Introduction to Ocean Sciences

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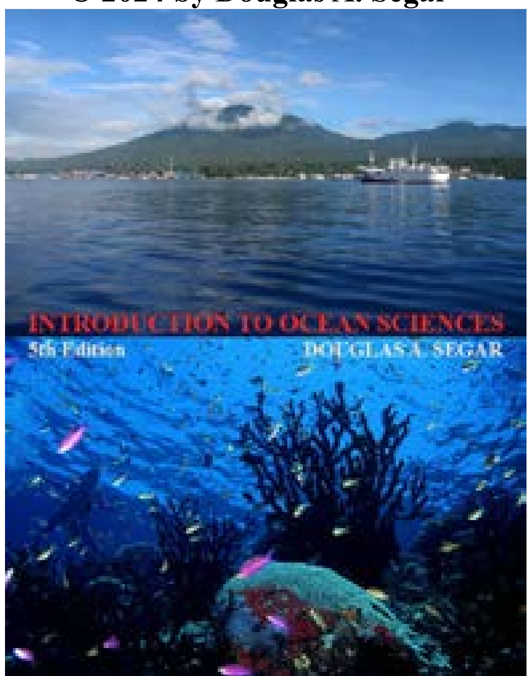

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CHAPTER 12

Foundations of Life in the Oceans

CRITICAL CONCEPTS USED IN THIS CHAPTER
CC4 Particle Size, Sinking, Deposition, and Resuspension
CC8 Residence Time
CC10 Modeling
CC14 Phototrophy, Light, and Nutrients
CC15 Food Chain Efficiency

Although it takes many wonderful forms, life in the oceans is all made possible by a few simple physical and chemical processes. When we found it, this midring blue-ringed octopus (Hapalochlaena sp., Indonesia) was a drab, dark color and blended in almost totally with the background. After we approached, it changed color rapidly and displayed the blue rings as a warning. A very closely related species of blue-ringed octopus is venomous with a toxin in its saliva for which there is no antidote. This species is thought to be less toxic, but little is known about it. This individual octopus entertained us by swimming and stopping several times, all the while displaying the blue rings and rapidly varying its body color before it settled and assumed the shape and color to blend perfectly with the rock on which it had landed

In many ways the oceans are an ideal **environment** for life. Temperatures are much more uniform than on land, so most marine organisms do not have to contend with the temperature variations and extremes that terrestrial organisms experience. In addition, all elements essential to life are present as dissolved **ions** in seawater, albeit sometimes at very low concentrations, and they are readily available to marine **archaea**, **bacteria**, and **algae,** which perform the task of converting these dissolved substances into living matter**.**

Living in the ocean also presents special problems, and the abundance of ocean life is limited by a variety of physical and chemical factors. This chapter examines the basic processes of life in the oceans, and the physical and chemical parameters that control the quantities and types of organisms in different regions of open oceans. The parameters that determine the distribution of life include the physical and chemical nature of seawater, the distribution of winds and **currents,** and even **plate tectonics.** Chapter 13 discusses how life in coastal and **estuarine** zones differs from open-ocean marine life as a result of the different physical and chemical environments.

HOW DO WE DESCRIBE LIFE?

Before we examine the many complex physical, chemical, and biological interactions that are the foundations of life in the oceans, it will help to look briefly at how biologists group and

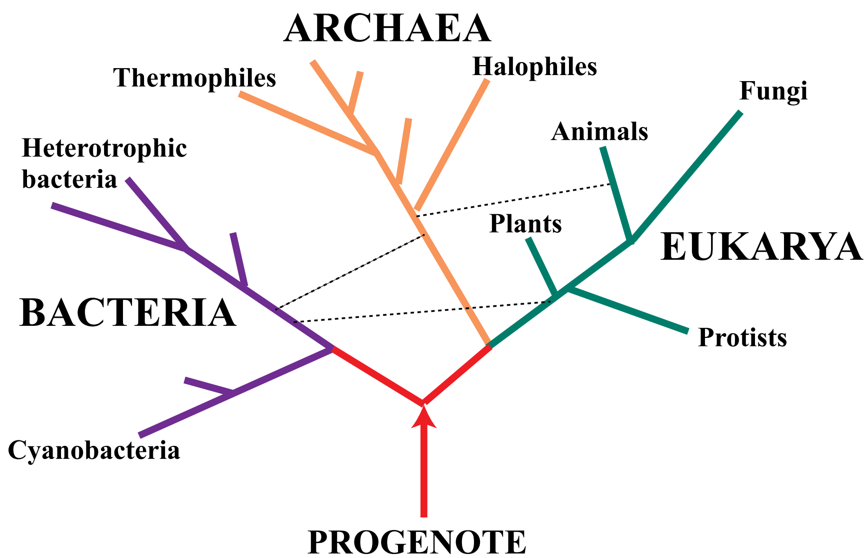


FIGURE 12-1 The tree of life. The prokaryotes—Bacteria and Archaea—are single-celled organisms with no membrane-bound (enclosed by a membrane) nucleus. The eukaryotes (Eukarya)—protists, fungi, plants, and animals— are single- or multi-celled organisms whose cells contain a membrane-bound nucleus. All life is assumed to derive from a common ancestor (the Progenote). Bacteria and Archaea are known to have developed before Eukarya (to which humans belong). DNA indicates that the Eukarya developed from Archaea but Eukarya also inherited one or more genes from Bacteria most likely through horizontal gene transfer (represented conceptually by the dashed lines in the figure). Horizontal gene transfer (transfer of one or more gene between species) is now known to be common so the original Darwinian theory of evolution of one species into another in a linear fashion that was the basis for the tree of life concept must now be revised. Protists include diatoms, dinoflagellates, foraminifera, radiolaria, marine algae and others (see **Table 12-1**).

classify living organisms. All living things are arranged into formal groups according to their anatomy, physiology, and, more recently, **genetic** differences, through a system known as "taxonomy." Taxonomy is discussed more fully in Appendix 3. For now, we need to know that, at the highest level of organization, called the "tree of life," all **species** are classified into one of three domains (**Fig. 12-1**, **Table 12-1**): Bacteria, Archaea, and Eukarya.

Archaea were once considered part of the Bacteria domain but are now considered separately. In addition, there is now some evidence that suggests that the tree of life might only contain two branches with the Eukarya being considered simply a subbranch of Archaea.

Together, bacteria and archaea make up a group of species known as **prokaryotes.** All other living species belong to a group called **eukaryotes**, which includes four kingdoms: Protista (**protists**), Fungi (**fungi**), Plantae (plants), and Animalia (animals). Viruses have traditionally been considered to be non-living (since they cannot reproduce without a host). However, this view is now changing and viruses may soon be recognized as a new classification of life. In addition, there is now evidence that viruses may have preceded all of the other kingdoms and that they stand at the base of the tree of life and may have evolved into cellular organisms and the progenote, the last common ancestor of all species of cellular life. However, the origin of viruses remains unknown and the issue of whether they are a branch of "life" remains controversial.

As discussed in Appendix 3, species within each kingdom are classified into groups that are arranged in a hierarchy containing a number of levels. All species eventually are given a formal name that consists of **genus** and species, the two lowest levels in the hierarchy. For example, humans are genus *Homo*, species *sapiens*; we are all members of the species *Homo sapiens* (note the italics always used for genus and species names).

Although the formal taxonomic classification of species addresses the need to classify organisms according to their physiological and genetic differences, it does not always serve well to

TABLE 12-1 The Major Taxonomic Groupings of Living Organisms

PROKARYOTES: Generally microscopic, single-celled organisms that have no membrane-bound (enclosed by a membrane) nucleus or internal structure. May be photosynthetic, chemosynthetic, or heterotrophic. **Two Domains**	
Domain Bacteria	Generally, microscopic and relatively simple single-celled organisms. Bacteria have no organelles (membrane-bound nucleus or internal structural features). However, most possess a carbohydrate-based cell wall.
Domain Archaea	Archaea are similar to bacteria but have different cell wall structures, different constituent organic compounds, and many different genes. Many archaea live in extreme environments, such as those found at hydrothermal vents, those where the temperature exceeds the boiling point of water (e.g., geysers), those where salinities are extremely high, or those that are strongly acidic or alkaline. Some archaea are single-celled, whereas others form filaments or aggregates.
EUKARYOTES: Single-celled or multi-celled organisms whose cells have a nucleus and other internal structure. Generally larger than prokaryotes. **Domain Eukarya**	
Kingdom Protista	A very diverse group of species, including all the eukaryotes except for the plants, fungi, and animals. The vast majority of protists are single-celled organisms, typically only 0.01 to 0.5 mm in size, yet generally larger than the prokaryotes. Examples are diatoms and dinoflagellates, foraminifera, radiolaria, marine algae, and seaweeds. Protists commonly can survive dry periods in the form of cysts; some are important parasites; a few forms are multicelled—for example, the brown and red algae.
Kingdom Fungi	Mostly single-celled, including many decomposers and parasites that infect animals and plants. Fungi release enzymes that break down organic matter that they absorb for food and energy. Examples are molds and mushrooms.
Kingdom Plantae	Multicelled photosynthetic autotrophs. Flowering plants, including sea grasses, mangroves, ferns, and mosses. Note that marine algae and seaweeds are *not* generally considered to be plants.
Kingdom Animalia	Multicelled heterotrophs, including all invertebrates and vertebrates.

classify species with regard to their functions in the **ecosystem.** Therefore, many other functional grouping schemes are used for specific situations. For example, marine biologists may group organisms according to whether they live in the water column or on the seafloor, or whether they are able to swim against currents or primarily drift with the water, or whether they are capable of synthesizing living organic matter from inorganic matter or not.

PRODUCTION, CONSUMPTION, AND DECOMPOSITION

Life is based on the production of an enormous variety of organic compounds, each of which serves a different function in the cells of living organisms. Organic compounds are created when carbon atoms are combined in chains or rings. Chemical properties of a compound are determined by the number of carbon atoms and how they are arranged, and by the number, position, and elements in other groups of atoms (containing, for example, oxygen, nitrogen, sulfur, or phosphorus) attached to the carbon chains or rings. Organic compounds made by living organisms can contain hundreds of carbon atoms and attached groups arranged in an enormous number of ways. Even the simplest living organisms consist of a bewildering array of organic compounds.

The most important use of organic molecules by living organisms is to provide energy for the **biochemical** processes that control their growth, movement, feeding, and reproduction. Energy is needed to combine carbon atoms into organic compounds. This energy can be released from organic compounds by decomposition of their molecules to carbon dioxide and water. All living organisms use a decomposition process called **respiration** to provide their needed energy.

There are two fundamental types of organisms. Those of the first type, **autotrophs,** create their own food from inorganic compounds by using an external source of energy. The process of converting inorganic compounds to organic matter is called **primary production.** Autotrophs use up some of the food they synthesize to fuel their own life processes through respiration. Plants, algae, and some bacteria and archaea are autotrophs. Organisms of the second fundamental type, **heterotrophs,** cannot make organic compounds from inorganic compounds and must obtain organic matter as food. Animals and most bacteria and archaea are heterotrophs. Recent research has shown that the distinction between autotrophs and heterotrophs is not as simple as once thought. There is now strong evidence that certain microbial species in the oceans possess the genetic machinery for both autotrophy and heterotrophy and it is likely that these species can behave either as an autotroph or a heterotroph depending on the availability of light, nutrients and dissolved food (carbon in organic compounds that can be "burned" to produce fuel for metabolic processes.

The distribution of life depends on the distribution and growth rate of autotrophs. Heterotrophs can live only where and when autotrophs supply enough food and **nutrients.** Autotrophs synthesize organic matter by one of two fundamentally different mechanisms: **phototrophy** (predominately **photosynthesis)** and **chemosynthesis.**

Phototrophy

The dominant process of primary production in the surface mixed layer of the oceans is photosynthesis (**CC14**). The basic raw materials needed for photosynthesis are carbon dioxide, water, and nutrients. An ample supply of carbon dioxide is dissolved in seawater in the form of carbonate and bicarbonate ions (**Chap. 5**). Of course, water is readily available. The source of energy used to combine carbon atoms is solar radiation. Therefore, light availability is an important determinant of where photosynthesis can occur and at what rate. Photosynthesis in the oceans is dominated by phytoplankton that include species of algae and cyanobacteria.

The general term for organisms using light energy to produce organic matter for growth of living organisms is **phototroph** (**CC14**). Certain archaea and possibly bacteria are phototrophs that do not use chlorophyll or photosynthesis and do not release oxygen. Instead they use a simpler metabolic pathway to capture light energy using compounds called **rhodopsins** to capture light energy for growth. These microbes are important at least in waters where nutrient concentrations are very low. Recent research also shows that certain marine diatoms may use the rhodopsin based pathway to supplement photosynthesis. The significance of the rhodopsin based light gathering mechanism to primary production in the oceans is not yet known.

Nutrient elements, such as nitrogen, phosphorus, magnesium, and sulfur, are also necessary for **phototrophy**. For example, nitrogen atoms are part of all protein molecules and of the molecules of **chlorophyll**, which is essential to most photosynthesis (**CC14**). The following sections of this chapter explain how the distribution of light and nutrients and the processes that affect their distribution control the distribution of life in most of the oceans.

Chemosynthesis

Some types of bacteria and archaea can convert carbon dioxide and water to organic matter by using energy from chemical reactions rather than from light. This process, called "chemosynthesis," uses energy obtained from chemical reactions including the oxidation of:

- hydrogen sulfide to sulfate,
- metals from a reduced to an oxidized form (including iron, arsenic, manganese and uranium),
- hydrogen to water,
- ammonia to nitrite,
- nitrite to nitrate, or of
- methane to carbon dioxide and water.

Note that "oxidation" does not necessarily require oxygen atoms to be present. Oxidation is the general term for a chemical reaction in which an electron is removed from a molecule that is being oxidized so certain molecules or atoms that do not contain oxygen atoms can also be used as the electron acceptor for example in the conversion (oxidation) of compounds of ferrous iron (Fe^{2+}) to compounds of ferric iron (Fe^{3+}). Some organisms can perform chemosynthesis in the complete absence of oxygen so chemosynthesis is possible almost anywhere on Earth and other planets even if they have no free oxygen. Indeed, there was no oxygen in Earth's atmosphere or free dissolved oxygen in Earth's oceans when life first evolved and the first life forms were chemosynthetic. It took billions of years for chemosynthetic organisms that produce oxygen to raise the oxygen concentrations in the atmosphere and oceans to where they are at present.

Hydrogen sulfide, metal sulfides, hydrogen, and methane are all oxidized readily by chemical processes in environments where oxygen is present. Therefore, most of the reduced compounds that fuel chemosynthesis are not currently present in the atmosphere or in most ocean waters, because these environments contain appreciable concentrations of oxygen. In reducing

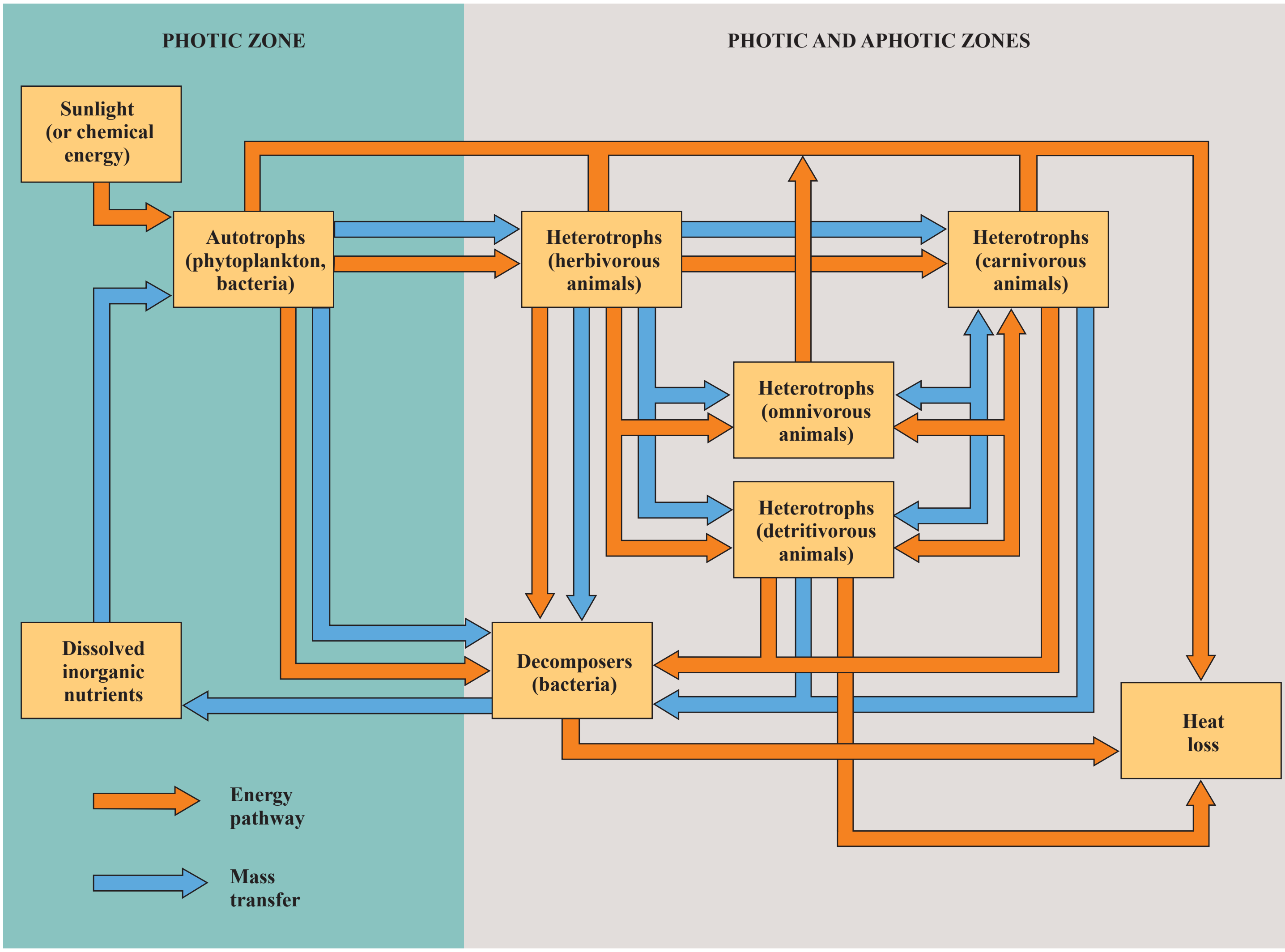


FIGURE 12-2 Simplified model of the energy and mass (organic matter and nutrient element) cycles in a marine ecosystem. Sunlight (or chemical energy) and dissolved nutrients are essential for autotrophs to perform the phototrophic (or chemosynthetic) primary production of organic matter from carbon dioxide. Energy collected and mass produced by autotrophs is cycled through various heterotrophs, followed by decomposers. The mass is transferred back to solution by decomposers, and the energy is eventually released as heat. Primary production of organic matter takes place only in the photic zone (except for limited areas where chemosynthesis occurs). All other steps in the ecosystem take place partly in the photic zone and partly in the aphotic zone.

environments where chemosynthetic fuels are abundant, free oxygen is absent because it has been consumed by respiration or chemical reactions. In the oceans chemosynthesis currently occurs in geographically limited environments where both reducing and oxygenated waters meet and mix, including hydrothermal vents and some seeps. Chemosynthesis also occurs in seafloor or near seafloor anaerobic environments such as **sediment** pore waters and oxygen free dead zones (Chap 13). It also occurs in transitional environments, such as oxygen minimum zones discussed later in this chapter, where dissolved oxygen is not totally depleted but where complex microbial communities include chemosynthetic species.

Chemosynthesis is common near **hydrothermal vents** on **oceanic ridges** and volcanoes, but it also occurs in water released to the oceans by vents or in seeps from ocean **sediment**. Some vents or seeps are in **subduction zones**, where water with dissolved methane and hydrogen sulfide is squeezed out of **subducted** ocean sediment. Others are in certain areas of the **continental shelf** where **groundwater** from the continents migrates through the sediment and accumulates methane or hydrogen sulfide. Chemosynthesis also occurs in the surface sediments of **salt marshes** and swamps, at the interface between oxygenated surface waters and oxygen-deficient bottom waters in **fjords**, and in other ocean areas where oxygen is depleted. Living microorganisms have been found in many extreme environments, including deep within ocean sediments and even within oceanic **crust** that is millions of years old. Many of these organisms are probably chemosynthetic, obtaining their energy needs by chemical reactions such as the combination of hydrogen and carbon dioxide to form methane.

Secondary Production and Decomposers

Nonautotrophic marine organisms are heterotrophic and must obtain food to supply all or part of their needs for organic matter and energy. Heterotrophs convert organic compounds to carbon dioxide and water during respiration, thereby releasing energy that was originally captured from the sun by phototrophy or chemosynthesis. The released energy fuels the metabolic processes of the heterotrophs.

Heterotrophs include all animals and many species of archaea, bacteria and fungi. Animals eat plants, algae, bacteria, archaea, other animals, and organic **detritus** formed by the partial decomposition of dead organisms. Animals that are **herbivores** eat photosynthetic organisms, **carnivores** eat only animals, **omni-**

FIGURE 12-3 Many species of macroalgae have gas enclosures within their structure that enable them to float and stay in the surface waters where there is ample light for photosynthesis. (a) The round ball-like structures in this kelp frond (*Macrocystis sp.*) are gas-filled. (b) Masses of kelp (*Macrocystis sp.*) grow in this cove near Monterey, California. The plants are anchored to the seafloor, but you can see the upper ends of the kelp fronds covering much of the water surface, held up by their gas enclosures.

vores eat both herbivores, carnivores or other omnivores, and **detritivores** eat detritus. The production of animal **biomass** by animals that consume primary producers is called "secondary production."

Heterotrophs use food inefficiently (**CC15**). They **excrete** part of their food as solid waste organic particles, called **fecal pellets**, or as dissolved organic matter in liquid excretions. Humans are no exception to this rule.

Many species of microorganisms, including some bacteria, archaea, and fungi, are heterotrophs but are also called **decomposers**. Decomposers obtain energy from organic particles or dissolved organic compounds, which they convert to carbon dioxide and water. Some species of microorganisms are capable of growing either autotrophically or heterotrophically, depending on their environment.

Phototrophic and chemosynthetic organisms, as well as food-eating and decomposing organisms, function together as a **community** within an ecosystem (**Fig. 12-2**). In an ecosystem, carbon dioxide, water, and nutrients are synthesized to organic matter, which is then processed through herbivores, carnivores, omnivores, detritivores, and decomposers. Each of the organisms in this **food chain** breaks down some organic matter and releases carbon dioxide, water, and nutrient elements back to solution.

Nutrients and other elements are recycled through ecosystems (**Fig. 12-2**). Recycling is an important factor in the distribution and abundance of ocean life. In parts of the oceans, life is limited because nutrients are not recycled fast enough to support photosynthesis.

MICROBES IN CHARGE

At the end of the twentieth century and the beginning of this century, marine science came to recognize that ocean ecosystems were dominated by microscopic organisms in a manner that would also change our perception of what constitutes the true foundation of life on our planet. To understand this, we first need to review just a few of the startling findings that have now revealed the dominance of **microbial** organisms on our planet. First, we have learned that there are about 10^6 bacteria in each milliliter of ocean water (or $5{\bullet}10^6$ per teaspoon) and viruses are about 10 times more abundant. This means that Earth's ocean is estimated to contain 10^{29} bacteria which is a number one hundred million times greater than the total estimated number of stars in the universe (10^{21}). The total mass of bacteria and other single celled organisms in the ocean exceeds the combined mass of all living organisms that are non-microbial by 5-10 times. Note that microbe and microbial are terms to identify those groups of tiny ocean organisms that are less than about 60 µm which is smaller than the approximately 100 µm smallest object that a normal human eye can see clearly. These organisms are so small that they have received relatively little scientific study to date. In practice, the oceans contain a continuum of sizes and this distinction is not a precise one, although most species of the bacteria and archaea domains and viruses all fit into the microbial category.

Microbial organisms perform essential all of the primary production in the oceans, a role played by plants in terrestrial ecosystem and despite microbes small size, total primary production in the oceans is estimated to approximately equal to total primary production on land. One type (a genus) of primary producer a cyanobacteria called *Prochlorocccus* is among the smallest primary producers (about 0.5-0.7 µm) but, despite it small size it is estimated to be responsible for about 5% of the total primary production on Earth. *Prochlorocccus* is able to do this because it is believed it may be the most plentiful genus of species on our planet with an estimated 10^{27} individuals.

If it were not for microbes, no animals, including humans, would ever have lived on the planet. Earth's early atmosphere and oceans had no free oxygen. Microbial photosynthesis is thought to have developed in cyanobacteria and the abundant free oxygen in the atmosphere and oceans that all animals depend on was generated by microbes (cyanobacteria) in the oceans, reaching concentrations in the oceans and atmosphere comparable to the current concentrations about 1 billion years ago.

The facts about ocean microbes listed above demonstrate the dominance of microbial organisms in the oceans. However, the dominance of microbial organisms is probably much greater still because they have the ability to metabolize at rates far exceeding those of larger organisms. This is because the ratio of surface area to volume generally is greater for smaller than for larger organisms. We can visualize why if we consider an apple cut into two halves. The apple's total volume does not change when it is cut,

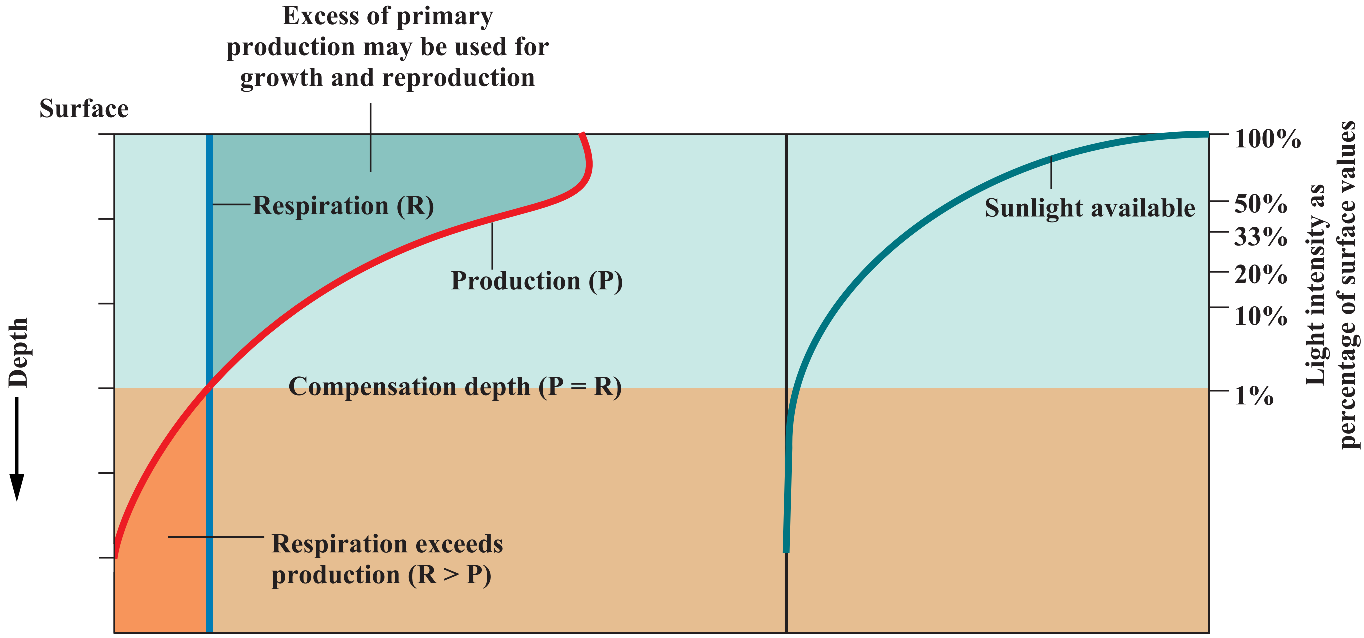


FIGURE 12-4 Photosynthesis depends on the availability of light energy. Therefore, the rate of primary production by phytoplankton decreases with decreasing light intensity and, thus, with depth. The rate of metabolic energy use and, thus, respiration by phytoplankton remains almost constant regardless of depth. The depth at which the rate of phytoplankton primary production equals the rate of phytoplankton respiration is called the "compensation depth." Below this depth, phytoplankton use more organic matter for respiration than they can produce by photosynthesis. The water column above the compensation depth is the photic zone, and everything below this depth is in the aphotic zone.

but the total surface area is increased by the area of the newly exposed interior surface of each apple half. If the apple is cut again, the total volume still remains the same, but the total surface area again increases. All organic and inorganic nutrients, oxygen, and waste products have to pass through the cell surface. Because of its much greater ratio of surface area to volume a microorganism 1 micrometer (one thousandth of a millimeter) in diameter can metabolize about 100,000 times faster than a human. To put this in context, for one oceanic bacterium that divides every 10 minutes (not unusually fast for bacteria if appropriate nutrients are available) the energy throughput of mass of the bacteria equal to a human would have an energy throughput of about 20 megawatts enough to provide power and heat for about 10,000 homes in the United States.

Because they are a large fraction of the total biomass and because they have high metabolic rates when nutrients are available, microbes dominate the movement of energy and biologically important elements in the oceans. Because the microbial community includes primary producers, consumers and decomposers all with fast metabolic rates, most of the total primary production in the oceans is recycled through microbes and only a small faction moves far enough up the food chain to reach non-microscopic eukaryotes. It is estimated that less than 1-2% of the total production is available for non-microscopic eukaryotes.

The rapid rate of division of microbial species also suggests that these microbial species are far more adept at adjusting to changing environmental conditions than larger longer lived organisms. It has been found, through genetic studies of microbes in ocean water, that ocean microbial **biomes** are as small as a single drop of water and that complex ecological and evolutionary processes take place in each such biomes. Thus, although global climate change may cause many species to become extinct, ocean microbes will almost certainly evolve, adapt and survive as they have done for billions of years.

PHOTOTROPIC PRIMARY PRODUCTION AND LIGHT

Seawater absorbs sunlight, so no light at all reaches ocean depths greater than a few hundred meters, even in the clearest open-ocean waters (Chap. 5). In coastal waters with high concentrations of **suspended sediments**, **turbidity** is high and light is more effectively absorbed and **scattered**. Turbidity is generally highest in shallow coastal waters where bottom sediments are **resuspended** by waves and in estuaries fed by rivers with high suspended sediment loads. In such waters, light penetrates a few meters at most, and only centimeters in extreme cases.

Phototrophy, including photosynthesis, cannot take place without light. Light is absorbed by the water, and its intensity is reduced with depth. Light of sufficient intensity to support photosynthesis, usually thought to be about 1% of the intensity at the surface, rarely penetrates more than about 100 m, and photosynthesis is restricted to the water column above this depth. This upper layer is called the **photic zone**.

Terrestrial plants must obtain nutrients from soil or, in some cases, from raindrops. In contrast, marine organisms can extract nutrients from the surrounding seawater. As a result, they do not have to be attached or rooted to the seafloor. Furthermore, attached marine photosynthesizers can receive enough light for photosynthesis only if they are attached to the limited areas of seafloor that are shallower than the depth of the photic zone. Consequently, most marine photosynthetic species live in the water column and are not attached to the seafloor.

Because they need light and therefore must remain near the surface, even where the water is deep, most marine phototrophs must avoid sinking. Pockets of gas or air contained within some species of algae enable them to float. The bubblelike lumps on some seaweeds (Fig. 12-3a) are such pockets. Some species that live attached to the seafloor also use these devices to keep their upper fronds in the light, including the giant **kelp** in California coastal waters (Fig. 12-3b).

Phytoplankton include algae, and those species of bacteria and archaea that are autotrophs (either phototrophic or chemosynthetic). Phytoplankton are the major primary producers in the oceans and are abundant especially in productive ocean waters. Most phytoplankton species are microscopic and drift freely in the photic zone. Due their small size and the relatively high **viscosity** of water (**Chap. 5**), phytoplankton cells sink very slowly (**CC4**), even if their **density** is higher than that of seawater and this helps them to remain in the photic zone. As discussed elsewhere in this chapter, the microscopic size and, therefore large ratio of surface area to volume, of most phytoplankton species also aids them in taking up dissolved substances.

In addition to sinking very slowly due to their small size, **turbulence** due to waves and currents counteracts the tendency of small phytoplankton to sink (**CC4**). Some species of **diatoms**, which are among the largest phytoplankton, store oils that increase their **buoyancy**, and many also have spines or aggregate in chains, which also reduces their tendency to sink. **Dinoflagellates**, another group of phytoplankton species, are able to counteract sinking because they have whiplike **flagella** that provide them with limited motility.

Phototrophy, Light, and Depth

Until near the end of the 20th century, it was thought that almost all ocean life ultimately depends on photosynthetic primary production for food. Other food sources, other phototrophic and chemosynthetic primary production (especially in hydrothermal vent communities) and the dissolved or particulate organic matter supplied by rivers, were previously considered insignificant in comparison. Research in hydrothermal vent areas and studies in estuarine and coastal waters have shown that these sources are probably much more important than previously thought. Because the relative importance of these other sources is not yet well known, we will focus heavily on photosynthetic primary production in this chapter.

Because photosynthesis requires light energy, most of the primary production in the oceans takes place in the upper layer of the water column, down to the depth that sunlight penetrates. Light intensity at any given depth is determined by the intensity of sunlight reaching the sea surface, the **angle of incidence** of the sun's light to the sea surface, and the water turbidity. The intensity of sunlight reaching the sea surface varies with the seasons, throughout the day as the angle of incidence of the sun changes, and as cloud cover varies. Light intensity at a given depth changes continuously. Fortunately, at any given location and depth, the variation of daily mean light intensity within a season is relatively small in comparison with the variation between seasons. Hence, the daily average intensity is a reasonable measure of the amount of light available for photosynthesis at any location and depth.

Light intensity decreases rapidly with depth (**Fig. 5-16**). In the clearest ocean waters, light intensity is reduced to 1% of the surface intensity at a depth of about 100 m. In coastal-ocean waters, the corresponding depth is variable, but it is often about 5 to 10 m. The rate at which photosynthesis can occur is reduced as light intensity decreases (**Fig. 12-4**). In contrast, the rate of respiration remains virtually constant at all depths because the energy needed to fuel the life processes of all species including photosynthetic autotrophs do not change significantly with depth. At relatively shallow depths, the rate of photosynthesis exceeds the rate of respiration, and photosynthetic autotrophs can grow larger and reproduce. At depths where the respiration rate exceeds the photosynthetic rate, autotrophs must metabolize more organic matter than they create by photosynthesis in order to survive. At least some species of photosynthetic autotrophs can survive for a limited time at these depths, but they cannot grow or reproduce. Although many species die if they do not return to conditions in which photosynthesis exceeds respiration, some species are capable of entering a resting phase, much as terrestrial plant seeds do, and can survive prolonged periods below the photic zone. Some microbial photosynthesizers also appear to be capable of switching from autotrophy to heterotrophy when insufficient light energy is available.

The depth at which photosynthesis equals respiration is called the **compensation depth**. The water column between the ocean surface and the compensation depth is the photic zone, and depths below this region constitute the **aphotic zone**. The compensation depth identifies the depth range within which phytoplankton and other photosynthesizers can produce more organic carbon than they consume. The compensation depth lies approximately where light intensity is reduced to 1% of that at the surface. Hence, the photic zone is rarely deeper than 100 m and is much shallower in turbid coastal waters (**Fig. 5-16**). Except in tropical regions, where the day length does not vary much, the compensation depth generally increases during local summer because the angle of incidence of the sun is smaller and the days are longer. However, in some regions where phytoplankton reproduce more rapidly, the additional phytoplankton cells and increased numbers of **zooplankton** that eat them contribute additional "particles" that absorb and scatter light. Consequently, in these regions the **plankton** reduce light penetration and the compensation depth, offsetting the effect of greater light intensity in summer.

Primary Production and the Ozone Hole

Although the rate of photosynthesis usually decreases with increasing depth (**Fig. 12-4**), in many areas it is often lower in water immediately below the surface than at a depth of several meters. One reason for the lower photosynthetic rate near the surface is that high light intensity, especially ultraviolet light, appears to interfere with photosynthesis. Because ultraviolet light is absorbed rapidly in the first few meters of seawater (**Chap. 5**) the maximum photosynthesis often occurs slightly below the surface.

Chapter 7 discussed depletion of the Earth's **ozone layer** by synthetic chemicals that may cause an increase in ultraviolet light intensity at the Earth's surface. Higher ultraviolet light intensity may significantly increase near-surface inhibition of photosynthesis, reduce the total food supply, and adversely affect ocean ecosystems.

PRIMARY PRODUCTION AND NUTRIENTS

Phototrophic organisms require many elements for growth. Carbon, hydrogen, and oxygen are obtained from dissolved carbon dioxide and water. Because carbon dioxide is abundant in seawater (**Chap. 5**), carbon is plentiful in the ocean. Several other elements are required, each in different amounts. Some, such as magnesium and sulfur, are present in high concentrations in seawater. As with carbon dioxide and water, they are always available in plentiful amounts. Other elements, such as nitrogen, phosphorus, iron, zinc, cobalt, and, for some species, silicon, are needed sometimes in substantial quantities but are present in low concentrations in seawater. In some areas, uptake by organisms or by processes such as **adsorption** on **lithogenous** particles can remove enough of these elements from solution that the remain-

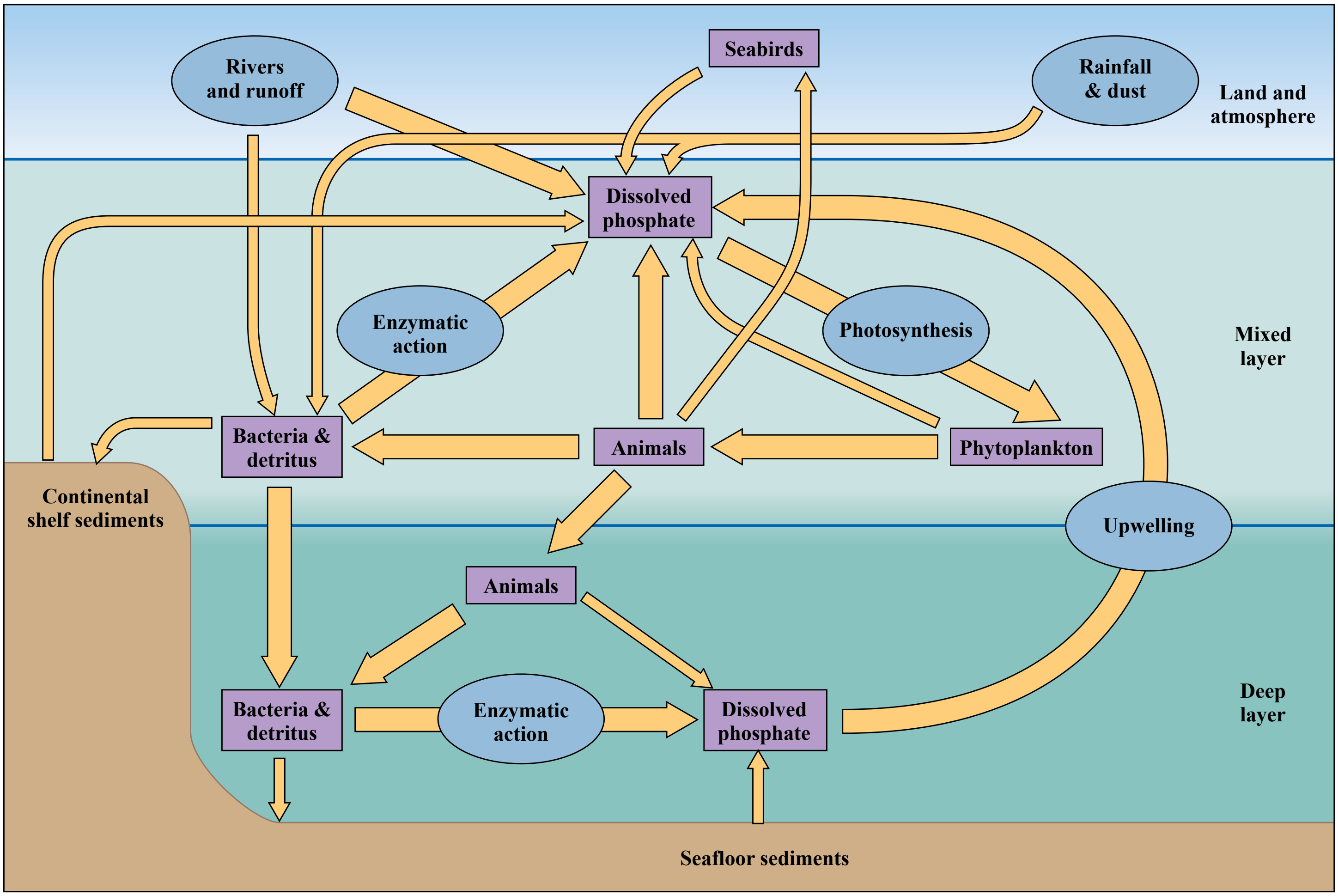


FIGURE 12-5 Simplified representation of the phosphorus cycle in the oceans. The boxes represent compartments (**CC10**) or components of the system among which the phosphorus is distributed. The ovals represent processes that transport or convert the phosphorus between these compartments. Thicker arrows show more important pathways. Phosphorus is recycled rapidly between solution and organisms in the photic zone. Thus, although some phosphorus is progressively transported below the thermocline, the low concentrations present in some ocean surface waters are still usually sufficient to support phytoplankton growth.

ing concentrations are too low to meet the needs of some species of autotrophs. Growth of phytoplankton, marine algae, and other species can be limited by the unavailability of a single essential element. In this condition, the system is said to be **nutrient-limited.**

Where growth is slowed or prevented because the concentration of a particular element is too low, that element is called a **limiting nutrient**. The most important limiting nutrients are nitrogen as dissolved inorganic ions nitrate (NO_3^-), nitrite (NO_2^-), and ammonia (ammonium ion [NH^{4+}] and NH_3); phosphorus (phosphate ion, PO_4^{3-}), iron; and silica (probably present in seawater as silicic acid–H_2SiO_4). When inorganic nitrogen and phosphorus ions are at very low concentrations, phytoplankton will often use organic nitrogen and/or phosphorus compounds. Although other nutrient elements, such as cobalt and zinc, are present only as trace elements, biological requirements for trace elements are so small that these elements generally do not limit phototrophic growth. Some marine species that are otherwise autotrophs may need certain organic compounds that they are unable to synthesize for themselves. In certain circumstances, including some newly **upwelled** water in **coastal upwelling** zones (**Chap. 15**), **primary productivity** may be limited by lack of such organic nutrients.

Nutrient Uptake

Phytoplankton and other autotrophs obtain nutrients from seawater through their outer membrane relying on the random movements of molecules to the nutrient ions to that membrane. At lower nutrient concentrations the nutrient ions are farther apart and the probability that an ion can diffuse to the cell outer membrane is lower. More nutrient ions will be in contact with a cell that has a larger surface area. Hence, autotrophs improve their chances of capturing nutrient ions if they have a large surface area. Because phytoplankton and other autotrophs are composed of similar organic compounds, their nutrient needs are approximately proportional to their volume. Recall that, the ratio of surface area to volume generally is greater for smaller than for larger organisms. Thus, phytoplankton compete more effectively for nutrients at low concentrations if they are small (their surface area is large in relation to their volume). This is one reason that most marine autotrophs are small, particularly where nutrient concentrations are low.

Small size is not the only adaptation that allows phytoplankton to compete for a limited supply of nutrients. When phytoplankton grow in seawater with relatively high nutrient concentrations, they take up more nutrients than are immediately needed. The excess nutrients are stored and can be used as a reserve to support growth and reproduction after nutrients have been depleted to concentrations that would otherwise limit growth. If concentrations remain growth-limiting for more than a few days, even the stored nutrients will be used up and primary productivity will slow. However, phototrophy is not completely halted, because some nutrients are continuously made available by recycling (**Fig. 12-2**).

Nutrient Recycling

Nutrients are recycled to solution when organic matter is decomposed during animal and decomposer respiration. Animals excrete nutrients in fecal material and in dissolved form, either in the equivalent of urine or by **diffusion** losses through external membranes. Bacteria and other decomposers release nutrients as they extract energy from dead organisms, fecal material, and dissolved organic compounds. The four most important limiting nutrients are recycled at different rates: phosphorus is recycled very rapidly, nitrogen more slowly, and iron and silica more slowly yet.

Phosphorus

Phosphorus recycling is relatively simple (**Fig. 12-5**). Phosphate is returned to solution rapidly after the death of any organism by the action of **enzymes** within the organisms that break phosphorus away from organic molecules with which it is combined. Phosphorus is converted directly to phosphate and released to solution. Enzyme-mediated release of phosphate also occurs within living zooplankton and other animals as they digest their food. Certain zooplankton species are known to excrete as much as 60% of the phosphorus taken in with their food. More than half of what remains is disposed in fecal pellets, from which it is rapidly released by continued enzyme activity as the fecal material is attacked by decomposers.

Because it is recycled rapidly, phosphorus is usually not a limiting nutrient in the oceans. In contrast, phosphorus is often the limiting nutrient in lakes. As a result, phosphate-free detergents are required by law in many areas, primarily to prevent **eutrophication** in lakes and rivers.

Nitrogen

Nitrogen, which occurs in living tissue mainly in **amino acids,** is released during the decomposition of organic matter, primarily as the ammonium ion (**Fig. 12-6**). Animals also release nitrogen in their liquid excretions as **soluble** organic compounds, such as urea and uric acid, which are broken down by decomposers to the ammonium ion. Decomposition of particulate organic matter to release ammonium is much slower than processes that release phosphorus. Consequently, nitrogen often becomes the limiting nutrient in the marine environment.

The ammonium ion is used as a source of energy by specialized bacteria and archaea that oxidize ammonium to nitrite. In turn, nitrite is oxidized to nitrate by another group of bacteria. Conversions from ammonium to nitrite and nitrate take place relatively slowly. Nevertheless, in waters below the photic zone this process can be completed, and nitrate is the principal form of

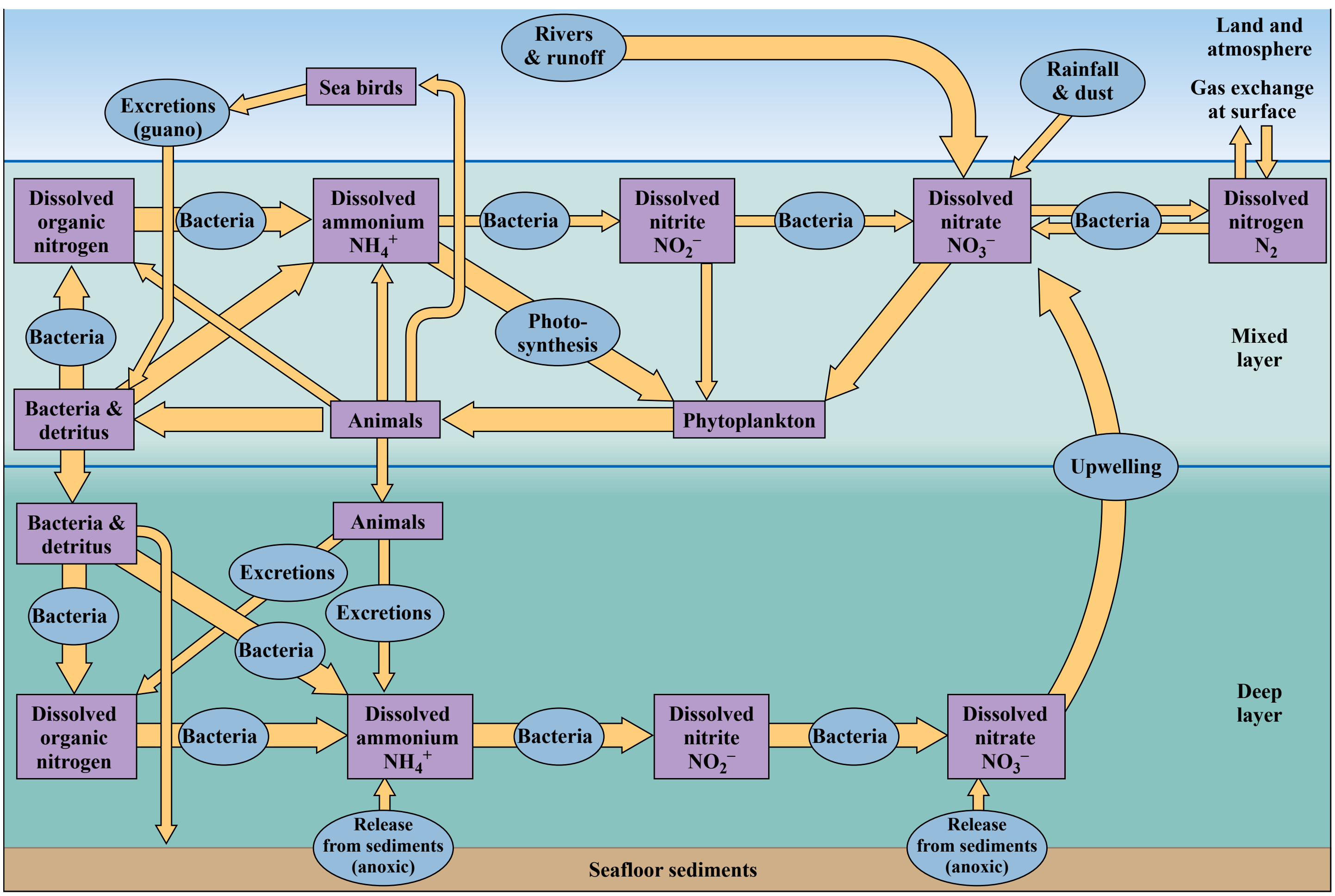


FIGURE 12-6 Simplified representation of the nitrogen cycle in the oceans. The boxes represent compartments (**CC10**) or components of the system among which the nitrogen is distributed. The ovals represent processes that transport the nitrogen or convert its chemical form between these compartments. Thicker arrows show more important pathways. Unlike phosphorus, nitrogen is not recycled rapidly in the photic zone, and it tends to be transported below the thermocline. Thus, nitrogen is often the limiting nutrient. Nitrogen can be recycled from shallow seafloor sediments (as depicted for phosphorus in Figure 12-5), but these pathways have been omitted in this figure to reduce its complexity.

dissolved nitrogen other than molecular nitrogen. Conversion to nitrate may also be completed in temperate **latitudes** during winter, when reduced light availability limits primary productivity. Such seasonal variations are discussed in **Chapter 13**. Because nitrogen may be predominantly ammonium, nitrite, or nitrate ions at different times and locations, primary producers are generally able to utilize nitrogen in each of these forms. Nitrogen and phosphorus are both supplied to the oceans by river flow, **erosion,** and **weathering** from the land, and, in small amounts, in rain and dust (**Figs. 12-5, 12-6**). The **biogeochemical cycle** (**Chap. 5**) is balanced in each case by the removal of equivalent amounts of nitrogen and phosphorus to the ocean sediment in detritus particles. This balance may be seriously disturbed by human activities, particularly through the use of agricultural fertilizers and the discharge of sewage (**Chaps. 13, 16**). The supply to and removal from the oceans of biologically available nitrogen are complicated by the exchange of molecular nitrogen gas between the atmosphere and ocean waters. Molecular nitrogen dissolved in ocean waters is biologically available only to nitrogen-fixing bacteria and archaea that are able to convert molecular nitrogen to nitrate. Other types of bacteria and archaea, called "denitrifying," can convert nitrate to molecular nitrogen. Although nitrogen fixation and denitrification are very limited, nitrogen fixation in particular is thought to be extremely important in some nutrient-poor environments, such as **coral reefs** and the centers of **subtropical gyres.** Phosphorus does not usually become the limiting nutrient because it is readily released from detritus back into solution in the photic zone and, as a result, only a small fraction of the phosphorus remains in the detritus that sinks below the photic zone. However, if the supply of nitrogen through nitrogen fixation is continuous, even if very slow, phosphorus can eventually be depleted and become the limiting nutrient.

Silica

Silicon is essential for the construction of **hard parts** (the shells or skeletons) of a variety of marine organisms, of which diatoms (**Fig. 8.5**) are the most important. Diatoms are larger than many other types of phytoplankton and are covered by an external silica **frustule.**

Because silica is not utilized or released to solution by decomposers, silica hard parts must dissolve chemically in seawater before silicate ions are again biologically available. Silica dissolves very slowly (**Fig. 8.9**). Consequently, once silicate is depleted in the photic zone, silicate limitation inhibits the growth and reproduction of organisms with silica hard parts. Because phytoplankton that do not have silica hard parts are not affected, silicate depletion can lead to a change in the dominant species, but it does not limit primary productivity. Silicate is supplied to the oceans in large quantities by rivers and is slowly dissolved from ocean sediment. Therefore, silicate limitation is generally only a temporary situation that develops in locations where diatoms undergo an explosive population growth called a **bloom.**

Iron

Iron is essential to certain reactions within the process of photosynthesis. Iron is supplied to the surface waters of the oceans from the land, primarily in **runoff,** but also through the transport and **deposition** of airborne dust. Iron is also continuously transported below the photic zone in detritus. As a result, iron can become the limiting nutrient in areas of the oceans where inputs from the continents are too small to replace the iron that is lost from the surface layers by sinking of detritus.

Iron is now thought to be the nutrient that limits primary production in large areas of the open oceans where river and dust inputs of iron are low.

High Nutrient Low Chlorophyll (HNLC) Areas

In approximately one third of the area of the oceans there is always sufficient biologically available nitrogen (and phosphorus) but chlorophyll concentrations are very low. These are known as high nutrient, low-chlorophyll (HNLC) areas. Chlorophyll concentration and primary production are closely related so chlorophyll is a proxy measurement of primary production. HNLC areas, have plentiful nitrogen and phosphorus but low chlorophyll concentrations indicating low primary productivity so some factor other than nitrogen and phosphorus must limit primary production in these regions.

There are at least three different possible reasons for the low primary productivity of HNLC areas.

- In some areas wind mixing can be strong enough to transport phytoplankton to mix the surface waters well below the depth of the photic zone. Phytoplankton cells can then spend too large a percentage of their time without sufficient light for phototrophy. This mechanism appears to be important in limited area and only during strong wind events but it is likely to apply in some areas including parts of the Southern Ocean.
- Phytoplankton biomass is kept extremely low due to very high rates of predation by zooplankton. High rates of predation can reduce the average length of time during which each phytoplankton cell lives and can photosynthesize. There is strong evidence for this mechanism being effective in parts of the subarctic North Pacific Ocean and of the eastern equatorial Pacific Ocean
- Phytoplankton growth is limited by the lack of availability of nutrients other than nitrogen and phosphorus such as iron, or zinc

Although lack of other nutrients such as zinc may be possible in some areas, a lack of available iron is now thought to be the primary mechanisms limiting productivity in most of the world's HNLC areas. Iron is supplied to the oceans primarily from rivers and wind blown dust and it is highly insoluble in oxygenated sea water. HNLC areas are, therefore, in the open ocean far from the continental shelf and river inputs, but in areas that do not receive large inputs of iron containing wind blown dust. These areas include the sub-Arctic Pacific Ocean, large areas of the equatorial Pacific Ocean, and much of the Southern Ocean.

Nutrient Transport and Supply

Substantial quantities of nutrients are supplied to the oceans by rivers, and smaller quantities are supplied in rainfall (and for some elements wind blown dust). In the open ocean remote from river influences, nutrients in the photic zone are depleted rapidly by growing phytoplankton and other autotrophs. Therefore, if primary production is to continue, nutrients must be resupplied. Some nutrients are continuously recycled and resupplied directly to the photic zone by decomposition. However, there must also be nutrient resupply by upwelling from below the photic zone because a proportion of the nutrients taken up by primary producers is released back to solution in waters below this zone.

Nutrients are transported from the photic zone to the aphotic zone by two major mechanisms. Almost all phytoplankton

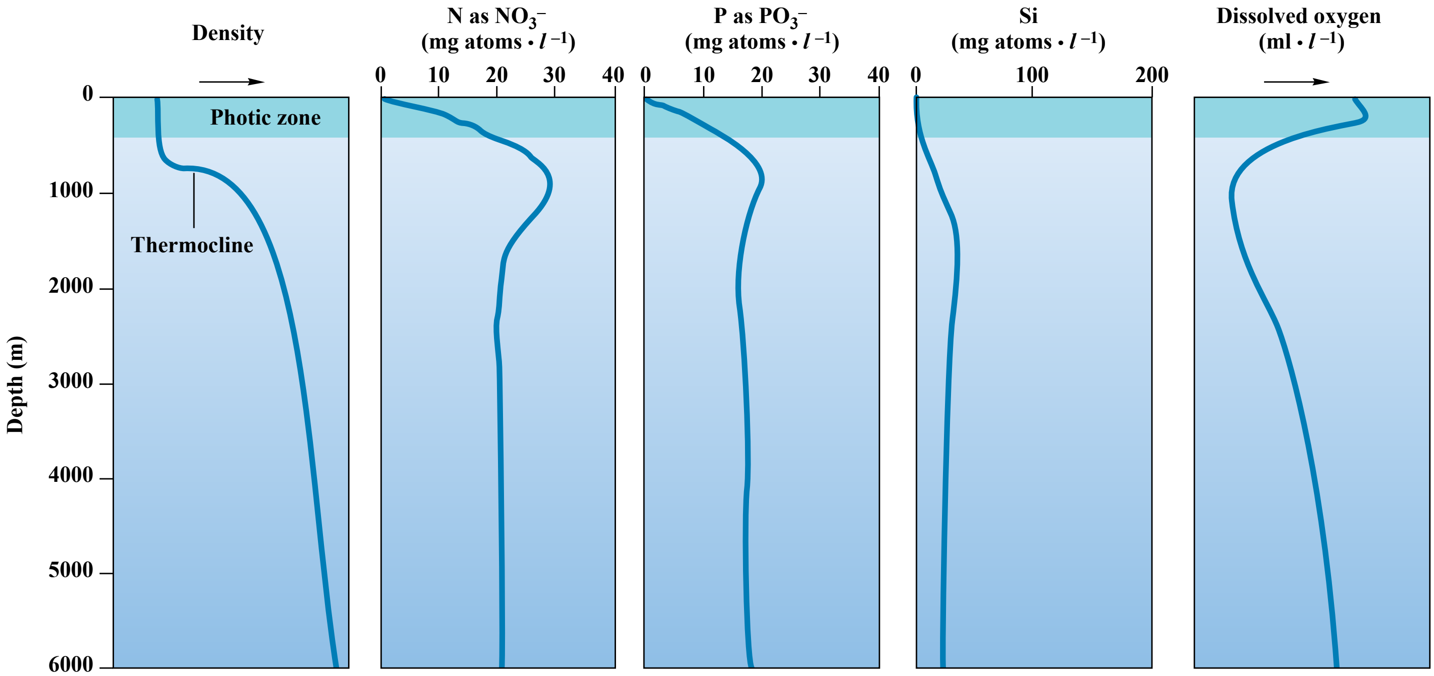


FIGURE 12-7 General representation of the vertical profiles of water density, nitrate, phosphate, silicate, and dissolved oxygen concentrations in the center of the Atlantic Ocean basin. Dissolved oxygen concentration is high above the thermocline, reaches a minimum just under the thermocline, and then increases to somewhat higher levels in the deep water masses formed by cooling of surface water at high latitudes. Nutrients (nitrate, phosphate, silicate) are generally depleted in the photic zone, increase rapidly in concentration until they reach a maximum at about the same depth as the dissolved oxygen minimum, then remain at relatively constant high levels in the deep water masses.

are eaten by **grazers** (herbivores or omnivores). Although these grazers are mainly small zooplankton, most are much larger than phytoplankton. Much of these animals' undigested waste material is excreted as fecal pellets. Fecal pellets from even the smallest zooplankton are packages of partially digested remains of numerous phytoplankton cells. Consequently, fecal pellets are larger than phytoplankton and sink much faster (CC4). As they sink, fecal pellets provide food for other heterotrophs, bacteria and fungi and are progressively decomposed with some or all of the nutrient elements being released to solution. Much of the decomposition and release of nutrients occurs below the photic zone, including on the ocean floor.

The second major mechanism of nutrient removal from the photic zone is the vertical migration of zooplankton and other animals. Phytoplankton generally remain in the photic zone unless carried out of it by turbulence or **downwelling.** However,

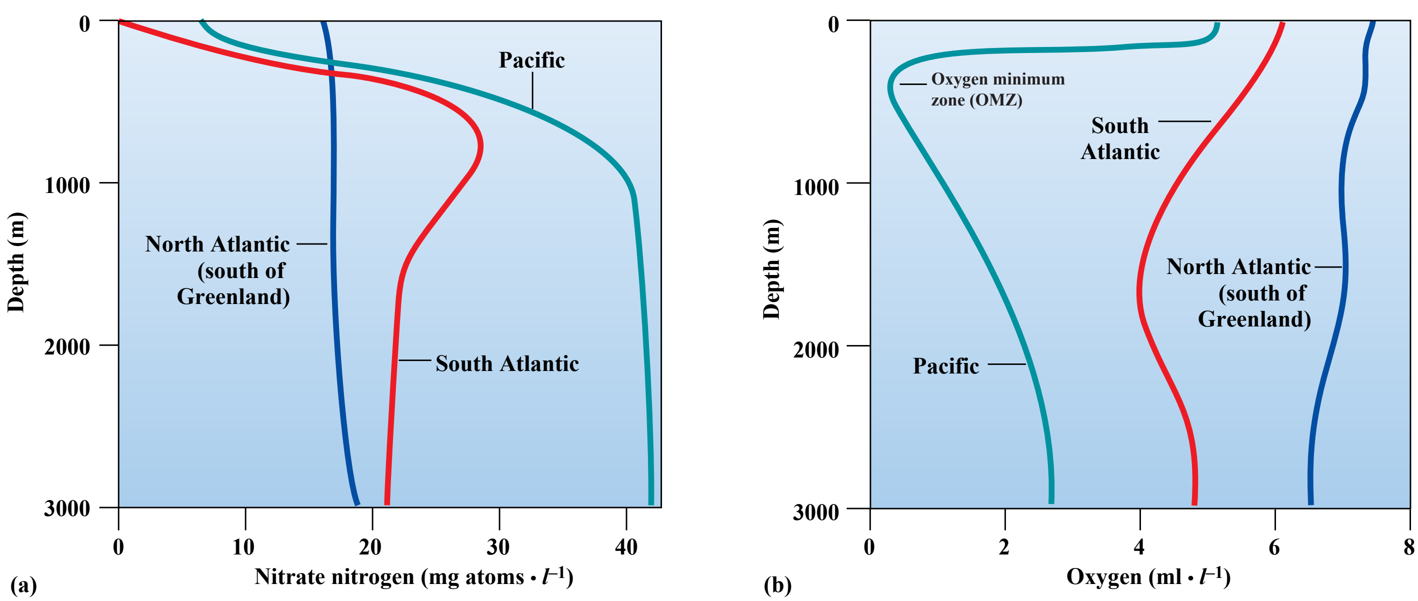


FIGURE 12-8 The vertical profiles of nitrate nitrogen and dissolved oxygen in the North Atlantic (south of Greenland), South Atlantic, and North Pacific Oceans are very different. In the North Atlantic, where cooled surface water is sinking to form North Atlantic Deep Water (NADW), the concentrations vary little with depth. During its passage southward to the South Atlantic, this water mass loses oxygen and gains dissolved nitrate as respiration by animals and decomposers uses oxygen and releases dissolved nitrate. This process continues as the water mass moves around Antarctica and northward into the deep water of the Pacific Ocean. Thus, the ratio of nitrate concentration to oxygen concentration is an indication of the "age" of the water mass since it left the surface layer. Higher ratios indicate "older" water. The "oldest" water has too little oxygen for animal life to survive in and areas with this low level of oxygen are call oxygen minimum zones (OMZs).

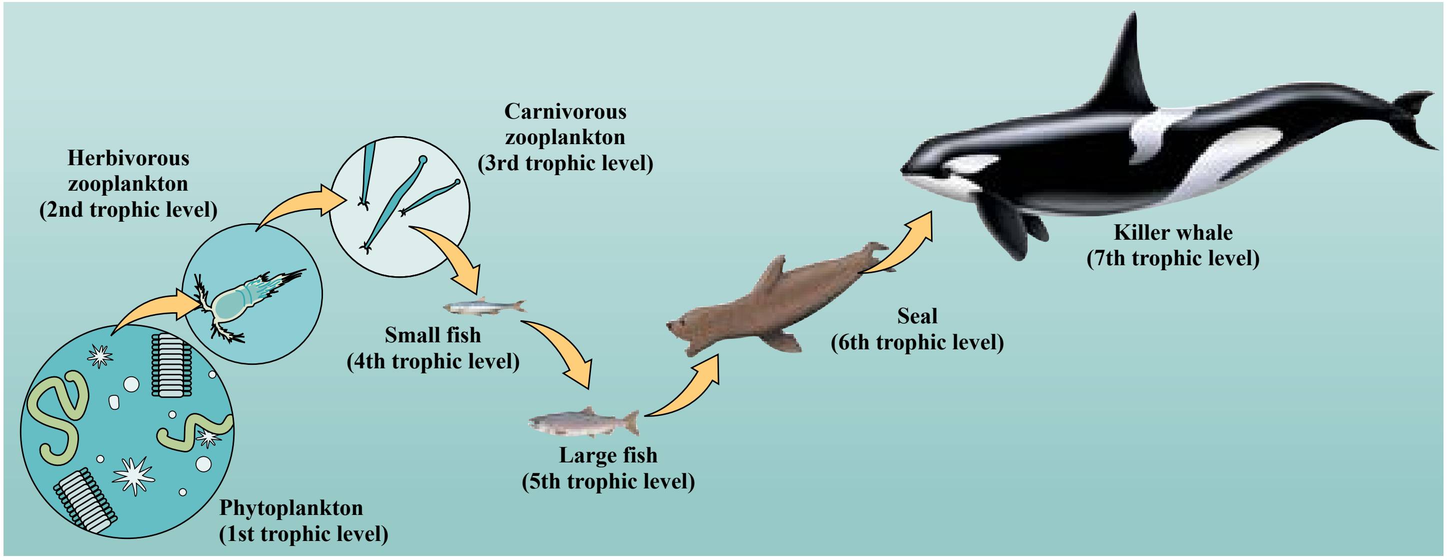


FIGURE 12-9 A simple food chain. Phytoplankton are eaten by herbivorous zooplankton, which are eaten by carnivorous zooplankton, which are eaten by small fishes, which are eaten by large fishes, which are eaten by seals, which are eaten by killer whales. Each step in this chain is one trophic level higher.

many species of zooplankton and other animals migrate vertically between the photic and aphotic zones each day, rising into the photic zone at night to feed, and then sinking or swimming down to waters below the photic zone during the day. This **diurnal** migration is probably a defensive mechanism that prevents many potential predators from feeding on the zooplankton when it is light enough to see them easily. Zooplankton and other animals that practice diurnal migration continue to digest food and excrete fecal pellets and liquid wastes during the day when they are below the photic zone. Consequently, much of the organic matter that they consume is transported below the photic zone, where it is released, with its nutrients, to the decomposer community.

Vertical Distribution of Nutrients

The photic zone is usually less than 100 m deep in the open oceans and normally restricted to water above the permanent **thermocline** (Chap. 8). Phytoplankton and nutrients are distributed throughout the **mixed layer** above the thermocline by turbulent motions of wind and wave mixing (Chap. 8). Where light is sufficient to support primary production in the open oceans away from terrestrial sources of supply, nutrients are continuously transported below the thermocline by the mechanisms already described. Below the thermocline, these nutrients are released by decomposers, but the water into which they are released does not mix with the mixed-layer or photic-zone water above, because

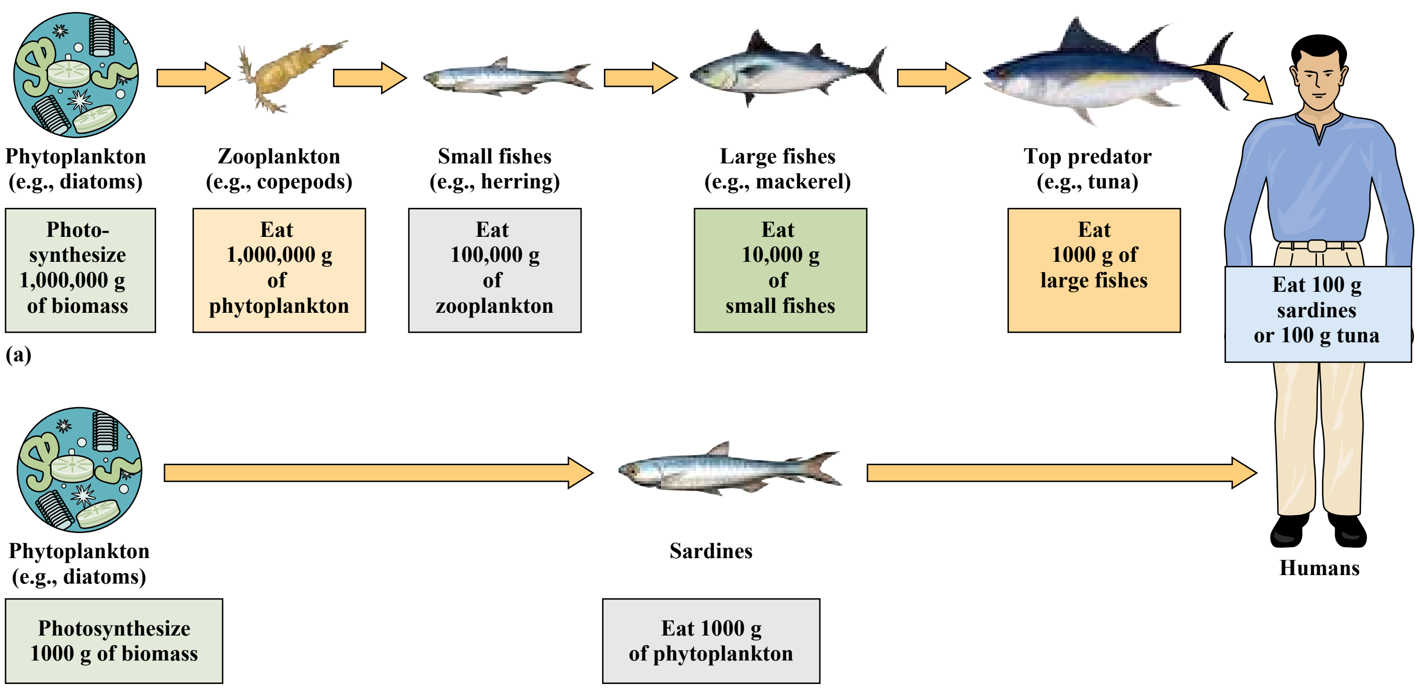


FIGURE 12-10 The food chains leading to (a) tuna and humans, and (b) sardines and humans, assuming that the trophic efficiency at each trophic level is 10%. Phytoplankton must photosynthesize 1 kg of organic matter to feed the human 100 g of sardines, but must photosynthesize 1000 kg (1 tonne) of organic matter to feed the human 100 g of tuna. However, because sardine species feed on both phytoplankton and zooplankton, their overall trophic efficiency is somewhat less than depicted. In addition, some tuna feed on both small and large fishes, so their overall trophic efficiency is somewhat better than depicted.

vertical mixing is inhibited by the density difference across the thermocline. Consequently, the mixed layer becomes nutrient-depleted, while deeper water becomes more nutrient-rich (**Fig. 12-7**).

Organic matter is decomposed continuously at all depths in the oceans, although the rate of decomposition varies with depth. Hence, water that leaves the surface to form deep **water masses** progressively accumulates recycled dissolved nutrients. Nutrient concentrations are usually highest in water immediately below the thermocline layer. The primary reason for this nutrient maximum is that this is the "oldest" deep water because it is formed by slow upward mixing of bottom waters that were formed near the poles (**Chap. 8**). The effect of water-mass "age" in determining nutrient concentrations is illustrated by the nutrient concentration differences between the deep waters of the Atlantic Ocean and the much older deep waters of the Pacific Ocean (**Fig. 12-8**).

Several additional factors cause concentrations of nutrients to be higher in waters just below the bottom of the thermocline than in bottom waters. First, bacterial decomposition processes are slowed at the low temperatures and high pressures near the deep-ocean floor. Second, the most easily oxidizable organic matter is decomposed long before it reaches the ocean floor. Third, animals that migrate vertically generally do not descend far below the permanent thermocline. However, these influences on the vertical distribution of nutrients, even taken together, are less important than the age of the water and the length of time during which recycled dissolved nutrients have accumulated in it.

The permanent thermocline is a persistent and widely distributed feature. Primary productivity above the thermocline is nutrient-limited except in areas where nutrients are transported into the mixed-layer waters by inputs from the continents or by upwelling of nutrient-rich water from below the thermocline. Major zones of high primary productivity and highly productive fisheries are found in coastal upwelling regions, off the mouths of rivers (which discharge nutrients), and in shallow areas where nutrients in sediments are returned to solution by decomposition and then released directly into the photic zone.

FOOD WEBS

Heterotrophic species from the smallest microbe to the largest whale depend on autotrophs to produce organic matter for food. Herbivores eat primary producers directly, whereas carnivores eat herbivores and other carnivores.

In the simplified food chain in **Figure 12-9**, photosynthetic organisms are eaten by herbivorous zooplankton, which are eaten by carnivores, which are eaten by larger carnivores, and so on. Each step in this food chain is a **trophic level**. As organisms at one trophic level are consumed by those at the next-higher trophic level, the ingested food biomass is not used entirely to create biomass of the consumer species at the higher trophic level. An average of only about 10% (varying from 1% to 40%) of food consumed at each level is used for growth. The remaining 90% is used during respiration to provide the consumer with energy or is excreted as waste. Clearly, the transfer of food energy in food chains is inefficient (**CC15**).

The consequences of food chain inefficiency are illustrated by the food chains in **Figure 12-10**. A good-sized tuna sandwich may contain about 100 g of tuna. For each 100 g of tuna produced, a tuna must eat about 1000 g of a large fish (e.g., mackerel). In turn, mackerel must eat 10 times their weight of smaller fishes (e.g., **herrings**), herrings must eat 10 times their weight of zooplankton (e.g., copepods), and copepods must eat 10 times their weight of phytoplankton (e.g., diatoms). The next time you eat a tuna sandwich, remember that phytoplankton synthesized about 1 million g (1 metric ton, or tonne) of phytoplankton biomass to produce your 100 g of tuna. In contrast, 100 g of sardines represent only 10 kg of primary production (**Fig. 12-10b**). We use ocean food resources 100 times more efficiently when we eat sardines instead of tuna.

Marine animals usually eat organisms that are not much smaller than themselves. Therefore, most large marine animals are high-trophic-level predators at the top of long food chains. **Baleen** whales are spectacular exceptions. The blue whale, the largest known ocean animal, can be 30 m long and weigh more than 100 tonnes. This magnificent creature eats only shrimplike **crustaceans** called **krill**, each of which is only a few centimeters long. Thus, blue whales are at the same trophic level as herrings (**Figs. 12-10a, 12-11**).

Food relationships in the ocean are far more complex than the simplified food chains depicted in **Figure 12-10** because they almost always include opportunistic carnivores that eat animals from several different trophic levels. The killer whale in the Antarctic marine ecosystem is a good example (**Fig. 12-11**). Complex food relationships, such as that shown in **Figure 12-11**, are called **food webs**. Food webs are further complicated by omnivorous species that will eat almost any living organism and sometimes even detritus. Detritus feeders eat particulate organic matter produced as waste products and/or dead tissues of organisms of all trophic levels. Certain detritus-based food webs are somewhat independent of phytoplankton-based food webs, although they depend ultimately on primary producers to synthesize organic matter that becomes their detrital food.

There are also microbial food loops. By some estimates, about one-half of the primary production in the oceans is performed by microscopically small phototrophic eukaryotes and bacteria. The microbial loop also uses dissolved and particulate organic matter. Heterotrophic bacteria and archaea can absorb this material and utilize it to grow. These organisms may then be consumed by **protozoa** and by other organisms that are themselves consumed by organisms in the higher levels of the food chain. Free-living heterotrophic bacteria in the water column help to recycle elements lost from the food web back into the food web through the microbial loop, or by releasing them as they consume organic matter for energy and growth.

GEOGRAPHIC VARIATION IN PRIMARY PRODUCTION

All marine animals ultimately depend for food on phototophic or chemosynthetic primary producers, which are mostly phytoplankton. Consequently, zooplankton, fishes, and other **pelagic** animals are most abundant in areas of high primary productivity. Most **benthos** rely on the rain of detritus from above. Exceptions are some species that live in limited areas where the seafloor is shallower than the photic-zone depth and in hydrothermal vent and other chemosynthetic communities. The quantity of detritus depends on the abundance of organisms in the overlying water, so **benthic** communities are also more abundant in areas of high primary productivity.

Phytoplankton biomass (**standing stock**) is determined by phytoplankton growth and reproduction rate versus consumption rate. If the productivity is high and the rate of grazing of

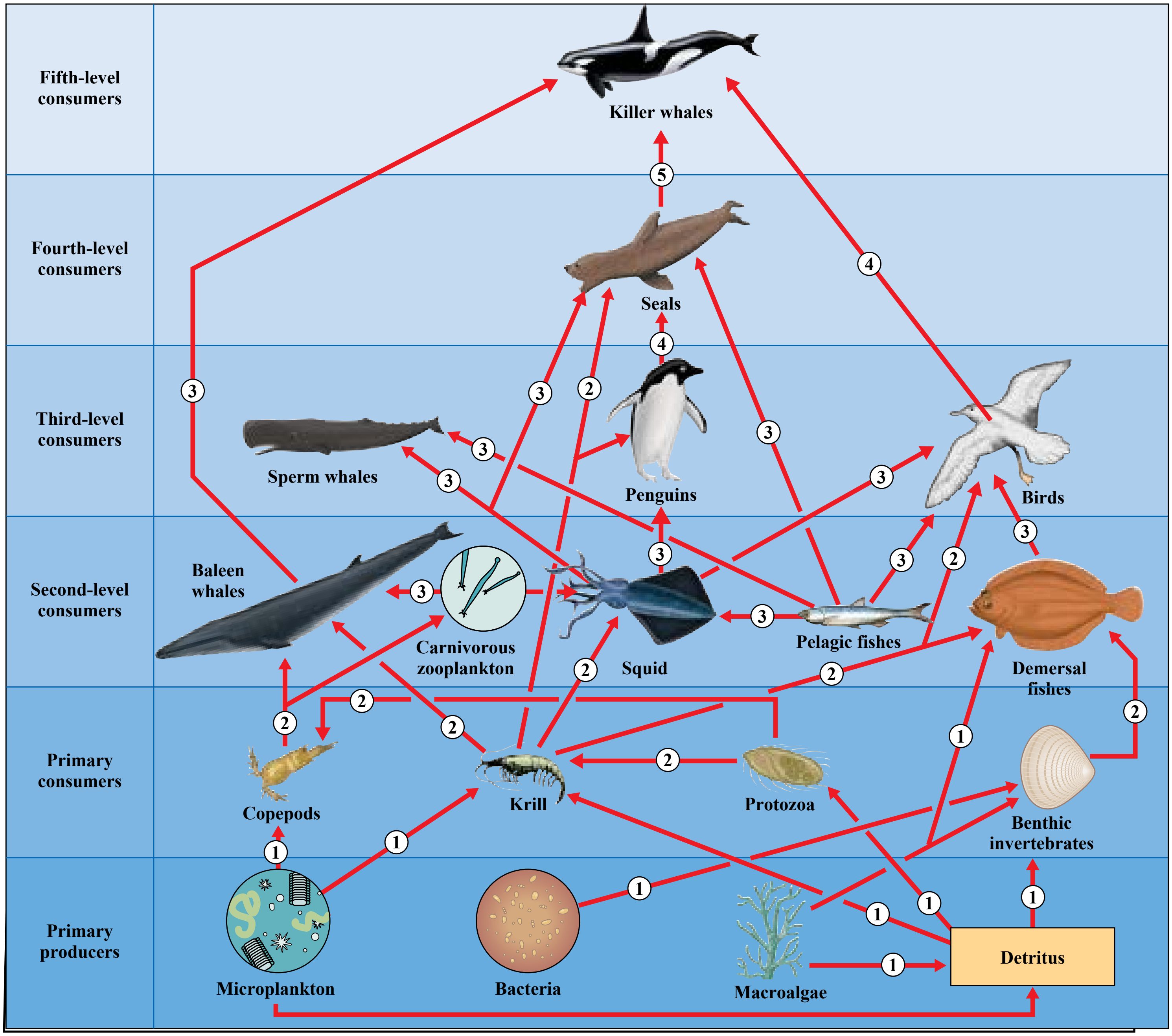


FIGURE 12-11 Simplified representation of the pelagic food web of the Southern Ocean. The number beside each arrow represents the trophic level at which the consuming organism is feeding. Note that many species feed at more than one level. For simplicity in this diagram, a number of pathways have been left out. For example, pelagic fishes feed on various prey including phytoplankton, zooplankton, and krill.

phytoplankton by zooplankton is low, phytoplankton biomass increases, and vice versa.

Zooplankton populations and biomass adjust to changes in food supply, but the changes lag days or weeks behind changes in phytoplankton biomass. As a result, phytoplankton biomass initially increases when phytoplankton productivity increases, but it may fall when zooplankton biomass increases, even if there is no change in phytoplankton productivity. Thus, phytoplankton biomass does not vary in concert with phytoplankton productivity. Fortunately, averaged over several months, phytoplankton biomass is reasonably related to the average primary productivity. **Figure 12-12** shows the seasonal variation in the distribution of chlorophyll (**CC14**) in ocean surface waters measured by satellites. The concentration of chlorophyll is a good indicator of the abundance or biomass of phytoplankton and also provides a reasonable approximation of the distribution of primary productivity.

The most productive parts of the ocean are coastal regions (**Fig. 12-12**), particularly along the western margins of continents, where coastal upwelling brings nutrients from deep waters into the photic zone (**Chap. 13**). Most of the open ocean has low productivity, the exceptions being certain high-latitude regions and the equatorial upwelling band across the eastern Pacific and, to a lesser degree, across other oceans (**Fig. 12-12**).

Throughout most of the tropical and subtropical open oceans, a permanent thermocline begins at a depth of about 100 to 200 m. Light intensity is relatively high, and the photic zone extends throughout most or all of the mixed layer above the thermocline. Nutrients are depleted in the photic zone, and the steep thermocline inhibits vertical mixing that would be necessary to resupply nutrients from the nutrient-rich water below the thermocline.

High productivity in tropical and subtropical open oceans is limited to areas of upwelling. The band of high productivity across the equator, particularly in the eastern Pacific, coincides with upwelling at the tropical **convergence** along the equator (**Fig. 10.2**). During **El Niño,** primary productivity is dramatically reduced in this region because upwelling is inhibited (**Chaps. 9, 10**; **Fig. 9.18**).

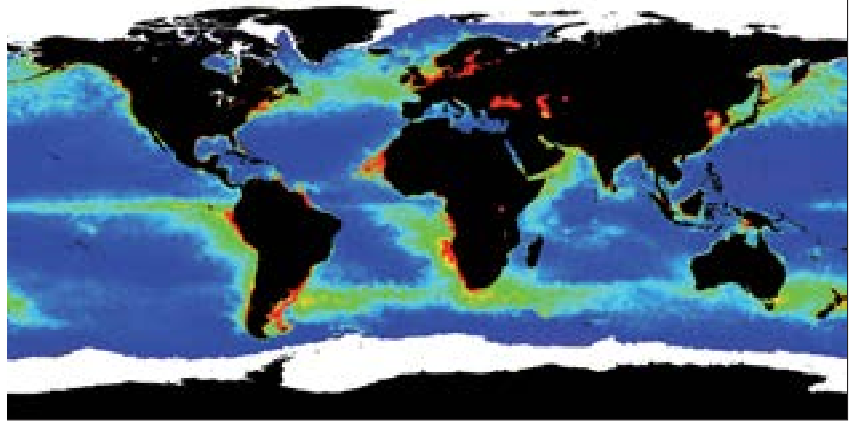
Upwelling at the Antarctic Divergence (**Fig. 10.2**) is responsible for high productivity in the ocean around Antarctica. The Northern Hemisphere has no comparable **divergence**, primarily because of the presence of continents. At high latitudes in the North Atlantic and North Pacific Oceans, productivity is seasonally high because cooling of surface waters, strong **westerly** winds, and **extratropical cyclones** effectively mix surface and subsurface waters during winter, when light levels are low. Nutrients supplied by winter mixing support high productivity when light intensity increases in spring.

Productivity is lowest in the interior of subtropical gyres in each ocean. These regions are remote from nutrient inputs in runoff, have low rainfall (which can carry small amounts of nutrients), and are characterized by downwelling and deep thermoclines (**Fig. 10.14**). Light is plentiful, but lack of nutrients limits phytoplankton growth. Ocean waters are a brilliant blue in these regions because of the lack of suspended particles. However, areas of the Sargasso Sea (the interior of the North Atlantic subtropical gyre) are covered by vast rafts of *Sargassum* seaweed, despite the lack of nutrients (**Chap. 15**).

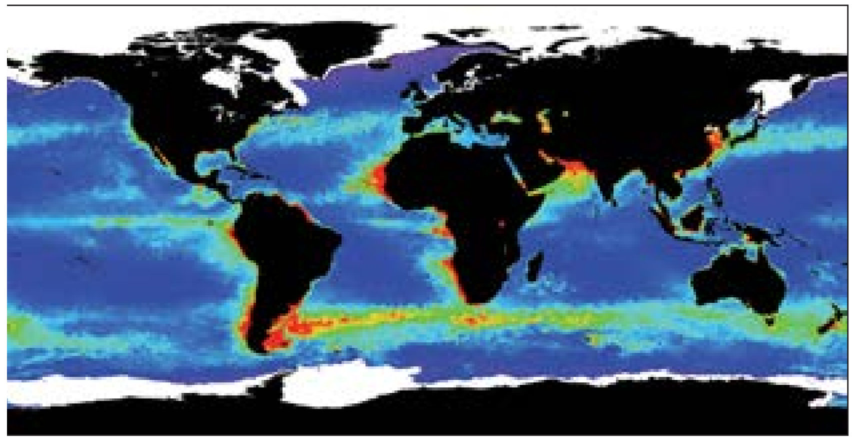
DISSOLVED OXYGEN AND CARBON DIOXIDE

Oxygen is released to solution during photosynthesis and consumed during respiration. The distribution of dissolved oxygen is controlled by these processes and by exchanges between atmosphere and ocean.

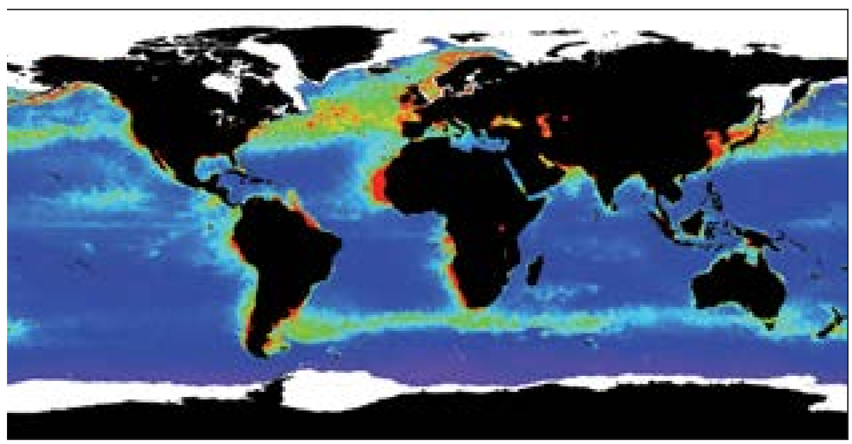
Oxygen is exchanged continuously between atmosphere and ocean. Hence, dissolved oxygen concentrations in the upper few meters of ocean water almost always equal the **saturation solubility** for the water temperature (**Fig. 5-6**). However, oxygen is produced by photosynthesis much faster than it is consumed by respiration in this layer, particularly when primary productivity is intense. As a result, oxygen concentration increases and the water becomes **supersaturated.** The depth and concentration of the oxygen maximum in the photic zone depend on the depth of maximum pri-



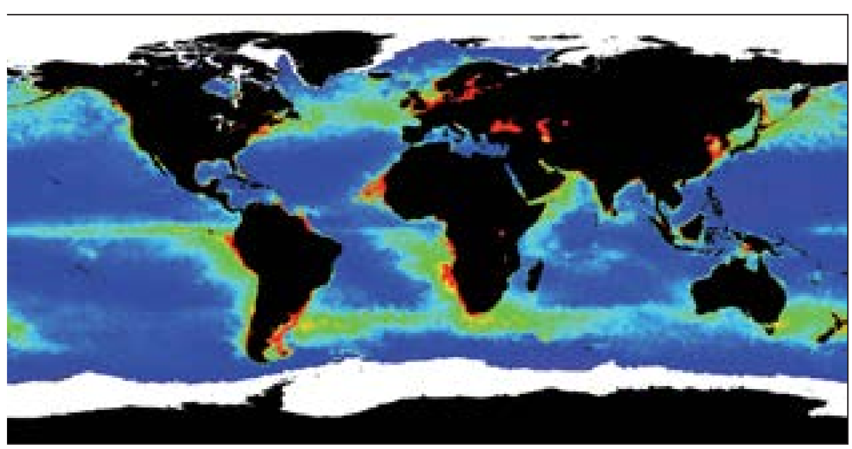
(a) September–November 1998



(b) December 1998–February 1999



(c) March–May 1999



(d) June–August 1999

FIGURE 12-12 Seasonal variations in the distribution of chlorophyll in the surface waters of the world oceans. Chlorophyll concentration is a reasonable measure of primary production. The data were obtained by a satellite sensor that measures ocean surface color within several wavelength bands. Red indicates the highest chlorophyll concentrations. White indicates areas where there were no data, because of cloud or ice cover or the limited orbital coverage of the satellite near the poles. (a) Northern fall. (b) Northern winter. (c) Northern spring. (d) Northern summer. Note the high productivity of many coastal regions and of the high-latitude seas in the Northern Hemisphere.

mary productivity and the depth and intensity of wind mixing that brings water to the surface, where excess oxygen can be released to the atmosphere. By many estimates, marine photosynthesizers contribute more oxygen to our atmosphere than land plants.

As they release oxygen to ocean waters and atmosphere, phytoplankton also remove dissolved carbon dioxide. Carbon dioxide is highly soluble in seawater as it reacts to form carbonate and bicarbonate ions (**Chap. 5**). The carbon dioxide concentration in seawater is so high that its removal by photosynthesis does not produce a marked minimum concentration of carbon dioxide at the oxygen maximum. Nevertheless, much of the carbon dioxide that primary producers remove from ocean waters is carried down into the deep ocean, where it is removed from contact with the atmosphere for hundreds of years.

It has been estimated that almost half of all carbon dioxide released to the atmosphere by human activity since the Industrial Revolution has entered the oceans. Substantial research is now focused on identifying the fate of this carbon dioxide. Predictions of future **climate** change depend on the rate at which carbon dioxide is transported into the deep ocean. Global climate models are limited by a lack of understanding of this rate and of various other critical ocean processes. For example, we do not know whether and to what degree increased carbon dioxide concentrations might increase ocean primary productivity, or how much of the additional organic matter that might be produced by such an increase would be transported below the thermocline. Proposals have been made to lessen or avoid global climate changes due to the increasing carbon dioxide concentrations in the atmosphere by injecting some of the carbon dioxide into the deep. The effectiveness of placing more carbon dioxide in the deep oceans would depend on the mode and location of introduction and would need to ensure that the carbon dioxide was stored in sediments or rocks as, otherwise ocean circulation would simple return the carbon dioxide to the atmosphere. The likely effectiveness and possible adverse side effects of implementing such carbon dioxide storage in the deep oceans cannot be properly assessed, given the present state of knowledge of the biogeochemical cycles of the oceans.

Organic matter transported below the thermocline as detritus or through animal migration is decomposed, releasing nutrients and carbon dioxide. At the same time, the processes that decompose this organic matter consume dissolved oxygen. The continuous decomposition of organic matter progressively reduces the dissolved oxygen concentration of deep water. An oxygen concentration minimum below the bottom of the thermocline coincides with the nutrient maximum (**Fig. 12-7**).

At present, oxygen is fully depleted only in limited areas of the oceans, mainly where the **residence time** of subthermocline water is extremely long and/or where mixed-layer primary productivity is exceptionally high. Such conditions are present, for example, in the Baltic Sea, where water residence time is long and primary productivity high because of large **anthropogenic** nutrient inputs. Oxygen depletion also occurs in many fjords, where water residence time is very long. Once dissolved oxygen has been completely depleted, the water is **anoxic.** Most marine species cannot survive in anoxic water. However, certain bacteria and archaea in anoxic water can obtain energy by reducing molecules that contain oxygen. First, bacteria that reduce nitrate (NO_3^-) to ammonium (NH_4^+) thrive, and then, when all nitrogen compounds are reduced, they are replaced by other species that reduce sulfate (SO_4^{2-}) to sulfide (S^{2-}). Sulfide is highly toxic and can be released from anoxic bottom waters into the overlying photic zone if vertical mixing is temporarily enhanced. In some cases, water containing hydrogen sulfide reaches the surface, and its foul smell is released to the atmosphere. Anoxic conditions are becoming more common and widespread in some coastal-ocean regions and estuaries because of inputs of nutrients from sewage and agricultural chemicals. In addition, there is a large area of the North Pacific Ocean where there is strong oxygen minimum zone below the **pycnocline**. Similar strong oxygen minimum zones have also been observed in the Atlantic Ocean off the coast of Southern Africa (Angola and Namibia) and in the Indian Ocean off both coasts of India (Arabian Sea and Bay of Bengal).

There is evidence that the North Pacific oxygen minimum zone is expanding and deepening. Oxygen depleted water from this water mass now seasonally moves onto the Oregon continental shelf in most years to form a dead zone (**Chap. 13**). Expansion of the oxygen minimum zone in the North Pacific could be related to a slowdown of the ocean conveyor belt circulation (**Chap 8**) since this would increase the age of this water mass and, therefore the length of time during which oxygen was consumed by respiration and decomposition. Alternatively, the expansion could be related to an increase in overall ocean primary productivity that would increase the rate of transport of oxidizable organic matter below the thermocline. Both a slowdown of the ocean conveyor belt circulation and an increase in primary production are effects of anthropogenic carbon dioxide and nutrient releases that are predicted by some of the mathematical climate models.

It should also be noted that one proposed approach to mitigation of climate change is that we should fertilize the oceans (primarily with iron in areas where it is the limiting nutrient) so that some of our released carbon dioxide would be transported into the deep oceans as organic detritus. If this were to be done successfully one of the undesirable side effects would be deoxygenation. The oxygen minimum zone would almost certainly deepen and expand further, perhaps eventually causing mass extinctions of ocean species as has occurred in the past when oxygen has become depleted in the deep oceans. In any event, ocean fertilization is a temporary solution at best. The deep oceans would only be a temporary storage location for our excess carbon dioxide since the excess carbon dioxide would be released back to the atmosphere within the next few generations as the deep water was mixed back to the surface.

Anoxic conditions have been more widespread in the oceans in the past. During anoxia, detritus that falls into the anoxic layer is no longer subject to decomposition by **aerobic** respiration, because there is no oxygen. Also, animals and other species that require dissolved oxygen can no longer live in the deep oceans. In such circumstances, organic matter can accumulate in large quantities in sediments. Oil and gas deposits are probably the result of **diagenetic** changes to such sediments over the millennia.

ORGANIC CARBON

Most organic matter in the oceans is nonliving and exists as both dissolved compounds and particulate matter (detritus). The reason most organic matter is nonliving is that organic matter created by phytoplankton and other marine algae undergoes a series of transfers between organisms, and conversions among physical and chemical forms, before finally being converted back to dissolved inorganic constituents by decomposers.

Under normal conditions, about 10% of the organic carbon that phytoplankton create by photosynthesis is excreted to seawater as dissolved substances. When phytoplankton are stressed by low nutrient or low light levels, nonoptimal temperatures, or other unfavorable factors, they may excrete 50% or more of the organic matter they create by photosynthesis. Although most phytoplankton are eaten before they die, those that are not eaten excrete substantial amounts of dissolved and particulate organic material as they reach the end of the life cycle. In addition, dissolved and particulate organic matter are released when phytoplankton cells are ruptured by **viruses** and during inefficient feeding by herbivores.

The distinction between dissolved and particulate matter is arbitrary. Oceanographers usually consider compounds to be dissolved if they pass through a filter with a pore size of 0.5 μm (human hair is about 100 μm in diameter), although filters used to separate dissolved and organic matter often have pore sizes somewhat larger or smaller than this value. Material that collects on such a filter is called "particulate." Much of the "dissolved" material that passes through a 0.5-μm filter is not truly dissolved, because it consists of **colloidal**-sized (**CC4**) inorganic or organic particles in addition to living organisms (such as microbacteria and archaea) and viruses. Nevertheless, the distinction between dissolved and particulate is useful. "Particles" less than 0.5 μm in diameter are believed to be too small to be eaten by most species in food chains that lead to higher animals, such as fishes.

Both particulate and dissolved organic matter are produced continuously wherever organisms are present in the oceans. Most organic matter is released in the photic zone, where marine organisms are concentrated. Many organic particles, such as fecal pellets and phytoplankton or zooplankton fragments, are relatively large (ranging from about 1 μm to more than 1 mm in diameter) and sink relatively fast (**Chap. 6**, **CC4**).

Marine bacteria, archaea and fungi utilize organic particles and dissolved organic matter that is present throughout the ocean depths. These decomposers rapidly break down the more easily oxidized organic compounds in solution and in detritus. As particles are decomposed, smaller particles and more dissolved organic matter are released. Decomposition continues until all organic matter is converted to carbon dioxide and water, which may take many years or even centuries. There are three reasons for the long-term persistence of some dissolved and particulate organic matter. First, many organic compounds are extremely resistant to oxidation. Second, the rate of bacterial decomposition is very slow in the cold temperatures and high pressures of the deep oceans. Finally, dissolved organic molecules and microbial decomposers are so small and well dispersed in seawater that encounters between particles and decomposer are rare events.

The mass of dissolved and particulate matter in the oceans far exceeds the mass of living organisms because dissolved and particulate organic matter is produced continuously but much of it is decomposed only very slowly. In the photic zone, dissolved and particulate nonliving organic matter usually makes up 95% or more of the total organic carbon. An unknown proportion of the "dissolved" organic matter is, in fact, living microbes (including microbacteria and archaea) and viruses. Although the number of these microorganisms is extremely large, they are very small and their total biomass is thought usually to be only a small fraction of the nonliving organic matter. The declines in total mass of carbon from phytoplankton to zooplankton and from zooplankton to fishes reflect the low efficiency of food transfer between trophic levels (**CC15**).

Relatively little is known about the composition of dissolved or particulate organic matter. These materials are extremely difficult to study because they consist of hundreds of thousands or millions of chemical compounds, each present in extremely small concentrations.

The concentration of particulate organic carbon is generally higher in the upper layers of the oceans than in deep waters. Within the surface layer, the concentration is lowest in areas where phytoplankton productivity is high. This seemingly paradoxical situation is created by the abundant populations of zooplankton and other **filter-feeding** organisms that thrive in productive waters because of the continuously abundant food supply. Particulate organic matter concentrations are high in deep waters below such productive areas because large numbers of fecal particles fall from the abundant filter-feeding organisms.

Organic particles generally account for about one-quarter of the suspended particles in ocean waters. In most areas, the majority of suspended particles are fragments of algae and animal hard parts with lesser amounts of lithogenous particles (**Chap. 6**).

BIOLOGICAL PROVINCES AND ZONES

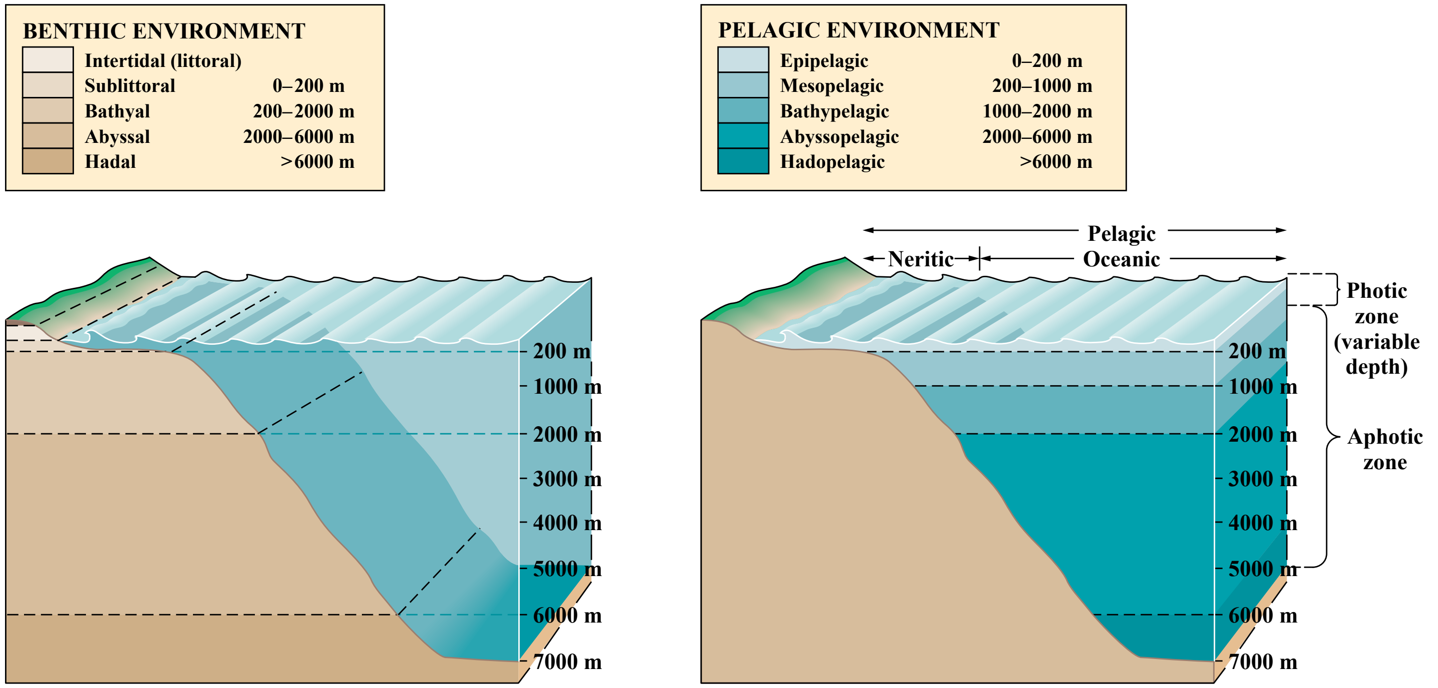
The communities of organisms in different parts of the oceans are as distinct and different from one another as the species that live in tropical rainforests, deserts, and Arctic tundra. The oceans are separated into distinct biological zones delineated by the availability of light, nutrients, and food, and by the temperature and **salinity** characteristics of the water.

Differences between communities that live in or on the seafloor and those that inhabit the water column are so great that the two locations are considered to be separate environments. The seafloor is the benthic environment, and the water column is the pelagic environment. In contrast to pelagic organisms, benthic organisms do not have to swim or control their density and/or size to avoid sinking, which can be energetically advantageous, but they must compete with each other much more intensely for living space and food. Although the pelagic and benthic environments support different communities, many species live part of the life cycle in one environment, then change form (in some species as dramatically as the **metamorphosis** of caterpillars into butterflies) and live in the other.

Benthic Environment

The benthic environment is separated into zones by depth. The deepest zone, the **hadal zone** (**Fig. 12-13a**), which occupies less than 1% of the ocean floor, is limited to the seafloor of deep-ocean **trenches** at depths greater than 6000 m. The seafloor between 2000 and 6000 m is the **abyssal zone,** and corresponds roughly to the **abyssal plains.** The hadal and abyssal zones are generally covered with soft, fine-grained muds. Much of these zones is below the **carbonate compensation depth** (**CCD; Chap. 6**), and the surface muds generally contain little or no calcium carbonate.

Sediment characteristics are important to the species composition of the benthos. For example, some polychaete worms feed by passing sediment through the gut to digest microbes and organic matter in the sediment, just as earthworms do. Such polychaetes are more successful in soft, fine-grained muds than in coarse-grained sediment, particularly if the muds contain a significant amount of detritus. Where sediments are coarse-grained with little organic matter, many benthic animals live on the sediment



(a) Benthic zones **(b) Pelagic zones**

FIGURE 12-13 The oceans are separated into zones. The assemblage of species in each zone is different from that found in the other zones. (a) The benthic environment is separated into a number of zones, each of which spans a different depth range. (b) The pelagic environment (water column) is separated into a neritic province (water over the continental shelf) and an oceanic province. The oceanic province is divided into several zones that each span a different depth range

surface and obtain food from particles or other animals in the water column. Benthic animals are called **infauna** if they live much or all their life in sediments, and **epifauna** if they live on or attached to the seafloor.

The seafloor environment between 2000 m and the approximate depth of the continental **shelf break** (about 200 m) is the **bathyal zone** (**Fig. 12-13a**). Because sediments in the bathyal zone are more variable than those in the abyssal and hadal zones, the benthos is more variable in composition in the bathyal zone.

The hadal and abyssal zones and almost all of the bathyal zone are below the photic zone, so no photosynthetic organisms are present in the benthos. Instead, benthos in these zones are dependent on food transported to them from the overlying photic zone, primarily as detritus. All benthic communities in these zones thus belong to the detrital food web, with some exceptions. One is the unusual benthic communities around hydrothermal vents. These organisms are supported by a chemosynthesis-based food web (**Chap. 15**). A second exception occurs in locations where methane and other hydrocarbons are abundant, and methane based chemosynthesis occurs, generally at seeps of oil and gas (most of which are natural seeps). A third, and minor, exception occurs in the shallowest parts of the bathyal zone in areas of the clearest waters, where light levels are very low but sufficient to support limited photosynthesis by species adapted to very low light levels. Such conditions are generally present only on some **seamounts** far from land.

The benthic environment between the continental shelf break (200 m depth) and the land is divided into three major zones. The **sublittoral zone** (subtidal zone) is the continental shelf floor that is permanently covered by water. It extends from the **low-tide line** to the depth of the continental shelf break (200 m). The **intertidal zone** (**littoral zone**) is the region between the low-tide line and the **high-tide line** and is covered with water during only a part of each tidal cycle. The **supralittoral zone,** often called the "splash zone," is the region above the high-tide line that is covered by water only when large storm waves or **tsunamis** reach the **coast** or during extremely high **tides** or **storm surges.**

Organisms that live in the supralittoral and intertidal zones must endure much more extreme conditions than other marine organisms. Such conditions include exposure to the temperature extremes of the atmosphere, loss of body fluids by evaporation while exposed to the atmosphere, salinity variations due to rainfall, predation by both marine and terrestrial species, and mechanical shock and turbulence created by breaking waves. In intertidal zones with sand or mud sediments, most organisms bury themselves to avoid extreme conditions. This is why **beaches** and mudflats appear to be unpopulated. Most sediment-covered **shores** support an abundance of infauna living a few centimeters beneath the sediment surface. Organisms that live in **rocky intertidal zones** adapt to their changeable environment in other ways (**Chap. 17**).

Pelagic Environment

The pelagic environment consists of the neritic province and the oceanic province. The neritic province is the water column between the sea surface and seafloor in water depths to about 200 m. Thus, it consists of the water overlying the continental shelf and shallow banks (**Fig. 12-13b**). The neritic province experiences greater variability in salinity, temperature, and suspended sediment concentrations than the oceanic province (**Chap. 13**). Further, the mixed layer reaches the seafloor in most of the neritic zone, at least for part of the year, which is important to nutrient cycles (**Chap. 13**).

The oceanic province comprises the entire water column of the open oceans beyond the continental shelf. It consists of several zones, each of which is a water layer distinct from the layer above or below because of differences in salinity, temperature, and light intensity. The **epipelagic zone** extends between the surface and 200 m, the approximate depth where light intensity becomes too low for photosynthesis. Note that this depth is not the same as the shallower (usually less than 100 m) compensation depth, where photosynthesis occurs just rapidly enough to match respiration (**Fig. 12-4**). The epipelagic zone is the only zone in the deep oceans in which food can be produced directly by phototrophy. In all deeper zones, the original source of food is primarily detritus falling from the epipelagic zone. Minor additional food sources include vertically migrating animals and chemosynthesis, especially at hydrothermal vents (**Chap. 15**).

Below the epipelagic zone, between 200 and 1000 m is the mesopelagic zone (**Fig. 12-13b**). Although light intensity is too low to support phototrophy, many organisms in this zone have photoreceptors or eyes adapted to detect very low light levels (**Chap. 15**). Some of these species migrate upward into the epipelagic zone at night to feed and return to the mesopelagic zone during the day. Below the mesopelagic zone are the bathypelagic zone (1000–2000 m), the abyssopelagic zone (2000–6000 m), and the hadopelagic zone (>6000 m). These are zones of perpetual darkness, high pressure, and low temperature, and their inhabitants feed on detritus or on each other (**Chap. 15**). The boundary between the bathypelagic and abyssopelagic zones is essentially the boundary between relatively young bottom water masses of the ocean basins and older overlying deep water masses (**Chap. 8**). The hadopelagic zone is restricted to the deep trenches, in which water movements are generally very slow and water residence time is long (**CC8**).

Latitudinal Zones

Most benthic and pelagic environments below the photic zone are relatively uniform at a given depth. Latitudinal variations in temperature and salinity are less in waters or sediment below the photic zone than in the epipelagic zone and in the pelagic and benthic environments of the continental shelf. Most marine organisms are adapted to live successfully within a narrow range of environmental conditions, particularly a narrow range of temperatures.

Variations in water temperature with latitude (**Figs. 9.13, 9.23**) act as effective barriers to latitudinal dispersal of many marine species. Hence, the marine **biota** of each biological zone varies with latitude (although the variation is small in the abyssal benthos and the abyssopelagic zone). For example, coral reefs are present in warm-water areas in all oceans, but not at cold, high latitudes. The **fauna** and **flora** of the Arctic and Antarctic regions are also very different. Polar bears and most penguin species live only at high latitudes, but polar bears live only in the Arctic region, and most penguin species live only in the Antarctic.

In some cases, continents act as geographic barriers to the distribution of marine species. The tropical Atlantic Ocean is effectively separated from the tropical Pacific and Indian Oceans by the continents. To move between the Atlantic Ocean and either the Pacific Ocean or the Indian Ocean, marine organisms would have to pass around the southern tip of Africa or South America or through the Arctic Ocean. Many tropical species could not tolerate the low water temperatures they would encounter in such journeys. Therefore, almost all tropical Atlantic species are different from those in the tropical Pacific and Indian Oceans. In contrast, the tropical Pacific and Indian Oceans (the Indo-Pacific) have many species in common because they are connected at tropical latitudes.

Tropical Atlantic and Indo-Pacific species, although different, are more closely related than Arctic and Antarctic species. The reason is that the continents have drifted to their present positions in the latter stages of the present **spreading cycle** (**Chap. 4**). Previously, all the oceans were connected at tropical latitudes, and tropical species could move freely around the globe during this relatively recent period in evolutionary history.

PLANKTON

The term *plankton* includes all marine organisms and viruses that do not swim or are very weak swimmers and that do not live on or attached to the seafloor (**Fig. 12-14**). Plankton generally do not settle to the seafloor, and they have very limited or no control of their horizontal movements, so they drift with the ocean currents. Phytoplankton are the phototrophic autotrophs that produce more than 99% of the food used by marine animals. Zooplankton are planktonic herbivores, carnivores, or omnivores.

Plankton are often categorized by size. The largest, which are almost exclusively zooplankton, are the macroplankton (>2 mm). Most plankton are microplankton (20 μm–2 mm), nannoplankton (5–20 μm), or ultraplankton (2–5 μm), and these size ranges are dominated by phytoplankton. The smallest plankton are picoplankton (0.2–2 μm), thought to be predominantly bacteria and archaea, and femtoplankton (<0.2 μm), thought to be primarily viruses. Because even the finest mesh nets used by biologists are too coarse to collect the smaller species, they have not been well studied. Less is known about nannoplankton than about microplankton and macroplankton, and very little is known about the even smaller plankton or their **ecological** importance. For this reason, in the following sections we discuss what is known about the microbial part of the food web that consists of bacteria, archaea and viruses in the nannoplankton size range or smaller and then describe those groups of phytoplankton and zooplankton that are better studied. Most species among these better studied plankton groups are larger than nannoplankton and fall into the macroplankton or microplankton size range. However, it is important to remember that the distinction we make between the very small, less well understood plankton and the larger better-known plankton is a necessity driven by the relative

FIGURE 12-14 A typical plankton sample (photographed at 3× magnification) contains many species of both phytoplankton and zooplankton. This image shows mostly zooplankton.

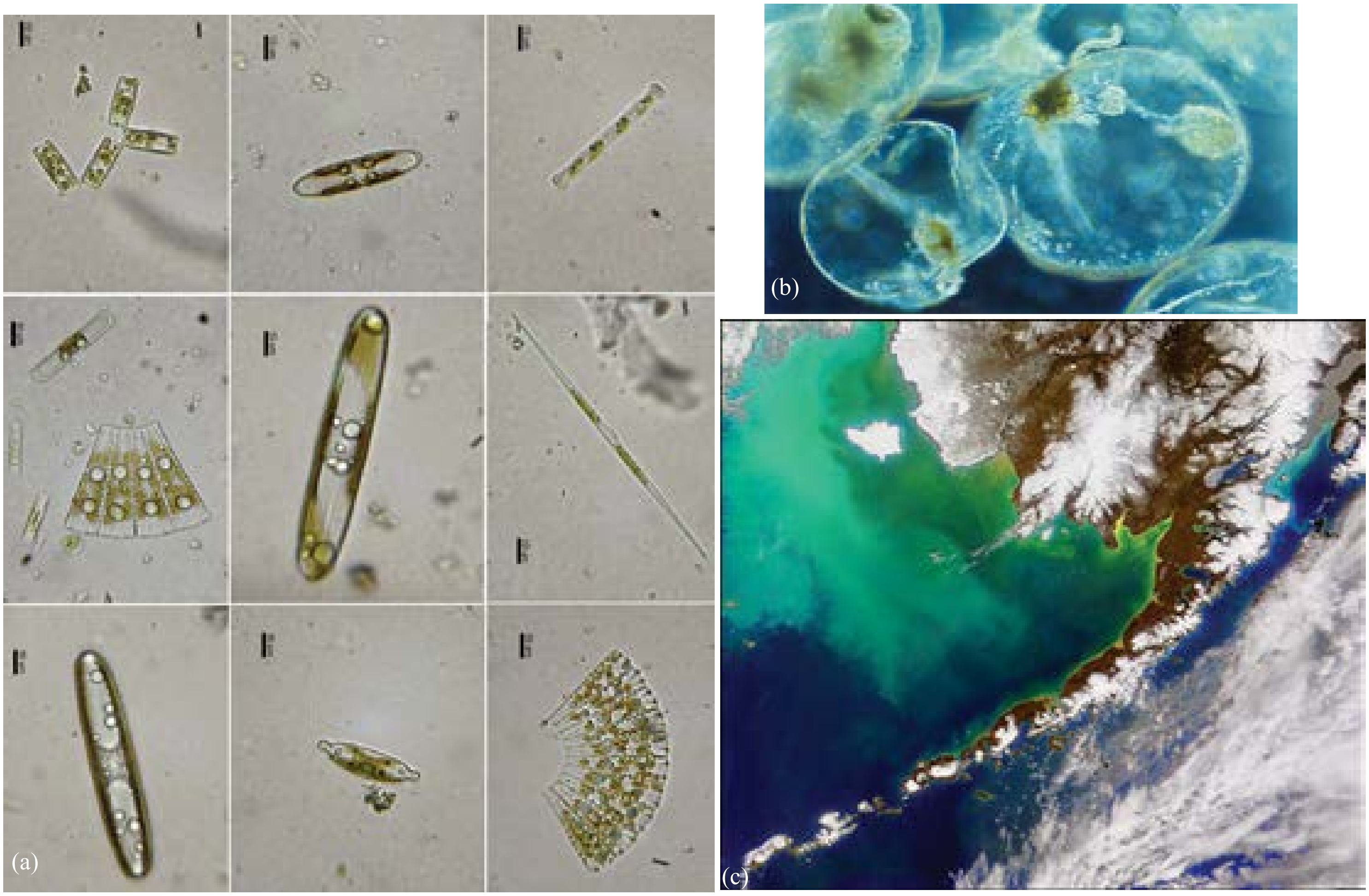


FIGURE 12-15 There are many varieties and species of phytoplankton (a) Various species of diatoms - approximately 20x magnification. (b) Bioluminescent dinoflagellates (*Noctiluca scintillans*, each individual is about 200-2000 micrometers across. (c) a bloom of coccolithophores seen from space. Since each individual coccolithophore is only about 40 micrometers across (about 100 times too small to see with the naked eye) there must be an almost unimaginable number of individuals that make up this bloom..

lack of knowledge of the very small plankton. There are autotrophic and heterotrophic plankton in all size ranges and they act together in an ocean ecosystem that is dominated in most areas by microbial communities that are nannoplankton or smaller. As our knowledge of these microbes improves it is certain that a new organizational structure will develop to replace the long-standing but now incorrect view of an ocean food chain starting at large phytoplankton plus a microbial food chain that operates mostly independently and contributes little to the animal biomass in the oceans.

The better-known large marine plants and **macroalgae,** including kelp, seaweeds, and **sea grasses,** constitute only a tiny fraction of the photosynthetic species in the oceans and so are not described in this text. Macroalgae normally grow attached to the seafloor and are found on the beach only when they have been broken loose by storm waves or animals.

Bacteria and Archaea

The majority of plankton biomass is now known to be outnumbered by plankton species so tiny that they escaped detection until the 1990s. These poorly studied, microbial plankton are dominated by species of bacteria and archaea. Viruses are also included in this group although viruses are not considered by many to be living organisms. Extremely sophisticated techniques are needed to isolate and identify bacteria and especially archaea and viruses, but they exist in vast numbers in all ocean water. As stated above, concentrations of bacteria in ocean water average around 1 million per milliliter. Archaea and virus concentrations of millions per milliliter are also believe to be not unusual.

One group of photosynthetic bacteria, *Prochlorococcus,* absorbs blue light efficiently at low light intensities, so it can grow throughout the depth of the photic zone. *Prochlorococcus* may be the most abundant component of the phytoplankton, especially in the tropical and subtropical oceans, and it is estimated to contribute 30% to 80% of the total photosynthesis in areas of the oceans where nutrients are scarce and in HNLC areas. Until recently it was thought that archaea existed primarily in extreme environments, but it is now known that archaeal species are found throughout the ocean environment and that some are phototrophic primary producers

We are only just beginning to study the microbial populations of the oceans and the role that they play in life on our planet. However, what we do know is that these microbes are responsible for regenerating dissolved nutrients and metals previously removed from solution by living organisms. Thus, without microbes, the ocean productivity and the entire ocean food web would quickly stop entirely.

Although there are millions of microbes in each milliliter of seawater, which might suggest that ocean water is a thick biological soup, in reality microbes are so small that their environment is 99.99999% water or dissolved ions. As a result, from the microbe's perspective life consists being separated from its neighbors by, what to it are long distances (hundreds of body lengths), and of waiting around for an occasional encounter with an organic particle or an occasional plume of nutrient from the waste liquids of larger organisms. In response to this, microbial bacteria and archaea have developed the ability to slow their metabolism, sometimes even essentially stop their metabolism and form a resting phase until they encounter food or the chemical energy source they need to grow and divide. Microbes have also developed abilities to rapidly adapt to changing opportunities and environments. They do so by transferring genes among themselves. Although this particular mechanism has not been fully demonstrated yet, the concept can be illustrated by the example that a species adapted to live in deep water might be able to pick up the gene for photosynthesis if it is transported into the upper layers where there is light. Interestingly much of this gene transfer may take place through virus-like gene-containing fragments of the host species chromosome. We do not know what all of the roles are that viruses play in ocean ecosystems. Mounting evidence suggests that they cause diseases in marine organisms spanning the entire range from the smallest bacteria to the largest whales but likely they also have a major role in gene transfer and adaptation in bacteria and archaea and even in animals and plants and they are now thought to have been the ultimate ancestors of all other life .

The discovery of the abundance and central role of bacteria and archaea, together with the discovery that viruses are even more abundant throughout the oceans and perform essential roles in microbial effects on biogeochemical cycles and likely also in evolutionary processes, has revolutionized ocean sciences. Extensive research efforts are currently directed toward gathering a better understanding of these organisms and viruses and details of their role in ocean ecosystems. A billion or more years ago, the microbial food web in the oceans became a self sustaining community of organisms, likely even before photosynthesis developed. The non-microbial world, including all eukaryotes, are late comers on the planet and are completely dependent on the microbes.

Phytoplankton

There are only three known planktonic species of macroalgae, all of the genus *Sargassum*. *Sargassum* grows in dense rafts, often many square kilometers in area, floating at the surface of the Sargasso Sea (**Chap. 15**).

Phytoplankton are generally much smaller than 1 mm in diameter—mostly too small to be seen clearly by the naked eye. The oceans contain an abundance of phytoplankton dispersed throughout the surface waters at concentrations that may exceed 1 billion individuals per liter. There are tens of thousands of species of phytoplankton. A sampled phytoplankton assemblage always consists of many species, but in any individual sample one species is often dominant and far outnumbers all others (as pine trees do in a pine forest).

Phytoplankton communities consist of different species in different climatic regions, and concentrations range from very low in some areas (equivalent to deserts) to very high in others (equivalent to rain forests). Unlike most land plant communities, phytoplankton communities can vary dramatically in composition and concentration within hours or days. Such variability occurs in part because phytoplankton are often concentrated in patches (tens to hundreds of meters across) that drift with ocean currents. Patches of phytoplankton can develop when rapid reproduction exceeds the rate of dispersal by mixing processes. Because phytoplankton can double their population within a day, or in even less time under favorable conditions, patches may develop quickly in calm seas. Phytoplankton are also concentrated by **Langmuir circulation** (**Chap. 8**). Smaller or less dense cells tend to concentrate at the surface convergence between Langmuir cells. Larger or higher-density cells, which tend to sink, may be concentrated below the surface where subsurface Langmuir cell currents converge (beneath surface divergences). Phytoplankton can also be concentrated within mesoscale eddies.

Individual phytoplankton species respond favorably to slightly different light intensity levels, temperatures, and nutrient concentrations. Under favorable conditions, one or more species can reproduce rapidly and become the dominant species. If conditions change and another phytoplankton species prospers in the changed conditions, the second species can become dominant within a few days because grazing zooplankton can rapidly remove the previously dominant species.

Diatoms

Diatoms (**Fig. 12-15a**) are among the most abundant types of phytoplankton in many of the more productive areas of the oceans. They are relatively large single cells (up to about 1 mm in diameter) with a hard, organically coated external **siliceous** casing called a "frustule," which is made of two halves much like a pillbox. The frustule is porous, allowing dissolved substances to diffuse through it and to be taken into or excreted from the cell. Because silica is denser than seawater, most diatoms contain a tiny droplet of a lighter-than-water natural oil to reduce their density and thus their sinking rate. Many diatoms have protruding, threadlike appendages and may link to form chains (**Fig. 12-15a**). These adaptations also reduce the cell's tendency to sink and may decrease predation by small zooplankton. The threadlike appendages also increase the surface area over which nutrients can be taken up and light collected for photosynthesis.

Their oil droplet and relatively large size make diatoms a favored food source for many species of juvenile fishes and zooplankton. Consequently, food chains based on diatoms are generally shorter than those based on smaller classes of phytoplankton. Smaller phytoplankton must usually be eaten by small

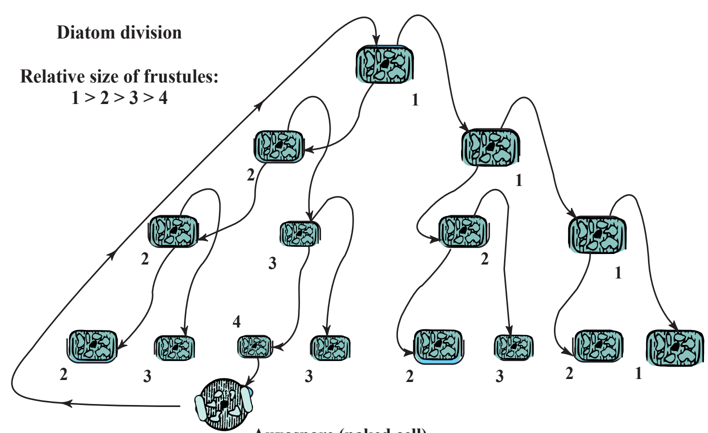


FIGURE 12-16 Most diatoms reproduce primarily by cell division. At each division, the two halves of the diatom frustule separate, and each half secretes a new half to its frustule. However, because one of the new halves is smaller than its parents, the mean size of the diatom is reduced with progressive divisions. Eventually, a small diatom reproduces sexually by producing an auxospore that at first has no frustule. After some period of growth, the auxospore secretes a new frustule.

zooplankton before they can provide food for juvenile fishes and larger herbivorous and omnivorous zooplankton.

Diatoms reproduce asexually by cell division. At each division, which may follow the previous one by less than a day, the frustule separates, with one-half taken by each of the two new cells, and each cell then manufactures a new half. Consequently, one of the new cells is smaller than its parent (**Fig. 12-16**). After several such divisions, the now much smaller cells may reproduce sexually, restoring the cell size to its maximum.

Dinoflagellates

Dinoflagellates range widely in size, but many are nannoplankton, smaller than most species of diatoms (**Fig. 12-15b**). Most species of dinoflagellates have two hairlike projections, called "flagella," that they use in whiplike motions to provide a limited propulsion ability. Some dinoflagellate species use this propulsion mechanism to migrate vertically and maintain a depth where light levels are optimal. Consequently, dinoflagellates of some species tend to concentrate around a single depth within the photic zone.

Many dinoflagellate species have an armored external cell wall made of cellulose, but others are "naked." Because cellulose is decomposed relatively easily by bacteria and other decomposers, dinoflagellates do not contribute significantly to deep-ocean bottom sediments. Dinoflagellates are not always autotrophs. Some species are able to use dissolved or particulate organic matter as food, and some are predators. Indeed, many species can live and grow both autotrophically and heterotrophically.

Dinoflagellates are more abundant than diatoms in the open oceans far from land because the silica needed to construct diatom frustules is in short supply. However, phytoplankton biomass is substantially lower in most such open-ocean areas (**Fig. 12-17a**). Silica can also be scarce in coastal waters at certain times of year. These temporary silica-deficient conditions can lead to explosive blooms of dinoflagellates if other nutrient, temperature, and light conditions permit (**Chap. 13**).

Coccolithophores and Other Types of Phytoplankton

Coccolithophores (**Fig. 12-15c**) are generally nannoplankton, and they are smaller and less abundant than diatoms and most dinoflagellates. Coccolithophores are single-celled **flagellates** whose external cell surface is covered by a mosaic of tiny **calcareous** plates (**Fig. 12-15c**). In certain areas, these plates are a major component of seafloor sediments (**Chap. 6**). Coccolithophores make up a greater fraction of the phytoplankton biomass in relatively nonproductive temperate and tropical open ocean waters than they do in coastal waters.

In most of the oceans, microplankton consist primarily of diatoms, dinoflagellates, and coccolithophores (**Fig. 12-15a–c**). However, there are several other types of phytoplankton, including silicoflagellates (which have an intricate silica shell). cryptomonads, chrysomonads, green algae, and **cyanobacteria** (**bluegreen algae**).

Zooplankton.

Zooplankton are animals that do not swim strongly enough to overcome currents and so drift with the ocean water. As is the case for phytoplankton, and for similar reasons, the distribution of zooplankton is patchy. Dense patches of zooplankton attract fishes and other predators. **Nekton,** marine animals that swim strongly enough to move independently of ocean currents, are distributed nonuniformly because they are attracted to food sources, and they often exhibit **schooling** behavior, which is discussed in **Chapter 14**. The nonuniform distribution of both plankton and nekton, together with the temporal variability of their populations, makes it difficult for biologists to obtain precise population estimates, even when large numbers of samples are taken.

Zooplankton consist of a bewildering array of species from many different groups of organisms. Many zooplankton species tolerate only narrow ranges of environmental conditions, especially temperature. Consequently, zooplankton species composition changes from one water mass to another and with depth. At any one location, many species are represented, including species that are bacteriovores (bacteria eaters), herbivores, carnivores, and omnivores.

Zooplankton belong to one of two categories based on the life history of the species. Species that live their entire life cycles as plankton are known as **holoplankton**. The **larvae** (juvenile stages) of species that later become free swimmers or benthic species are **meroplankton**. Meroplankton include many species of fishes, **sea stars**, crabs, oysters, clams, **barnacles**, and other **invertebrates**. Holoplankton are the dominant zooplankton in surface ocean waters, whereas meroplankton are more numerous

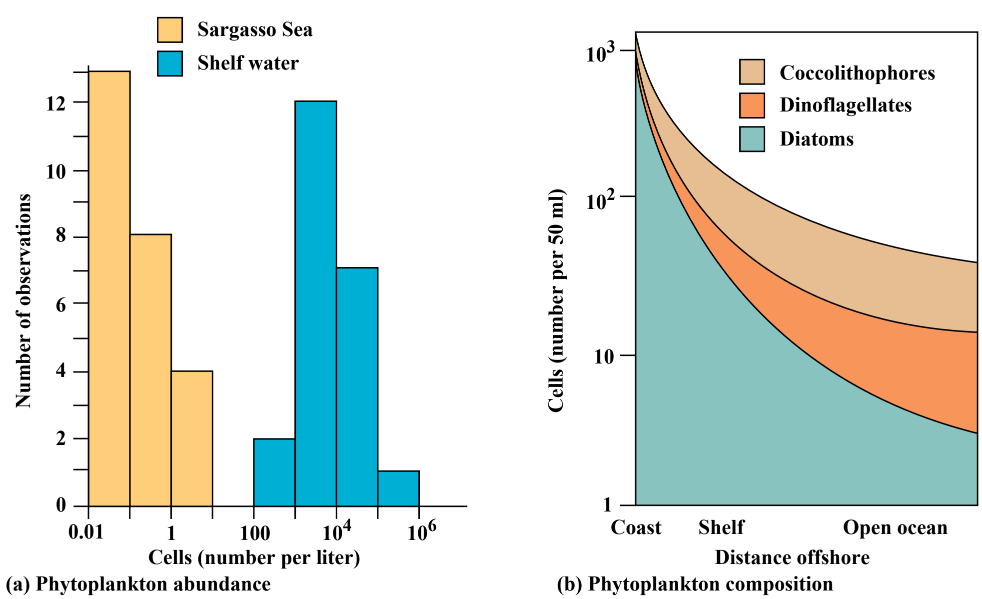


FIGURE 12-17 The composition of the phytoplankton community is different in coastal, offshore, and open ocean waters. (a) Phytoplankton are much more abundant (note the logarithmic scale) in the surface layer waters of the continental shelf than they are in the Sargasso Sea, where nutrients are depleted. (b) In many areas, the relative proportion of diatoms generally decreases with distance offshore, reflecting the lower availability of dissolved silicate in the offshore waters. These data were obtained from the Caribbean Sea

in continental shelf and coastal waters. In tropical coastal waters, larvae of benthic species make up as much as 80% of all zooplankton.

Many zooplankton species tend to concentrate at the same depth and collectively migrate between the photic zone and aphotic zone each day, but the depth to which this diurnal migration takes place differs depending on the species. Zooplankton also tend to collect at density interfaces between water layers because these interfaces inhibit (but do not prevent) vertical migration and sinking and thus collect food particles. When zooplankton are present in large numbers within a thin layer below the surface, they scatter or reflect sound and are observed by echo sounders as a "deep scattering layer." This layer changes depth during the day as the zooplankton make their daily migration between the photic and aphotic zones.

There are too many important species of zooplankton to describe in this text, but the characteristics of the major groups of holoplankton and meroplankton are described briefly in the sections that follow.

Holoplankton

The most abundant holoplankton are **copepods** (Fig. 12-18a) **euphausiids** (Fig. 12-18b) and **amphipods**, (Fig. 12-18c) which constitute 60% to 70% of all zooplankton in most locations. Copepods and euphausiids are both crustaceans, a class of invertebrates that includes crabs and lobsters. In the open oceans, most copepod species are herbivorous, whereas many coastal forms are omnivores. Copepods eat about half their body weight in phytoplankton or other food each day. They are abundant throughout the oceans and can double their population within a few weeks. Euphausiids are generally larger and reproduce more slowly than copepods. Euphausiid population doubling times are typically several months. Many euphausiids are omnivorous, eating smaller zooplankton, as well as their major food, phytoplankton.

Euphausiids called "krill" are especially abundant in waters around Antarctica, and they constitute the principal food source of the abundant marine animals there. Baleen whales, including the blue, humpback, sei, and finback, feed directly on krill. These baleen whales gulp large volumes of water, then squeeze

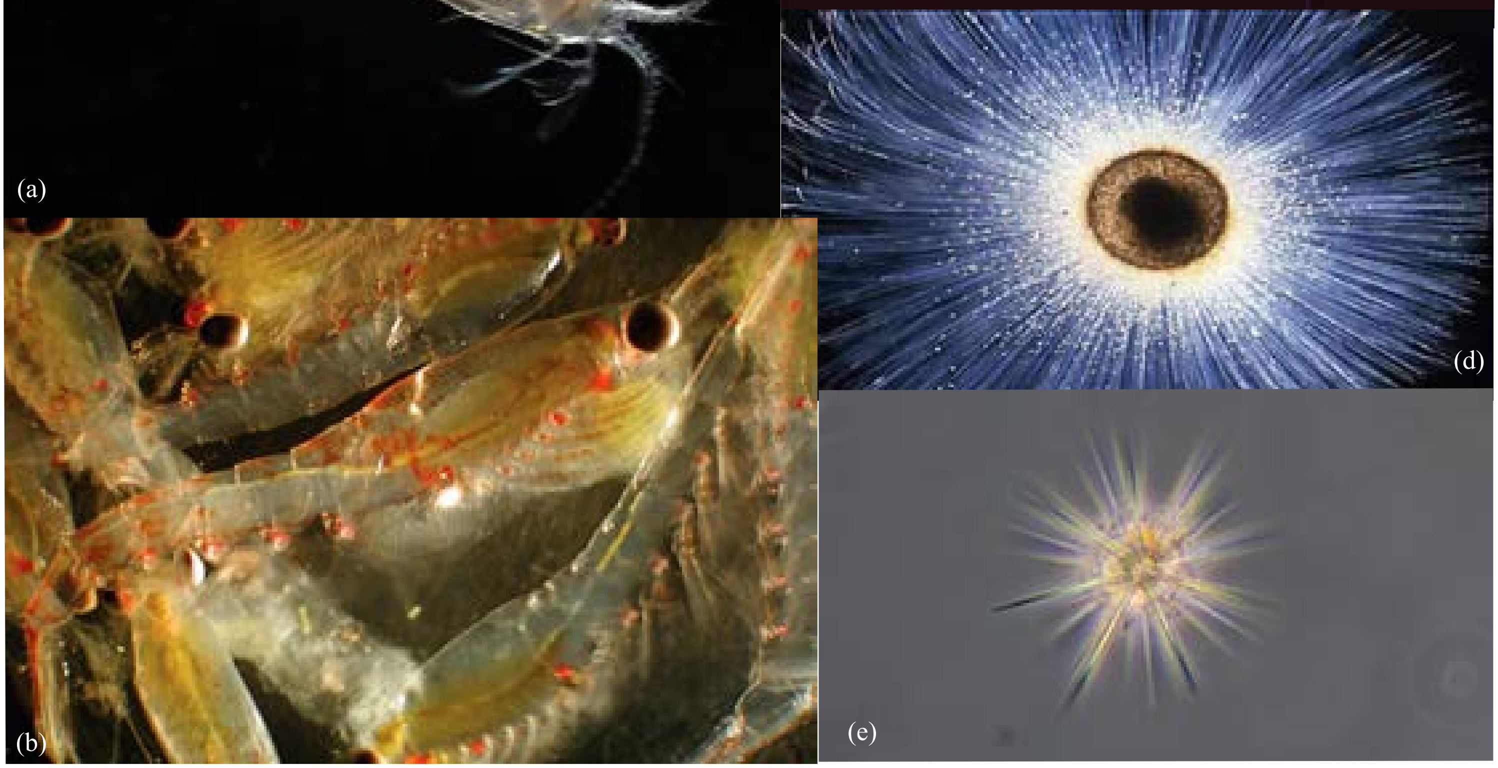
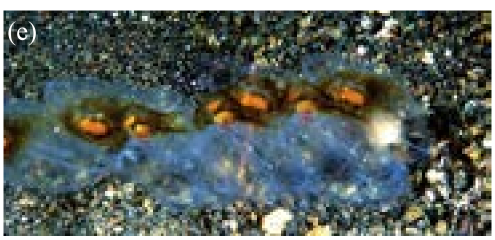


FIGURE 12-18 Typical holoplankton. (a) Copepods such as this *Scaphocalanus acrocephalus* are extremely abundant in some regions of high primary productivity. (b) Euphausiids. (c) Amphipods (possibly *Ampeliscidae*) are a major food source for fishes (d) Foraminifera *Orbulina universa*. Only the spherical inner shell will remain in sediments. The central spherical chamber is about 0.5 mm diameter and the many brightwhite spots are symbiotic dinoflagellates. (e) Radiolarian (class prob. Acantharea),northeast Pacific Ocean, approx 160x magnification, cell body approx 50 micrometers across.

FIGURE 12-19 Typical gelatinous holoplankton. (a) Jelly *Aurelia sp.* This one was in a unique marine lake called Jellyfish Lake in Palau. (b) This upside-down jelly (*Cassiopeia andromeda*, Papua New Guinea, about 10–15 cm across) generally lies on its "back" on the shallow seafloor to provide light to the symbiotic algae that live in its tentacles. (c) The Portuguese man-of-war (*Physalia physalis*) is a colonial jelly whose long tentacles bear stinging cells that can severely injure a swimmer. (d) Ctenophores, like this *Mertensia ovum*, propel themselves by pulsating the columns of bright hairlike cilia visible through the body. (e) Each individual of this colonial salp species, photographed after it had floated into shallow water and settled on the sand in Indonesia, may be 10 cm or more across. The colonies, which normally drift through open-ocean surface waters, may exceed several meters in length.



it out through net-like baleen plates suspended from the roofs of their mouths. Krill collect on the baleen and are removed by the tongue and ingested.

Two groups of single-celled **amoeba**-like microplankton have hard parts that become important components of sediment in some areas: **foraminifera** (**Fig. 12-18d**), with shells composed of calcium carbonate, and **radiolaria** (**Fig. 12-18e**), with shells composed of silica. Both are holoplankton and feed on diatoms, small protozoa, and bacteria, often capturing them on their many long, sticky, spikelike projections. Radiolaria and foraminifera are most abundant in warm waters. Individual species, especially of foraminifera, are very sensitive to small changes in water temperature and salinity. Because of the sensitivity to temperature, the species compositions of radiolaria and foraminifera in sediments are important indicators of past climates. **Isotopic** compositions of the shells of these organisms also provide a record of the temperature at the time they lived (**Chap. 6**).

The **pteropods** (**Fig. 8.7b**), another group of holoplankton, are also important in marine sediments. Pteropods are **mollusks** and are related to slugs and snails. In pteropods, the "foot" on which slugs or snails crawl is modified into a delicate transparent wing that undulates and propels the organism like a fin. This modified foot enables pteropods to migrate vertically hundreds of meters each day. Some pteropod species are carnivorous and do not have a shell. Others are herbivorous and have a calcareous shell that contributes to sediment, especially in tropical regions (**Chap. 6**), where they often occur in dense swarms.

Gelatinous Holoplankton

Many holoplankton differ from other holoplankton species because they have gelatinous bodies and are apparently not part of the food webs that lead to fishes and other marine animals exploited by humans. Although these species consume large amounts of other zooplankton, their gelatinous bodies provide little or no food for species at higher trophic levels.

The most familiar group of gelatinous holoplankton, the **jellies** (commonly but incorrectly called **jellyfish** or sea jellies but they are not fish and are not restricted to seawater), are **cnidar-**

ians (phylum Cnidaria, or Coelenterata), a phylum which also include **corals** and **anemones**. All cnidarians have stinging cells, called “cnidocysts,” within which they have harpoon-like structures called “nematocysts” that can fire into their prey to inject toxins. In some species, the toxins are extremely strong and can paralyze or kill large fishes or even people.

Some jelly species (**Fig. 12-19a–c**) are very large in comparison with most other holoplankton, perhaps because their food value is low and they have relatively few predators. Some, such as the moon jelly *Aurelia* (**Fig. 12-19a**) and *Cyanea*, are holoplankton. Others are meroplankton that spend part of their lives in the plankton, then settle to the seafloor, where they attach with their stinging tentacles extended upward. In the benthos they resemble their close relatives: anemones and corals.

Among the most unusual jellies are species, such as the Portuguese man-of-war (**Fig. 12-19c**), that appear to be a single organism but in fact are a colony. In colonial forms, many individuals of the same species form a cooperative group that appears to be a single organism. Each colony member has a specialized task, such as protecting the colony, gathering food, digesting food, or reproducing. In the Portuguese man-of-war, one colony member is filled with gas to provide flotation and a “sail” that can partially control the colony’s drift.

Widely occurring gelatinous plankton that are not jellies include **ctenophores** and **salps**. Ctenophores are transparent, **bioluminescent** organisms, some of which have long, trailing tentacles (**Fig. 12-19d**). Ctenophores propel themselves through the water by beating eight columns of hairlike cilia that are usually visible through the ctenophore’s body (**Fig. 12-19d**) and that give these species their common name, “comb jellies.” Small, rounded species of ctenophores are often called “sea walnuts” or “sea gooseberries.”

Salps (**Fig. 12-19e**) are the holoplankton species of **tunicates**, most of which are benthos. Tunicates are among the most advanced invertebrates. They are **chordates** (phylum Chordata), a phylum which also includes the **vertebrates** (fishes and mammals). This close relationship is difficult to envision from the simple form of the adult salps or other tunicates, but tunicate larvae closely resemble vertebrate larvae. Adult tunicates have a simple baglike form with two openings. Water is pumped into one opening (**incurrent** opening) and out the other (**excurrent** opening). Food particles are removed from the water by a mucous layer spread over the interior of the tunicate’s body.

Many salps are hollow and barrel-shaped, with incurrent and excurrent openings at opposite ends (**Fig. 12-19e**). They propel themselves slowly by pumping water through their bodies. Several salp species are bioluminescent. I witnessed a “magic moment” one moonless night on a research vessel sailing through an exceptionally dense patch of salps in the tropical Atlantic Ocean. For miles, the ship’s wake was a brilliant, sparkling light show, as a continuous stream of salps was disturbed by the wake and emitted pulses of light.

Meroplankton

Meroplankton are the eggs, larvae, and juveniles of species that spend their adult lives as benthos or nekton. Larvae or juvenile forms of the majority of benthic species, including clams, oysters, crabs, snails, lobsters, sea stars, **sea urchins**, corals, and **sea cucumbers,** spend their first few weeks of life as meroplankton. Many fish species also release eggs to the water column. These eggs, the larvae that hatch from them, and juvenile fishes that emerge from the larvae are meroplankton until the fishes become big enough to swim actively against currents as nekton. The

FIGURE 12-20 Typical meroplankton. (a) A crustacean larvae. (b) A blue king crab larvae, zoeal stage 2 (*Paralithodes platypus*) (c) The first larval stage of a starfish. This stage is called a bipinnaria.

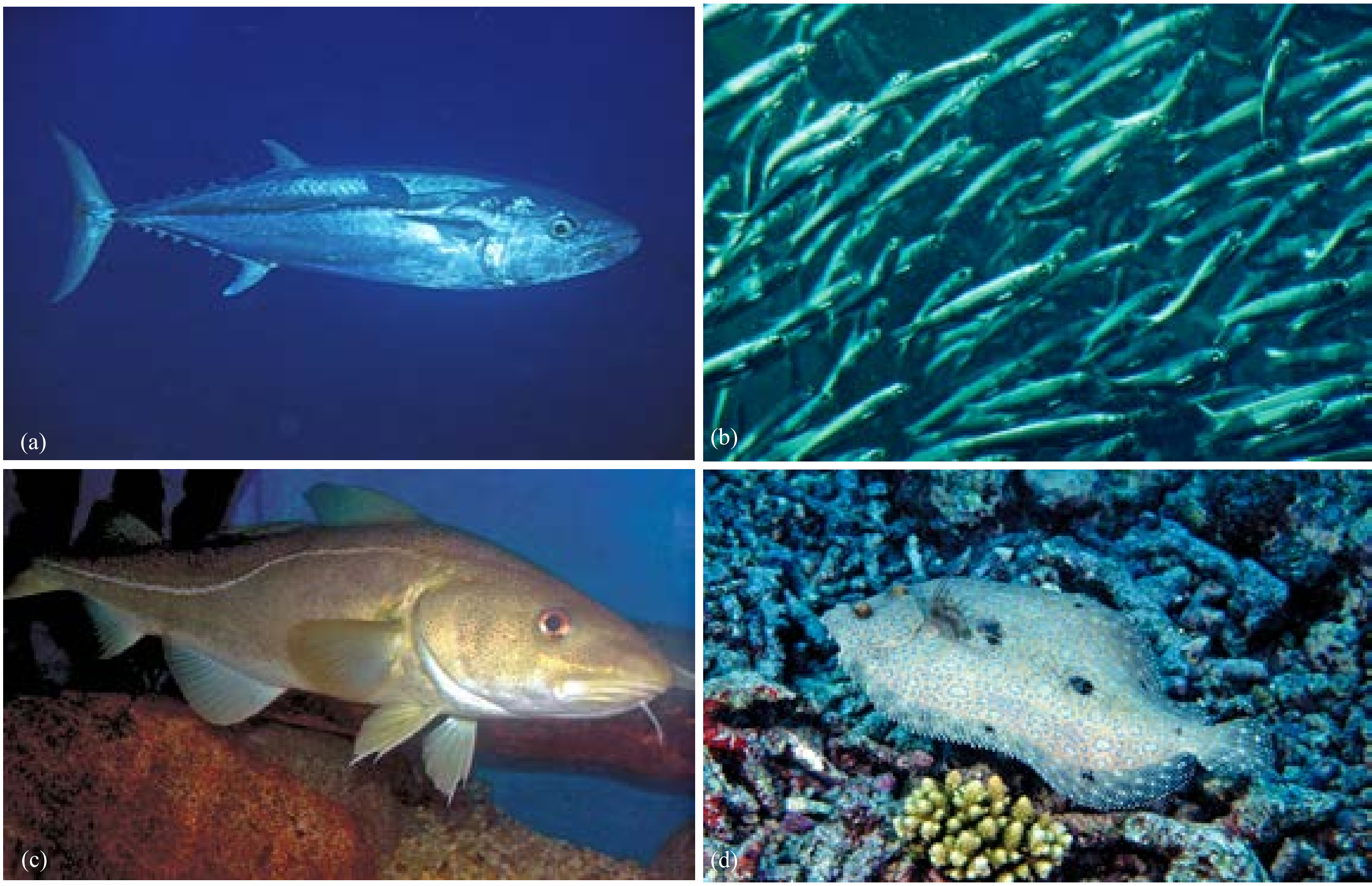


FIGURE 12-21 Representative species of fishes. (a) The dogtooth tuna (Gymnosarda unicolor, Papua New Guinea) is an oceanic predator. (b) A school of Pacific sardines (Sardinops sagax) . (c) The Atlantic cod (Gadus morrhua) was once extremely abundant, but its populations have now been substantially reduced by overfishing. (d) The flowery flounder (Bothus mancus, Solomon Islands) spends much of its life lying camouflaged on the seafloor.

release of eggs and larvae as meroplankton is an effective means of distributing species over wide areas (**Chap. 14**).

Many species of meroplankton larvae do not remotely resemble their adult forms (**Fig. 12-20**). In the past, numerous meroplankton have been named and classified as separate species, even though their adult forms were already well known. Modern scientific methods, particularly genetic studies, now enable us to match meroplankton with their adult forms.

NEKTON

Nekton are animals that swim strongly enough to move independently of ocean currents. Most nekton are vertebrates, which are organisms that have an internal skeleton, spinal cord, and brain. Marine vertebrates include fishes, **reptiles,** birds, and **marine mammals.** Some invertebrates, such as squid, are also nekton. The nekton are dominated by the varied and abundant fish species. There are three types of fishes: primitive jawless fishes including hagfishes and eels; fishes that have cartilage skeletons, including sharks and rays; and bony fishes that have bone (largely calcium carbonate and calcium phosphate) skeletons. More than 95% of all living species of fishes are bony fishes.

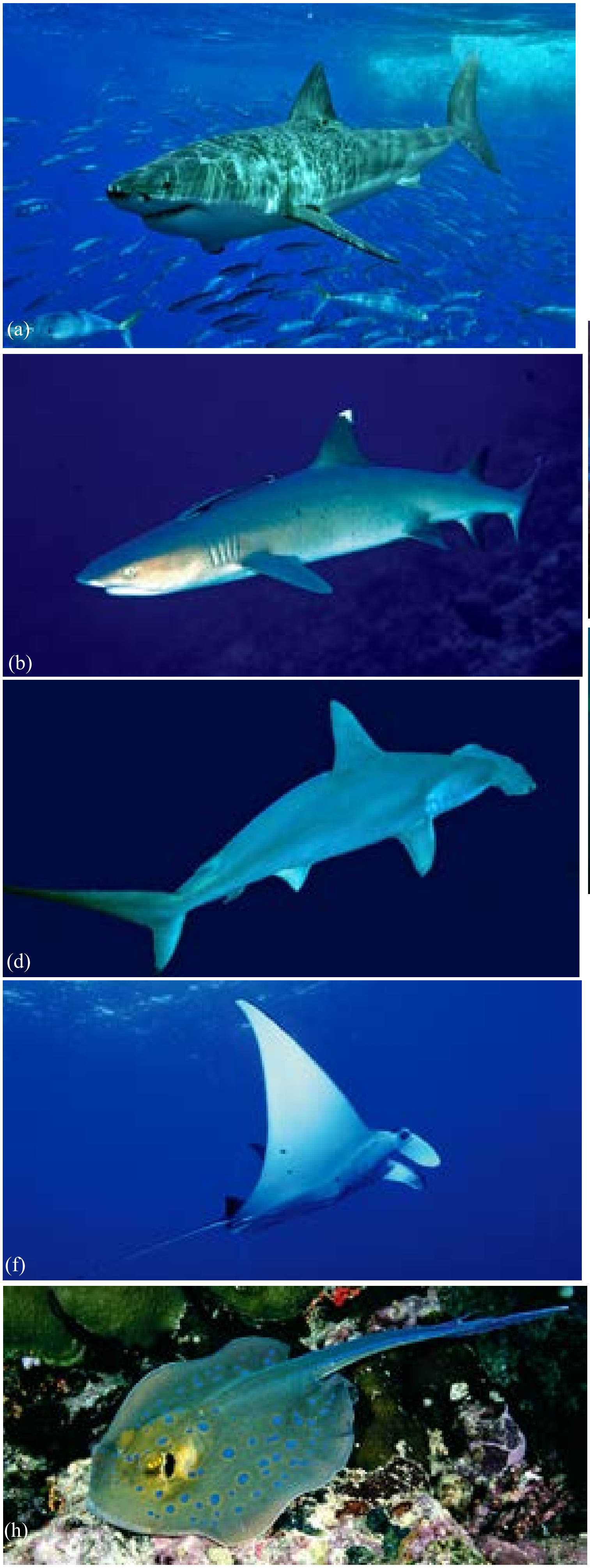
Bony Fishes

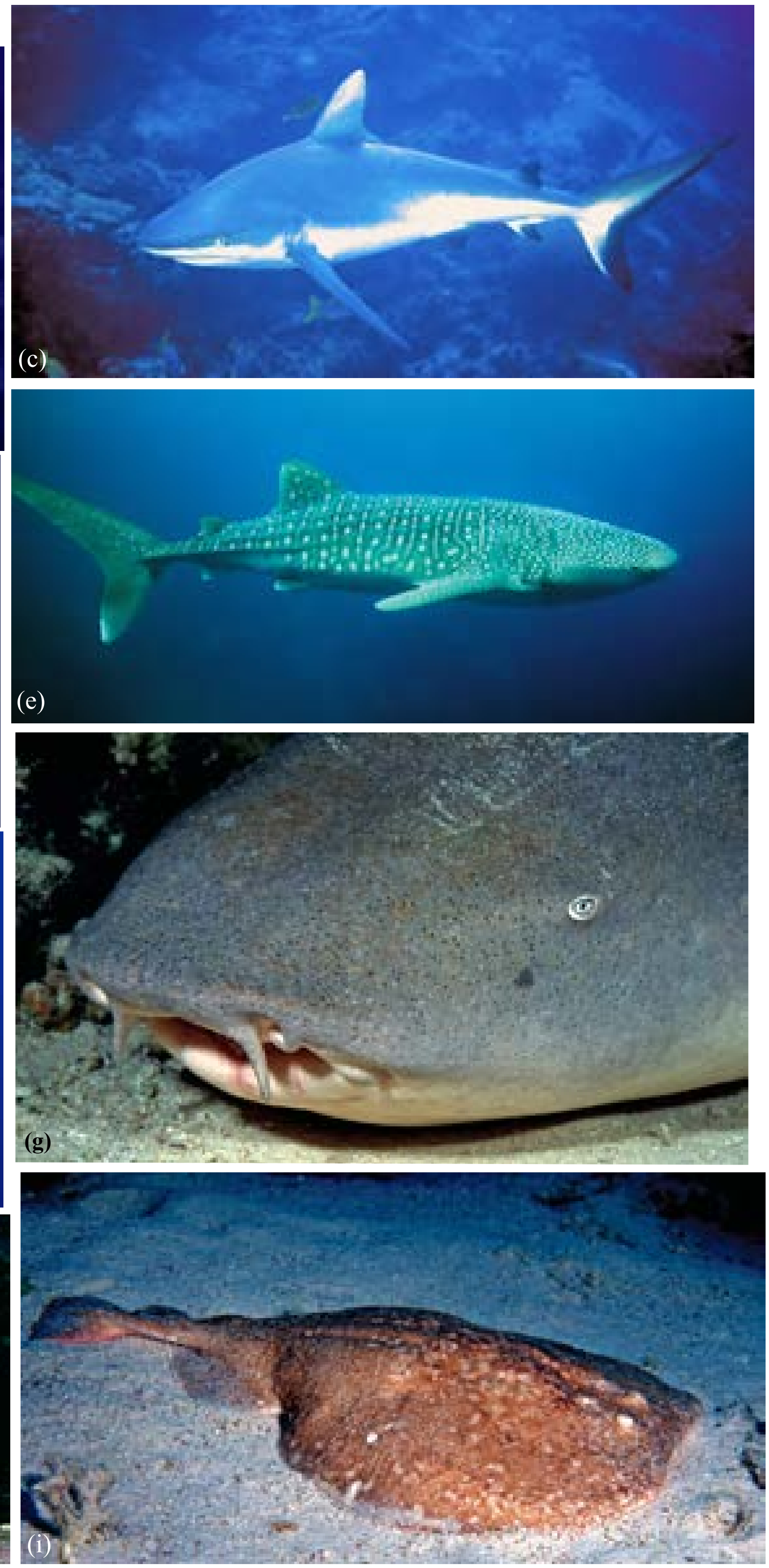
Bony nektonic fishes have a wide variety of body forms and range in length from just a few centimeters to more than a meter. Such pelagic giants as tuna (**Fig. 12-21a**) or swordfish can exceed 3 m. Species of fishes that live on or near the seafloor are called "demersal" fishes, and those living predominantly in the water column are called "pelagic" fishes.

The most abundant fishes in coastal waters are various species of silver-bodied schooling fishes including herrings, anchovies, pilchards, sardines (**Fig. 12-21b**), and menhaden. Because these fishes generally do not exceed a few tens of centimeters in length and have oily tissues, they are generally not valued for human consumption. Nevertheless, their numbers are so vast that the world's most productive commercial fisheries target these species. Much of the catch is processed and used as animal feed, fish oils for paints and diet supplements, soaps, and lubricants. These species have each been **overfished,** and their historical populations have been decimated in many coastal regions (**Chap. 16**). Various species of cod (**Fig. 12-21c**) are extremely abundant in mid and high latitudes, especially in the Northern Hemisphere, and they are commercially very valuable. Cod live most of their lives on or near the ocean floor, where they feed on invertebrates and small fishes.

The body shapes of fishes are determined primarily by their swimming habits (**Chap. 14**). Species that are members of the flatfish group have bodies modified to enable them to lie flat on the seafloor, where they remain well camouflaged (**Fig. 12-21d**). Juvenile flatfishes, like other fishes, have eyes on each side of their body. As they mature, one eye migrates across the body so

FIGURE 12-22 Representative sharks and rays. (a) Great white shark (*Carcharodon carcharias*), attracted to a diver's bait. (b) Reef whitetip shark (*Triaenodon obesus*, Papua New Guinea) with a sharksucker, or remora (*Echeneis naucrates*) attached. (c) Gray reef shark (*Carcharhinus amblyrhynchos*, Fiji), which is called a "bronze whaler" in Fiji. (d) Scalloped hammerhead shark (*Sphyrna lewini*, Papua New Guinea). (e) The whale shark (*Rhincodon typus*, Papua New Guinea) is the largest known shark species. This one was quite small, only about 8 to 10 m long. (f) The graceful manta ray (Manta birostris, Philippines). (g) Up close and personal with a nurse shark (*Nebrius concolor*, Philippines). (h) Blue-spotted rays (*Taeniura lymma*, Red Sea) have a dangerous barb on the tail. (i) The torpedo ray (family Torpedinidae, Red Sea) can inflict a powerful electric shock. The whale shark and manta ray are plankton feeders, the nurse shark eats benthic invertebrates, and the other sharks are scavengers and carnivores.





that both eyes are on the same side of the head (**Fig. 12-21d**). If the eye migrates to the left side of the body, the species is usually called a "flounder." If it migrates to the right side, the species is usually called a "sole." However, some species, such as the starry flounder, have both left- and right-eyed forms.

Many fishes contain **swim bladders** filled with a gas that is usually a mixture of oxygen and carbon dioxide. Swim bladders are used to maintain buoyancy, and, at least in some species, they appear to be used in the fish's "hearing" mechanism. Because gas expands or contracts as pressure changes with depth, fishes with swim bladders must add or remove gas from their swim bladders as they move vertically. Some fishes absorb the gas back into the bloodstream, and others, such as herrings, can release the gas as bubbles. Many fishes bloat and die if brought rapidly to the surface because they cannot purge their swim bladders fast enough. Fish species that migrate vertically each day often have no swim bladders, but maintain buoyancy through high concentrations of lighter-than-water oils.

Sharks and Rays

Sharks and rays are more primitive than other fishes, and many species have existed essentially unchanged for millions of years. Unlike bony fishes, sharks and rays have skeletons made of cartilage. Sharks and rays have reproductive cycles that require eggs to be fertilized inside the female. Most other fish species reproduce by the simultaneous release of eggs and sperm by female and male. In many **cartilaginous** fish species, the fertilized eggs are hatched and develop into the adult form within the mother (or in some species the father) before being released in a live birth.

The common perception of sharks is that they are fearsome predators that will hunt and kill anything, including people (**Fig. 12-22a**). Although many species are able to hunt and kill large fishes and marine mammals, only a few species are known to attack people. Because humans are not the natural prey of sharks, most shark attacks on humans are thought to be cases of mistaken identity. The fact that most carnivorous sharks are opportunistic hunters, honing in on weak and dying prey, belies their reputa-

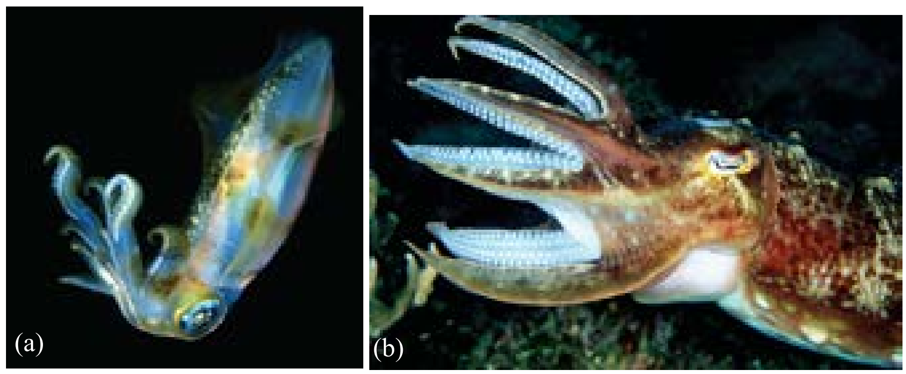
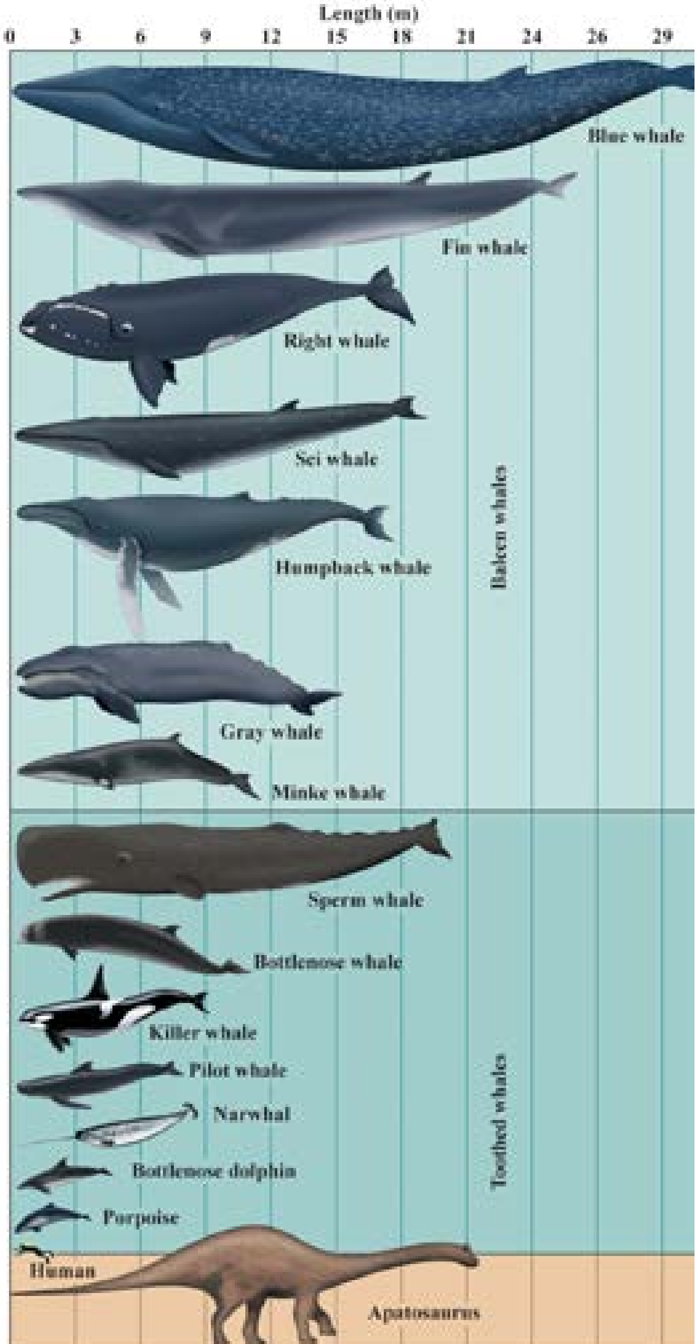


FIGURE 12-23 Cephalopod mollusks. (a) A common reef squid (*Sepioteuthis lessoniana*, Indonesia) photographed at night. (b,c) Broadclub cuttlefish (*Sepia latimanus*, Indonesia and Papua New Guinea). (d) Stumpy spined cuttlefish (*Sepia bandanensis*, Indonesia). (e) Nautilus (*Nautilus pompilius*, Papua New Guinea), captured at a depth of several hundred meters in a trap similar to a lobster pot, which was baited with fish. The Nautilus was released to swim back to its deepwater home after this photograph was taken. (f) This sectioned Nautilus shell shows the internal chambers that are filled with gas at low pressure to provide buoyancy. Because these chambers are incompressible, Nautilus can safely migrate great vertical distances.



(a)


(b)


(c)


(d)


(e)

FIGURE 12-24 Cetaceans and sea cows. (a) The relative sizes of various toothed and baleen whales, compared to humans and the largest known dinosaur, *Apatosaurus.* (b) Killer Whale (*Orcinus orca*) (c) Pacific White Side dolphins (*Lagenorhynchus obliquidens*) (c) Humpback whale (*Megaptera novaengliae*). (c) Killer whale, often called "Orca" (*Orcinus orca*). (d) Manatees (*Trichechus manatus*) in the Crystal River, Florida.

tion.

Species such as the reef whitetip, gray reef, and hammerhead (**Fig. 12-22b–d**) are regularly attracted to dead fishes set as bait by **scuba** divers. I have witnessed several occasions when these sharks ate such bait while swimming frantically among surrounding divers. Even when agitated, these sharks do not attack the divers and can almost always be chased away easily on the extremely rare occasions when they do attack. Other shark species, such as the tiger and great white, are more dangerous, and cautious divers will leave the water when they appear.

Although many sharks eat fishes and marine mammals, a number of shark species feed only on plankton. Plankton-eating sharks include basking sharks that grow to 12 m in length and whale sharks (**Fig. 12-22e**) that grow to more than 15 m. The beautiful and graceful manta ray is also a plankton eater (**Fig. 12-22f**). Plankton-eating sharks and rays swim with mouths wide open. Large volumes of water pass into the mouth and are filtered to capture the plankton before flowing out of the **gills.** The nurse shark (**Fig. 12-22g**) and many species of rays (**Fig. 12-22h,i**) feed only on mollusks and other benthic animals.

Many rays, such as the blue-spotted sting ray (**Fig. 12-22h**), have a barbed stinger embedded in the tail. They use the stinger as a defensive weapon against natural predators, such as sharks, and occasionally against a human foot. Torpedo rays (**Fig. 12-22i**) deliver a strong electric shock that can be lethal to humans, as much as 200 volts, from an organ in the head.

Squid and Their Relatives

Squid (**Fig. 12-23a**), nektonic mollusks of the class Cephalopoda, are extremely abundant in the oceans. Squid normally live in schools that can contain huge numbers of individuals. They are extremely fast swimmers (using their fins) and voracious predators of small fishes. They can also jet-propel themselves by ingesting water and forcibly squirting it out through a special cavity. They can even propel themselves several meters into the air. Most squid species live below the photic zone during the day and migrate to the mixed layer at night to feed. The largest squid species, the giant squid, can grow to 16 m or more in length (6 m of body and 10 m of tentacles). It lives in the deep ocean and is rarely caught or seen, but it is known to be a favorite food of sperm whales.

Cuttlefish (**Fig. 12-23b–d**) are **cephalopods** that have an unusual internal single "bone" or shell (the "cuttlebone" that is typically hung in parakeet cages). *Nautilus* species (**Fig. 12-23e**) have a calcium carbonate shell with a series of internal gas-filled chambers (**Fig. 12-23f**). They are an ancient form of cephalopod that has changed little over millions of years. All cephalopods are believed to have had external shells at one time. *Nautilus* species, cuttlefish, and squid represent steps in cephalopod evolution in which the external shell, an excellent means of defense, has been discarded in favor of greater swimming speed, which is also an excellent means of defense, but more valuable for hunting prey.

Marine Mammals

Marine mammals, which include seals and sea lions, dolphins and other whales, and a number of other less familiar animals, are warm-blooded and breathe air. Their young are born live and nursed by their mothers, just as terrestrial mammals are.

The **cetaceans,** which include dolphins, porpoises, and other whales, live their entire lives in the water. The largest whales—the blue, finback, right, sei, and humpback (**Fig. 12-24a,b,c,d**)—are baleen whales that feed on plankton. The smaller gray whale, also a baleen whale, is unique because it feeds mainly on small

FIGURE 12-25 Pinnipeds and otters. (a) Harbor seals (*Phoca vitulina*) haul out on the rocks near Monterey, California. (b) A scientist measures the length of an adult male elephant seal (*Mirounga angustirostris*) at the Año Nuevo State Reserve, California. This can be a dangerous job for the scientist because the elephant seal may weigh well over a tonne, can move surprisingly fast, and can be very aggressive when disturbed. (c) California sea lion (*Zalophus californianus*) populations are growing very quickly and becoming a nuisance in many harbors, where they aggressively compete for space when they haul out on any convenient platform, especially boat docks like this one in Monterey, California. (d) Walrus (*Odobenus rosmarus*) apparently use their tusks as the equivalent of sled runners that enable them to glide along the seafloor as they feed by sucking or slurping up sediments with their whiskered mouths. (e) Sea otters (*Enhydra lutris*, California) sometimes eat shellfish by resting the shellfish on their chests and pounding them open with a stone while floating on their backs.

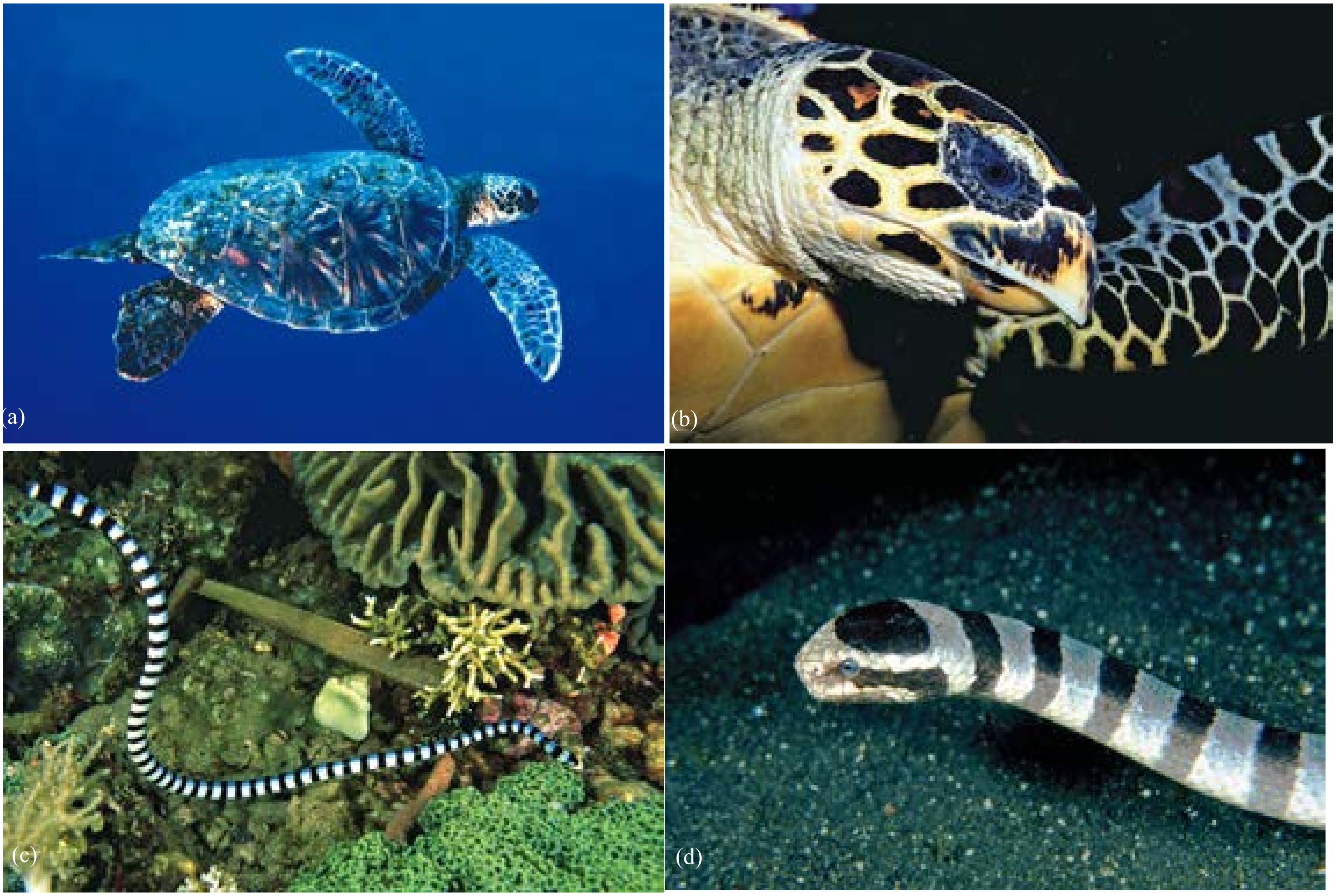


FIGURE 12-26 There are only a small number of marine reptile species. (a) Green sea turtle (Chelonia mydas, Hawaii). (b) Hawksbill turtle (Eretmochelys imbricata, Fiji). (c,d) Banded sea snake (Laticauda colubrine, Indonesia). (e,f) Marine iguana (Amblyrhynchus cristatus), which lives only in the Galápagos Islands

crustaceans, mollusks, and worms that it stirs up from muddy sediments with its snout. Sperm whales (**Fig. 12-24c**) feed primarily on squid, whereas most small whales, including the pilot and beluga whales, dolphins, and porpoises, eat mostly fishes. However, the killer whale (**Fig. 12-24c**) lives up to its name by hunting and eating fishes, seals, sea lions, and even other whales. Killer whales often hunt in packs like wolves. On several occasions, pods of killer whales have been filmed systematically harassing a California gray whale mother and calf until they were separated. If they successfully separate the mother and calf, the killer whales, as a pack, set upon the calf, which they then kill and eat.

Manatees (**Fig. 12-24e**) and dugongs, commonly called "sea cows," are herbivorous sirenians that graze on vegetation in the shallow tropical coastal waters where they live. Sea cows are considered to be the source of the mermaid (or siren) legend.

Seals (**Fig. 12-25a,b**), sea lions (**Fig. 12-25c**), and walrus (**Fig. 12-25d**) are **pinnipeds**. Pinnipeds live and feed in the oceans for most of their lives, but they must haul themselves out of the water to breed and bear young and to rest and conserve body heat. The elephant seal (**Fig. 12-25b**), whose bizarre-looking adult males weigh 2 tonnes, is the largest pinniped. Most pinnipeds eat fishes, but walrus (**Fig. 12-25d**) eat clams and other **shellfish** from the sediment, and Antarctic leopard seals will eat invertebrates, seabirds, and other mammals.

The sea otter (**Fig. 12-25e**) is a unique shellfish-eating mammal that, unlike all other marine mammals, lacks an insulating layer of **blubber**. Instead, sea otters retain body heat with soft, thick fur that they must continuously groom if it is to retain its insulating properties.

Many marine mammals were once hunted intensively for their fur, meat, and oil. Because they have long life cycles, hunting quickly reduced some species to critically low population levels. Although certain species are still hunted, the hunting of marine mammals was stopped by most nations several decades ago. Most marine mammal populations that were decimated by hunting are now recovering slowly. However, some species are still threatened by the destruction of **habitat** (particularly pinniped breeding areas), by **pollution**, and by some fishing methods, such as the use of **drift nets** that kill mammals as well as targeted fishes (**Chap. 16**).

Reptiles

Only a small number of reptiles, which are air-breathing animals, live in the oceans. The best known are sea turtles, of which four large species are widely distributed in the oceans: the green (**Fig. 12-26a**), hawksbill (**Fig. 12-26b**), leatherback, and loggerhead. Green turtles are herbivorous and graze on sea grasses that grow in shallow **lagoons**. One common species of sea grass is known as "turtle grass" because it is a favorite food of these turtles. The hawksbill lives in tropical waters and eats mostly **sponges**. The loggerhead also eats sponges, but it adds crabs and mollusks to its diet. The biggest turtle, the leatherback, can weigh as much as 650 kg and is among the few large animals in the ocean that eat jellies.

Turtles have been hunted for centuries. They are easy to catch and, if placed on their backs out of water, live for many weeks but cannot escape. For this reason, turtles were an ideal source of fresh meat on sailing vessels before refrigeration was developed. Turtles were common just 200 years ago, but all turtle species have been decimated by humans, and most are threatened or endangered by extinction. The Kemp's ridley turtle, a relatively small species that lives only in the Gulf of America (Golfo de México) and South Atlantic, is especially in danger of extinction.

Turtles lay their eggs in beach sands above the high-tide line. The eggs hatch in several weeks, and the young turtles immediately head to the sea. Turtle eggs are considered a delicacy in many areas, and the fact that they are easily dug out of the sand by human and other predators has contributed to the decline of turtle populations. In addition, turtles are easy for predators to catch when they climb onto the beach to lay their eggs and when they emerge as hatchlings.

Turtles use relatively few beaches throughout the world for breeding. They almost always return to lay eggs on the same beach where they hatched and usually will not lay eggs on any other beach. Because they are reluctant to lay eggs where human development has altered a beach, they have abandoned many traditional breeding beaches. The reduction in the number of breeding beaches that are suitably protected has seriously affected turtle populations.

The Pacific and Indian Oceans have about 50 species of sea snakes (**Fig. 12-26c,d**). Most are highly venomous, and their bite is generally lethal to people. Fortunately, sea snakes have small mouths and small fangs that cannot easily break human skin, unless they catch a finger or other small appendage. Sea snakes are also relatively shy and do not attack unless threatened. They live near the shore so that they can slither out of the water onto rocks to sun themselves. They eat small fishes, can dive as deep as 100 m, and can stay submerged for more than 2 h before they must come up for air.

In certain areas of Asia and the Pacific Islands, saltwater species of crocodiles feed on fishes in coastal waters. American alligators are also known to enter coastal-ocean waters, but normally they are confined to freshwater. The only marine species of lizard is the Galápagos marine iguana (**Fig. 12-26e,f**), which lives on land but frequently enters shallow coastal waters to graze on marine algae.

Birds

Penguins (**Fig. 12-27a**) are flightless birds that live in the oceans and feed on fishes. They leave the water only to lay eggs and brood their young. Most species are restricted to the cold waters near Antarctica, and none are present in the Northern Hemisphere.

Many species of seabirds feed exclusively on ocean fishes. Some, including most seagulls (**Fig. 12-27b**), feed at the ocean surface, but many, like the brown pelican (**Fig. 12-27c**), dive into the water to catch their prey. Others, such as the cormorant (**Fig. 12-27d**), are excellent swimmers that can dive tens of meters deep and stay submerged for as much as several minutes in pursuit of prey.

BENTHOS

The challenges and opportunities for marine animals in the benthic environment are different from those in the pelagic environment. The physical nature of the seafloor can change dramatically over relatively short distances, especially in coastal areas. The seafloor can be covered with soft mud into which organisms can easily burrow to live, hide, or feed, or it can be solid rock that provides a stable surface for organisms to attach to or bore into. Benthic communities have evolved to take advantage of each different type of seafloor between these two extremes. Consequently, benthic communities are more varied than pelagic communities, particularly in the **coastal zone**, where seafloor character varies the most. Most deep-ocean benthos must obtain food from particulate organic matter that rains down from above or by preying on other organisms.

Chapter 14 discusses the constraints and strategies of life on the seafloor and the approaches that various species use to meet the challenges. **Chapter 15** describes benthos in some specific regions of the seafloor, including those of the deep-ocean seafloor, the unique hydrothermal vent communities of the deep sea, and the remarkably different coastal benthos communities of the coral reef, kelp forest, and rocky intertidal zone.

CHAPTER SUMMARY

Production, Consumption, Decomposition.

Almost all organic matter on which marine life depends for food is synthesized from carbon dioxide and nutrients by photosynthesis or chemosynthesis—a process called "primary production." Organisms are autotrophs if they synthesize their own food, and heterotrophs if they do not. Autotrophs and heterotrophs convert some organic matter to carbon dioxide and water in respiration. Heterotrophs can be herbivores, carnivores, omnivores, detritivores, or decomposers.

FIGURE 12-27 Swimming seabirds that feed in the marine environment. (a) King penguins (*Aptenodytes patagonicus),* Fortuna Bay, South Georgia. Adults and molting juveniles. (b) Herring gulls (*Larus argentatus*), California), one of the many species of seagulls. (c) Brown pelican (*Pelecanus occidentalis*, California). (d) Double-crested cormorants (*Phalacrocorax auritus*, Monterey, California), which are excellent underwater swimmers.

Microbes in Charge

The majority of the biomass in the oceans is now known to be microbial—consisting primarily of bacteria and archaea. Microbial species are responsible for much of the primary production and most of the decomposition of organic matter in the oceans and dominate the movement of energy and biologically important elements in the oceans.

Primary Production and Light.

Light is needed to provide energy for phototrophy (which includes photosynthesis). Light is absorbed by seawater and scattered by suspended particles. It penetrates to a depth of a few hundred meters in clear waters and much less in high-turbidity waters. The photic zone is the upper layer of the oceans where light is sufficient to support phototrophy. Most primary production is carried out by phytoplankton, which are floating microscopic algae and cyanobacteria. Benthic phototrophs are present only where the seafloor is within the photic zone. As light decreases with depth, phototrophy is slowed but respiration is not. The depth at which photosynthesis equals respiration is the compensation depth. This depth is shallower in winter and in high-turbidity water.

Primary Production and Nutrients.

Phytoplankton require nitrogen, phosphorus, iron, and other nutrients. If the concentration of a particular nutrient is too low to support growth, it is a limiting nutrient. Nutrients are taken up through the cell membrane. The small size of phytoplankton provides a large surface area (per volume) for this uptake and to retard sinking. Phosphorus is recycled rapidly to solution in liquid excretions of animals and during the decay of dead organisms. Nitrogen is recycled more slowly through several chemical forms and is more often the limiting nutrient in the ocean. In some areas where river runoff and atmospheric dustfall are both low, iron can become the limiting nutrient. Silica is an important nutrient for diatoms and other plankton that have silica-based hard parts and is recycled very slowly. Nutrients are carried below the mixed layer by the sinking of dead organisms and fecal pellets. Nutrients are provided to the photic zone primarily by rivers, recycling, and upwelling. They are relatively abundant in waters below the permanent thermocline.

Food Webs.

Phytoplankton are eaten by herbivores or omnivores, which are eaten by small carnivores, which in turn are eaten by larger carnivores. Each organism in this food chain is at a higher trophic level. The conversion efficiency of food to biomass is about 10% between each trophic level. Many carnivores and omnivores feed on organisms from more than one trophic level, forming a more complex food web.

Geographic Variation in Primary Production.

The highest primary productivity is in upwelling regions, most of which are in coastal waters along the western margins of continents. Upwelling also occurs around Antarctica and across parts of the equatorial regions. Primary productivity is lowest in the centers of the subtropical gyres.

Dissolved Oxygen and Carbon Dioxide.

Dissolved oxygen is released during photosynthesis and consumed during respiration. Gases are exchanged between ocean and atmosphere across the sea surface. Oxygen and carbon dioxide are saturated in surface waters. Oxygen can be supersaturated in shallow parts of the photic zone where photosynthesis exceeds respiration. Below the thermocline, oxygen is consumed in respiration and decomposition, and its concentration is below saturation. In some areas where the photic zone has high primary productivity and bottom waters have long residence time, bottom water is anoxic and may contain toxic hydrogen sulfide.

Organic Carbon.

Organic carbon is present in dissolved and suspended particulate forms and in phytoplankton and animal tissues. More than 95% is nonliving dissolved organic matter, and most of the rest is particulate detritus. Most of the dissolved and particulate organic matter is difficult to decompose and has limited nutritional value. Organic particles are more abundant in the photic zone and in areas of high primary productivity.

Biological Provinces and Zones.

The benthic and pelagic environments support fundamentally different biological communities. The benthic environment is divided into the hadal zone, which is the deep seafloor below 6000 m, the abyssal zone between 6000 and 2000 m, the bathyal zone between 2000 m and the continental shelf break, the sublittoral zone (water-covered continental shelf), and the intertidal zone. Benthic organisms in the hadal, abyssal, and most of the bathyal and sublittoral zones depend on detritus for food, with the exception of isolated chemosynthetic communities. The pelagic environment is separated into the neritic province in water less than 200 m deep, and the oceanic province in water deeper than 200 m. The oceanic province consists of the epipelagic zone, in which phototrophy (including photosynthesis) can occur; and the mesopelagic, bathypelagic, abyssopelagic, and hadopelagic zones, which are all below the photic zone. Communities of each of the benthic and pelagic zones are different, but there is some overlap.

In the sublittoral zone, the neritic province, and the epipelagic zone, latitudinal variations of temperature and salinity cause latitudinal zonation in biological communities. For example, tropical and polar regions support different species.

Plankton.

Plankton are organisms and viruses that drift freely with currents and include phytoplankton (which are microscopic photosynthetic algae and cyanobacteria) and zooplankton (which are herbivorous, carnivorous, or omnivorous animals). Phytoplankton are abundant in productive photic-zone waters, exceeding 1 billion individuals per liter, and have patchy distributions. Diatoms are relatively large phytoplankton with silica frustules. They are important in food chains that lead to commercially valuable species. Dinoflagellates are smaller than diatoms, and most lack hard parts. They dominate where silica is depleted, particularly in the open oceans, are not always autotrophic, and often bloom explosively. Generally less abundant types of phytoplankton include coccolithophores that are covered in tiny calcareous plates, and silicoflagellates that have a silica shell. Microscopically small ultraplankton, which include bacteria, archaea, and viruses, are extremely abundant but are not yet well characterized.

Zooplankton are either holoplankton that live their entire life cycles as plankton, or meroplankton that spend only their larval stages as zooplankton. Many zooplankton migrate to the surface layer at night to feed and return below the photic zone by day. Holoplankton include copepods, euphausiids, and other crustaceans, foraminifera, radiolaria, and pteropods, as well as gelatinous forms such as jellies, ctenophores, and salps. Meroplankton include eggs, larvae, and juveniles of many invertebrates and fishes.

Nekton.

Nekton are organisms that swim actively. They include many fish species. Sharks and rays are fishes that have cartilaginous skeletons. Many fishes have gas- or oil-filled swim bladders to maintain buoyancy. The nekton also include squid, which are extremely abundant, feed mostly near the surface at night, and migrate below the photic zone by day. Marine mammals, including dolphins, porpoises, other whales, seals, and sea lions, are also nekton. Sea turtles and sea snakes are nektonic reptiles.

Benthos.

Benthic organisms comprise a profusion of species adapted to live on or in the sediment or on hard substrates such as rocks and coral reefs

KEY TERMS

You should be able to recognize and understand the meaning of all terms that are in boldface type in the text. All of those terms are defined in the Glossary. The following are some less familiar or often misused key scientific terms that are used in this chapter and that are essential to know and be able to use in classroom discussions or on exams

abyssal zone	fungi
adsorption	genus
aerobic	gills
algae	grazers
anemones	hadal zone
angle of incidence	hard parts
anoxic	herbivore
anthropogenic	herring
aphotic zone	heterotroph
archaea	holoplankton
autotroph	infauna
bacteria	intertidal zone
baleen	invertebrates
barnacles	kelp
bathyal zone	krill
benthic	limiting nutrient
benthos	littoral zone
bioluminescent	macroalgae
biomass	marine mammals
bloom	meroplankton
calcareous	metamorphosis
carnivore	mixed layer
cartilaginous	mollusks
cephalopods	nekton
cetaceans	nutrient
chemosynthesis	omnivore
chlorophyll	overfishing
chordates	pelagic
cnidarians	photic zone

coccolithophores
colloidal
community
compensation depth
copepods
corals
crustaceans
ctenophores
decomposer
detritivore
detritus
diagenetic
diatoms
diffusion
dinoflagellates
diurnal
ecosystem
enzymes
epifauna
epipelagic zone
eukaryotes
euphausiids
eutrophication
excrete
fauna
fecal pellets
filter feeding
flagella (flagellates)
flora
food chain (web)
foraminifera
frustule
photosynthesis
phototroph
phototrophy
phytoplankton
pinnipeds
plankton
primary production
prokaryotes
protist
pteropods
radiolaria
reptiles
respiration
rocky intertidal zone
salps
saturation solubility
sea cucumbers
sea grasses
sea stars
sea urchins
shellfish
siliceous
species
sponges
standing stock
sublittoral zone
supralittoral zone
swim bladder
trophic level
tunicates
vertebrates
zooplankton

STUDY QUESTIONS

1. Why is it necessary to have primary producers, animals, and decomposers in a marine ecosystem?
2. Dissolved oxygen concentration varies substantially with depth. Describe and explain the distribution of dissolved oxygen in the deep ocean.
3. Why is nitrogen generally the limiting nutrient in the oceans? List the sources of biologically available nitrogen in the photic zone.
4. Of all the organic carbon in the oceans, 99% is in nonliving particulate or dissolved form. Why?
5. Why are most of the world's major fisheries in coastal waters? Why are many major fisheries off the west coasts of the continents? Why are the waters around Antarctica highly productive?
6. List and describe the principal differences between the pelagic and benthic environments. Why are the boundaries between zones of the benthic and pelagic environments defined by depth ranges?
7. At what depths in the pelagic and benthic environments would you expect to find substantial variation in the species composition of the fauna and flora between tropical, mid, and high latitudes? Why?
8. Describe the major types of plankton.
9. Why are phytoplankton small?
10. List the major categories of organisms that constitute the nekton. What are the principal distinguishing characteristics of each category?

CRITICAL THINKING QUESTIONS

1. Very high productivity is found in the circumpolar ocean around Antarctica. This is also the region most often under the hole in the ozone. (a) Does the high productivity indicate that the ozone hole does not have a significant adverse effect on the ocean ecosystem? Explain why or why not. (b) What other information did you use to reach your answer? (c) What other studies or data would you like to have to make sure that your answer is correct?
2. The enhanced greenhouse effect is expected to cause climate changes that will lead to warming of the mixed layer of the oceans by several degrees.
   (a) Hypothesize how this change might affect winds, the characteristics of the pycnocline, and ocean currents.
   (b) Would these changes affect the amount of nutrients available to phytoplankton? If so, how?
3. A number of years ago it was suggested that nuclear reactors should be placed on the seafloor in tropical deep-water areas and other areas of the oceans where the primary production in the mixed layer is nutrient-limited. The intention was that the heat generated by the reactor would cause artificial convection-driven upwelling, increase the supply of nutrients to the mixed layer, and increase primary production.
   (a) Would this proposal work? If not, why not?
   (b) If so, can you suggest reasons (other than the potential for the release of radioactivity) to explain why the idea was not adopted?
4. If you measured the dissolved oxygen concentration carefully in the photic zone during a spring bloom of phytoplankton, describe how you would expect it to change over 24 h and why. Would the changes in concentration during the 24 h be different at different depths within the photic zone? If so, describe how and why.
5. Pelagic food chains that lead to large predatory fishes in the deep oceans far from land tend to be much longer than in coastal regions. What might account for this difference?
6. What is a detritus-based food web? Would you expect detritus based food chains that lead to large fishes that feed on benthic animals to be longer than the pelagic food chains in the overlying water that lead to large carnivorous fishes? Why? Would your answer be different for coastal and deep-ocean regions? Why?
7. Many fewer species of reptiles and mammals live in the oceans than on land, and many more species of fishes and invertebrates live in the oceans than live on land and in freshwater. What do you think are the reasons for these differences?

CRITICAL CONCEPTS REMINDERS

CC4 **Particle Size, Sinking, Deposition, and Resuspension:** Suspended particles in ocean water, including plankton, sink at rates primarily determined by particle size: large particles or plankton sink faster than small particles. Larger plankton species have various adaptations to reduce their sinking rate. Small organic particles can be aggregated into fecal pellets that are larger than the individual particles and, thus, sink faster.

CC8 **Residence Time:** The residence time of seawater in a given segment of the oceans is the average length of time the water spends in the segment. In the deep ocean trenches water column water mass residence time can be long and this affects the character of the biota that inhabits this zone.

CC10 Modeling: Complex environmental systems including the cycling of nutrients among ocean water, living matter, suspended particles and sediments can best be studied by using conceptual and mathematical models. Many oceanographic and climate models are extremely complex and require the use of the fastest supercomputers.

CC14 Phototrophy, Light, and Nutrients: Phototrophy (which includes photosynthesis) and chemosynthesis are the two processes by which simple chemical compounds are made into the organic compounds of living organisms. Photosynthesis depends on the availability of carbon dioxide, light, and certain dissolved nutrient elements including nitrogen, phosphorus, and iron. Chemosynthesis does not use light energy and instead depends on the availability of chemical energy from reduced compounds which occur only in limited environments where oxygen is depleted.

CC15 Food Chain Efficiency: All organisms use some of their food as an energy source in respiration and for reproduction, and also lose some in excretions including wastes. On average, at each level in a food chain, only about 10% of food consumed is converted to growth and biomass of the consumer species.

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