.

- Island biogeography describes isolated populations.
- Conservation genetics is important in survival of endangere species.
- Population viability analysis calculates chances of survival.
- Metapopulations are important interconnections.

Practice Quiz

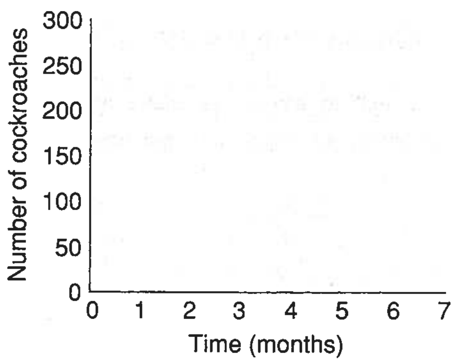
1. What caused the sudden collapse of Atlantic cod populations?
2. Define *exponential growth.*
3. Given a growth rate of 3 percent per year, how long will it take for a population of 100,000 individuals to double? How long will it take to double when the population reaches 10 million?
4. What is environmental resistance? How does it affect populations?
5. What is the difference between fertility and fecundity?
6. Describe the four major types of survivorship patterns and explain what they show about the role of the species in an ecosystem.
7. What are the main interspecific population regulatory inter actions? How do they work?
8. What is island biogeography and why is it important in con servation biology?
9. Why does genetic diversity tend to persist in large popula tions, but gradually drift or shift in small populations?
10. Draw a diagram showing gene flow between source and sink habitat in a metapopulation. Explain.

Critical Thinking and Discussion Questions

1. Compare the advantages and disadvantages to a species that result from exponential or logistic growth. Why do you think hares have evolved to reproduce as rapidly as possible, while lynx appear to have intrinsic or social growth limits?
2. Are humans subject to environmental resistance in the same sense that other organisms are? How would you decide whether a particular factor that limits human population growth is ecological or social?
3. Species differ greatly in birth and death rates, survivorship, and life spans. There must be advantages and disadvantages in living longer or reproducing more quickly. Why hasn't evolution selected for the most advantageous combination of characteristics so that all organisms would be more or less alike?
4. Abiotic factors that influence population growth tend to be density-independent, while biotic factors that regulate population growth tend to be density-dependent. Explain.
5. Some people consider stress and crowding studies of laboratory animals highly applicable in understanding human behavior. Other people question the cross-species transferability of these results. What considerations would be important in interpreting these experiments?
6. What implications (if any) for human population control might we draw from our knowledge of basic biological population dynamics?

DATA analysis Comparing Exponential to Logistic Population Growth

Exponential growth occurs in a series of time steps—days, months, years, or generations. Imagine cockroaches in a room multiplying (or some other species, if you must). Picture a population of ten cockroaches that together produce enough young to increase at a rate of 150 percent per month. What is r for this population?



To find out how this population grows, fill out the table shown. (*Hint:* r remains constant.) Remember, for time step 0 (the first month), you begin with ten roaches, and end (N_e) with a larger number that depends on r, the intrinsic rate of growth. The beginning of the second time step (1) starts with the number at the end of step 0. Round N to the nearest whole number. When you are done, graph the results. At the end of 7 months, how large did this population become? What is the shape of the growth curve?

Time Step (t)	Begin Step (N_b)	Intrinsic Growth Rate (r)	End Step (N_e)
0	10		15
1			
2			
3			
4			
5			
6			
7			

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