

## AQUATIC HABITATS

### 1. Introduction:

70.8% of the surface is covered with water. Of the estimated  $1.403 \times 10^9$  km<sup>3</sup> of water on the globe, 2% is ice pack (or glaciers), 97.61% is seawater, and only 0.3% is freshwater (in lakes, streams, and groundwater aquifers). Thus, despite their crucial role for maintaining plants, animals, and humans on land, freshwaters comprise only a small proportion of the global water resources. Because of its huge volume and relatively small fluxes of incoming and outgoing waters, the residence time for water in the oceans is long (~4000 years). In contrast, the residence time of water in lakes, ponds, and rivers is relatively brief (~2 weeks to infiltrating through subsoil and entering the subsurface, the incoming water may re-emerge in surface habitats within ~2 weeks or may be trapped in deep aquifers for as long as 10,000 years.

### 2. Fresh water habitats:

Major freshwater resources of the globe include glaciers in polar and/or high elevation zones. Lakes are termed *lentic* environments because their waters are calm and slow. Rivers and streams are *lotic* habitats because they feature water moving in response to gravity. Though only 0.0001% of the water on the Earth occurs in river channels, running waters are of enormous ecological and biogeochemical significance. They play key roles in the hydrologic cycle, deliver water across continents, and serve as critical habitats for many important aquatic species. Immediately derived from atmospheric precipitation, freshwaters generally have low dissolved concentrations of salts. After contacting fallen water, rock and soil generally contribute inorganic constituents to concentrations in the millimolar range. The major common ions in freshwaters are  $\text{SO}_4^{2-}$ ,  $\text{Cl}^-$ ,  $\text{Ca}^{+2}$ ,  $\text{Mg}^{+2}$ ,  $\text{Na}^+$ . Localized conditions throughout the globe contribute other dissolved and suspended aqueous constituents that determine major water quality characteristics such as pH, buffering capacity, dissolved organic matter, particulate organic matter, alkalinity, color, and turbidity.

#### 2.1 Freshwater Microbial Communities

Freshwater habitats contain much lower salt, usually less than 0.1%. The study of aquatic systems is called limnology. Like the marine water column, the profile of a lake water column is defined by depth, aeration, and temperature. Large, undisturbed lakes are usually **oligotrophic**, with dilute concentrations of nutrients and microbes. The warm upper water layer above the thermocline is called the epilimnion. The epilimnion water is warm, well mixed, and oxygenated relative to the lower layers of water that are isolated from the atmosphere. It supports oxygenic phototrophs such as algae and cyanobacteria.

Below the epilimnion lies a thermocline, a steep transition zone to colder, denser water below. The epilimnion reaches only about 10 m in depth, much shallower than the marine euphotic zone. In a lake, the depth of light penetration varies greatly, depending on the concentration of microbes and particulate matter.

At the edge of the lake, where the upper layer becomes shallow enough for rooted plants, is the **littoral zone**.

In the deeper water, below the epilimnion, lies the hypolimnion, a region that becomes anoxic in lakes that are eutrophic (rich in organic nutrients).

When deeper water is anoxic, it supports only anaerobic microbes. These include a series of anaerobic phototrophs that do not produce  $O_2$ . Enough light may penetrate to support anaerobic  $H_2S$ -splitting phototrophs such as *Chlorobium* and *Rhodospseudomonas*. Although  $H_2S$  photolysis provides less energy than oxygenic  $H_2O$  photolysis, these bacteria have evolved in a productive niche by using chlorophyll pigments whose spectrum extends into the infrared. Light in the red and infrared portions of the spectrum extends the deepest into the lake column. Light with wavelengths in this range cannot be used by oxygenic phototrophs because the photon energy is insufficient to split water. The less efficient  $H_2S$  photolyzers, however, can harness the energy of red and infrared radiation. The green and purple phototrophs overlap metabolically with anaerobic heterotrophs and lithotrophs that reduce oxidized minerals. Some bacteria, such as *Rhodospirillum rubrum*, can grow anaerobically with or without light; others grow only by anaerobic catabolism, unassisted by light. At the bottom of the water column, the water meets the sediment (benthos). In the benthic sediment, gradients develop in which successive electron acceptors become reduced by anaerobic respirers and lithotrophs. Electron acceptors that provide the most energy are consumed first; as each in turn is depleted, the electron acceptor with the most energy is consumed next. First, molecular oxygen is used to oxidize organic material and reduced minerals such as  $NH_4^+$ . As molecular oxygen falls off, bacteria use nitrate ( $NO_3^-$ ) from oxidized ammonium ion as an electron acceptor to respire on remaining organic material. As the nitrate is used up, still other bacteria use manganese ( $Mn^{4+}$ ) as an electron acceptor, followed by iron ( $Fe^{3+}$ ) and sulfate ( $SO_4^{2-}$ ). Reduction of sulfate leads to  $H_2S$ , which eventually returns to the upper layers supporting anaerobic photolysis. Reduction of  $CO_2$  by  $H_2$  produces methane ( $CH_4$ ). Methane collects below and sometimes ignites when it escapes to the surface. Methane is of global concern as a potent “greenhouse gas”.

Throughout the water column, fungi and protists serve as grazers and predators on algae and bacteria, respectively. They also interact with invertebrates and fish as parasites. Other important consumers are the viruses, which lyse about half of microbial populations in lakes, as they do in the ocean. Viruses serve an important function by limiting the number of microbes and keeping the water clear enough for light to penetrate. Note that all fish and invertebrates need access to the epilimnion for oxygen. Only anaerobic microbes can grow entirely in the anoxic hypolimnion. Thus, problems arise when effluents entering a lake carry high concentrations of nutrients causing overgrowth of phototrophs. Initially, the phototrophs increase the oxygen content of the epilimnion. But, the cell mass of the phototrophs sinks to the bottom, where overgrowth of heterotrophs depletes oxygen, causing **eutrophication**. So the anaerobic zone near the bottom of the lake grows larger, meaning that the boundary between the aerobic and anaerobic zones rises. In a eutrophied lake, fish die off owing to lack of oxygen, which heterotrophic microbes have

consumed. Such a lake is said to have a high level of biochemical oxygen demand (BOD). Common causes of eutrophication include:

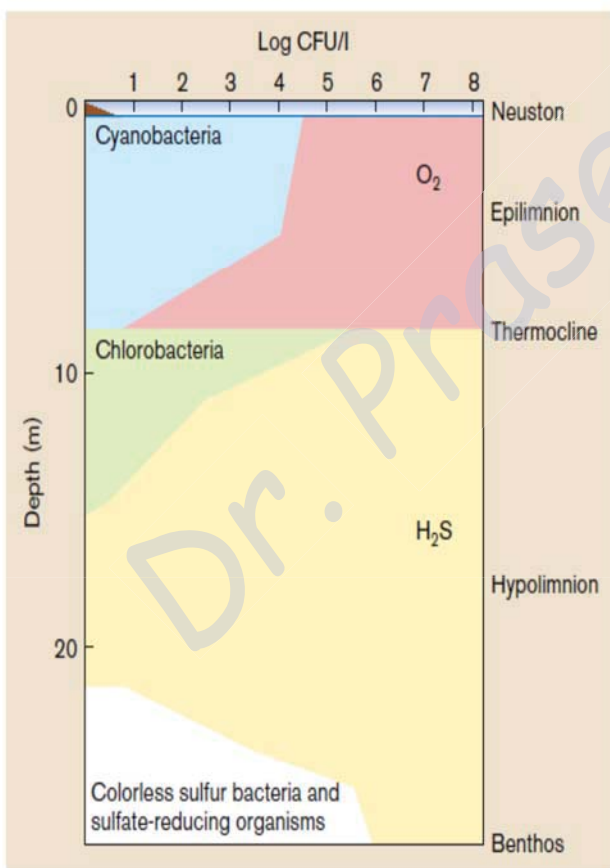
- **Phosphates.** Because phosphorus is commonly a **limiting nutrient** (nutrient in shortest supply) for algae, addition of phosphates from detergents and fertilizers can lead to an **algal bloom** in which algae overgrow the water surface. The algae die, and their consumption by heterotrophic bacteria depletes oxygen, suffocating fish.

- **Nitrogen** from sewage effluents can lead to algal blooms by relieving nitrogen limitation.

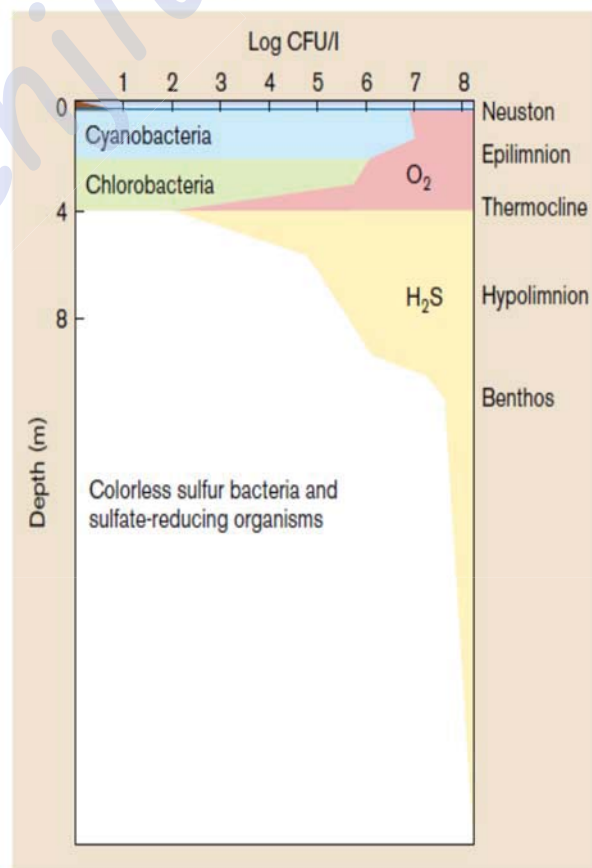
- **Organic pollutants** from sewage effluents overfeed heterotrophic bacteria, depleting the epilimnion of oxygen.

A **eutrophic lake** is one in which the lower layers have become depleted of oxygen as a result of overgrowth of microbial producers. Thermal stratification may break up, and the lake may mix one to several times per year, thus re-oxygenating the entire lake. A permanently **eutrophic** lake typically supports ten times the microbial concentrations of an oligotrophic lake, but shows greatly decreased animal life.

A. Oligotrophic lake (dilute nutrients)



B. Eutrophic lake (rich nutrients)



### 3. Oceanic habitat:

Each major oceanic basin (especially the Pacific, Atlantic, Indian, Antarctic, and North Atlantic) offers a unique set of geologic, physical, and biotic features. Oceanographers have defined key circulatory patterns of ocean waters that have major climatic and biotic implications. Major ocean currents result from a combination of the Earth's rotation and atmospheric forces. Vertical migration of ocean water also plays a critical role in biosphere function. The three major circulation loops into the Atlantic, Pacific and Indian Oceans, respectively, are driven by density gradients in which cold, saline waters descend to the ocean bottom. These zones of down-welling are balanced by zones of up-welling, often along continental margins. The horizontal and vertical circulation patterns lead to heterogeneous nutrient distribution patterns (especially for N, P, and Fe) that directly govern the productivity of photosynthetic phytoplankton in ocean waters. The oceans are nutritionally and biologically heterogeneous. Marine water is distinguished by its salt concentration, averaging 3.5%. The major ions are  $\text{Na}^+$  and  $\text{Cl}^-$ , with significant levels of sulfate, iodide, and bromide. Marine salt concentration is high enough to prevent growth of many aquatic and terrestrial bacteria such as *E. coli*, although salt-tolerant organisms such as *Vibrio cholerae* grow well over a broad range of salt concentration. Phytoplankton productivity indirectly governs fish productivity and harvest.

Characteristics	Marine habitat	Freshwater habitat	Groundwater habitat
<b>Physical</b>			
Global location	Ocean basins	Continental depressions, valleys, basins	Beneath continental subsoils
Global surface area (%)	70.8	0.2	29.0
Global water volume (%)	94	<0.01	4
Residence time for water	~4000 years	2 weeks to ~10 years	2 weeks to 10,000 years
Hydrologic regime	Relatively deep water; very low percentage solids; little, if any, unsaturated zone; hydrologic stratification	Relatively shallow water; low percentage solids; little, if any, unsaturated zone, though some streams are ephemeral; hydrologic stratification	Interstitial water in solid matrix of variable porosity and variable degree of saturation; unsaturated zone may be substantial; hydrologic and geologic stratification
<b>Biological</b>			
Biota	Multicellular and unicellular algae; animals, protists, fungi, and prokaryotes	Multicellular and unicellular algae; animals, protists, fungi, and prokaryotes	Primarily prokaryotes; protists, rare algae, and cave-dwelling animals
Food chain	Photosynthesis, rare chemosynthesis, heterotrophy	Photosynthesis, rare chemosynthesis, heterotrophy	Heterotrophy, chemosynthesis at depth
Nutrient status	Nutrient-poor regions; productivity in up-welling zones	Broad range of oligotrophic, mesotrophic, and eutrophic conditions	Low levels of DOC and other nutrients common, but many nutrient-rich waters, i.e., beneath landfills
Water flow	Flow paths well defined	Flow paths well defined	Flow paths difficult to define
DOC, dissolved organic carbon.			

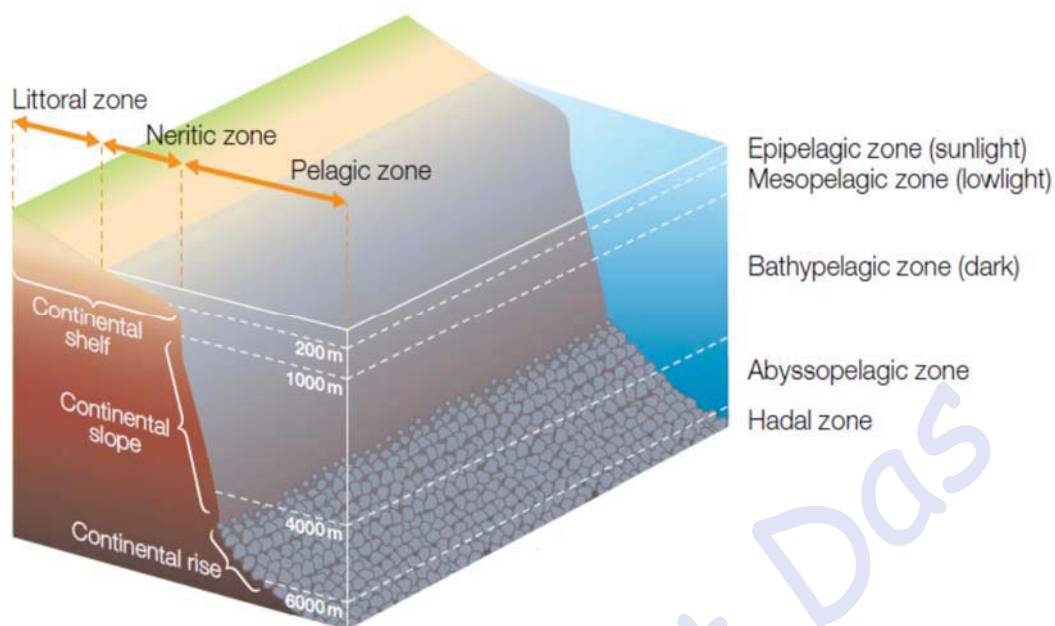
Marine waters vary considerably with respect to temperature, pressure, light penetration, and concentration of organic matter. The vast majority of the oceans are deep, dark, and cold. Ninety percent of the volume of ocean waters remains at the stable temperature of approximately 3°C. The rest may be influenced by sunlight at the surface, by hydrothermal vents that mark the boundaries of tectonic plates along mid-ocean ridges, and/or by the continental margins.

The dissolved materials currently present in the oceans are only a small fraction of those that have been delivered to the oceans by rivers over geologic time. Some constituents from incoming river waters are removed from the ocean, as mineral or other precipitates. Overall, the composition of seawater is regulated by two key complementary mechanisms:

- (i) Control by chemical equilibria between seawater and oceanic sediments; and
- (ii) Kinetic regulation by three interacting rates: supply of individual chemical components, biological processes, and mixing processes.

### 3.1 Zonation at the ocean–continent interface

- ✓ The **littoral zone** is the extremely shallow periphery influenced by waves and tidal action. Coastal regions show the highest concentration of nutrients and living organisms and considerable light penetration to sustain both photosynthetic and heterotrophic microorganisms.
- ✓ The **neritic zone** is a slightly deeper boundary along the continental shelf, rich in minerals and organic matter with moderate light penetration that harbors photosynthetic, heterotrophic and a few lithotrophic microorganisms.
- ✓ Deep ocean waters beyond the continental slope are known as the **pelagic zone**.
- ✓ Sunlight penetrates the upper pelagic (epipelagic) zone to about 200 m. Epipelagic layer may be further divided into the neuston and the euphotic zone. The **neuston** is the air-water interface. Although extremely thin, the neuston layer contains the highest concentration of microbes. Many algae and protists have evolved so as to “hang” from the layer of surface tension. The **euphotic zone**, or **photic zone**, is the upper part of the water column up to a depth of about 200 m that receives light for phototrophs.
- Beneath this is a zone of very dim light (**mesopelagic**) which extends an additional 800 m. Only heterotrophs and lithotrophs can grow in this oceanic sub-zone as phototrophs cannot grow here due to lack of sunlight, but this zone is rich in inorganic nutrients released from continental slope and hydrothermal vents.
- Deeper still are the **bathypelagic** and **abyssopelagic zones**, which are very dark with no ecological productivity and very little biodiversity.
- The **hadal** pelagic extreme is the Mariana Trench (in the Pacific Ocean northeast of Indonesia), 12,000 m below the ocean surface.



Vertical cross-section of the continental shelf.

**Benthos:** The **benthos** includes the region where the water column meets the ocean floor, as well as sediment below the surface. Organisms that live in the benthos, such as those of thermal vent communities, are called **benthic organisms**.

**Thermocline:** An important determinant of marine habitat is the **thermocline**, a depth at which temperature decreases steeply and water density increases. A thermocline typically exists in an unmixed region. At the thermocline, a population of heterotrophs will peak, feeding on organic matter that settles from above.

**Why hydrothermal vents are rich in lithotrophic microorganisms though oxygen is limited in that habitat?**

The open ocean is largely oligotrophic (extremely low concentration of nutrients and organisms). The concentration of heterotrophic microorganisms determines the **biochemical oxygen demand (BOD)**, the amount of oxygen removed from the water by aerobic respiration. The open ocean has such a low concentration of organisms that the BOD is extremely low; therefore, the dissolved oxygen content is high. This explains why enough oxygen reaches the ocean floor to serve lithotrophs growing at hydrogen sulfide thermal vents.

The term **plankton** refers to organisms that float passively in water. The term is used loosely, as it includes motile microorganisms. Microbial plankton are divided into groups based on their approximate size ranges as tabulated below-

**Table 21.4** Microbial plankton: size categories.

Size category	Microbial group	Size range (Micrometer)
Microplankton	Eukaryotes	20–200
	Microalgae—phytoplankton	
	Heterotrophs, ciliates—zooplankton	
	Mixotrophs and symbiotic protists	
	Microscopic multicellular plants and invertebrates	
Nanoplankton	Prokaryotes: Cyanobacteria (filamentous)	2–200
	Eukaryotes	2–20
	Nanoalgae	
Picoplankton	Heterotrophs and mixotrophs—flagellates	
	Prokaryotes	
	Bacteria	0.5–1.0
	Phototrophs (phytoplankton)	
	Prochlorophytes	0.5–2.0
	Cyanobacteria (coccoid)	1.0–2.0
	Lithotrophs (oxidize $\text{NH}_4^+$ , $\text{H}_2\text{S}$ , etc.)	0.3–1.0
	Heterotrophs (zooplankton)	0.3–1.0
	Archaea	
	Eukaryotes	
Picoalgae—phytoflagellates	1.0–2.0	
Heterotrophic protists—zooflagellates	1.0–2.0	
Femtoplankton	Viruses	0.01–0.02

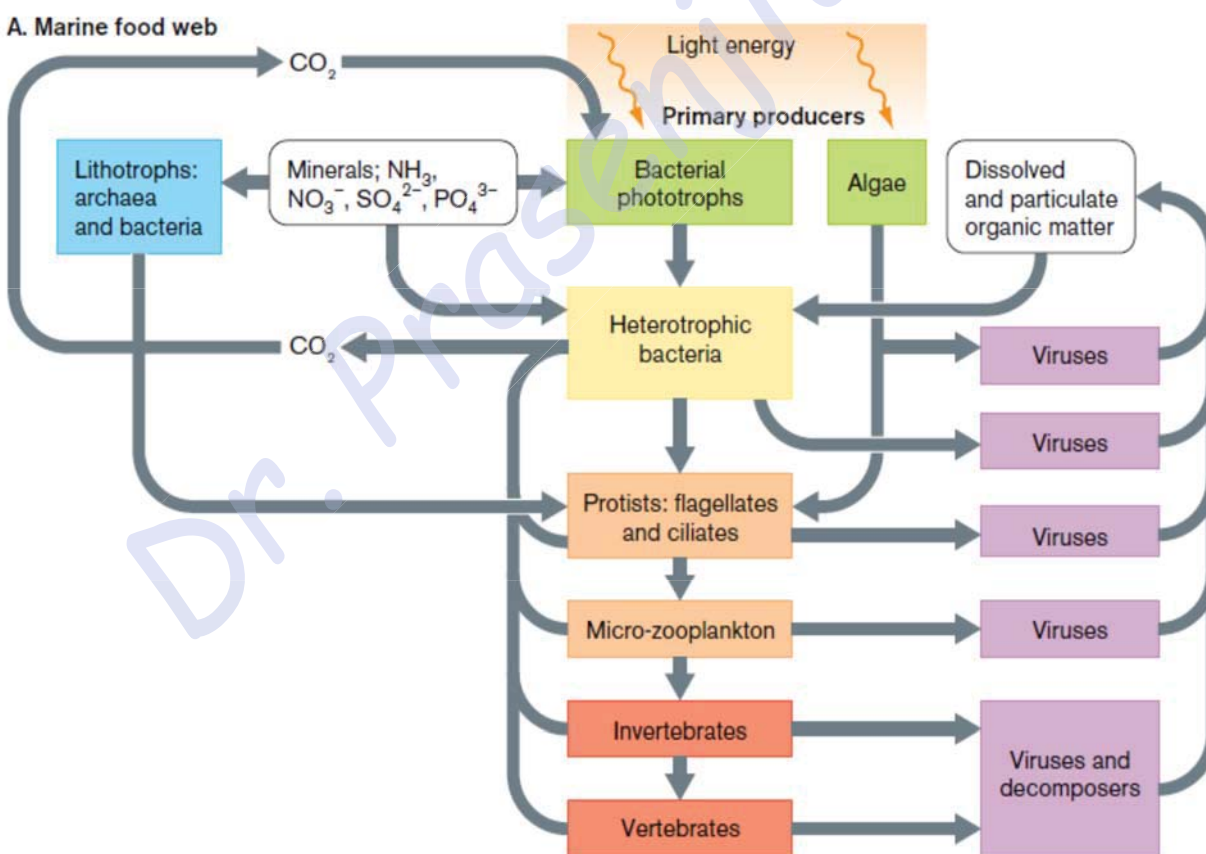
Source: Kirchner, D. 2000. *Microbial Ecology of the Ocean*.

### 3.2 Planktonic Food Webs

Marine plankton interact with each other as producers and consumers in a food web. The diagram of a food web is often called a “spaghetti diagram” because so many trophic interactions cross each other in various directions. The phototrophic producers are known as **phytoplankton**. Examples of phytoplankton include tiny *Prochlorococcus*, predominating in the upper photic layer, and *Synechococcus*, in a slightly deeper layer reached by longer wavelengths of light. In addition, there are myriad forms of algae, such as diatoms and dinoflagellates. Bacterial phototrophs (picoplankton and nanoplankton) are mainly consumed by protists and by heterotrophic bacteria and archaea. These, in turn, are consumed by larger protists, which feed small invertebrates, which feed larger invertebrates and ultimately vertebrates such as fish. All levels of microbial plankton, however, are subject to intense predation by viruses. The degree of viral predation is difficult to measure, but recent studies indicate that cell lysis by viruses

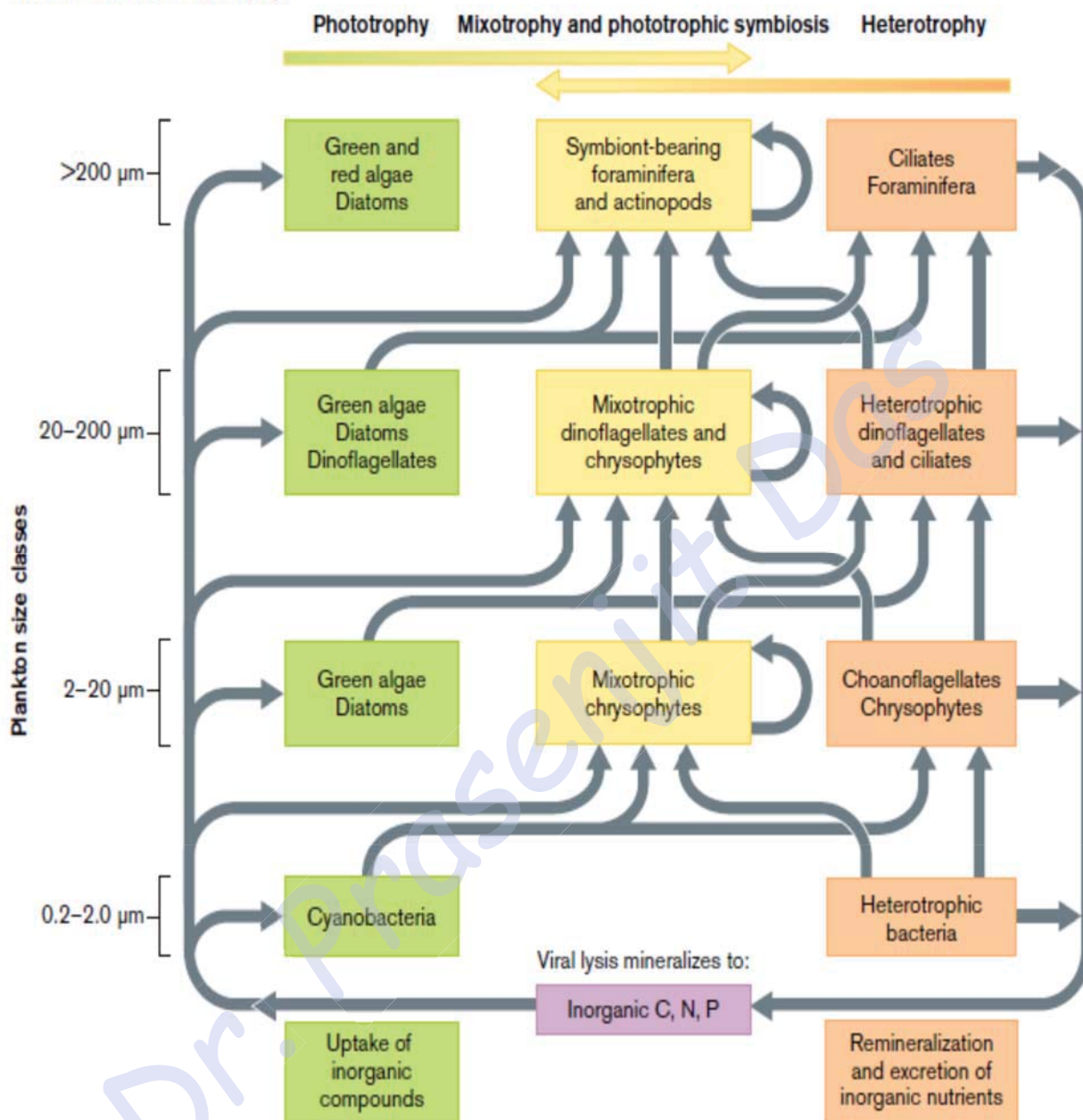
mineralizes (breaks down to  $\text{CO}_2$  and minerals) about half of microbial biomass. Virus particles represent a significant sink for carbon and nitrogen. They accelerate the return of minerals to producers and necessitate a larger base of producers to sustain the ecosystem. Ocean ecosystems contain a large number of trophic levels, of which the top consumers include fish and humans. Because each trophic level spends 90% of its biomass for energy, ecosystems require a huge lower foundation to sustain the highest-level consumers.

However, actual food webs are far more complex. One source of complexity is that many “algal protists” such as chrysophytes (golden algae) and dinoflagellates are actually **mixotrophs**, organisms conducting both photosynthetic and heterotrophic metabolism. Mixotrophs include secondary endosymbiont algae, such as Sargassum weed, as well as protists containing cyanobacterial or algal endosymbionts. The scheme is further complicated by the existence of elaborate mutualistic associations between different kinds of protists, algae, and bacteria. Microbial flora includes numerous unique species associated within or adherent to macroscopic organisms, including invertebrates, fish, and marine mammals.





### B. Food web with mixotrophy



### 3.3 The Ocean Floor

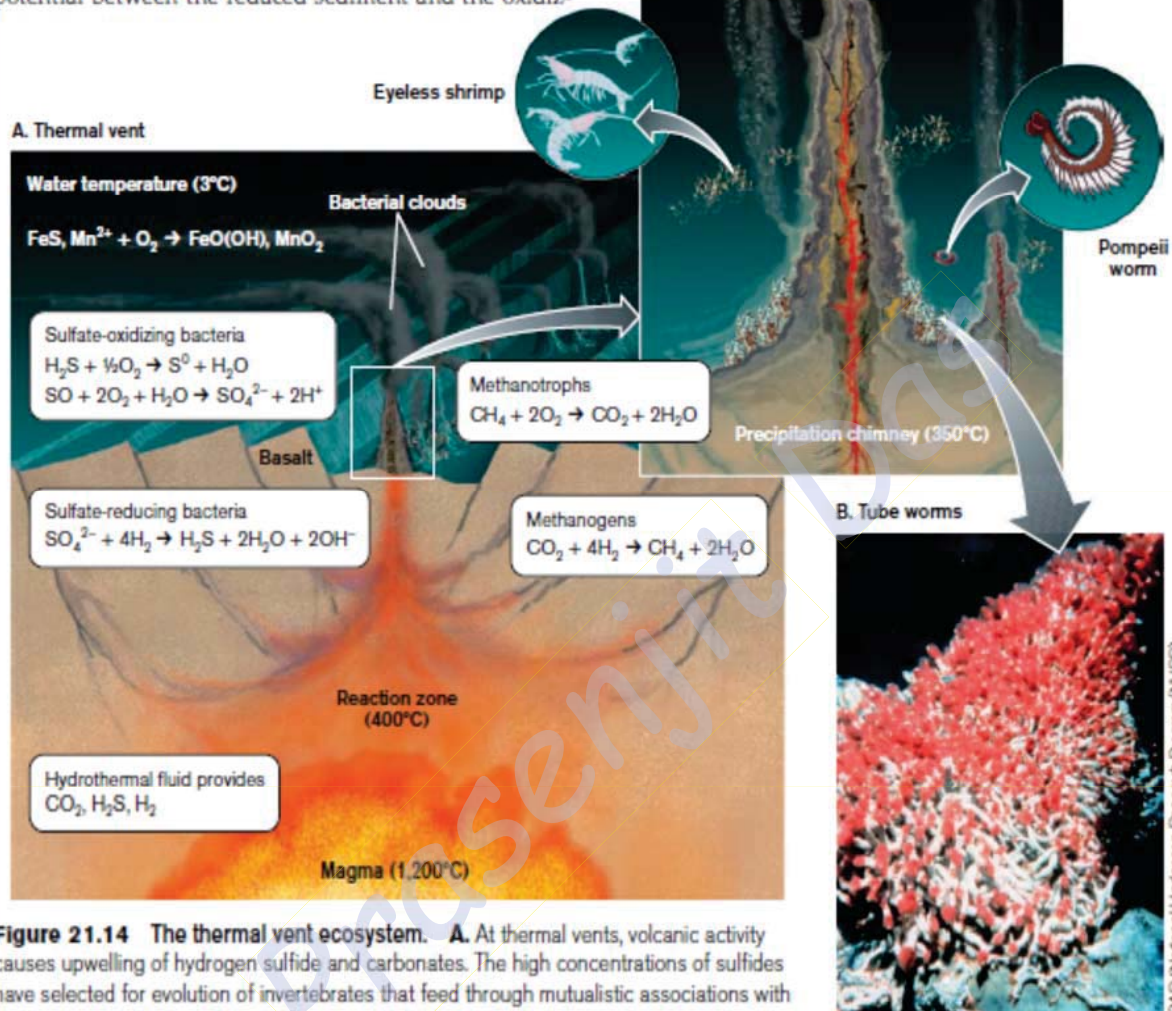
The ocean floor (benthos) experiences extreme pressure from the water column. Most organisms that live there are pressure-dependent species, known as **barophiles**. Barophiles require high pressure for growth, failing to grow when cultured at sea level. In the absence of light, heterotrophic bacteria depend on detritus from above as their carbon source; but by the time any material reaches the benthos, its food value has largely been depleted by prior consumers. Thus, at the benthos, with less food available, microbial decay occurs at a much lower rate than at sea level. The cold temperatures (about  $10^{\circ}\text{C}$ ) also limit microbial growth. The ocean floor provides reduced inorganic minerals such as iron sulfide ( $\text{FeS}$ ) and manganese

( $\text{Mn}^{2+}$ ) that can combine with dissolved oxygen to drive lithotrophy. Lithotrophic metabolism by microbes in the sediment generates a permanent voltage potential between the reduced sediment and the oxidizing water.

### **3.4 Hydrothermal Vent ecosystem**

The benthic redox gradient is enhanced dramatically at thermal vents, where volcanic activity causes upwelling of hydrogen sulfide ( $\text{H}_2\text{S}$ ),  $\text{H}_2$ , and carbonates. These minerals are brought up by seawater that seeps through the sediment until it reaches a magma pool, where it becomes superheated and rises to the surface as steam. Sulfate-reducing bacteria reduce sulfate from seawater with  $\text{H}_2$  upwelling from the vent fluids, to form  $\text{H}_2\text{S}$ . As the  $\text{H}_2\text{S}$  rises, it is oxidized by sulfur-oxidizing bacteria such as *Thiomicrospira*. The vent waters also support methanogens, and the methane they produce becomes oxidized by methanotrophs. The high concentrations of sulfides at thermal vents have selected for a remarkable evolution of invertebrate species that feed through mutualistic associations with  $\text{H}_2\text{S}$ -oxidizing bacteria. The  $\text{H}_2\text{S}$  oxidizers fix carbon from the carbonates, generating organic metabolites that feed their animal hosts—species of worms, anemones, and giant clams, all closely related to surface-dwelling species that would be poisoned by  $\text{H}_2\text{S}$ . The tube worm *Riftia* is colored bright red by a pigment carrying  $\text{H}_2\text{S}$  and  $\text{O}_2$  in its circulatory fluid. The worm has evolved such a complete dependence on its symbionts that it has lost its own digestive tract.

can combine with dissolved oxygen to drive nitrotrophy (discussed in Chapter 14). Lithotrophic metabolism by microbes in the sediment generates a permanent voltage potential between the reduced sediment and the oxidiz-



**Figure 21.14** The thermal vent ecosystem. **A.** At thermal vents, volcanic activity causes upwelling of hydrogen sulfide and carbonates. The high concentrations of sulfides have selected for evolution of invertebrates that feed through mutualistic associations with  $\text{H}_2\text{S}$ -oxidizing bacteria. The  $\text{H}_2\text{S}$  oxidizers fix carbon from the carbonates, generating organic metabolites that feed their animal hosts. **B.** Vent bacteria within the gills of tube worms provide energy from oxidation of hydrogen sulfide. Source: A. Maier, et al. *Environmental Microbiology*.