INTRODUCTION

The global ocean ecosystem – the interconnected physical, marine environment and communities of organisms – is critically dependent upon an often unseen, vast, poorly swimming, generally microscopic group of organisms called plankton. In particular, phytoplankton – photosynthesizing plankton – are the original source of food for nearly all higher microscopic and macroscopic marine organisms. As individuals, most phytoplankton are so small that they have very little consequence. However, taken as a whole, phytoplankton number overwhelm all other marine organisms, and represent a category of life on Earth with some of the most profound global effects. The environmental importance of phytoplankton cannot be overstated.

PLANKTON

Marine plankton are organisms which drift within the water column of the open ocean – in the vast region known as the pelagic zone. Pelagic organisms living in the surface waters are either unable to swim or have limited swimming ability. However, many of these plankton are able to control their vertical position in the water column. Nekton or nektonic organisms are those which expertly swim in the pelagic zone and are able to move both laterally and vertically. Benthic organisms (or benthos) live on, in, or near the seafloor, also known as the benthic zone. Those that live on the seafloor sediment are termed epifaunal. Organisms living near the seafloor can either be mobile – those that crawl or swim or sessile – those that are attached to a fixed structure. Lastly, infaunal benthos are the organisms that live within sediment.

PHYTOPLANKTON

Phytoplankton are the primary producers of the marine ecosystem and are the first link in the marine food web. Extraordinarily, these microscopic phytoplankton account for up to half of the total global primary production on planet Earth and have been critical in producing our oxygen-rich atmosphere. All phytoplankton are single-celled organisms and, other than the bacterioplankton, are protists. The most common and important phytoplankton are the coccoid cyanobacteria, diatoms, dinoflagellates, and the coccolithophores.

The coccoid cyanobacteria (blue-green algae) are so small (0.2-2.0 µm) that their relative contribution and importance was overlooked until just recently. In fact, the photosynthesizing bacterioplankton are the most abundant photosynthetic organisms on Earth and are estimated to compose half of all the photosynthetic biomass in the ocean! These bacterioplankton are difficult to culture in the lab, difficult to preserve, and difficult to observe with the common light microscope.

The diatoms are equally important primary producers in the ocean, estimated to contribute up to 45% of the total oceanic primary production. Diatoms are members of the algae (plant-like) protists. Diatoms produce a silica (SiO$_2$) mineralized cell wall (called a frustule or test), typically 20-200 µm in size, with some species reaching up to 2 mm in length. Some diatoms live as solitary single cells and some live in interconnected chains with others. Diatoms
lack flagella (small whip-like or tail-like filaments) that other groups commonly utilize to control suspension, so some diatoms regulate buoyancy with intracellular low-density fats to counter sinking due to the dense silica frustule. Diatoms also rely on turbulent mixing of surface waters through wind to keep them suspended in the euphotic zone. Diatoms mostly contain green chlorophyll, and in the case of very highly concentrated populations of diatoms, they may color the water green. In California, some coastal diatoms produce domoic acid, a toxin which accumulates at the top of food webs. In seabirds and sea lions the concentration of domoic acid can become high enough to cause illness, erratic behavior and death. A historic incident of domoic acid poisoning inspired the Alfred Hitchcock movie “The Birds”.

The **dinoflagellates**, next most in importance as marine primary producers, are members of the protozoa (animal-like) protists. Oddly, about half of all dinoflagellate species are phytoplanktonic photosynthesizers, and the other species are zooplanktonic heterotrophs. Dinoflagellates produce a toughened cell wall with cellulose (an organic complex carbohydrate) and are typically 0.1-2 mm in size. Dinoflagellates possess two flagella – a longitudinal posterior flagellum directs steering and a transverse encircling flagellum propels the dinoflagellate in a whirling motion. The flagella are set into orthogonal grooves – a lengthwise longitudinal groove and a waistline groove. Dinoflagellates are often adorned with spines or horns. Many dinoflagellates are noticeably bioluminescent and glow in the wakes of boats and in breaking waves. Dinoflagellates contain a red chlorophyll as well as a green chlorophyll, and mostly appear brown. Particularly visible phenomena of reddish brown accumulations of extremely concentrated (millions of dinoflagellates per milliliter) populations of dinoflagellates are often called **“red tides”**, a misnomer as they have no association with ocean tides. They are more properly called **algal blooms**. A few, but not all, “red tides” are associated with dangerous levels of toxins (concentrated from ordinarily harmless levels). Generally, red tides off the California coast are harmless by themselves, but they may indicate dangerously polluted water.

The **coccolithophores** are members of the algae protists. Coccolithophores are covered with ornate calcareous (calcium-carbonate, CaCO₃) plates or disks (called coccoliths), typically numbering 30 or more. During a coccolithophore’s lifetime, coccoliths may be shed and replaced. Coccolithophores, minute in comparison to the diatoms and dinoflagellates, are typically 2-20 µm in diameter, too small for common light microscopes.

**ZOOPLANKTON**

Zooplankton are composed of single-celled protozoan and multicellular animal (metazoan) species. Most zooplankton occupy the primary and secondary consumer trophic levels of the marine food web. The minute size of phytoplankton dictates that marine grazers are also very small. These herbivores and small carnivores play an exceptionally important role in marine ecosystem. Both nekton and benthic organisms depend on a zooplankton diet, directly or indirectly. The most common and important (primary and secondary consumer) zooplankton are the **copepods, krill, dinoflagellates, radiolarians, and foraminiferans**.

**Copepods**, a group of small crustaceans, are by far the most important primary consumer zooplankton. Copepods are covered in an armored exoskeleton composed of chitin (an organic complex carbohydrate), which they molt and replace routinely. Copepods are typically 1-2 mm in length, with some species as long as 10 mm. Slightly larger than the phytoplankton, and thus more visible, copepods are almost totally transparent to avoid predation. Some copepod species ascend to surface waters during the night to feed and descend up to several hundred meters to deeper, darker waters at daytime to avoid visually acute predators. Copepods are well suited for hunting other zooplankton and phytoplankton as they’re armed with capture appendages and
sensitive antennae. For motility, copepods possess swimming legs and head appendages, and long, feathered antennae ideal for drifting.

**Krill** are a group of small shrimp-like crustaceans, much larger than the copepods, and are an important food source for fish, seabirds, seals, manta rays, whale sharks, and the largest animals of all, the baleen whales. Most krill are 1-2 cm long, with some species as long as 15 cm. Krill assemble in dense swarms, a defensive tactic to confuse smaller predators that would like to pick out single individuals. They also practice vertical migration like copepods. Krill can swim against weak currents, thus they are in a gray zone between true plankton and nekton.

**Radiolarians** are amoeboid protozoans which produce amazingly complex and intricate silica (SiO$_2$) skeletons, typically 0.1-2 mm in size. Radiolarian skeletons have spherical and conical forms with geometrical latticework patterns, with or without numerous radial spines. Radiolarians regulate buoyancy with intracellular low-density fats and possess spiny exteriors which increase their surface area which helps counter sinking.

**Foraminiferans** are amoeboid protozoans which produce a globular or spiraled, chambered calcareous (calcium-carbonate, CaCO$_3$) test (shell), typically 0.1-1.5 mm in size. They capture food with reticulating pseudopoda, fine strands of cytoplasm that branch and merge to form a dynamic net.

**Macroplankton** are numerous. They include krill, discussed above, **pteropods**, which are planktonic snails, and many types of **gelatinous plankton**, the best known or which are jellyfish.

**THE BIOTIC COMMUNITY**

An ecosystem is composed of the physical (or abiotic) environment and the biotic community, interacting together. The biotic community is made up by the **producers**, **consumers**, and decomposers. **Autotrophs** are the producers in the food chain, which produce complex organic compounds (often by photosynthesis) from simple inorganic compounds (such as CO$_2$, nitrate, etc.) and an external, inorganic source of energy (such as sunlight) from the physical environment. **Heterotrophs** are the consumers in the food chain, which may feed on autotrophs or other heterotrophs for chemical-organic energy and organic-carbon compounds used for growth and development. **Saprotrophs**, or detritivores, are heterotrophs that are the decomposers and recyclers in the food chain. They obtain energy from wastes or dead organisms and return nutrients to the physical environment.

Plankton are divided into three trophic groups (depending on how they obtain energy) – the autotrophic **phytoplankton**, the heterotrophic **zooplankton**, and **bacterioplankton** (planktonic bacteria). Some bacterioplankton are saprotrophic and many are autotrophic. We’ll survey particularly important groups of phytoplankton and zooplankton in a later section.

A **food chain** is a simple arrangement of organisms according to the order of predation (representing the transfer of energy and organic compounds from autotrophs to heterotrophs). However, the food chain shows only a single possible pathway between organisms. Closer to reality, a **food web** represents the complex network of interactions among organisms. The food web is divided into **trophic levels**, composed of **primary producers** (the autotrophs) at the base, **primary consumers** (herbivorous heterotrophs which feed on primary producers), **secondary consumers** (carnivorous heterotrophs which prey on primary consumers and other heterotrophs), and so on, often up to a fifth-level consumer at the top, producing a trophic pyramid. Too often, figurative trophic pyramids neglect to include the crucial contribution of the decomposers. The abundance of the primary producers largely determines the abundances of the higher trophic levels. What limits the abundance of the primary producers?
The rate of synthesis of organic matter from inorganic materials by photosynthesis is called **primary productivity**. Primary productivity is expressed in grams of carbon bound into organic material per square-meter of ocean surface area per year (g\text{carbon}/m^2/yr). Most photosynthesizers utilize a pigment called **chlorophyll** to absorb sunlight. The organic material produced is usually glucose, C_6H_{12}O_6, a simple sugar or carbohydrate. The source of carbon for glucose is dissolved CO_2. In turn, phytoplankton and all heterotrophs respire in order to liberate needed metabolic energy.

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\text{Photosynthesis:} \quad 6\text{H}_2\text{O} + 6\text{CO}_2 + \text{sunlight} \rightleftharpoons \text{C}_6\text{H}_{12}\text{O}_6 + 6\text{O}_2
\]

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\text{Respiration:} \quad \text{C}_6\text{H}_{12}\text{O}_6 + 6\text{O}_2 \rightleftharpoons 6\text{H}_2\text{O} + 6\text{CO}_2 + \text{metabolic energy}
\]

**Limiting Physical Factors Affecting Phytoplankton Growth**

The availability of **sunlight** and **nutrients** are the two major factors controlling phytoplankton growth. In general, sunlight comes from above and nutrients come from below; only when both are adequate can the amount of phytoplanktonic primary production be high.

**Sunlight**

The single most important factor that determines the distribution of life in the oceanic province is the availability of sunlight. Seawater, with relatively high transparency, allows sunlight to penetrate to a depth of about 600 meters in clear, open ocean and approximately 100 meters in coastal waters. The actual depth depends on the amount of suspended sediment, detritus, and plankton in the water, the latitude, season, and the time of day.

![Diagram of the Ocean Zones](image)

**Figure:** Light only penetrates to a maximum depth of ~600 m.
Nutrients

Nutrients are compounds that are limited in supply but required for the production of organic or skeletal matter. Because carbon dioxide, CO$_2$, is not limited in supply, it is generally not considered a nutrient even though it is the major carbon source for biomass formation by photosynthesis. With a high solubility in seawater, CO$_2$ is usually available for photosynthesis. The main limiting nutrients required in primary productivity include nitrogen (as nitrate, NO$_3^-$; not as nitrogen gas, N$_2$) and phosphorus (as phosphate, PO$_4^{3-}$) – substances commonly used as fertilizers by gardeners and farmers. Compared to terrestrial soils, nitrates and phosphates are far less abundant in even the most fertile ocean water. Carbon, nitrogen, and phosphorus constitute the major elements taken up by marine phytoplankton in an average (molar) ratio of:

106 C to 16 N to 1 P

This is known as the Redfield ratio, and can be useful for predicting the amount of available CO$_2$ for conversion to organic matter given a set amount of N and P.

In addition to these, a nutrient in short supply during high productivity and rapid reproduction is dissolved silica (as SiO$_2^{2-}$ or H$_4$SiO$_4^{(aq)}$), necessary to construct tests or shells particular to certain planktonic species. Essential nutrients required by organisms in much lower concentrations are referred to as micronutrients, such as iron (Fe), copper (Cu), and selenium (Se). These are usually not limiting relative to the more commonly limited nitrate, phosphate, and silica.

Without replenishment, nutrients would quickly be depleted upon consumption by primary producers. Upwelling currents are particularly important sources of nutrient replenishment since cold waters derived from depths are enriched in nutrients (having little nutrient depletion) and contain high dissolved CO$_2$ concentrations. As discussed in the prior Ocean Circulation lab, coastal upwellings are found along the eastern boundaries of oceans where surface currents are moving toward the equator. Ekman transport moves surface water away from these coasts, so nutrient-rich water from depths of 200 to 1000 meters constantly rises to replace it. Equatorial upwelling, a region of diverging surface water, is another area of nutrient replenishment from below and causes high primary productivity. Thermohaline stratification of surface waters, more common at tropical and subtropical latitudes, may be a significant barrier against nutrient replenishment. Thus, the interiors of the large subtropical gyres are generally the regions with the lowest productivity in the oceans. Large storms may disrupt and mix limiting, stratified layers, and may form migrating, local zones of upwelling. Dead organic matter and excreted waste are consumed by the saprotrophic bacterioplankton which return nutrients to the ocean cycle.