

Marine Microbiology in the Oligotrophic Ocean
Expert Factsheets
Giovannoni Lab, Oregon State University

Lesson and materials developed by Chris Suffridge, Chih-Ping Lee, Stephen Noell, Quinn Washburn, and Sarah Wolf

Scientific Background

The ocean covers 70% of Earth's surface and has an average depth of 4000 meters. Every milliliter of seawater contains over a million microbial cells. Approximately 40% of the ocean is classified as oligotrophic, meaning it is a nutrient desert; in these conditions microbial life dominates (Polovina et al., 2008). All microorganisms living in the ocean are classified as plankton and cannot be seen with the naked eye. The term plankton is broad, it refers to any organisms unable to swim against ocean currents; instead, they drift with the movements of the ocean. There are many types and sizes of plankton, including: viruses (0.02 to 0.2 μm); bacteria, called bacterioplankton (0.2 to 2 μm); eukaryotic protists, including phytoplankton and grazers (1 μm to 20 μm); and small zooplankton like copepods and fish larvae (20 μm to 200 μm) (Figure 1) (Finkel et al., 2010; Sherr, E., & Sherr, B). Marine microorganisms form the basis of every marine food web. The carbon dioxide that phytoplankton fix with photosynthesis travels throughout the food web and up through trophic levels until it eventually becomes the carbon that makes up fish, sharks, whales and other megafauna that make up the apex trophic level (Worden et al., 2015).

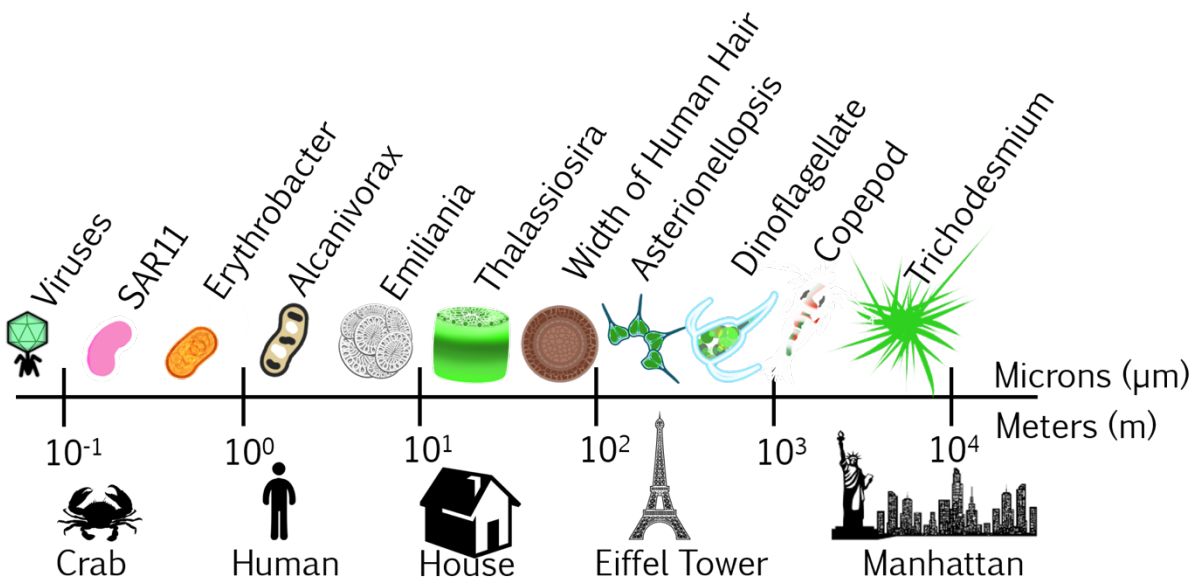


Figure 1: Comparing the size range of marine microbes (microns, top scale) with relative macroscale objects (meters, bottom scale). This figure is adapted with permission from Finkel et al. (2009).

Phytoplankton, including photosynthetic bacteria and eukaryotes, are responsible for about half of the global carbon fixation, which means that they also produce 50% of the Earth's

oxygen (Field et al., 1998). Much of the carbon fixed by phytoplankton in the oceans is rapidly returned to the atmosphere via the heterotrophic activity of bacterioplankton. SAR11 is a heterotrophic bacterioplankton, and the most abundant organism on Earth, estimated to make up 25% of the world's planktonic organisms (Morris et al., 2002). SAR11 cells alone consume between 6% and 37% of the carbon fixed by all of Earth's phytoplankton (White et al., 2019).

Up to 1.3% of the carbon dioxide that phytoplankton fix each year will remain trapped in the ocean for thousands to millions of years, due to a process called the Microbial Carbon Pump (Legendre et al., 2015). Marine microorganisms consume more carbon dioxide each year via photosynthesis than they produce via respiration making Earth's oceans a carbon dioxide sink. Carbon dioxide can be trapped in the ocean after it is made into sugars by phytoplankton photosynthesis. These sugars are converted into biomolecules like lipids and amino acids, that are then incorporated into the phytoplankton's cellular components. When these phytoplankton die, they begin to sink. As that sinking occurs, heterotrophic bacterioplankton consume the phytoplankton's biomass, using it either as an energy source or recycling the biological building blocks, like amino acids, into their own cells. Bacterioplankton use the most energy rich, easy-to-consume molecules first. As a result, the deep ocean becomes littered with energy-poor carbon compounds that very few organisms can use. In the final step of the Microbial Carbon Pump, the portions of each dead phytoplankton cell that are not consumed while sinking end up on the ocean floor where they are buried for millennia in thick sediment layers.

The amount of carbon dioxide stored in the Earth's oceans is 50 times greater than all of the carbon in the atmosphere (Rackley, 2010). The Microbial Pump has allowed the ocean to absorb and sequester the additional atmospheric carbon dioxide produced by anthropogenic activities over the past two centuries. However, we are now rapidly approaching a tipping point where the ocean's natural processes will no longer be able to compensate for the continued added carbon dioxide, which will result in global-scale environmental changes, including climate change. Understanding how marine microbes function individually and as communities helps scientists predict the outcomes of global scale changes brought on by anthropogenic carbon dioxide production (Bindoff et al., 2019).

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Abiotic Factors

Important non-living components of ecosystems.

Description: An ecosystem consists of not just living organisms and biotic interactions; abiotic factors, defined as all the non-living parts of an ecosystem, are equally important to the biotic components. Both physical conditions and chemical nutrients are critical because they interact with living organisms and determine the community structure. Physical conditions and **nutrient** availability are two primary abiotic factors. In the ocean, physical conditions, such as temperature, **salinity**, depth, and **dissolved oxygen** provide structure for the habitat for marine microbes. A change in physical conditions within an ecosystem can result in a shift of microbial **community structure**. For example, in winter when the temperature is lower and the wind above the sea surface is stronger, the water is colder and more turbulent compared to summer, resulting in a clear seasonal change in the microbial community structure. Nutrient availability can influence the growth of microbes because each microbe has its own requirements to grow and survive, and nutrients are rarely present in high enough concentrations to prevent competition between organisms. Sunlight is an energy source for phytoplankton via the process of photosynthesis. By taking up the available nutrients (like nitrogen, phosphorus, iron, etc.) into their cells, phytoplankton can increase their biomass. Sometimes an **algal bloom** can be found when temperature is warm, light intensity is increased, and high concentrations of nutrients are available. Heterotrophic Bacteria grow by using **dissolved organic matter (DOM)** which is produced by phytoplankton.

Carbon Cycle: Nutrients are the base of the trophic pyramid. Phytoplankton require light, CO₂, and nutrients in order to grow using photosynthesis. The biomass they produce can be consumed by bacteria or protists. Bacteria can take up the dissolved organic matter which is easily absorbed (**labile DOM**), leaving the less absorbed part of DOM (called **recalcitrant DOM**) in the ocean, a process called **microbial carbon pump**. When the microbes in the surface ocean dies, the cell debris may aggregate into particles and sink into the deep ocean. These sinking particles are called **marine snow** and are important transport of carbon from the surface of the ocean into deep ocean.

Ecosystem Role: In an ecosystem, abiotic factors not only provide what the living organisms need to grow, but also impose a pressure on them. When the abiotic factors change, the living organisms have to respond to such a change, either changing the size of their population, or changing the community structure. Therefore, the dynamics of abiotic factors is important in shaping the composition of living organisms in an ecosystem.

Key Terms

Nutrients: the chemicals required by living organisms to support their growth, survival, and reproduction. These chemicals include Carbon, Nitrogen, Phosphorus, Sulfur, and Iron. In the ocean most of these nutrients are not present in a surplus, so living organisms must compete with each other to acquire the nutrients they require.

Salinity: the content of salts in seawater. Salinity is important to microbes because they may not tolerate a large change of salinity, since the cells may shrink (or burst).

Dissolved oxygen: the content of oxygen dissolved in water. oxygen is necessary by many bacteria and protists due to its role for energy generation.

Community structure: the composition of all the living organisms in a given locale and at a specific time.

Algal bloom: a rapid increase of algal cells in freshwater or seawater systems. An occurrence of algal bloom may be associated with high input of nutrients and/or an optimal temperature for the algae. Algae

bloom may be identified by a change of color in the water, or sometimes even can be seen by satellite images.

Dissolved organic matter (DOM): the fraction of organic matter that is solubilized (usually $< 0.7 \mu\text{m}$ in their sizes) in water. The amount of carbon in the marine DOM is nearly comparable to the amount in the atmospheric CO_2 .

Labile DOM: the fraction of DOM that is easily used by bacteria. Labile DOM can often stay in the ocean from days to weeks.

Recalcitrant DOM: the fraction of DOM that is less easily used and hard to be degraded by bacteria. Recalcitrant DOM often stay in the ocean for more than thousand years.

Microbial carbon pump: a way of carbon storage from the atmosphere to the recalcitrant DOM in the ocean. Photosynthesis by phytoplankton can draw down CO_2 from the atmosphere. DOM can be produced by phytoplankton exudation, zooplankton grazing, and viral lysis. The labile fraction of the DOM will be degraded first by bacteria. The recalcitrant DOM remains intact in the ocean and the carbon inside can be regarded as a storage for the atmospheric carbon.

Marine snow: the cell debris and aggregates of organic matter sinking from surface to the deep ocean. Marine snow is a way to transport carbon into the deep ocean. It is also a food source for a lot of bacteria in the deep.

Light: an energy source for phytoplankton via photosynthesis. Light in the ocean is rapidly absorbed by seawater so light can only reach a top layer of the ocean less than $\sim 100 \text{ m}$.

Ultraviolet light (UV): a light with a high energy power and can damage cells.

Nitrogen (N): a nutrient and is a constitute of biochemical molecules like proteins or DNA.

Phosphorus (P): a nutrient and is a constitute of biochemical molecules like cell membranes or DNA.

Iron (Fe): a nutrient and is an important constitute by many enzymes in cells.

Arsenic (As): a toxin that can damage or kill cells.

More resources

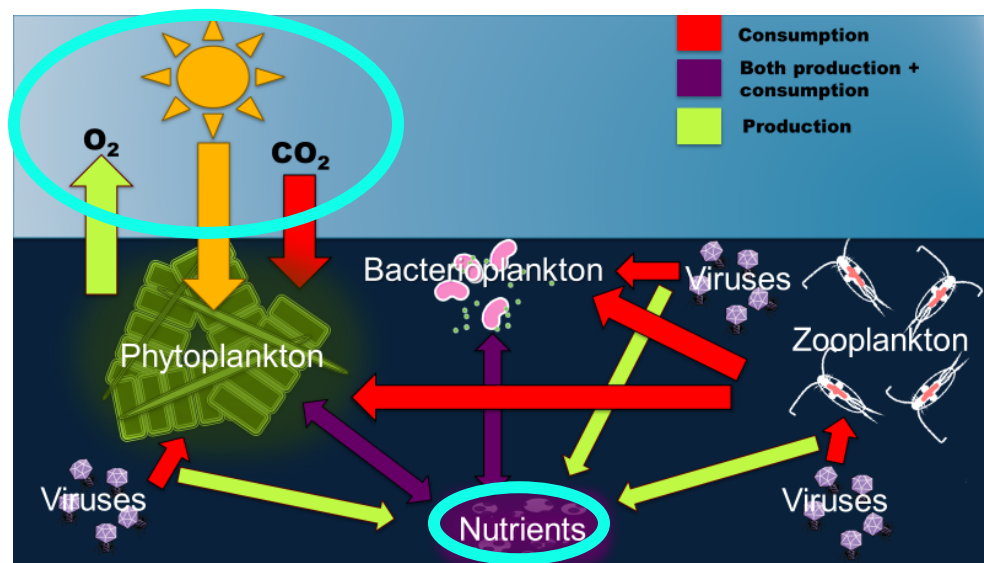
Abiotic & biotic factors in ecosystems: <https://tinyurl.com/yygx4ozq>

Coexisting in a sea of competition: <https://tinyurl.com/y34ky9pr>

Marine Snow and Fecal Pellets: The spring rain and food to the abyss: <https://tinyurl.com/yxsjwwaw>

What is a harmful algal bloom: <https://tinyurl.com/y59xf7un>

Microbial carbon pump in a changing ocean: building models for the future: <https://tinyurl.com/y3psdt3k>





Heterotrophs

Organisms that consume other organisms.

Description: Heterotrophs are defined as organisms that cannot produce their own food or energy. Unlike phototrophs who use light from the sun for energy, heterotrophs must consume other heterotrophs, plants, or organic matter to meet their nutritional requirements. **Heterotrophic** marine bacteria are called **bacterioplankton**. They need organic carbon and have to obtain it, either directly or indirectly from phytoplankton. **Secondary consumers** (Choanoflagellates and other protists) are organisms that feed on primary consumers (bacterioplankton). **Zooplankton** are small heterotrophic animals who play a role in aquatic food webs and act as a resource for consumers on higher trophic levels, including fish.

Carbon Cycle: Heterotrophs and autotrophs are partners in biological carbon exchange. Heterotrophs acquire organic carbon compounds from the autotrophs by consuming them and breaking them down via respiration for cellular energy.

Ecosystem Role: Heterotrophs function as consumers in the food chain. Secondary consumers, such as Zooplankton, depend on the success of primary consumers, bacterioplankton. Both primary and secondary heterotrophic consumers' use of organic matter for energy provides a critical link within the global carbon cycle, connecting trophic levels.

Key Terms

Actinobacteria: bacteria that grow in long strands and contribute to the breakdown and recycling of organic compounds.

Alcanivorax: rod-shaped bacteria found in seawater containing crude-oil because the bacteria use compounds in oil as a source of energy.

Alteromonas: a curved, rod-shaped bacterium found in various ocean waters worldwide that degrade aromatic carbon rings introduced through an oil spill.

Bacterioplankton: both primary producers and primary consumers and drive global biogeochemical cycling of elements essential for life.

Choanoflagellate: a free-living eukaryotic cell that has flagella (like a tail) that helps to propel the cell through the water in search of bacteria and dead matter to consume.

Herbivorous Copepod: small crustaceans found in nearly every saltwater habitat that consume phytoplankton. Because of their small size and hefty cumulative biomass, they contribute heavily to the global carbon cycle.

Erythrobacter: red-orange bacteria, a major player in the cycling of both inorganic and organic carbon and frequently found in nutrient-rich coastal seawaters.

Mixotroph: an organism that can use a mix of different sources of energy and carbon, both autotrophic and heterotrophic.

Oceanicola: a member of the Rhodobacterales order that has a diverse metabolism playing an important role in oceanic nutrient cycling.

Protist: any eukaryotic organism that is not an animal, plant or fungus. Heterotrophic protists have evolved many ways to obtain nutrients from their environment through consumption of detritus, bacteria, filter feeding, and more.

Pseudoalteromonas: a genus of bacteria that produce biologically active molecules that aid the organism in competition for nutrients. These molecules can inhibit or promote the survival of other marine organisms living nearby.

Roseobacter: clade of bacteria that are commonly found interacting with phytoplankton, macro algae and various marine animals in coastal ecosystems.

SAR11: the most abundant cell type in the ocean that oxidize organic compounds from primary production into CO₂.

SAR202: bacterioplankton found in the dark-ocean and play a role in cycling of recalcitrant carbon.

SAR86: abundant gammaproteobacteria in the surface ocean.

Vibrio: bacteria that form relationships (mutualistic, parasitic, or pathogenic) with other animals and are found in temperate waters.

Vibrio: rod-shaped bacteria that are bioluminescent (glowing) and are endosymbionts of squid or fish

Zooplankton: plankton that range from microscopic organisms to large species, such as jellyfish.

Zooplankton are found within large bodies of water, including oceans and freshwater systems.

More Resources

The Biological Productivity of the Ocean:

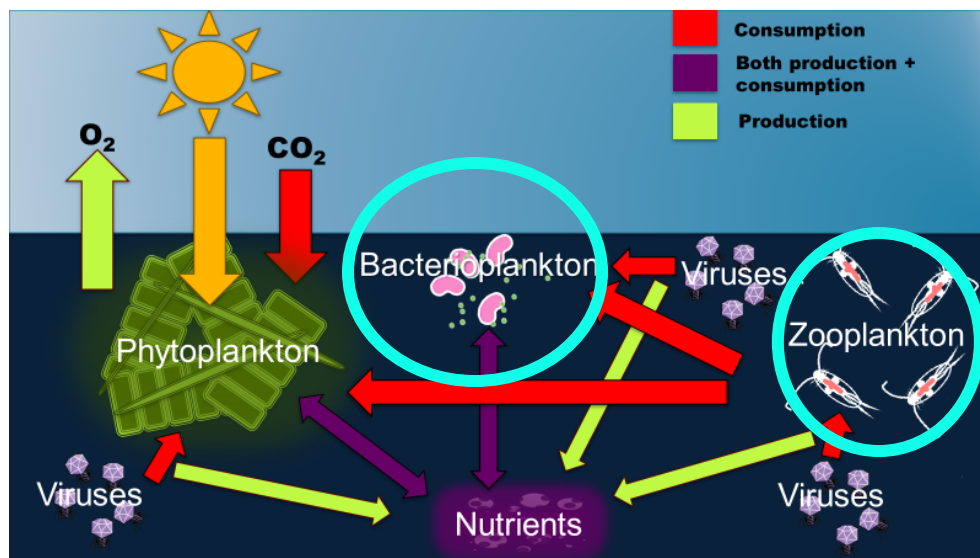
<https://www.nature.com/scitable/knowledge/library/the-biological-productivity-of-the-ocean-70631104>

Glowing Squid Video:

https://www.nsf.gov/news/special_reports/science_nation/glowingsquid.jsp

A Drop in the Ocean is Teeming with Life:

<https://www.whoi.edu/oceanus/feature/a-drop-in-the-ocean-is-teeming-with-life>



Phototrophs

Organisms that build themselves from CO₂ and Light

Description: Phytoplankton are defined as microscopic marine algae. Like microscopic versions of plants on land, they are **autotrophs**, using chlorophyll to harvest sunlight and CO₂ to make energy and grow. Because they need sunlight, they inhabit the upper, sunlit portions of the ocean. They also require inorganic nutrients (such as phosphorous, nitrogen, etc.) to grow, just as terrestrial plants require fertilizer. As a byproduct of their photosynthesis, they produce oxygen, accounting for over 50% of all oxygen in earth's atmosphere. In spring, as there is more sunlight available in the ocean, temperatures are warmer, and there are more nutrients available due to **upwelling** of nutrients from winter storms, phytoplankton reproduce in huge quantities. These major events in the ocean are called **phytoplankton blooms** and are similar to blooms that can be observed in lakes that produce green films on the surface of the water.

Carbon Cycle: Phytoplankton turn inorganic carbon (in the form of CO₂) into organic carbon (sugars, etc.) using photosynthesis. They then release some of this organic carbon into the ocean for other organisms (especially bacterioplankton) to consume. This release can be intentional, through the release of certain organic nutrients to attract certain bacterioplankton, or unintentional via the death of the phytoplankton cell (being burst by viruses, grazing by zooplankton, etc.).

Ecosystem Role: Phytoplankton serve as the base of the food web for the marine microbial ecosystem. They are consumed by a variety of larger organisms, including zooplankton, jellies, and fish.

Key Terms

Autotroph: An organism that produces its own food from inorganic sources, either sunlight and CO₂ (photoautotrophs) or other inorganic chemicals (chemoautotrophs).

Upwelling: A process in which deep, cold water rises toward the surface, bringing nutrients from the bottom of the water body to the top.

Phytoplankton bloom: A high concentration of phytoplankton due to explosive growth.

Dinoflagellate: a single-celled organism with two flagella, mainly marine but can also be found in freshwater. Most dinoflagellates are autotrophic, some are heterotrophic and some mixotrophic.

Emiliana: A type of coccolithophore found in almost all ocean ecosystems. It is known for the large blooms it forms in nutrient-depleted waters in the middle of summer. Like all other coccolithophores, it is a single-celled phytoplankton covered with uniquely ornamented calcite disks called coccoliths.

Diatoms: Single-celled, free-living phytoplankton that are the only organism on the planet with cell walls composed of transparent silica. They are highly abundant in marine and freshwater systems.

Pseudo-nitzschia: A type of marine diatom known to be capable of producing the neurotoxin domoic acid which is responsible for the neurological disorder known as amnesic shellfish poisoning.

Asterionellopsis: An abundant type of diatom that lives in cooler waters in the ocean. Especially abundant in the surf zone near the coast.

Mixotroph: An organism that can use a mix of different sources of energy and carbon, both autotrophic and heterotrophic.

Trichodesmium: A type of cyanobacteria that are found in nutrient poor tropical oceans. They are known for being able to fix atmospheric nitrogen into ammonium, a nutrient needed by other organisms. They account for half of global marine nitrogen fixation. They can live either as individual filaments, with tens

to hundreds of cells strung together, or in colonies consisting of tens to hundreds of filaments clustered together.

Zooxanthellae: They are photosynthetic single-celled dinoflagellates that usually live in symbiosis with diverse marine invertebrates including corals, jellies, and nudibranchs. During the day, they provide their symbiotic host with the organic nutrients from photosynthesis; in return, they receive nutrients, carbon dioxide, and an elevated position with access to sunshine.

Prochlorococcus: A type of very small (0.6 μm) unicellular marine photosynthetic cyanobacteria. These bacteria are probably the most abundant photosynthetic organism on Earth, found mostly in nutrient-poor ocean waters.

Synechococcus: A type of small (0.8 to 1.5 μm) marine and freshwater unicellular cyanobacteria. They are very widespread in the marine environment, found mostly in the nutrient-rich ocean waters.

More resources

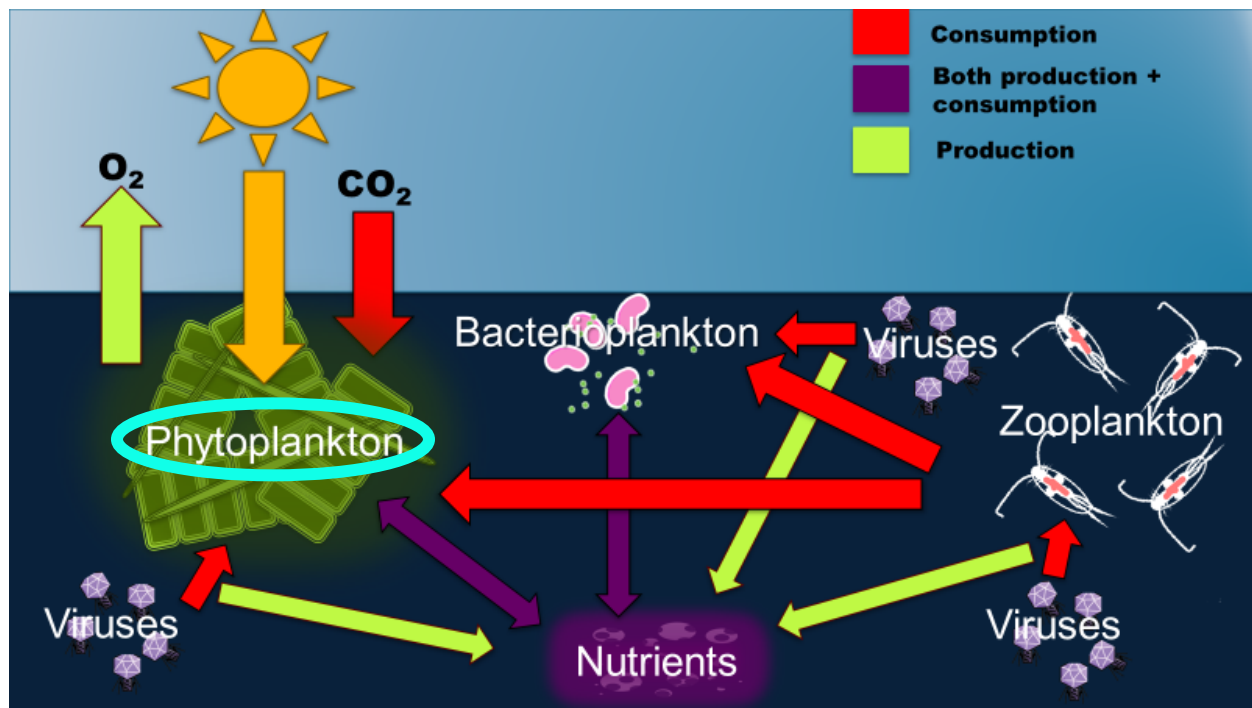
What are Phytoplankton?: <https://tinyurl.com/yxrzroqv>

Phytoplankton Blooms: The Basics: <https://tinyurl.com/y5ct49vv>

What is Upwelling?: <https://tinyurl.com/y2ze23qo>

Zooxanthellae and Coral Bleaching: <https://tinyurl.com/y5yv xv7e>

Meet the obscure microbe that influences climate, ocean ecosystems, and perhaps even evolution: <https://tinyurl.com/y4xr7rl3>



Viruses

Non-living protein and genetic material that parasitize organisms

Description: A virus is defined as an infective agent that typically consists of genetic material in a protein coat, is too small to be seen by light microscopy, and is able to multiply only within the living cells of a host. What distinguishes viruses from other organisms is that they are incapable of reproducing on their own and must first infect a host before being able to reproduce. Once a virus has infected a cell, they release their own genetic material (either **DNA** or **RNA**) and use the cellular machinery of the host cell to produce more copies of themselves. Eventually, once the host is filled with new viruses, it bursts (called **lysis**) and the new viruses are released back into the water. Different types of viruses are often specific to a few host organisms (see below for examples), but all organisms in the marine microbial ecosystem can be infected by viruses. A virus particle is comprised of the genetic material (DNA or RNA) surrounded by a virus-produced protein shell.

Carbon Cycle: With the lysis of host cells, a lot of cellular debris (nutrients; Dissolved Organic Matter) is released into the water, which can then be used as food for other microbes. Viruses thus release nutrients from cellular form into the dissolved form where other organisms can access them.

Ecosystem Role: When not infecting an organism, viruses are inactive and have no motility. Thus, they must find a new host by random encounters with potential hosts. The more there are of a virus' potential host, the more likely it is for a virus to encounter a new potential host, which in turn produces more of those viruses. In this way, viruses act as regulator of diversity in the ecosystem, keeping any one organism from taking over the ecosystem.

Key Terms

Lysis: the disintegration of a cell by rupture of the cell wall or membrane.

DNA: deoxyribonucleic acid, a molecule that carries the genetic information in all living cells.

RNA: ribonucleic acid, a molecule present in all living cells that acts as a messenger carrying instructions from DNA for controlling the production of proteins, although in some viruses RNA rather than DNA carries the genetic information.

DNA virus: a virus in which the genetic information is stored in the form of DNA.

RNA virus: a virus in which the genetic information is stored in the form of RNA.

Cyanophage: a type of virus that infects cyanobacteria, which are bacteria that obtain their energy through photosynthesis (autotrophs).

Membraned virus: a type of virus (also called an enveloped virus) that has a lipid membrane surrounding the protein shell.

Multi-host virus: a type of virus that is capable of infecting several different types of hosts.

Host-specific virus: a type of virus that is only capable of infecting a specific host.

Abundant virus: types of viruses that are very common in the ocean; many of the hosts for these viruses remain unknown.

More resources

Microbial Ecologies: The Role of Viruses in the Marine Environment: <https://tinyurl.com/y3yoypy2>

Differentiating RNA & DNA Viruses: <https://tinyurl.com/y6pdhag2>

Most abundant viruses in Earth's oceans identified: <https://tinyurl.com/y45734fj>

Virus Infections and Hosts: <https://tinyurl.com/y4ucqvxz>

