The Biosphere

29

Concept Outline

29.1 Organisms must cope with a varied environment.

The Environmental Challenge. Habitats vary in ways important to survival. Organisms cope with environmental variation with physiological, morphological, and behavioral adaptations.

29.2 Climate shapes the character of ecosystems.

The Sun and Atmospheric Circulation. The sun powers major movements in atmospheric circulation. Atmospheric Circulation, Precipitation, and Climate. Latitude and elevation have important effects on climate, although other factors affect regional climate.

29.3 Biomes are widespread terrestrial ecosystems.

The Major Biomes. Characteristic communities called biomes occur in different climatic regions. Variations in temperature and precipitation are good predictors of what biomes will occur where. Major biomes include tropical rain forest, savanna, desert, grassland, temperate deciduous forest, temperate evergreen forest, taiga, and tundra.

29.4 Aquatic ecosystems cover much of the earth.

Patterns of Circulation in the Oceans. The world's oceans circulate in huge circles deflected by the continents.
Life in the Oceans. Most of the major groups of organisms originated and are still represented in the sea.
Marine Ecosystems. The communities of the ocean are delineated primarily by depth.
Freshwater Habitats. Like miniature oceans, ponds and lakes support different communities at different depths.
Productivity of Freshwater Ecosystems. Freshwater ecosystems are often highly productive.

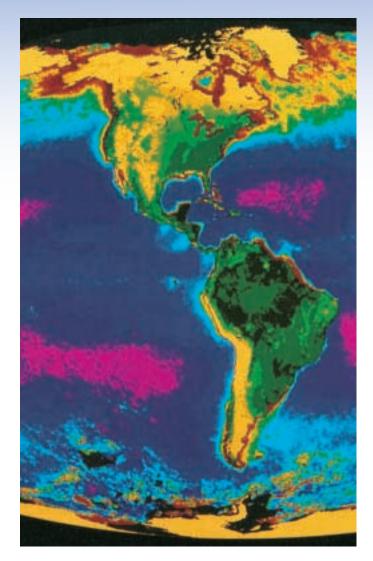


FIGURE 29.1

Life in the biosphere. In this satellite image, orange zones are largely arid. Almost every environment on earth can be described in terms of temperature and moisture. These physical parameters have great bearing on the forms of life that are able to inhabit a particular region.

The biosphere includes all living communities on earth, from the profusion of life in the tropical rain forests to the photosynthetic phytoplankton in the world's oceans. In a very general sense, the distribution of life on earth reflects variations in the world's environments, principally in temperature and the availability of water. Figure 29.1 is a satellite image of North and South America, collected over eight years, the colors keyed to the relative abundance of chlorophyll, a good indicator of rich biological communities. Phytoplankton and algae produce the dark red zones in the oceans and along the seacoasts. Green and dark green areas on land are dense forests, while orange areas like the deserts of western South America are largely barren of life.

29.1 Organisms must cope with a varied environment.

The Environmental Challenge

How Environments Vary

The nature of the physical environment in large measure determines what organisms live in a place. Key elements include:

Temperature. Most organisms are adapted to live within a relatively narrow range of temperatures and will not thrive if temperatures are colder or warmer. The growing season of plants, for example, is importantly influenced by temperature.

Water. Plants and all other organisms require water. On land, water is often scarce, so patterns of rainfall have a major influence on life.

Sunlight. Almost all ecosystems rely on energy captured by photosynthesis; the availability of sunlight influences the amount of life an ecosystem can support, particularly below the surface in marine communities.

Soil. The physical consistency, pH, and mineral composition of soil often severely limit plant growth, particularly the availability of nitrogen and phosphorus.

Active and Passive Approaches to Coping with Environmental Variation

An individual encountering environmental variation may choose to maintain a "steady-state" internal environment, an approach known as maintaining **homeostasis**. Many animals and plants actively employ physiological, morphological, or behavioral mechanisms to maintain homeostasis. The beetle in figure 29.2 is using a behavioral mechanism to cope with drastic changes in water availability. Other animals and plants simply conform to the environment in which they find themselves, their bodies adopting the temperature, salinity, and other aspects of their surroundings.

Responses to environmental variation can be seen over both the short and the long term. In the short term, spanning periods of a few minutes to an individual's lifetime, organisms have a variety of ways of coping with environmental change. Over longer periods, natural selection can operate to make a population better adapted to the environment.

Individual Response to Environmental Change

Physiology. Many organisms are able to adapt to environmental change by making physiological adjustments. Thus, your body constricts the blood vessels on the surface of your face on a cold day, reducing heat loss (and also giving your face a "flush"). Similarly, humans who visit high



FIGURE 29.2 Meeting the challenge of obtaining moisture in a desert. On the dry sand dunes of the Namib Desert in southwestern Africa, the beetle *Onymacris unguicularis* collects moisture from the fog by holding its abdomen up at the crest of a dune to gather condensed water.

Table 29.1 Physiological changes at high altitude that increase the amount of oxygen delivered to body tissues

Increased rate of breathing

Increased erythrocyte production, increasing the amount of hemoglobin in the blood

Decreased binding capacity of hemoglobin, thus increasing the rate at which oxygen is unloaded in body tissues

Increased density of mitochondria, capillaries, and muscle myoglobin

Based on Table 14-11 in A. J. Vander, J. H. Sherman, and D. S. Luciano, *Human Physiology*, 5th Ed., McGraw-Hill, 1990.

altitudes, such as in the Andes, initially experience altitude sickness—the symptoms of which include heart palpitations, nausea, fatigue, headache, mental impairment and, in serious cases, pulmonary edema—because of the lower atmospheric pressure and consequent lower oxygen availability in the air. After several days, however, the same people will feel fine, because of a number of physiological changes that increase the delivery of oxygen to body (table 29.1).

Some insects avoid freezing in the winter by adding glycerol "antifreeze" to their blood; others tolerate freezing by converting much of their glycogen reserves into alcohols that protect their cell membranes from freeze damage.

Morphology. Animals that maintain a constant internal temperature (endotherms) in a cold environment have adaptations that tend to minimize energy expenditure. Many other mammals grower thicker coats during the winter, utilizing their fur as insulation to retain body heat during the winter. In general, the thicker the fur, the greater the insulation (figure 29.3). Thus, a wolf's fur is some three times as thick in winter as summer and insulates more than twice as well. Other mammals escape some of the costs of maintaining a constant body temperature during winter by hibernating during the coldest season, behaving, in effect, like conformers.

Behavior. Many animals deal with variation in the environment by moving from one patch of habitat to another, avoiding areas that are unsuitable. The tropical lizards in figure 29.4 manage to maintain a fairly uniform body temperature in an open habitat by basking in patches of sun, retreating to the shade when they become too hot. By contrast, in shaded forests, the same lizards do not have the opportunity to regulate their body temperature through behavioral means. Thus, they become conformers and adopt the temperature of their surroundings.

Behavioral adaptations can be extreme. The spadefoot toad *Scaphiophus*, which lives in the deserts of North America, can burrow nearly a meter below the surface and remain there for as long as nine months of each year, its metabolic rate greatly reduced, living on fat reserves. When moist cool conditions return, the toads emerge and breed. The young toads mature rapidly and burrow back underground.

Evolutionary Responses to Environmental Variation

These examples represent different ways in which organisms may adjust to changing environmental conditions. The ability of an individual to alter its physiology, morphology, or behavior is itself an evolutionary adaptation, the result of natural selection. The results of natural selection can also be detected by comparing closely related species that live in different environments. In such cases, species often exhibit striking adaptations to the particular environment in which they live.

For example, animals that live in different climates show many differences. Mammals from colder climates tend to have shorter ears and limbs (Allen's Rule) and larger bodies (Bergmann's Rule) to limit heat loss. Both mechanisms reduce the surface area across which animals lose heat. Lizards that live in different climates exhibit physiological adaptations for coping with life at different temperatures. Desert lizards are unaffected by high temperatures that would kill a lizard from northern Europe, but the northern lizards are capable of running, capturing prey, and digesting food at cooler temperatures at which desert lizards would be completely immobilized.

Many species also exhibit adaptations to living in areas where water is scarce. Everyone knows of the camel, and other desert animals, which can go extended periods without drinking water. Another example of desert adaptation is seen in frogs. Most frogs have moist skins through which water permeates readily. Such animals could not survive in arid climates because they would rapidly dehydrate and dry. However, some frogs have solved this problem by greatly reducing the rate of water loss through the skin. One species, for example, secretes a waxy substance from specialized glands that waterproofs its skin and reduces rates of water loss by 95%.

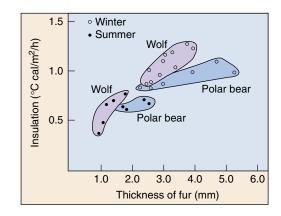


FIGURE 29.3

Morphological adaptation. Fur thickness in North American mammals has a major impact on the degree of insulation the fur provides.

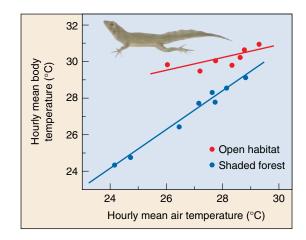


FIGURE 29.4

Behavioral adaptation. The Puerto Rican lizard *Anolis cristatellus* maintains a relatively constant temperature by seeking out and basking in patches of sunlight; in shaded forests, this behavior is not possible and body temperature conforms to the surroundings.

Adaptation to different environments can also be studied experimentally. For example, when strains of *E. coli* are grown at high temperatures (42°C), the speed at which resources are utilized improves through time. After 2000 generations, this ability increased 30% over what it had been when the experiment started. The mechanism by which efficiency of resource use was increased is still unknown and is the focus of current research.

Organisms use a variety of physiological, morphological, and behavioral mechanisms to adjust to environmental variation. Over time, species evolve adaptations to living in different environments.

29.2 Climate shapes the character of ecosystems.

The distribution of biomes (see discussion later in this chapter) results from the interaction of the features of the earth itself, such as different soil types or the occurrence of mountains and valleys, with two key physical factors: (1) the amount of solar heat that reaches different parts of the earth and seasonal variations in that heat; and (2) global atmospheric circulation and the resulting patterns of oceanic circulation. Together these factors dictate local climate, and so determine the amounts and distribution of precipitation.

The Sun and Atmospheric Circulation

The earth receives an enormous quantity of heat from the sun in the form of shortwave radiation, and it radiates an equal amount of heat back to space in the form of longwave radiation. About 10²⁴ calories arrive at the upper surface of the earth's atmosphere each year, or about 1.94 calories per square centimeter per minute. About half of this energy reaches the earth's surface. The wavelengths that reach the earth's surface are not identical to those that reach the outer atmosphere. Most of the ultraviolet radiation is absorbed by the oxygen (O_2) and ozone (O_3) in the atmosphere. As we will see in chapter 30, the depletion of the ozone layer, apparently as a result of human activities, poses serious ecological problems.

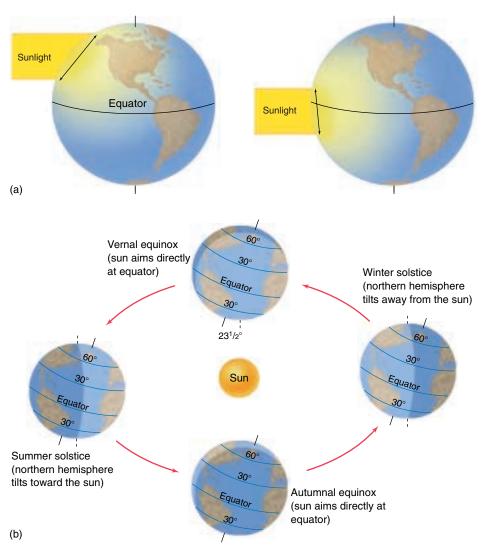
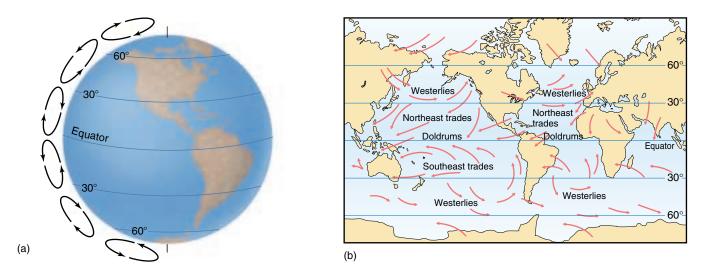


FIGURE 29.5

Relationships between the earth and the sun are critical in determining the nature and distribution of life on earth. (a) A beam of solar energy striking the earth in the middle latitudes spreads over a wider area of the earth's surface than a similar beam striking the earth near the equator. (b) The rotation of the earth around the sun has a profound effect on climate. In the northern and southern hemispheres, temperatures change in an annual cycle because the earth tilts slightly on its axis in relation to the path around the sun.

Why the Tropics Are Warmer

The world contains a great diversity of biomes because its climate varies so much from place to place. On a given day, Miami, Florida, and Bangor, Maine, often have very different weather. There is no mystery about this. Because the earth is a sphere, some parts of it receive more energy from the sun than others. This variation is responsible for many of the major climatic differences that occur over the earth's surface, and, indirectly, for much of the diversity of biomes. The tropics are warmer than temperate regions because the sun's rays arrive almost perpendicular to regions near the equator. Near the poles the angle of incidence of the sun's rays spreads them out over a much greater area, providing less energy per unit area (figure 29.5a).



General patterns of atmospheric circulation. (*a*) The pattern of air movement toward and away from the earth's surface. (*b*) The major wind currents across the face of the earth.

The earth's annual orbit around the sun and its daily rotation on its own axis are both important in determining world climate (figure 29.5*b*). Because of the annual cycle, and the inclination of the earth's axis at approximately 23.5° from its plane of revolution around the sun, there is a progression of seasons in all parts of the earth away from the equator. One pole or the other is tilted closer to the sun at all times except during the spring and autumn equinoxes.

Major Atmospheric Circulation Patterns

The moisture-holding capacity of air increases when it warms and decreases when it cools. High temperatures near the equator encourage evaporation and create warm, moist air. As this air rises and flows toward the poles, it cools and loses most of its moisture (figure 29.6). Consequently, the greatest amounts of precipitation on earth fall near the equator. This equatorial region of rising air is one of low pressure, called the **doldrums**, which draws air from both north and south of the equator. When the air masses that have risen reach about 30° north and south latitude, the dry air, now cooler, sinks and becomes reheated. As the air reheats, its evaporative capacity increases, creating a zone of decreased precipitation. The air, still warmer than in the polar regions, continues to flow toward the poles. It rises again at about 60° north and south latitude, producing another zone of high precipitation. At this latitude there is another low-pressure area, the polar front. Some of this rising air flows back to

the equator and some continues north and south, descending near the poles and producing another zone of low precipitation before it returns to the equator.

Air Currents Generated by the Earth's Rotation

Related to these bands of north-south circulation are three major air currents generated mainly by the interaction of the earth's rotation with patterns of worldwide heat gain. Between about 30° north latitude and 30° south latitude, the trade winds blow, from the east-southeast in the southern hemisphere and from the east-northeast in the northern hemisphere. The trade winds blow all year long and are the steadiest winds found anywhere on earth. They are stronger in winter and weaker in summer. Between 30° and 60° north and south latitude, strong prevailing westerlies blow from west to east and dominate climatic patterns in these latitudes, particularly along the western edges of the continents. Weaker winds, blowing from east to west, occur farther north and south in their respective hemispheres.

Warm air rises near the equator, descends and produces arid zones at about 30° north and south latitude, flows toward the poles, then rises again at about 60° north and south latitude, and moves back toward the equator. Part of this air, however, moves toward the poles, where it produces zones of low precipitation.

Atmospheric Circulation, Precipitation, and Climate

As we have discussed, precipitation is generally low near 30° north and south latitude, where air is falling and warming, and relatively high near 60° north and south latitude, where it is rising and cooling. Partly as a result of these factors, all the great deserts of the world lie near 30° north or south latitude. Other major deserts are formed in the interiors of large continents. These areas have limited precipitation because of their distance from the sea, the ultimate source of most moisture.

Rain Shadows

Other deserts occur because mountain ranges intercept moisture-laden winds from the sea. When this occurs, the air rises and the moisture-holding capacity of the air decreases, resulting in increased precipitation on the windward side of the mountains—the side from which the wind is blowing. As the air descends the other side of the mountains, the leeward side, it is warmed, and its moisture-holding capacity increases, tending to block precipitation. In California, for example, the eastern sides of the Sierra Nevada Mountains are much drier than the western sides, and the vegetation is often very different. This phenomenon is called the **rain shadow effect** (figure 29.7).

Regional Climates

Four relatively small areas, each located on a different continent, share a climate that resembles that of the Mediterranean region. So-called Mediterranean climates are found in portions of Baja, California, and Oregon; in central Chile; in southwestern Australia; and in the Cape region of South Africa. In all of these areas, the prevailing westerlies blow during the summer from a cool ocean onto warm land. As a result, the air's moisture-holding capacity increases, the air absorbing moisture and creating hot rainless summers. Such climates are unusual on a world scale. In the five regions where they occur, many unique kinds of plants and animals, often local in distribution, have evolved. Because of the prevailing westerlies, the great deserts of the world (other than those in the interiors of continents) and the areas of Mediterranean climate lie on the western sides of the continents.

Another kind of regional climate occurs in southern Asia. The monsoon climatic conditions characteristic of India and southern Asia occur during the summer months. During the winter, the trade winds blow from the eastnortheast off the cool land onto the warm sea. From June to October, though, when the land is heated, the direction of the air flow reverses, and the winds veer around to blow

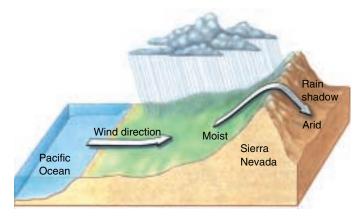


FIGURE 29.7

The rain shadow effect. Moisture-laden winds from the Pacific Ocean rise and are cooled when they encounter the Sierra Nevada Mountains. As their moisture-holding capacity decreases, precipitation occurs, making the middle elevation of the range one of the snowiest regions on earth; it supports tall forests, including those that include the famous giant sequoias (*Sequoiadendron giganteum*). As the air descends on the east side of the range, its moisture-holding capacity increases again, and the air picks up rather than releases moisture from its surroundings. As a result, desert conditions prevail on the east side of the mountains.

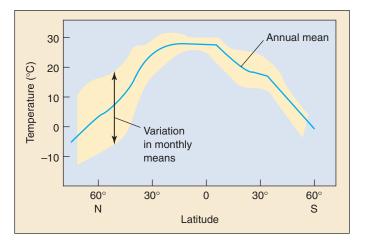
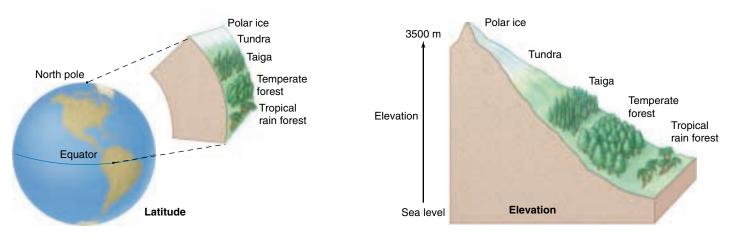


FIGURE 29.8

Temperature varies with latitude. The blue line represents the annual mean temperature at latitudes from the North Pole to Antarctica.

onto the Indian subcontinent and adjacent areas from the southwest bringing rain. The duration and strength of the monsoon winds spell the difference between food sufficiency and starvation for hundreds of millions of people in this region each year.



Elevation affects the distribution of biomes much as latitude does. Biomes that normally occur far north and far south of the equator at sea level also occur in the tropics at high mountain elevations. Thus, on a tall mountain in southern Mexico or Guatemala, one might see a sequence of biomes like the one illustrated here.

Latitude

Temperatures are higher in tropical ecosystems for a simple reason: more sunlight per unit area falls on tropical latitudes. Solar radiation is most intense when the sun is directly overhead, and this only occurs in the tropics, where sunlight strikes the equator perpendicularly. As figure 29.8 shows, the highest mean global temperatures occur near the equator (that is, 0 latitude). Because there are no seasons in the tropics, there is little variation in mean monthly temperature in tropical ecosystems. As you move from the equator into temperate latitudes, sunlight strikes the earth at a more oblique angle, so that less falls on a given area. As a result, mean temperatures are lower. At temperate latitudes, temperature variation increases because of the increasingly marked seasons.

Seasonal changes in wind circulation produce corresponding changes in ocean currents, sometimes causing nutrient-rich cold water to well up from ocean depths. This produces "blooms" among the plankton and other organisms living near the surface. Similar turnover occurs seasonally in freshwater lakes and ponds, bringing nutrients from the bottom to the surface in the fall and again in the spring.

Elevation

Temperature also varies with elevation, with higher altitudes becoming progressively colder. At any given latitude, air temperature falls about 6°C for every 1000meter increase in elevation. The ecological consequences of temperature varying with elevation are the same as temperature varying with latitude (figure 29.9). Thus, in North America a 1000-meter increase in elevation results in a temperature drop equal to that of an 880-kilometer increase in latitude. This is one reason "timberline" (the elevation above which trees do not grow) occurs at progressively lower elevations as one moves farther from the equator.

Microclimate

Climate also varies on a very fine scale within ecosystems. Within the litter on a forest floor, there is considerable variation in shading, local temperatures, and rates of evaporation from the soil. Called **microclimate**, these very localized climatic conditions can be very different from those of the overhead atmosphere. Gardeners spread straw over newly seeded lawns to create such a moisture-retaining microclimate.

The great deserts and associated arid areas of the world mostly lie along the western sides of continents at about 30° north and south latitude. Mountain ranges tend to intercept rain, creating deserts in their shadow. In general, temperatures are warmer in the tropics and at lower elevations.

29.3 Biomes are widespread terrestrial ecosystems.

The Major Biomes

Biomes are major communities of organisms that have a characteristic appearance and that are distributed over a wide land area defined largely by regional variations in climate. As you might imagine from such a broad definition, there are many ways to classify biomes, and different ecologists may assign the same community to different biomes. There is little disagreement, however, about the reality of biomes as major biological communities—only about how to best describe them.

Distribution of the Major Biomes

Eight major biome categories are presented in this text: tropical rain forest, savanna, desert, temperate grassland, temperate deciduous forest, temperate evergreen forest, taiga, and tundra. These biomes occur worldwide, occupying large regions that can be defined by rainfall and temperature. Six additional biomes are considered by some ecologists to be subsets of the eight major ones: polar ice, mountain zone, chaparral, warm moist evergreen forest, tropical monsoon forest, and semidesert. They vary remarkably from one another because they have evolved in regions with very different climates.

Distributions of the 14 biomes are mapped in figure 29.10. Although each is by convention named for the dominant vegetation (deciduous forest, evergreen forest, grassland, and so on) each biome is also characterized by particular animals, fungi, and microorganisms adapted to live as members of that community. Wolves, caribou or reindeer, polar bears, hares, lynx, snowy owls, deer flies, and mosquitoes inhabit the tundra all over the world and are as much a defining characteristic of the tundra biomes as the low, shrubby, matlike vegetation.

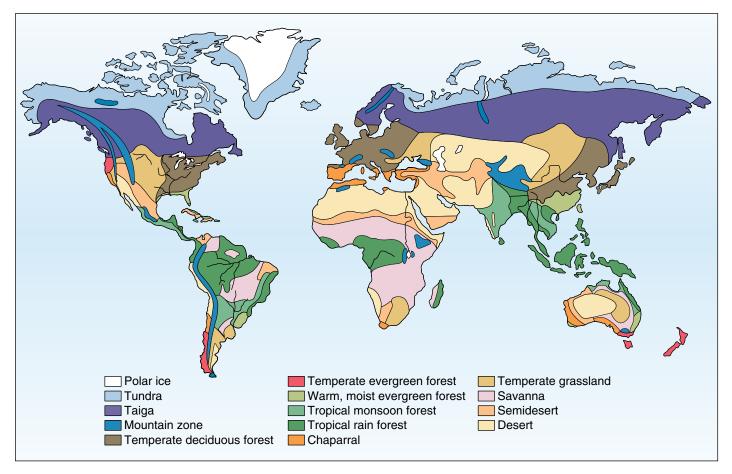


FIGURE 29.10

The distribution of biomes. Each biome is similar in structure and appearance wherever it occurs on earth.

Biomes and Climate

Many different environmental factors play a role in determining which biomes are found where. Two key parameters are available moisture and temperature. Figure 29.11 presents data on ecosystem productivity as a function of annual precipitation and of annual mean temperature: ecosystem productivity is strongly influenced by both. This is not to say that other factors such as soil structure and its mineral composition (discussed in detail in chapter 39), or seasonal versus constant climate, are not also important. Different places with the same annual precipitation and temperature sometimes support different biomes, so other factors must also be important. Nevertheless, these two variables do a fine job of predicting what biomes will occur in most places, as figure 29.12 illustrates.

If there were no mountains and no climatic effects caused by the irregular outlines of continents and by different sea temperatures, each biome would form an even belt around the globe, defined largely by latitude. In truth, these other factors also greatly affect the distribution of biomes. Distance from the ocean has a major impact on rainfall, and elevation affects temperature—the summits of the Rocky Mountains are covered with a vegetation type that resembles the tundra which normally occurs at a much higher latitude.

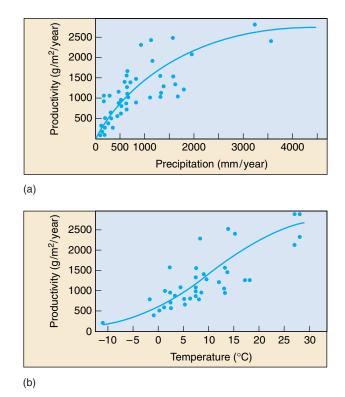


FIGURE 29.11

The effects of precipitation and temperature on primary productivity. The net primary productivity of ecosystems at 52 locations around the globe depends significantly upon (*a*) mean annual precipitation and (*b*) mean annual temperature.

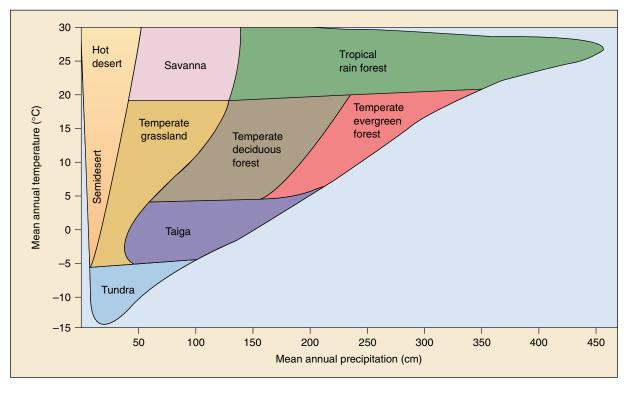


FIGURE 29.12

Temperature and precipitation are excellent predictors of biome distribution. At mean annual precipitations between 50 and 150 cm, other factors such as seasonal drought, fire, and grazing also have a major influence on biome distribution.

Tropical Rain Forests

Rain forests, which receive 140 to 450 centimeters of rain a year, are the richest ecosystems on earth (figure 29.13). They contain at least half of the earth's species of terrestrial plants and animals-more than 2 million species! In a single square mile of tropical forest in Rondonia, Brazil, there are 1200 species of butterflies-twice the total number found in the United States and Canada combined. The communities that make up tropical rain forests are diverse in that each kind of animal. plant, or microorganism is often represented in a given area by very few individuals. There are extensive tropical rain forests in South America, Africa, and Southeast Asia. But the world's rain forests are being destroyed, and countless species, many of them never seen by humans, are disappearing with them. A quarter of the world's species will disappear with the rain forests during the lifetime of many of us.



FIGURE 29.13 Tropical rain forest.

Savannas

In the dry climates that border the tropics are the world's great grasslands, called savannas. Savanna landscapes are open, often with widely spaced trees, and rainfall (75 to 125 centimeters annually) is seasonal. Many of the animals and plants are active only during the rainy season. The huge herds of grazing animals that inhabit the African savanna are familiar to all of us. Such animal communities lived in North America during the Pleistocene epoch but have persisted mainly in Africa. On a global scale, the savanna biome is transitional between tropical rain forest and desert. As these savannas are increasingly converted to agricultural use to feed rapidly expanding human populations in subtropical areas, their inhabitants are struggling to survive. The elephant and rhino are now endangered species; lion, giraffe, and cheetah will soon follow.

Deserts

In the interior of continents are the world's great deserts, especially in Africa (the Sahara), Asia (the Gobi) and Australia (the Great Sandy Desert). **Deserts** are dry places where less than 25 centimeters of rain falls in a year—an amount so low that vegetation is sparse and survival depends on water conservation. Plants and animals may restrict their activity to favorable times of the year, when water is present. To avoid high temperatures, most desert

vertebrates live in deep, cool, and sometimes even somewhat moist burrows. Those that are active over a greater portion of the year emerge only at night, when temperatures are relatively cool. Some, such as camels, can drink large quantities of water when it is available and then survive long, dry periods. Many animals simply migrate to or through the desert, where they exploit food that may be abundant seasonally.

Temperate Grasslands

Halfway between the equator and the poles are temperate regions where rich grasslands grow. These grasslands once covered much of the interior of North America, and they were widespread in Eurasia and South America as well. Such grasslands are often highly productive when converted to agricultural use. Many of the rich agricultural lands in the United States and southern Canada were originally occupied by prairies, another name for temperate grasslands. The roots of perennial grasses characteristically penetrate far into the soil, and grassland soils tend to be deep and fertile. Temperate grasslands are often populated by herds of grazing mammals. In North America, huge herds of bison and pronghorns once inhabited the prairies. The herds are almost all gone now, with most of the prairies having been converted to the richest agricultural region on earth.

Temperate Deciduous Forests

Mild climates (warm summers and cool winters) and plentiful rains promote the growth of deciduous (hardwood) forests in Eurasia, the northeastern United States, and eastern Canada (figure 29.14). A deciduous tree is one that drops its leaves in the winter. Deer, bears, beavers, and raccoons are familiar animals of the temperate regions. Because the temperate deciduous forests represent the remnants of more extensive forests that stretched across North America and Eurasia several million years ago, the remaining areas in eastern Asia and eastern North America share animals and plants that were once more widespread. Alligators, for example, are found today only in China and in the southeastern United States. The deciduous forest in eastern Asia is rich in species because climatic conditions have historically remained constant. Many perennial herbs live in areas of temperate deciduous forest.



FIGURE 29.14 Temperate deciduous forest.

Temperate Evergreen Forests

Temperate evergreen forests occur in regions where winters are cold and there is a strong, seasonal dry period. The pine forests of the western United States and California oak woodlands are typical temperate evergreen forests. Temperate evergreen forests are characteristic of regions with nutrient-poor soils. Temperate-mixed evergreen forests represent a broad transitional zone between temperate deciduous forests to the south and taiga to the north. Many of these forests are endangered by overlogging, particularly in the western United States.

Taiga

A great ring of northern forests of coniferous trees (spruce, hemlock, and fir) extends across vast areas of Asia and North America. Coniferous trees are ones with leaves like needles that are kept all year long. This ecosystem, called **taiga**, is one of the largest on earth. Here, the winters are long and cold, and most of the limited precipitation falls in the summer. Because the taiga has too short a growing season for farming, few people live there. Many large mammals, including elk, moose, deer, and such carnivores as wolves, bears, lynx, and wolverines, live in the taiga. Traditionally, fur trapping has been extensive in this region, as has lumber production. Marshes, lakes, and ponds are common and are often fringed by willows or birches. Most of the trees occur in dense stands of one or a few species.

Tundra

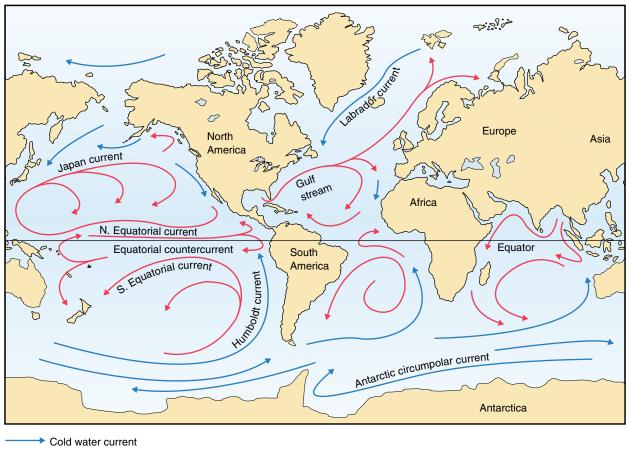
In the far north, above the great coniferous forests and south of the polar ice, few trees grow. There the grassland, called tundra, is open, windswept, and often boggy. Enormous in extent, this ecosystem covers one-fifth of the earth's land surface. Very little rain or snow falls. When rain does fall during the brief arctic summer, it sits on frozen ground, creating a sea of boggy ground. Permafrost, or permanent ice, usually exists within a meter of the surface. Trees are small and are mostly confined to the margins of streams and lakes. As in taiga, herbs of the tundra are perennials that grow rapidly during the brief summers. Large grazing mammals, including musk-oxen, caribou, reindeer, and carnivores, such as wolves, foxes, and lynx, live in the tundra. Lemming populations rise and fall on a long-term cycle, with important effects on the animals that prey on them.

Major biological communities called biomes can be distinguished in different climatic regions. These communities, which occur in regions of similar climate, are much the same wherever they are found. Variation in annual mean temperature and precipitation are good predictors of what biome will occur where.

Patterns of Circulation in the Oceans

Patterns of ocean circulation are determined by the patterns of atmospheric circulation, but they are modified by the locations of landmasses. Oceanic circulation is dominated by huge surface gyres (figure 29.15), which move around the subtropical zones of high pressure between approximately 30° north and 30° south latitude. These gyres move clockwise in the northern hemisphere and counterclockwise in the southern hemisphere. The ways they redistribute heat profoundly affects life not only in the oceans but also on coastal lands. For example, the Gulf Stream, in the North Atlantic, swings away from North America near Cape Hatteras, North Carolina, and reaches Europe near the southern British Isles. Because of the Gulf Stream, western Europe is much warmer and more temperate than eastern North America at similar latitudes. As a general principle, western sides of continents in temperate zones of the northern hemisphere are warmer than their eastern sides; the opposite is true of the southern hemisphere. In addition, winds passing over cold water onto warm land increase their moisture-holding capacity, limiting precipitation.

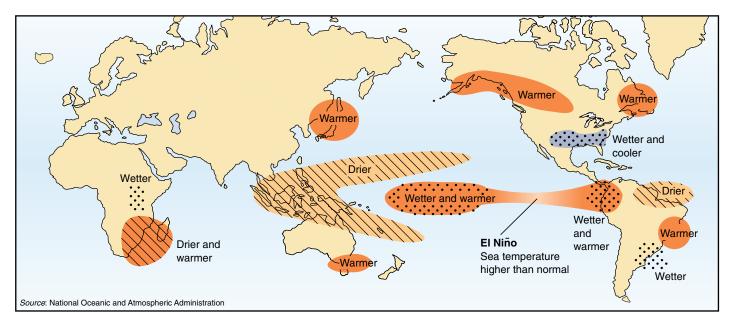
In South America, the Humboldt Current carries phosphorus-rich cold water northward up the west coast. Phosphorus is brought up from the ocean depths by the upwelling of cool water that occurs as offshore winds blow from the mountainous slopes that border the Pacific Ocean. This nutrient-rich current helps make possible the abundance of marine life that supports the fisheries of Peru and northern Chile. Marine birds, which feed on these organisms, are responsible for the commercially important, phosphorus-rich, guano deposits on the seacoasts of these countries.



Warm water current

FIGURE 29.15

Ocean circulation. Water moves in the oceans in great surface spiral patterns called gyres; they profoundly affect the climate on adjacent lands.



An El Niño winter. El Niño currents produce unusual weather patterns all over the world as warm waters from the western Pacific move eastward.

El Niño and Ocean Ecology

Every Christmas a tepid current sweeps down the coast of Peru and Ecuador from the tropics, reducing the fish population slightly and giving local fishermen some time off. The local fishermen named this Christmas current *El Niño* (literally, "the child," after "the Christ Child"). Now, though, the term is reserved for a catastrophic version of the same phenomenon, one that occurs every two to seven years and is felt not only locally but on a global scale.

Scientists now have a pretty good idea of what goes on in an El Niño. Normally the Pacific Ocean is fanned by constantly blowing east-to-west trade winds that push warm surface water away from the ocean's eastern side (Peru, Ecuador, and Chile) and allow cold water to well up from the depths in its place, carrying nutrients that feed plankton and hence fish. This surface water piles up in the west, around Australia and the Philippines, making it several degrees warmer and a meter or so higher than the eastern side of the ocean. But if the winds slacken briefly, warm water begins to slosh back across the ocean.

Once this happens, ocean and atmosphere conspire to ensure it keeps happening. The warmer the eastern ocean gets, the warmer and lighter the air above it becomes, and hence more similar to the air on the western side. This reduces the difference in pressure across the ocean. Because a pressure difference is what makes winds blow, the easterly trades weaken further, letting the warm water continue its eastward advance.

The end result is to shift the weather systems of the western Pacific Ocean 6000 km eastward. The tropical rainstorms that usually drench Indonesia and the Philippines are caused when warm seawater abutting these islands causes the air above it to rise, cool, and condense its moisture into clouds. When the warm water moves east, so do the clouds, leaving the previously rainy areas in drought. Conversely, the western edge of South America, its coastal waters usually too cold to trigger much rain, gets a soaking, while the upwelling slows down. During an El Niño, commercial fish stocks virtually disappear from the waters of Peru and northern Chile, and plankton drop to a twentieth of their normal abundance.

That is just the beginning. El Niño's effects are propagated across the world's weather systems (figure 29.16). Violent winter storms lash the coast of California, accompanied by flooding, and El Niño produces colder and wetter winters than normal in Florida and along the Gulf Coast. The American midwest experiences heavier-than-normal rains, as do Israel and its neighbors.

Though the effects of El Niños are now fairly clear, what triggers them still remains a mystery. Models of these weather disturbances suggest that the climatic change that triggers El Niño is "chaotic." Wind and ocean currents return again and again to the same condition, but never in a regular pattern, and small nudges can send them off in many different directions—including an El Niño.

The world's oceans circulate in huge gyres deflected by continental landmasses. Circulation of ocean water redistributes heat, warming the western side of continents. Disturbances in ocean currents like El Niño can have profound influences on world climate.

Life in the Oceans

Nearly three-quarters of the earth's surface is covered by ocean. Oceans have an *average* depth of more than 3 kilometers, and they are, for the most part, cold and dark. Heterotrophic organisms inhabit even the greatest ocean depths, which reach nearly 11 kilometers in the Marianas Trench of the western Pacific Ocean. Photosynthetic organisms are confined to the upper few hundred meters of water. Organisms that live below this level obtain almost all of their food indirectly, as a result of photosynthetic activities that occur above.

The supply of oxygen can often be critical in the ocean, and as water temperatures become warmer, the water holds less oxygen. For this reason, the amount of available oxygen becomes an important limiting factor for organisms in warmer marine regions of the globe. Carbon dioxide, in contrast, is almost never limited in the oceans. The distribution of minerals is much more uniform in the ocean than it is on land, where individual soils reflect the composition of the parent rocks from which they have weathered.

Frigid and bare, the floors of the deep sea have long been considered a biological desert. Recent close-up looks taken by marine biologists, however, paint a different picture (figure 29.17). The ocean floor is teeming with life. Often miles deep, thriving in pitch darkness under enormous pressure, crowds of marine invertebrates have been found in hundreds of deep samples from the Atlantic and Pacific. Rough estimates of deep-sea diversity have soared to millions of species. Many appear endemic (local). The diversity of species is so high it may rival that of tropical rain forests! This profusion is unexpected. New species usually require some kind of barrier in order to diverge (see chapter 22), and the ocean floor seems boringly uniform. However, little migration occurs among deep populations, thus allowing populations to diverge and encouraging local specialization and species formation. A patchy environment may also contribute to species formation there; deep-sea ecologists find evidence that fine but nonetheless formidable resource barriers arise in the deep sea.

Another conjecture is that the extra billion years or so that life has been evolving in the sea compared with land may be a factor in the unexpected biological richness of its deep recesses.

Despite the many new forms of small invertebrates now being discovered on the seafloor, and the huge biomass that occurs in the sea, more than 90% of all *described* species of organisms occur on land. Each of the largest groups of organisms, including insects, mites, nematodes, fungi, and plants has marine representatives, but they constitute only a very small fraction of the total number of described species. There are two reasons for this. First, barriers between habitats are sharper on land, and variations in elevation, parent rock, degree of exposure, and

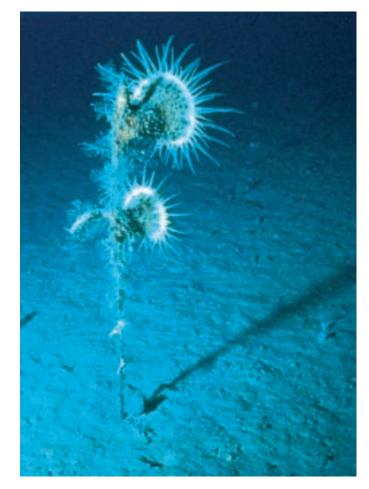


FIGURE 29.17

Food comes to the ocean floor from above. Looking for all the world like some undersea sunflower, the two sea anemones (actually animals) use a glass-sponge stalk to catch "marine snow," food particles raining down on the ocean floor from the ocean surface miles above.

other factors have been crucial to the evolution of the millions of species of terrestrial organisms. Second, there are simply few taxonomists actively classifying the profusion of ocean floor life being brought to the surface.

In terms of higher level diversity, the pattern is quite different. Of the major groups of organisms—phyla most originated in the sea, and almost every one has representatives in the sea. Only a few phyla have been successful on land or in freshwater habitats, but these have given rise to an extraordinarily large number of described species.

Although representatives of almost every phylum occur in the sea, an estimated 90% of living species of organisms are terrestrial. This is because of the enormous evolutionary success of a few phyla on land, where the boundaries between different habitats are sharper than they are in the sea.

Marine Ecosystems

The marine environment consists of three major habitats: (1) the **neritic zone**, the zone of shallow waters along the coasts of continents; (2) the **pelagic zone**, the area of water above the ocean floor; and (3) the **benthic zone**, the actual ocean floor (figure 29.18). The part of the ocean floor that drops to depths where light does not penetrate is called the **abyssal zone**.

The Neritic Zone

The **neritic zone** of the ocean is the area less than 300 meters below the surface along the coasts of continents and islands. The zone is small in area, but it is inhabited by large numbers of species (figure 29.19). The intense and sometimes violent interaction between sea and land in this zone gives a selective advantage to well-secured organisms that can withstand being washed away by the continual beating of the waves. Part of this zone, the **intertidal region**, sometimes called the **littoral region**, is exposed to the air whenever the tides recede.

The world's great fisheries are in shallow waters over continental shelves, either near the continents themselves or in the open ocean, where huge banks come near the surface. Nutrients, derived from land, are much more abundant in coastal and other shallow regions, where upwelling from the depths occurs, than in the open ocean. This accounts for the great productivity of the continental shelf fisheries. The preservation of these fisheries, a source of high-quality protein exploited throughout the world, has become a growing concern. In Chesapeake Bay, where complex systems of rivers enter the ocean from heavily populated areas, environmental stresses have become so severe that they not only threaten the continued existence of formerly highly productive fisheries, but also diminish the quality of human life in these regions. Increased runoff from farms and sewage effluent in areas like Chesapeake Bay add large amounts of nutrients to the water. This increased nutrient supply allows an increase in the numbers of some marine organisms. The increased populations then use up more and more of the oxygen in the water and thus may disturb established populations of organisms such as oysters. Climatic shifts may magnify these effects, and large numbers of marine animals die suddenly as a result.

About three-fourths of the surface area of the world's oceans are located in the tropics. In these waters, where the water temperature remains about 21°C, coral reefs can grow. These highly productive ecosystems can successfully concentrate nutrients, even from the relatively nutrient-poor waters characteristic of the tropics.

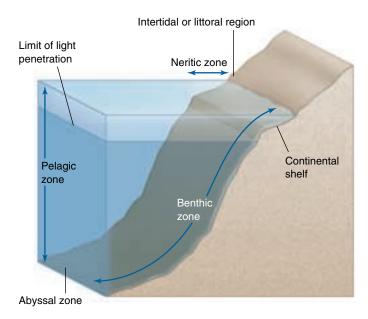


FIGURE 29.18

Marine ecosystems. Ecologists classify marine communities into neritic, pelagic, benthic, and abyssal zones, according to depth (which affects how much light penetrates) and distance from shore.

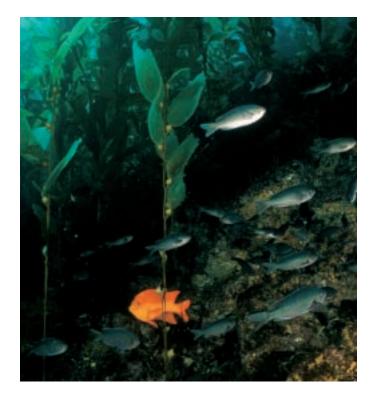


FIGURE 29.19

Diversity is great in coastal regions. Fishes and many other kinds of animals find food and shelter among the kelp beds in the coastal waters of temperate regions.

The Pelagic Zone

Drifting freely in the upper waters of the pelagic zone, a diverse biological community exists, primarily consisting of microscopic organisms called plankton. Fish and other larger organisms that swim in these waters constitute the *nekton*, whose members feed on plankton and one another. Some members of the plankton, including protists and some bacteria, are photosynthetic. Collectively, these organisms account for about 40% of all photosynthesis that takes place on earth. Most plankton live in the top 100 meters of the sea, the zone into which light from the surface penetrates freely. Perhaps half of the total photosynthesis in this zone is carried out by organisms less than 10 micrometers in diameter-at the lower limits of size







FIGURE 29.20

(a)

Life in the abyssal and benthic zones. (*a*) The luminous spot below the eye of this deepsea fish results from the presence of a symbiotic colony of luminous bacteria. Similar luminous signals are a common feature of deep-sea animals that move about. (*b*) These giant beardworms live along vents where water jets from fissures at 350°C and then cools to the 2°C of the surrounding water.

for organisms—including cyanobacteria and algae, organisms so small that their abundance and ecological importance have been unappreciated until relatively recently.

Many heterotrophic protists and animals live in the plankton and feed directly on photosynthetic organisms and on one another. Gelatinous animals, especially jellyfish and ctenophores, are abundant in the plankton. The largest animals that have ever existed on earth, baleen whales, graze on plankton and nekton as do a number of other organisms, such as fishes and crustaceans.

Populations of organisms that make up plankton can increase rapidly, and the turnover of nutrients in the sea is great, although the productivity in these systems is quite low. Because nitrogen and phosphorus are often present in only small amounts and organisms may be relatively scarce, this productivity reflects rapid use and recycling rather than an abundance of these nutrients.

The Benthic Zone

The seafloor at depths below 1000 meters, the **abyssal zone**, has about twice the area of all the land on earth. The seafloor itself, sometimes called the **benthic zone**, is a thick blanket of mud, consisting of fine particles that have settled from the overlying water and accumulated over millions of years. Because of high pressures (an additional atmosphere of pressure for every 10 meters of depth), cold temperatures (2° to 3°C), darkness, and lack of food, biologists thought that nothing could live on the seafloor. In fact, recent work has shown that the number of species that live at great depth is quite high. Most of these animals are only a few millimeters in size, although larger ones also occur in these regions. Some of the larger ones are bioluminescent (figure 29.20*a*) and thus are able to communicate with one another or attract their prey.

Animals on the sea bottom depend on the meager leftovers from organisms living kilometers overhead. The low densities and small size of most deep-sea bottom animals is in part a consequence of this limited food supply. In 1977, oceanographers diving in a research submarine were surprised to find dense clusters of large animals living on geothermal energy at a depth of 2500 meters. These deep-sea oases occur where seawater circulates through porous rock at sites where molten material from beneath the earth's crust comes close to the rocky surface. A series of these areas occur on the Mid-Ocean Ridge, where basalt erupts through the ocean floor.

This water is heated to temperatures in excess of 350°C and, in the process, becomes rich in reduced compounds. These compounds, such as hydrogen sulfide, provide energy for bacterial primary production through chemosynthesis instead of photosynthesis. Mussels, clams, and large red-plumed worms in a phylum unrelated to any shallowwater invertebrates cluster around the vents (figure 29.20b). Bacteria live symbiotically within the tissues of these animals. The animal supplies a place for the bacteria to live and transfers CO₂, H₂S, and O₂ to them for their growth; the bacteria supply the animal with organic compounds to use as food. Polychaete worms (see chapter 46), anemones, and limpets live on free-living chemosynthetic bacteria. Crabs act as scavengers and predators, and some of the fish are also predators. This is one of the few ecosystems on earth that does not depend on the sun's energy.

About 40% of the world's photosynthetic productivity is estimated to occur in the oceans. The turnover of nutrients in the plankton is much more rapid than in most other ecosystems, and the total amounts of nutrients are very low.

Freshwater Habitats

Freshwater habitats are distinct from both marine and terrestrial ones, but they are limited in area. Inland lakes cover about 1.8% of the earth's surface, and running water (streams and rivers) covers about 0.3%. All freshwater habitats are strongly connected with terrestrial ones, with marshes and swamps constituting intermediate habitats. In addition, a large amount of organic and inorganic material continuously enters bodies of fresh water from communities growing on the land nearby (figure 29.21a). Many kinds of organisms are restricted to freshwater habitats (figure 29.21b,c). When organisms live in rivers and streams, they must be able to swim against the current or attach themselves in such a way as to resist the effects of current, or risk being swept away.



(a)

FIGURE 29.21

A nutrient-rich stream. (*a*) Much organic material falls or seeps into streams from communities along the edges. This input increases the stream's biological productivity. (*b*) This speckled darter and (*c*) this giant waterbug with eggs on its back can only live in freshwater habitats.



(b





Ponds and Lakes

Small bodies of fresh water are called ponds, and larger ones lakes. Because water absorbs light passing through it at wavelengths critical to photosynthesis (every meter absorbs 40% of the red and about 2% of the blue), the distribution of photosynthetic organisms is limited to the upper **photic zone;** heterotrophic organisms occur in the lower **aphotic zone** where very little light penetrates.

Ponds and lakes, like the ocean, have three zones where organisms occur, distributed according to the depth of the water and its distance from shore (figure 29.22). The *littoral zone* is the shallow area along the shore. The *limnetic zone* is the well-illuminated surface water away from the shore, inhabited by plankton and other organisms that live in open water. The *profundal zone* is the area below the limits where light can effectively penetrate.

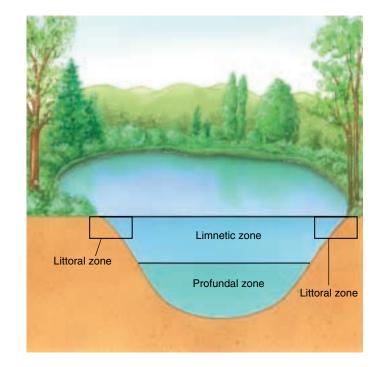
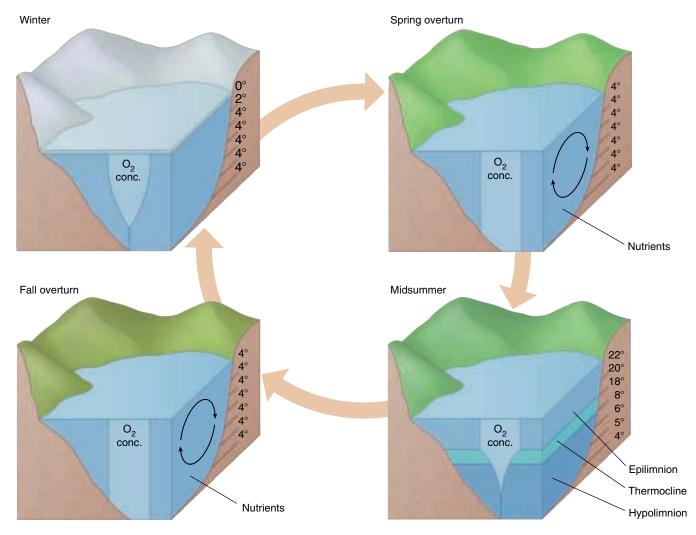


FIGURE 29.22

The three zones in ponds and lakes. A shallow "edge" (littoral) zone lines the periphery of the lake, where attached algae and their insect herbivores live. An open-water surface (limnetic) zone lies across the entire lake and is inhabited by floating algae, zooplankton, and fish. A dark, deep-water (profundal) zone overlies the sediments at the bottom of the lake and contains numerous bacteria and wormlike organisms that consume dead debris settling at the bottom of the lake.



Stratification in fresh water. The pattern stratification in a large pond or lake in temperate regions is upset in the spring and fall overturns. Of the three layers of water shown, the hypolimnion consists of the densest water, at 4°C; the epilimnion consists of warmer water that is less dense; and the thermocline is the zone of abrupt change in temperature that lies between them. If you have dived into a pond in temperate regions in the summer, you have experienced the existence of these layers.

Thermal Stratification

Thermal stratification is characteristic of larger lakes in temperate regions (figure 29.23). In summer, warmer water forms a layer at the surface known as the *epilimnion*. Cooler water, called the *hypolimnion* (about 4°C), lies below. An abrupt change in temperature, the thermocline, separates these two layers. Depending on the climate of the particular area, the epilimnion may become as much as 20 meters thick during the summer.

In autumn the temperature of the epilimnion drops until it is the same as that of the hypolimnion, 4°C. When this occurs, epilimnion and hypolimnion mix—a process called fall overturn. Because water is densest at about 4°C, further cooling of the water as winter progresses creates a layer of cooler, lighter water, which freezes to form a layer of ice at the surface. Below the ice, the water temperature remains between 0° and 4°C, and plants and animals can survive. In spring, the ice melts, and the surface water warms up. When it warms back to 4°C, it again mixes with the water below. This process is known as spring overturn. When lake waters mix in the spring and fall, nutrients formerly held in the depths of the lake are returned to the surface, and oxygen from surface waters is carried to the depths.

Freshwater habitats include several distinct life zones. These zones shift seasonally in temperate lakes and ponds. In the spring and fall, when their temperatures are equal, shallower and deeper waters of the lake mix, with oxygen being carried to the depths and nutrients being brought to the surface.

Productivity of Freshwater Ecosystems

Some aquatic communities, such as fast-moving streams, are not highly productive. Because the moving water washes away plankton, the photosynthesis that supports the community is limited to algae attached to the surface and to rooted plants.

The Productivity of Lakes

Lakes can be divided into two categories based on their production of organic matter. **Eutrophic lakes** contain an abundant supply of minerals and organic matter. As the plentiful organic material drifts below the thermocline from the well-illuminated surface waters of the lake, it provides a source of energy for other organisms. Most of these are oxygen-requiring organisms that can easily deplete the oxygen supply below the thermocline during the summer months. The oxygen supply of the deeper waters cannot be replenished until the layers mix in the fall. This lack of oxygen in the deeper waters of some lakes may have profound effects, such as allowing relatively harmless materials such as sulfates and nitrates to convert into toxic materials such as hydrogen sulfide and ammonia.

In **oligotrophic lakes**, organic matter and nutrients are relatively scarce. Such lakes are often deeper than eutrophic lakes and have very clear blue water. Their hypolimnetic water is always rich in oxygen.

Human activities can transform oligotrophic lakes into eutrophic ones. In many lakes, phosphorus is in short supply and is the nutrient that limits growth. When excess phosphorus from sources such as fertilizer runoff, sewage, and detergents enters lakes, it can quickly lead to harmful effects. In many cases, this leads to perfect conditions for the growth of blue-green algae, which proliferate immensely. Soon, larger plants are outcompeted and disappear, along with the animals that live on them. In addition, as these phytoplankton die and decompose, oxygen in the water is used up, killing the natural fish and invertebrate populations. This situation can be remedied if the continual input of phosphorus can be diminished. Given time, lakes can recover and return to prepollution states, as happened with Lake Washington pictured in figure 29.24.

The Productivity of Wetlands

Swamps, marshes, bogs, and other **wetlands** covered with water support a wide variety of water-tolerant plants, called hydrophytes ("water plants"), and a rich diversity of invertebrates, birds, and other animals. Wetlands are among the most productive ecosystems on earth (table 29.2). They also play a key ecological role by providing water storage basins that moderate flooding. Many wetlands are being disrupted by human "development" of

Table 29.2 The Most Productive Ecosystems	
Ecosystem	Net Primary Productivity per Unit Area (g/m²)
Coral reefs	2500
Tropical rain forest	2200
Wetlands	2000
Tropical seasonal forest	1600
Estuaries	1500
Temperate evergreen forest	1300
Temperate deciduous forest	1200
Savanna	900
Boreal forest	800
Cultivated land	650
Continental shelf	360
Lake and stream	250
Open ocean	125
Extreme desert, rock, sand, and ice	3

Source: Whitaker, 1975.



FIGURE 29.24

Oligotrophic lakes are highly susceptible to pollution. Lake Washington is an oligotrophic lake near Seattle, Washington. The drainage from fertilizers applied to the plantings around residences, business concerns, and recreational facilities bordering the lake poses an ever-present threat to its deep blue water. By supplying phosphorus, the drainage promotes algal growth. Aerobic bacteria decomposing dead algae deplete the lake's oxygen, killing much of the lake's life.

what is sometimes perceived as otherwise useless land, but government efforts are now underway to protect the remaining wetlands.

The most productive freshwater ecosystems are wetlands. Most lakes are far less productive, limited by lack of nutrients.

