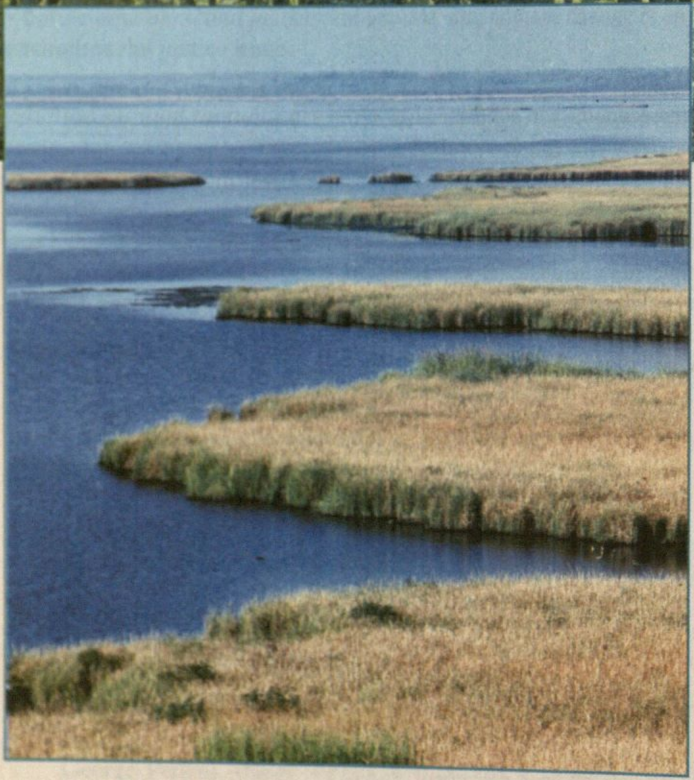
3

Ecosystems and Energy



Cordgrass (*Spartina*) in a Chesapeake Bay salt marsh.
(Stephen J. Krasemann/Photo Researchers, Inc.)

A salt marsh in the Chesapeake Bay on the East Coast of the United States contains an assortment of organisms that interact with one another and are interdependent in a variety of ways. This bay is an estuary, a semi-enclosed body of water found where fresh water from a river drains into the ocean. Estuaries, which are complex *systems* under the influence of tides, gradually change from unsalty fresh water to salty ocean water. In the Chesapeake Bay, this change results in freshwater marshes at the head of the bay, brackish (moderately salty) marshes in the middle bay region, and salt marshes on the ocean side of the bay.

A Chesapeake Bay salt marsh consists of flooded meadows of cordgrass (see photo). Few other plants are found because high salinity and tidal inundations produce a challenging environment in which only a few plants survive. Both cordgrass and microscopic algae (photosynthetic aquatic organisms) are eaten directly by some animals, and when they die, their remains provide food for other salt marsh inhabitants.

If you visited a salt marsh, you would observe two major kinds of animal life: insects and birds. Insects, particularly mosquitoes and horseflies, number in the millions. Birds nesting in the salt marsh include seaside sparrows, laughing gulls, and clapper rails. Study the salt marsh carefully and you will find it has many other species. Large numbers of invertebrates, such as shrimps, lobsters, crabs, barnacles, worms, clams, and snails, seek refuge in the water surrounding the cordgrass. Here they eat, hide from predators to avoid being eaten, and reproduce.

Chesapeake Bay marshes are an important nursery for numerous marine fishes—spotted sea trout, Atlantic croaker, striped bass, and bluefish, to name just a few. These fishes typically reproduce in the open ocean, and the young then enter the estuary, where they grow into juveniles.

Almost no amphibians inhabit salt marshes—the salty water dries out their skin—but a few reptiles, such as the northern diamondback terrapin (a semi-aquatic turtle), have adapted. The terrapin spends its time basking in the sun or swimming in the water searching for food—snails, crabs, worms, insects, and fish. Although a variety of snakes live in the dry areas adjacent to salt marshes, only the northern water snake, which preys on fish, is adapted to salty water.

The meadow vole is a small rodent that lives in the salt marsh. Meadow voles are excellent swimmers and scamper about the salt marsh day and night. Their diet consists mainly of insects and the leaves, stems, and roots of cordgrass.

Add to all these visible plants and animals the unseen microscopic world of the salt marsh—countless algae, protozoa, fungi, and bacteria, and you can begin to appreciate the complexity of a saltmarsh community.

In this chapter you begin your study of ecology, which is central to environmental science. Throughout the chapter, which focuses on energy flow, you will encounter many examples from the salt marsh community.

In Your Own Backyard...

Water quality in the Chesapeake Bay has deteriorated over the years as increasing levels of sediment, sewage, and fertilizer from the land have polluted the water. Identify a body of water near where you live. Does it have similar pollution problems? Why or why not?

What Is Ecology?

LEARNING OBJECTIVES

- Define *ecology*.
- Distinguish among the following ecological levels: population, community, ecosystem, landscape, and biosphere.

ecology: The study of systems that include interactions among organisms and between organisms and their abiotic environment.

Ernst Haeckel, a 19th-century scientist, developed the concept of **ecology** and named it—*eco* from the Greek word for "house" and *logy* from the Greek word for "study." Thus, *ecology* literally means "the study of one's house." The environment—one's house—consists of two parts, the **biotic** (living) environment, which includes all organisms, and the **abiotic** (nonliving, or physical) surroundings, which include living space, temperature, sunlight, soil, wind, and precipitation (**Figure 3.1**).

Ecologists study the vast complex web of relationships among living organisms and their physical environment. Areas of study include, but are not limited to, why organisms are distributed the way they are, why some species are more abundant than others, the ecological roles of different organisms in their environment, and how the interactions between organisms and their environment helps to maintain the overall health of our living world.

The focus of ecology is local or global, specific or generalized, depending on what questions the scientist is trying to answer. One ecologist might determine the temperature or light requirements of a single oak, another might study all the organisms that live in a forest where the oak is found, and another might examine how nutrients flow between the forest and surrounding areas.

Ecology is the broadest field within the biological sciences, and it is linked to every other biological discipline. The universality of ecology links subjects that are not traditionally part of biology. Geology and earth science are extremely important to ecology, especially when ecologists examine the physical environment of planet Earth. Chemistry and physics are also important; in this chapter, for example, you are studying chemistry when you read about photosynthesis and physics when you read about the laws of thermodynamics. Humans are biological organisms, and our activities have a bearing on ecology. Even economics and politics have profound ecological implications, as was discussed in Chapter 2.

How does the field of ecology fit into the organization of the biological world? As you may know, one of the characteristics of life is its high degree of organization. Atoms are organized into molecules, which in turn are organized into cells. In multicellular organisms, cells are organized into tissues, tissues into organs such as a bone or stomach, organs into body systems such as the nervous system and digestive system, and body systems into individual organisms such as dogs and ferns.

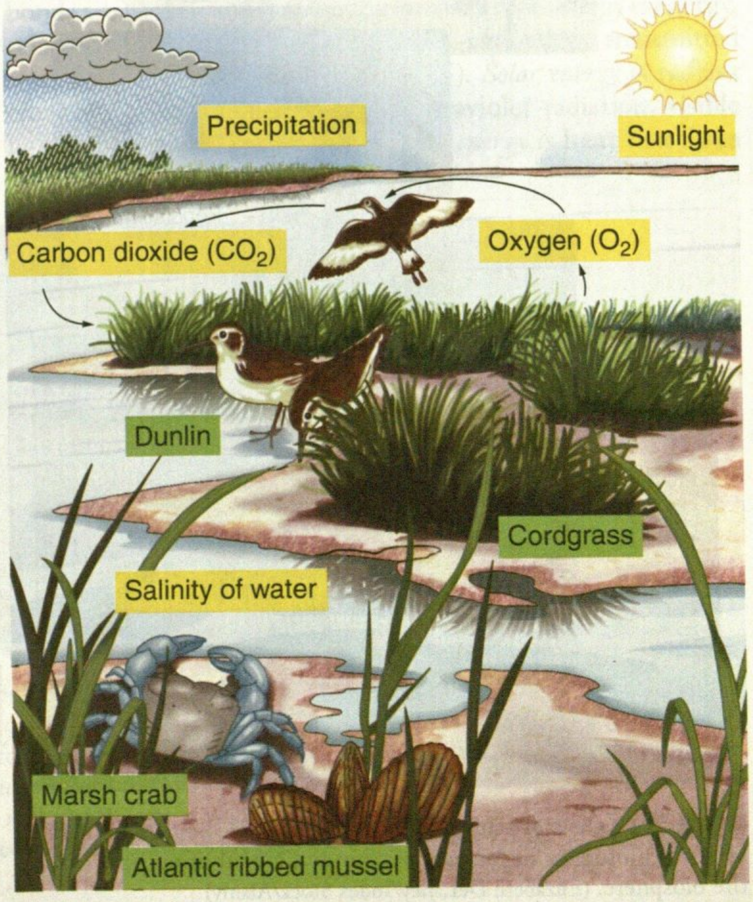


Figure 3.1 Some abiotic and biotic components of a Chesapeake Bay salt marsh. Shown is a mudflat at low tide. Abiotic (nonliving) components are labeled in yellow and biotic (living) components, in green.

species: A group of similar organisms whose members freely interbreed with one another in the wild to produce fertile offspring; members of one species generally do not interbreed with other species of organisms.

Ecologists are most interested in the levels of biological organization that include or are above the level of the individual organism (**Figure 3.2**). Individuals of the same **species** occur in **populations**. A population ecologist might study a population of polar bears or a population of marsh grass. Population ecology is discussed in Chapter 5, and human populations in Chapters 8 and 9. Species are considered further in Chapter 16.

population: A group of organisms of the same species that live in the same area at the same time.

community: A natural association that consists of all the populations of different species that live and interact within an area at the same time.

Populations are organized into **communities**. Ecologists characterize communities by the number and kinds of species that live there, along with their relationships with one another. A community ecologist might study how organisms interact with one another—including feeding relationships (who eats whom)—in an alpine meadow community or in a coral reef community (**Figure 3.3**).

Ecosystem is a more inclusive term than *community*. An **ecosystem** includes all the biotic interactions of a community as well as the interactions between organisms and their abiotic environment. Like other *systems*, an ecosystem consists of multiple interacting and inseparable parts and processes that form a unified whole. An ecosystem—whether it is a forest, a pond, or the ocean—is a system in which all the biological, physical, and chemical components of an area form a complex, interacting network of energy flow and materials cycling. An ecosystem ecologist might examine how energy, nutrients, organic (carbon-containing) materials, and water affect the organisms living in a desert ecosystem or a coastal bay ecosystem.

ecosystem: A community and its physical environment.

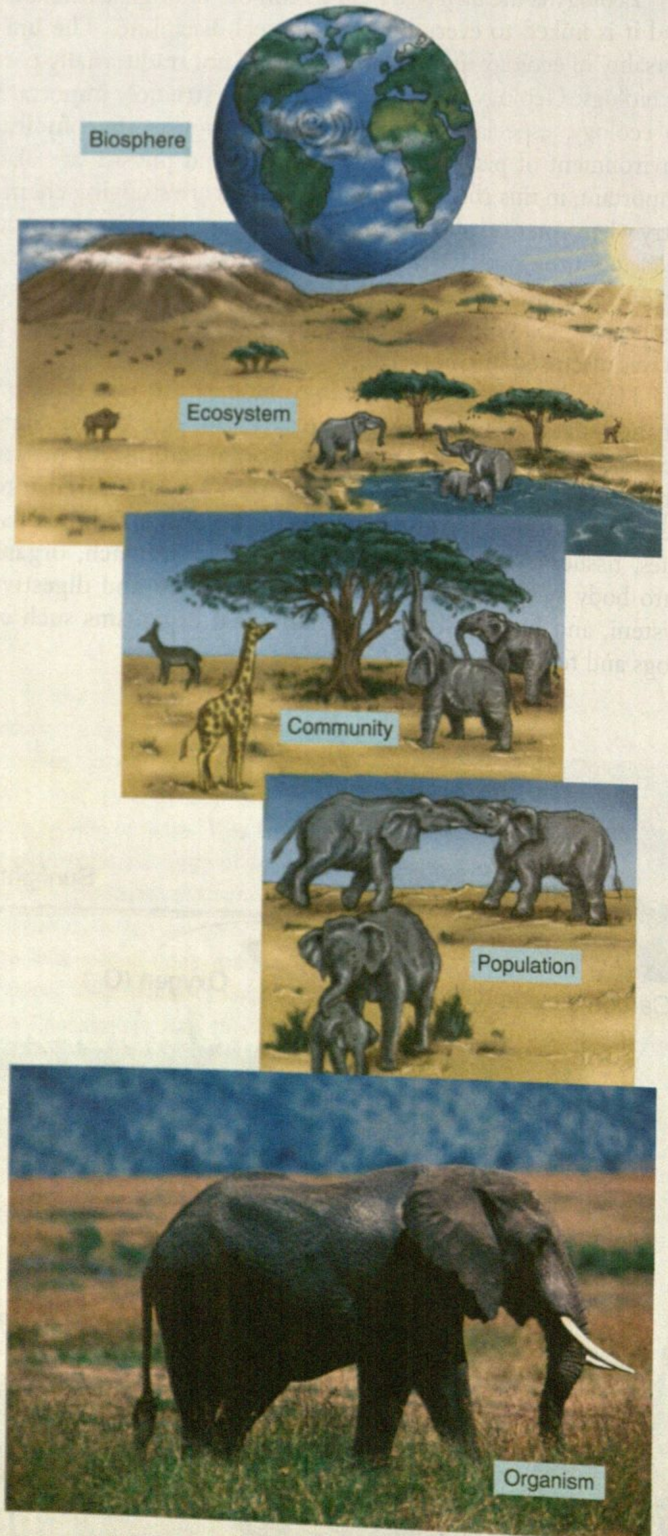


Figure 3.2 Levels of ecological organization. Ecologists study the levels of biological organization from individual organisms to the biosphere. (Elizabeth DeLaney/Index Stock/Alamy)

Figure 3.3 Coral reef community. Coral reef communities have the greatest number of species and are the most complex aquatic community. This close-up of a coral reef in the Caribbean Sea off the coast of Mexico shows a green moray eel, French grunts, and several species of coral. Today many coral reefs worldwide are threatened by global climate change. How can they be protected from warming temperatures? (Gerald Nowak/WaterFrame/Age Fotostock America, Inc.)

The ultimate goal of ecosystem ecologists is to understand how ecosystems function. This is not a simple task, but it is important because ecosystem processes collectively regulate the global cycles of water, carbon, nitrogen, phosphorus, and sulfur essential to the survival of humans and all other organisms. As humans increasingly alter ecosystems for their own uses, the natural functioning of ecosystems is changed, and we must determine whether these changes will affect the sustainability of our life-support system.

Landscape ecology is a subdiscipline of ecology that studies ecological processes that operate over large areas. Landscape ecologists examine the connections among ecosystems found in a particular region. Consider a simple **landscape** consisting of a forest ecosystem located adjacent to a pond ecosystem. One connection between these two ecosystems might be great blue herons, which eat fishes, frogs, insects, crustaceans, and snakes along the shallow water of the pond but often build nests and raise their young in the secluded treetops of the nearby forest. Landscapes, then, are based on larger land areas that include several ecosystems.

landscape: A region that includes several interacting ecosystems.

The organisms of the **biosphere**—Earth's communities, ecosystems, and landscapes—depend on one another and on the other realms of Earth's physical environment: the atmosphere, hydrosphere, and lithosphere (**Figure 3.4**). The **atmosphere** is the gaseous envelope surrounding Earth; the **hydrosphere** is Earth's supply of water—liquid and frozen, fresh and salty, groundwater and surface water; and the **lithosphere** is the soil and rock of Earth's crust. Ecologists who study the biosphere examine global interrelationships among Earth's atmosphere, land, water, and organisms.

biosphere: The parts of Earth's atmosphere, ocean, land surface, and soil that contain all living organisms.

The biosphere is filled with life. Where do these organisms get the energy to live? And how do they harness this energy? Let's examine the importance of energy to organisms, which survive only as long as the environment continuously supplies them with energy. You will revisit the importance of energy as it relates to human endeavors in many chapters throughout this text.

REVIEW

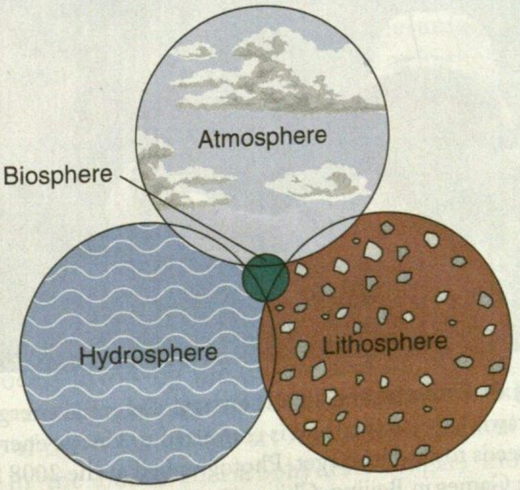
1. What is ecology?
2. What is the difference between a community and an ecosystem? Between an ecosystem and a landscape?

The Energy of Life

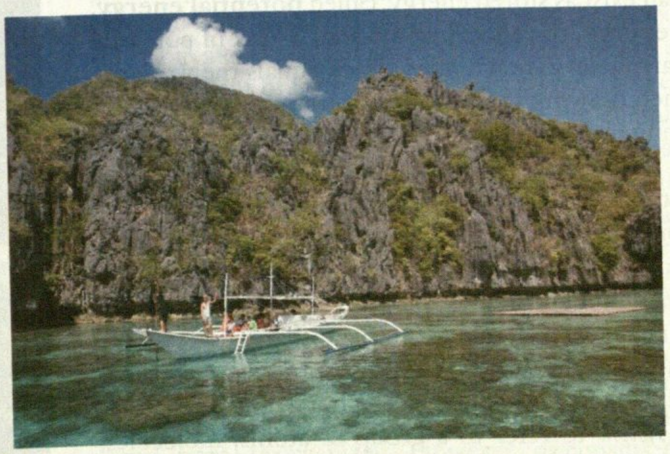
LEARNING OBJECTIVES

- Define *energy* and explain how it is related to work and to heat.
- Use an example to contrast potential energy and kinetic energy.
- Distinguish between open and closed systems.
- State the first and second laws of thermodynamics, and discuss the implications of these laws as they relate to organisms.
- Write summary reactions for photosynthesis and cellular respiration, and contrast these two biological processes.

Energy is the capacity or ability to do work. In organisms, any biological work, such as growing, moving, reproducing, and maintaining and repairing damaged tissues, requires energy. Energy exists in several forms: chemical, radiant, thermal, mechanical, nuclear, and electrical. *Chemical energy* is energy stored in the bonds of molecules; for example, food contains chemical energy; organisms use the energy released when chemical bonds are broken and new bonds form. *Radiant energy* is energy, such as radio waves, visible light, and X-rays, that is transmitted as electromagnetic waves (**Figure 3.5**). *Solar energy* is radiant energy from the sun; it includes ultraviolet radiation, visible light, and infrared radiation. *Thermal energy* is **heat** that flows



(a) Earth's four realms, represented as intersecting circles, are a system of interrelated parts.



(b) In this scene, photographed on Palawan Island, Philippines, the atmosphere contains a cumulus cloud, which indicates warm, moist air. The jagged rocks, formed from volcanic lava flows that have eroded over time, represent the lithosphere. The shallow water represents the hydrosphere. The biosphere includes the green vegetation and humans in the boat as well as the coral reefs visible as darker areas in the water. (© Jon Arnold Images Ltd./Alamy)

Figure 3.4 Earth's four realms.

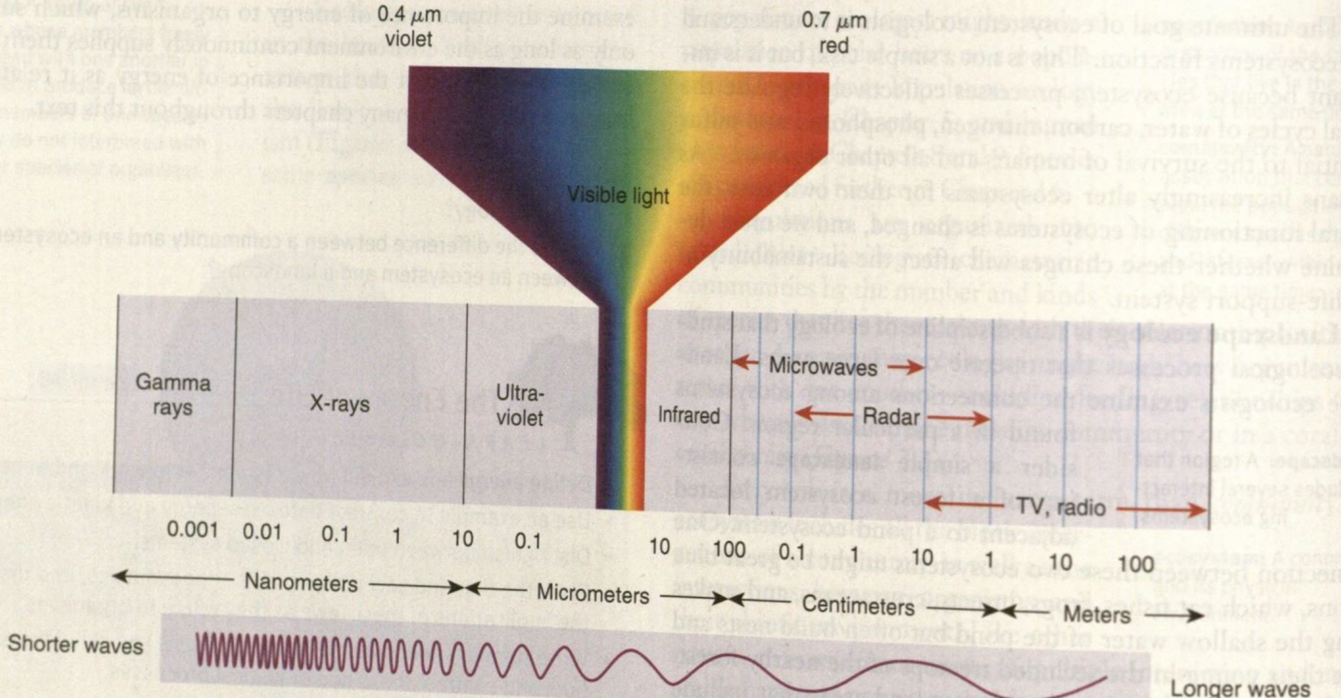


Figure 3.5 The electromagnetic spectrum. The shortest wavelengths are gamma rays, and the longest are TV and radio waves. Visible light occurs between ultraviolet and infrared radiation.

from an object with a higher temperature (the heat source) to an object with a lower temperature (the heat sink). *Mechanical energy* is energy in the movement of matter. Some of the matter contained in atomic nuclei can be converted into *nuclear energy*. *Electrical energy* is energy that flows as charged particles. You will encounter these forms of energy throughout the text.

Biologists generally express energy in units of work (*kilojoules, kJ*) or units of heat (*kilocalories, kcal*). One kilocalorie, the energy required to raise the temperature of 1 kg of water by 1°C, equals 4.184 kJ. The kcal is the unit that nutritionists use to express the energy content of the foods we eat.

Energy can exist as stored energy, called **potential energy**, or as **kinetic energy**, the energy of motion. Think of potential energy as an arrow on a drawn bow, which equals the work the archer did when drawing the bow to its position (**Figure 3.6**). When the string is released, the bow's potential energy is converted to the arrow's kinetic energy of motion. Similarly, the cordgrass that a meadow vole eats has chemical potential energy in the bonds of its molecules. As molecular bonds are broken by cellular respiration, this energy is converted to kinetic energy and heat as the meadow vole swims in the salt marsh. Thus, energy changes from one form to another.

The study of energy and its transformations is called **thermodynamics**. When considering thermodynamics, scientists use the word *system* to refer to a group of atoms, molecules, or objects being studied.[1] The rest of the universe other than the system is known as the *surroundings*. A **closed system** is self-contained; that is, it does not exchange energy with its surroundings (**Figure 3.7**).[2] Closed systems are very rare in nature. In contrast, an **open system** exchanges energy with its surroundings. This text discusses many kinds of open systems. For example, a city is an open system with an input of energy (as well as food, water, and consumer goods). Outputs from a city system include energy (as well as manufactured goods, sewage, and solid waste). On a global scale, Earth is an open system dependent on a continual supply of energy from the sun.

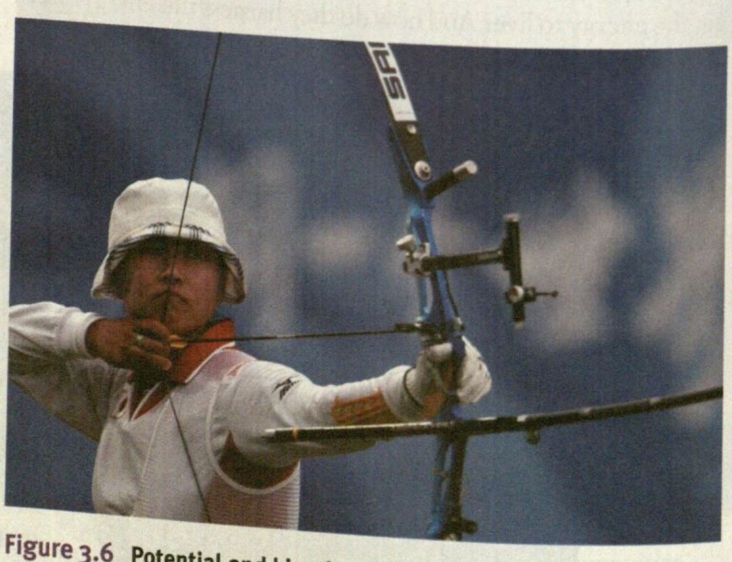
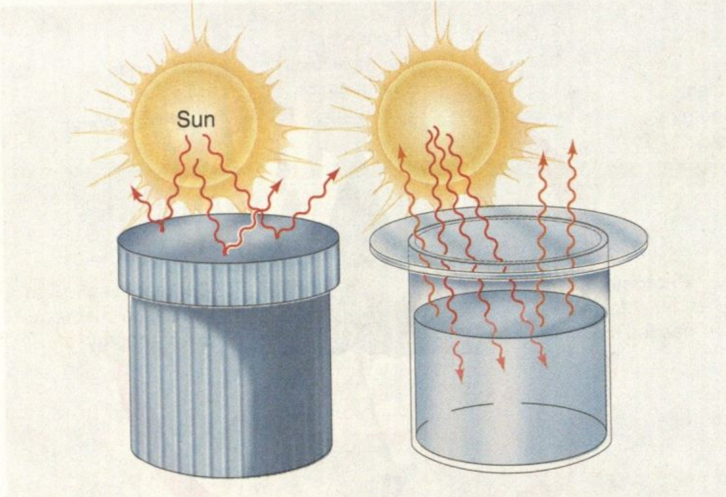


Figure 3.6 Potential and kinetic energy. Potential energy is stored in the drawn bow (shown) and is converted to kinetic energy as the arrow speeds toward its target. Photographed at the 2008 Summer Olympic Games in Beijing, China. (© Aflo Foto Agency/Alamy)

[1]The meaning of *system* in thermodynamics is different from the meaning of *system* in environmental science (a set of components that interact and function as a whole).

[2]In thermodynamics, an *isolated system* does not exchange energy *or* matter with the surroundings.



(a) Closed system. Energy is not exchanged between a closed system and its surroundings. A thermos bottle is an approximation of a closed system. Closed systems are rare in nature.

(b) Open system. Energy is exchanged between an open system and its surroundings. Earth is an open system because it receives energy from the sun, and this energy eventually escapes Earth as it dissipates into space.

Figure 3.7 Closed and open systems, with regard to energy.

Regardless of whether a system is open or closed, two laws about energy apply to all things in the universe: the first and second laws of thermodynamics.

THE FIRST LAW OF THERMODYNAMICS

first law of thermodynamics: Energy cannot be created or destroyed, although it can change from one form to another.

According to the **first law of thermodynamics**, an organism may absorb energy from its surroundings, or it may give up some energy into its surroundings, but the total energy content of the organism and its surroundings is always the same. As far as we know, the energy present in the universe at its formation, approximately 15 billion to 20 billion years ago, equals the amount of energy present in the universe today. This is all the energy that will ever be present in the universe. Similarly, the energy of any system and its surroundings is constant. A system may absorb energy from its surroundings, or it may give up some energy into its surroundings, but the total energy content of that system and its surroundings is always the same.

The first law of thermodynamics specifies that an organism cannot create the energy it requires to live. Instead, it must capture energy from the environment to use for biological work, a process involving the transformation of energy from one form to another. In photosynthesis, plants absorb the radiant energy of the sun and convert it into the chemical energy contained in the bonds of carbohydrate (sugar) molecules. Similarly, some of that chemical energy may later be transformed by an animal that eats the plant into the mechanical energy of muscle contraction, enabling it to walk, run, jump, slither, fly, or swim.

THE SECOND LAW OF THERMODYNAMICS

As each energy transformation occurs, some energy is changed to heat that is released into the cooler surroundings. No other organism can ever reuse this energy for biological work; it is "lost" from the biological point of view. It is not really gone from a thermodynamic point of view because it still exists in the surrounding physical environment. The use of food to enable us to walk or run does not destroy the chemical energy once present in the food molecules. After we have performed the task of walking or running, the energy still exists in the surroundings as heat.

second law of thermodynamics: When energy is converted from one form to another, some of it is degraded into heat, a less usable form that disperses into the environment.

According to the **second law of thermodynamics**, the amount of usable energy available to do work in the universe decreases over time. The second law of thermodynamics is consistent with the first law; that is, the total amount of energy in the universe is not decreasing with time. However, the total amount of energy in the universe available to do work decreases over time.

Less usable energy is more diffuse, or disorganized. **Entropy** is a measure of this disorder or randomness; organized, usable energy has low entropy, whereas disorganized energy such as heat has high entropy. Entropy is continuously increasing in the universe in all natural processes, and entropy is not reversible. Billions of years from now, all energy may exist as heat uniformly distributed throughout the universe. If that happens, the universe as a closed system will cease to operate because no work will be possible. Everything will be at the same temperature, so there will be no way to convert the thermal energy of the universe into usable mechanical energy. Another way to explain the second law of thermodynamics, then, is that entropy, or disorder, in a system increases over time.

An implication of the second law of thermodynamics is that no process requiring an energy conversion is ever 100% efficient because much of the energy is dispersed as heat, resulting in an increase in entropy. (*Efficiency* in this context refers to the amount of useful work produced per total energy input.) An automobile engine, which converts the chemical energy of gasoline to mechanical energy, is between 20% and 30% efficient. That is, only 20% to 30% of the original energy stored in the chemical bonds of the gasoline molecules is actually transformed into mechanical energy, or work. In our cells, energy use for metabolism is about 40% efficient, with the remaining energy given to the surroundings as heat.

Organisms are highly organized and at first glance appear to refute the second law of thermodynamics. As organisms grow and develop, they maintain a high level of order and do not become more disorganized. However, organisms maintain their degree of order over time only with the constant input of energy. That is why plants must photosynthesize and why animals must eat food. When relating the second law of thermodynamics to living organisms, the organisms' surroundings must also be considered. Throughout its life, as a plant takes in solar energy and photosynthesizes, it continually breaks down the products of photosynthesis to supply its own energy needs. This break-down releases heat into the environment. Similarly, as an animal eats and processes food to meet its energy needs, it releases heat into the surroundings. When an organism and its surroundings are taken into account, both laws of thermodynamics are satisfied.

PHOTOSYNTHESIS AND CELLULAR RESPIRATION

Energy is stored in living things as carbon compounds. **Photosynthesis** is the biological process in which light energy from the sun is captured and transformed into the chemical energy of carbohydrate (sugar) molecules (**Figure 3.8**). Photosynthetic pigments such as *chlorophyll*, which gives plants their green color, absorb radiant energy. This energy is used to manufacture the carbohydrate glucose ($C_6H_{12}O_6$) from carbon dioxide (CO_2) and water (H_2O), with the liberation of oxygen (O_2).

Photosynthesis:

$$6CO_2 + 12H_2O + \text{radiant energy} \rightarrow C_6H_{12}O_6 + 6H_2O + 6O_2$$

The chemical equation for photosynthesis is read as follows: 6 molecules of carbon dioxide plus 12 molecules of water plus light energy are used to produce 1 molecule of glucose plus 6 molecules of water plus 6 molecules of oxygen. (See Appendix I for a review of basic chemistry.)

Plants, some bacteria, and algae perform photosynthesis, a process essential for almost all life. Photosynthesis provides these organisms with a ready supply of energy in carbohydrate molecules, which they use as the need arises. The energy can also be transferred from one organism to another—for example, from plants to the organisms that eat plants. Oxygen, which many organisms require when they break down glucose or similar foods to obtain energy, is a by-product of photosynthesis.

The chemical energy that plants store in carbohydrates and other molecules is released within the cells of plants, animals, or other organisms through **cellular respiration**. In *aerobic* cellular respiration, molecules such as glucose are broken down in the presence of oxygen and water into carbon dioxide and water, with the release of energy (see Figure 3.8).

Aerobic cellular respiration:

$$C_6H_{12}O_6 + 6O_2 + 6H_2O \rightarrow 6CO_2 + 12H_2O + \text{energy}$$

Cellular respiration makes the chemical energy stored in glucose and other food molecules available to the cell for biological work, such as moving around, courting, and growing new cells and tissues. All organisms, including green plants, respire to obtain energy. Some organisms do not use oxygen for this process. *Anaerobic* bacteria that live in waterlogged soil, stagnant ponds, animal intestines, or hydrothermal vents respire in the absence of oxygen.

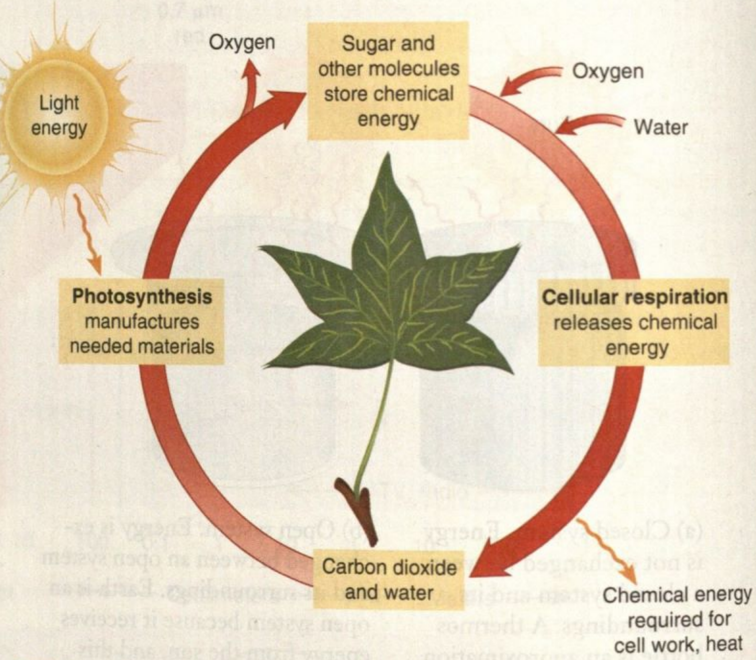


Figure 3.8 Photosynthesis and cellular respiration make up a system. These processes occur continuously in the cells of living organisms. Note that energy flow is *not* cyclic; energy enters living organisms as radiant energy and leaves organisms for the surroundings as heat energy. Given that increasing levels of CO_2 in the atmosphere are linked to climate warming, which process—photosynthesis or cellular respiration—could help reduce warming if it was increased significantly? Explain your answer.

CASE IN POINT

LIFE WITHOUT THE SUN

The sun is the energy source for almost all ecosystems. A notable exception was discovered in the late 1970s in a series of deep-sea **hydrothermal vents** in the Eastern Pacific where seawater had penetrated and been heated by the radioactive rocks below. During its time within Earth, the water had been charged with inorganic compounds, including hydrogen sulfide (H_2S).

Although no light is available for photosynthesis, hydrothermal vents support a rich ecosystem that contrasts with the surrounding "desert" of the deep-ocean floor. Giant, blood-red tube worms almost 3 m (10 ft) in length cluster in great numbers around the vents (**Figure 3.9**). Other animals around the hydrothermal vents include shrimp, crabs, clams, barnacles, and mussels.

Scientists initially wondered what the ultimate source of energy for the species in this dark environment is. Most deep-sea ecosystems depend on the organic material that drifts down from surface waters; that is, they depend on energy derived from photosynthesis. But hydrothermal vent ecosystems, now known to exist in hundreds of places, are too densely clustered and too productive to depend on chance encounters with organic material from surface waters.

The base of the *food web* in these aquatic oases consists of certain bacteria that survive and multiply in water so hot

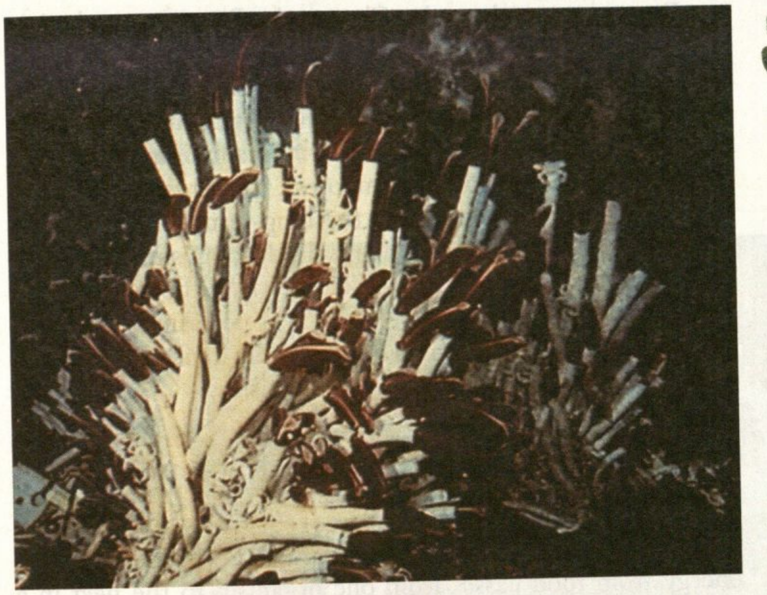


Figure 3.9 Hydrothermal vent ecosystem. Bacteria living in the tissues of these tube worms extract energy from hydrogen sulfide to manufacture organic compounds. These worms lack digestive systems and depend on the organic compounds the bacteria provide, along with materials filtered from the surrounding water. Also visible in the photograph are some crabs (white). (Dr. Ken Macdonald/Photo Researchers, Inc.)

(exceeding 200°C, or 392°F) that it would not remain in liquid form were it not under such extreme pressure. These bacteria function as producers, but they do not photosynthesize. Instead, they obtain energy and make carbohydrate molecules from inorganic raw materials by **chemosynthesis.** Chemosynthetic bacteria possess enzymes (organic catalysts) that cause the inorganic molecule hydrogen sulfide to react with oxygen, producing water and sulfur or sulfate. Such chemical reactions provide the energy to support these bacteria and other organisms in deep-ocean hydrothermal vents. Many of the vent animals consume the bacteria directly by filter feeding. Others, such as the giant tube worms, obtain energy from chemosynthetic bacteria that live symbiotically inside their bodies. ■

REVIEW

1. Distinguish among energy, work, and heat.
2. Is water stored behind a dam an example of potential or kinetic energy? What would cause the water to convert to the other form of energy?
3. Is a rabbit an example of a closed system or an open system? Why?
4. When coal is burned in a power plant, only 3% of the energy in the coal is converted into light in a lightbulb. What happens to the other 97% of the energy? Explain your answer using the laws of thermodynamics.
5. Distinguish between photosynthesis and cellular respiration. Which organisms perform each process?

The Flow of Energy Through Ecosystems

LEARNING OBJECTIVES

- Define *energy flow*, *trophic level*, and *food web*.
- Summarize how energy flows through a food web, mentioning producers, consumers, and decomposers in your explanation.
- Describe typical pyramids of numbers, biomass, and energy.
- Distinguish between gross primary productivity and net primary productivity, and discuss human impact on the latter.

With the exception of a few ecosystems such as hydrothermal vents, energy enters ecosystems as radiant energy (sunlight), some of which plants trap during photosynthesis. The energy, now in chemical form, is stored in the bonds of organic molecules such as glucose. To obtain energy, animals eat plants or eat animals that ate plants. All organisms—plants, animals, and microorganisms—respire to obtain some of the energy in organic molecules. When cellular respiration breaks these molecules apart, the energy becomes available for work such as repairing tissues, producing body heat, or reproducing. As the work is accomplished, the energy escapes the organism and dissipates into the environment as heat (recall the second law of thermodynamics). Ultimately, this heat radiates into space. Once an organism has used energy, it becomes unusable for all other organisms. The movement of energy just described is called **energy flow.**

energy flow: The passage of energy in a one-way direction through an ecosystem.

PRODUCERS, CONSUMERS, AND DECOMPOSERS

The organisms of an ecosystem are divided into three categories on the basis of how they obtain nourishment: producers, consumers, and decomposers (**Figure 3.10**). Virtually all ecosystems contain representatives of all three groups, which interact extensively, both directly and indirectly, with one another.

Producers, also called **autotrophs** (Greek *auto*, "self," and *tropho*, "nourishment"), manufacture organic molecules from simple inorganic substances, generally CO_2 and water, usually using the energy of sunlight. In other words, most producers perform the process of photosynthesis. Producers incorporate the chemicals they manufacture into their own bodies, becoming potential food resources for other organisms. Whereas plants are the most significant producers on land, algae and certain types of bacteria are important producers in aquatic environments. In the salt marsh ecosystem discussed in the chapter introduction, cordgrass, algae, and photosynthetic bacteria are important producers.

Animals are **consumers** that use the bodies of other organisms as a source of food energy and bodybuilding materials. Consumers are also called **heterotrophs** (Greek *heter*, "different," and *tropho*, "nourishment"). Consumers that eat producers are **primary consumers** or **herbivores** (plant eaters). Rabbits and deer are examples of primary consumers, as is the marsh periwinkle, a type of snail that feeds on algae in the salt marsh ecosystem.

Secondary consumers eat primary consumers, whereas **tertiary consumers** eat secondary consumers. Both secondary and tertiary consumers are flesh-eating **carnivores** that eat other animals. Lions, lizards, and spiders are examples of carnivores, as are the northern diamondback terrapin and the northern water snake in the salt marsh ecosystem. Other consumers, called **omnivores**, eat a variety of organisms, both plant and animal. Bears, pigs, and humans are examples of omnivores; the meadow vole, which eats both insects and cordgrass in the salt marsh ecosystem, is an omnivore.

Some consumers, called **detritus feeders** or **detritivores**, consume detritus, organic matter that includes animal carcasses, leaf litter, and feces. Detritus feeders, such as snails, crabs, clams, and worms, are especially abundant in aquatic environments, where they burrow in the bottom muck and consume the organic matter that collects there. Marsh crabs are detritus feeders in the salt marsh ecosystem. Earthworms, termites, beetles, snails, and millipedes are terrestrial (land-dwelling) detritus feeders. An earthworm actually eats its way through the soil, digesting much of the organic matter contained there. Detritus feeders work with microbial decomposers to destroy dead organisms and waste products.

Decomposers, also called **saprotrophs** (Greek *sapro*, "rotten," and *tropho*, "nourishment"), are heterotrophs that break down dead organic material and use the decomposition products to supply themselves with energy. They typically release simple inorganic molecules, such as CO_2 and mineral salts, that producers can reuse. Bacteria and fungi are important decomposers. For example, during the decomposition of dead wood, sugar-metabolizing fungi first invade the wood and consume simple carbohydrates, such as glucose and maltose. When these carbohydrates are exhausted, other fungi, often aided by termites with symbiotic bacteria in their guts, complete the digestion of the wood by breaking down cellulose, the main carbohydrate of wood.

Ecosystems such as the Chesapeake Bay salt marsh contain a variety of producers, consumers, and decomposers, all of which have indispensable roles in ecosystems. Producers provide both food and oxygen for the rest of the community. Consumers play an important role by maintaining a balance between producers and decomposers. Detritus feeders and decomposers are necessary for the long-term survival of any ecosystem because, without them, dead organisms and waste products would accumulate indefinitely. Without microbial decomposers, important elements such as potassium, nitrogen, and phosphorus would remain permanently in dead organisms, unavailable for new generations of organisms.

THE PATH OF ENERGY FLOW: WHO EATS WHOM IN ECOSYSTEMS

In an ecosystem, energy flow occurs in **food chains**, in which energy from food passes from one organism to the next in a sequence (see Figure 3.10). Each level, or "link," in a food chain is a **trophic level** (recall that the Greek *tropho* means "nourishment"). An organism is assigned a trophic level based on the number of energy transfer steps to that level. Producers (organisms that photosynthesize) form the first trophic level, primary consumers (herbivores) the second trophic level, secondary consumers (carnivores) the third trophic level, and so on. At every step in a food chain are decomposers, which respire organic molecules in the carcasses and body wastes of all members of the food chain.

trophic level: An organism's position in a food chain, which is determined by its feeding relationships.

Simple food chains rarely occur in nature because few organisms eat just one kind of organism. More typically, the flow

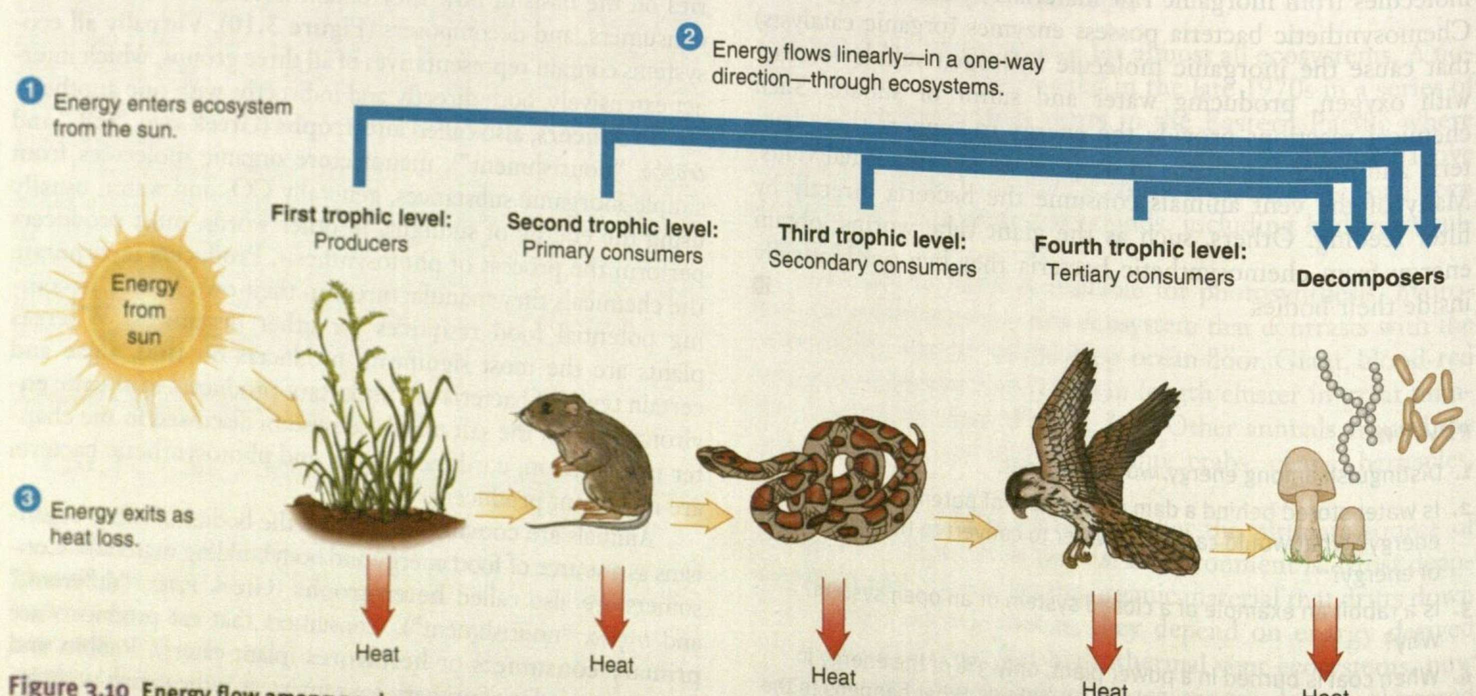


Figure 3.10 Energy flow among producers, consumers, and decomposers. In photosynthesis, producers use the energy from sunlight to make organic molecules. Consumers obtain energy when they eat producers or other consumers. Decomposers, such as bacteria and fungi, obtain energy from wastes and dead organic material from producers and consumers. During every energy transaction, some energy is lost to biological systems as it disperses into the environment as heat.

of energy and materials through an ecosystem takes place in accordance with a range of food choices for each organism involved. In an ecosystem of average complexity, numerous alternative pathways are possible. A hawk eating a rabbit is a different energy pathway than a hawk eating a snake. A **food web** is a more realistic **model** of the flow of energy and materials through an ecosystem (**Figure 3.11**). A food web helps us visualize feeding relationships that indicate how a community is organized.

food web: A representation of the interlocking food chains that connect all organisms in an ecosystem.

Figure 3.11 Food web at the edge of an eastern deciduous forest. This food web is greatly simplified compared to what actually happens in nature. Groups of species are lumped into single categories such as "spiders" and "fungi," other species are not included, and many links in the web are not shown.

The most important thing to remember about energy flow in ecosystems is that it is linear, or one way. Energy moves along a food chain or food web from one organism to the next as long as it has not been used for biological work. Once an organism has used energy, it is lost as heat and is unavailable for any other organism in the ecosystem.

CASE IN POINT

HOW HUMANS HAVE AFFECTED THE ANTARCTIC FOOD WEB

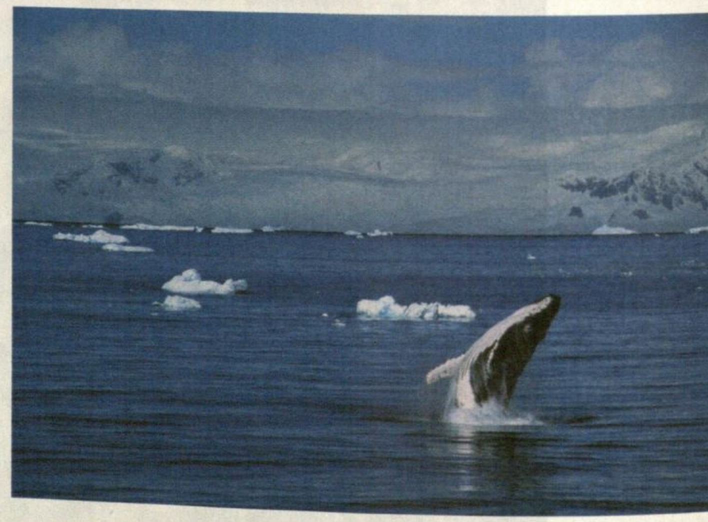
Although the icy waters around Antarctica may seem an inhospitable environment, a complex food web is found there. The base of the food web consists of microscopic, photosynthetic algae present in vast numbers in the well-lit, nutrient-rich water. A huge population of herbivores—tiny shrimplike **krill**—eat these marine algae (**Figure 3.12a**). Krill, in turn, support a variety of larger animals. A major consumer of krill is the baleen whale, which filters krill out of the frigid water. Baleen whales include blue whales, right whales, and humpback whales (**Figure 3.12b**). Squid and fishes also consume krill in great quantities. These, in turn, are eaten by other carnivores: toothed whales such as the sperm whale, elephant seals and leopard seals, king penguins and emperor penguins, and birds such as the albatross and the petrel.

Humans have had an impact on the Antarctic food web, as they have had on most other ecosystems. Before the advent of whaling, baleen whales consumed huge quantities of krill. Until a global ban on hunting large whales was enacted in 1986, whaling steadily reduced the number of large baleen whales in Antarctic waters. As a result of fewer whales eating krill, more krill became available for other krill-eating animals, whose populations increased.

Now that commercial whaling is regulated, it is hoped that the number of large baleen whales will slowly increase, and that appears to be the case for some species. However, the populations of most baleen whales in the Southern Hemisphere are still a fraction of their pre-whaling levels. It is not known whether baleen whales will return to their former position of dominance in terms of krill consumption in the food web. Biologists will monitor changes in the Antarctic food web as the whale populations recover.

Thinning of the ozone layer in the stratospheric region of the atmosphere over Antarctica has the potential to cause long-term effects on the entire Antarctic food web. Ozone thinning allows more of the sun's ultraviolet radiation to penetrate to Earth's surface. Ultraviolet radiation contains more energy than visible light and can break the chemical bonds of some biologically important molecules, such as deoxyribonucleic acid (DNA). Scientists are concerned that ozone thinning over Antarctica may damage the algae that form the base of the food web in the Southern Ocean. Increased ultraviolet radiation is penetrating the surface waters around Antarctica, and algal productivity has declined, probably as a result of increased exposure to ultraviolet radiation. (The problem of stratospheric ozone depletion is discussed in detail in Chapter 19.)

(a) Krill, tiny shrimplike animals, live in large swarms and eat photosynthetic algae in and around the pack ice. (Tom McHugh/Photo Researchers, Inc.)



(b) Whales, squid, and fishes consume vast numbers of krill. Shown is a humpback whale in the Antarctic. (© Media Bakery)

Figure 3.12 Antarctic food web.

Another human-induced change that may be responsible for declines in certain Antarctic populations is global climate change. As the water has warmed in recent decades around Antarctica, less pack ice has formed during winter months. Large numbers of marine algae are found in and around the pack ice, providing a critical supply of food for the krill, which reproduce in the area. Years with below-average pack ice cover mean fewer algae, which mean fewer krill reproducing. Scientists have demonstrated that low krill abundance coincides with unsuccessful breeding seasons for penguins and fur seals, which struggle to find food during warmer winters. Scientists are concerned that climate change will continue to decrease the amount of pack ice, which will reverberate through the food web. (Global climate change, including the effect on Adélie penguins in Antarctica, is discussed in Chapter 20.)

To complicate matters, some commercial fishermen have started to harvest krill to make fishmeal for aquaculture industries (discussed in Chapter 18). Scientists worry that the human harvest of krill may endanger the many marine animals that depend on krill for food. ■

ECOLOGICAL PYRAMIDS

An important feature of energy flow is that most of the energy going from one trophic level to the next in a food chain or food web dissipates into the environment as a result of the second law of thermodynamics. **Ecological pyramids** often graphically represent the relative energy values of each trophic level. There are three main types of pyramids—a pyramid of numbers, a pyramid of biomass, and a pyramid of energy.

A **pyramid of numbers** shows the number of organisms at each trophic level in a given ecosystem, with greater numbers illustrated by a larger area for that section of the pyramid (**Figure 3.13**). In most pyramids of numbers, the organisms at the base of the food chain are the most abundant, and fewer organisms occupy each successive trophic level. In the Antarctic food web, the number of algae is far greater than the number of krill that feed on the algae; likewise, the number of krill is greater than the number of baleen whales, squid, and fishes that feed on krill.

Inverted pyramids of numbers, in which higher trophic levels have *more* organisms than lower trophic levels, are often observed among decomposers, parasites, tree-dwelling herbivorous insects, and similar organisms. One tree may provide food for thousands of leaf-eating insects, for example. Pyramids of numbers are of limited usefulness because they do not indicate the biomass of the organisms at each level, and they do not indicate the amount of energy transferred from one level to another.

A **pyramid of biomass** illustrates the total biomass at each successive trophic level. **Biomass** is a quantitative estimate of the total mass, or amount, of living material; it indicates the amount of fixed energy at a particular time. Biomass units of measure vary: Biomass is represented as total volume, as dry weight, or as live weight. Typically, pyramids of biomass illustrate a progressive reduction of biomass in succeeding trophic levels (**Figure 3.14**). For example, if one assumes about a 90% reduction of biomass for each trophic level, 10,000 kg of grass should support 1000 kg of grasshoppers, which in turn support 100 kg of toads. The 90% reduction in biomass is used for illustrative purposes only; actual field numbers for biomass reduction in nature vary widely. By this logic, however, the biomass of toad eaters such as snakes could be, at most, only about 10 kg. From this brief exercise, it is apparent that although carnivores do not eat vegetation, a great deal of vegetation is required to support them.

A **pyramid of energy** illustrates the energy content, often expressed as kilocalories per square meter per year, of the biomass of each trophic level (**Figure 3.15**). These pyramids always have large energy bases and get progressively smaller through succeeding trophic levels. Energy pyramids show that most energy dissipates into the environment when going from one trophic level to the next. Less energy reaches each successive trophic level from the level beneath it because organisms at the lower level use some energy to perform work, and some energy is lost. (Remember, because of the second law

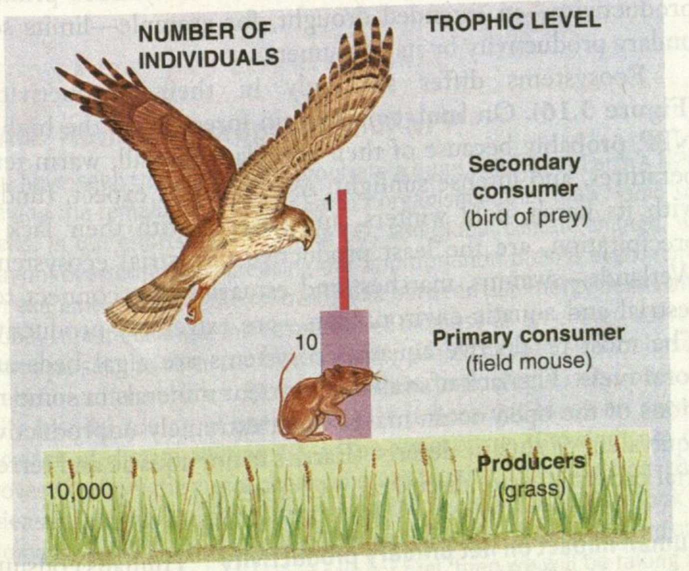


Figure 3.13 Pyramid of numbers. This pyramid is for a hypothetical area of temperate grassland; in this example, 10,000 grass plants support 10 mice, which support one bird of prey. Based on the number of organisms found at each trophic level, a pyramid of numbers is not as useful as other ecological pyramids. It provides no information about biomass differences or energy relationships between one trophic level and the next. (Note that decomposers are not shown.)

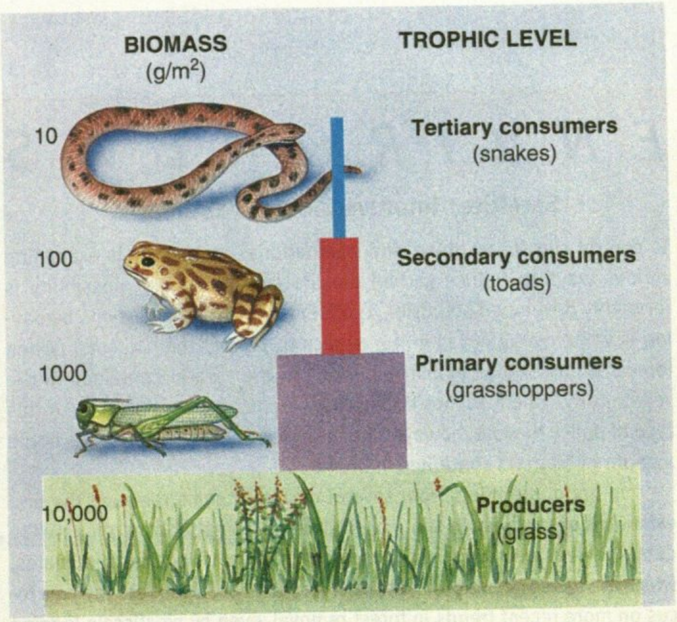


Figure 3.14 Pyramid of biomass. This pyramid is for a hypothetical area of temperate grassland. Based on the biomass at each trophic level, pyramids of biomass generally have a pyramid shape with a large base and progressively smaller areas for each succeeding trophic level. (Note that decomposers are not shown.)

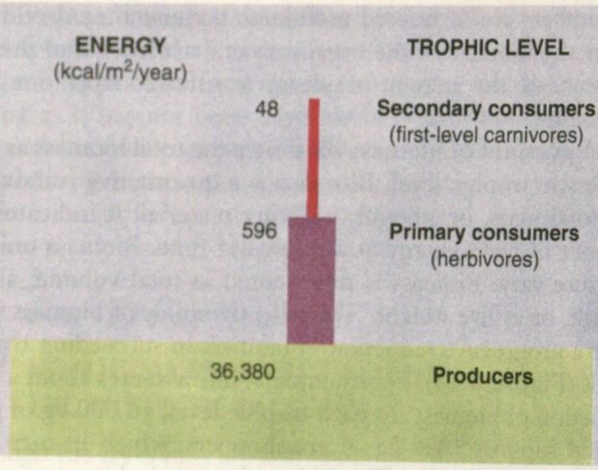


Figure 3.15 Pyramid of energy. This pyramid indicates how much energy is present in the biomass at each trophic level in a salt marsh in Georgia and how much is transferred to the next trophic level. Note the substantial loss of usable energy from one trophic level to the next; this loss occurs because of the energy used metabolically and given off as heat. (Note that decomposers are not shown. The 36,380 kcal/m^2/year for the producers is gross primary productivity, or GPP, discussed shortly.) (After J. M. Teal. Energy flow in the salt marsh ecosystem of Georgia. *Ecology*, Vol. 43 [1962])

of thermodynamics, no biological process is ever 100% efficient.) Energy pyramids explain why there are so few trophic levels: Food webs are short because of the dramatic reduction in energy content at each trophic level. (See You Can Make a Difference: Vegetarian Diets in Chapter 18 for a discussion of how the eating habits of humans relate to food chains and trophic levels.)

ENVIRONEWS

Satellites Improve Biomass Estimates

To control climate warming, the international community is examining various ways to reduce carbon dioxide emissions. One possibility is for highly developed countries to offset their carbon emissions by paying developing countries in the tropics to protect their forests. (When forests are cut down or burned, much of the carbon contained in the vegetation is released into the atmosphere as carbon dioxide.) For this type of policy to work, however, we must have accurate estimates of the amount of biomass contained in the forests.

In 2009, scientists from several research teams released the first estimates of biomass in the world's tropical forests based on satellite data. The data are accurate to a resolution of 1 km. Using these estimates, which are based on satellite data collected in 2000, scientists can now focus on more recent trends in forest removal, even by smallscale logging operations. Thus, scientists and policymakers will have a more accurate understanding of how the carbon locked in biomass is changing.

ECOSYSTEM PRODUCTIVITY

The **gross primary productivity (GPP)** of an ecosystem is the rate at which energy is captured during photosynthesis. (Gross and net primary productivities are referred to as *primary* because plants occupy the first trophic level in food webs.)

gross primary productivity (GPP): The total amount of photosynthetic energy that plants capture and assimilate in a given period.

Of course, plants respire to provide energy for their own use, and this acts as a drain on photosynthesis. Energy in plant tissues after cellular respiration has occurred is **net primary productivity (NPP)**. That is, NPP is the amount of biomass found in excess of that broken down by a plant's cellular respiration. NPP represents the rate at which this organic matter is actually incorporated into plant tissues for growth.

net primary productivity (NPP): Productivity after respiration losses are subtracted.

Net primary productivity (plant growth per unit area per unit time)	=	**Gross primary productivity** (total photosynthesis per unit area per unit time)	−	**Plant cellular respiration** (per unit area per unit time)

Both GPP and NPP are expressed as energy per unit area per unit time (kilocalories of energy fixed by photosynthesis per square meter per year) or as dry weight (grams of carbon incorporated into tissue per square meter per year).

Only the energy represented by NPP is available as food for an ecosystem's consumers. Consumers use most of this energy for cellular respiration to contract muscles (obtaining food and avoiding predators) and to maintain and repair cells and tissues. Any energy that remains is used for growth and for the production of young, collectively called *secondary productivity*. Any environmental factor that limits an ecosystem's primary productivity—an extended drought, for example—limits secondary productivity by its consumers.

Ecosystems differ strikingly in their productivities (**Figure 3.16**). On land, tropical rain forests have the highest NPP, probably because of their abundant rainfall, warm temperatures, and intense sunlight. As you might expect, tundra, with its harsh, cold winters, and deserts, with their lack of precipitation, are the least productive terrestrial ecosystems. Wetlands—swamps, marshes, and estuaries that connect terrestrial and aquatic environments—are extremely productive. The most productive aquatic ecosystems are algal beds and coral reefs. The lack of available nutrient minerals in some regions of the open ocean makes them extremely unproductive, equivalent to aquatic deserts. (Earth's major aquatic and terrestrial ecosystems are discussed in Chapter 6.)

Human impact on net primary productivity Humans consume far more of Earth's resources than any other of the millions of animal species. **Peter Vitousek** and colleagues at Stanford University calculated in 1986 how much of the global NPP is appropriated for the human economy and therefore not transferred to other organisms. When both direct and indirect

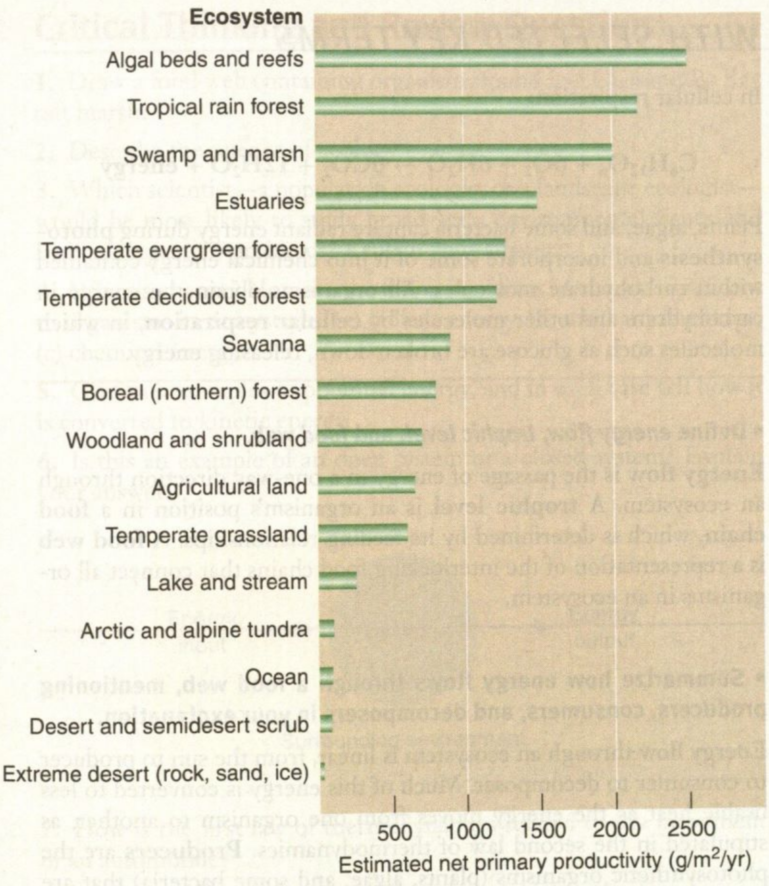


Figure 3.16 Estimated annual net primary productivities (NPP) for selected ecosystems. NPP is expressed as grams of dry matter per square meter per year ($g/m^2/yr$). (After R.H. Whittaker, *Communities and Ecosystems*, 2nd edition. New York: Macmillan [1975])

human impacts are accounted for, Vitousek estimated that humans use 32% of the annual NPP of land-based ecosystems. This is a huge amount considering that we humans represent about 0.5% of the total biomass of all consumers on Earth.

In 2001 **Stuart Rojstaczer** and colleagues at Duke University reexamined Vitousek's groundbreaking research. Rojstaczer used contemporary data sets, many of which are satellite-based and more accurate than the data Vitousek had. Rojstaczer's mean value for his conservative estimate of annual land-based NPP appropriation by humans was 32%, like Vitousek's, although Rojstaczer arrived at that number using different calculations.

In 2007, **K. Heinz Erb** at Klagenfurt University in Vienna and his colleagues plugged agricultural and forestry statistics that account for 97% of Earth's ice-free land into a computer model. Erb's model indicates that humans appropriate about 25% of Earth's land-based NPP for food, forage (for livestock), and wood.

These studies provide us with estimates, not actual values. However, the take-home message is simple: Human use of global productivity is competing with other species' energy needs. Our use of so much of the world's productivity may contribute to the loss of many species, some potentially useful to humans, through extinction. Human consumption of global NPP could become a serious threat to the planet's ability to support both its nonhuman and human occupants. If we want our planet to operate sustainably, we must share terrestrial photosynthesis products—that is, NPP—with other organisms.

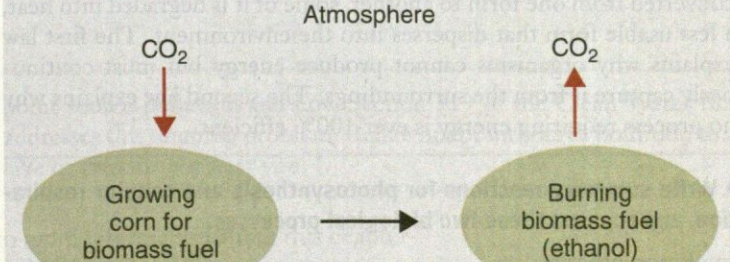
REVIEW

1. What is a food web?
2. How does energy flow through a food web consisting of producers, consumers, and decomposers?
3. What is a pyramid of energy?
4. What is gross primary productivity? Net primary productivity?

ENERGY AND CLIMATE CHANGE

Human Appropriation of NPP

You have seen that humans appropriate a huge amount of Earth's NPP, leaving the remainder for all of Earth's organisms other than *Homo sapiens*. In our efforts against rising CO_2 and global climate change, we may inadvertently be increasing our appropriation of NPP even more. For example, consider the following link between our energy needs and global climate change: increased use of biomass as an energy source. Biomass, such as corn, can be chemically altered to yield alcohol-based fuels for motor vehicles. Biomass is often considered an environmentally friendly source of energy because it does not cause an overall increase of climate-altering CO_2 in the atmosphere. (Growing corn removes CO_2 from the atmosphere, whereas burning fuel made from corn releases CO_2 into the atmosphere; see the figure.) But a closer look at biomass shows it is not so environmentally friendly. If we grow corn and other biomass crops on a large scale for fuel, then we will be taking an even larger share of global NPP, which would leave even less for the planet's organisms. At some point, our use of global NPP will compromise Earth's systems that sustain us. Indeed, we may have already exceeded the sustainable consumption of NPP.



Carbon stored as biomass in the world's tropical forest.

View video on this subject in your ***WileyPLUS*** course.