Phytoplankton

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Synonyms

Algae; Microalgae

Definition

The term plankton comes from the Greek meaning to drift or wander and was introduced in 1887 by Victor Hensen to refer to biological matter that drifts in bodies of water (Mills 1989). The term phytoplankton refers to the photosynthetic species of the plankton community. Phytoplankton are a genetically diverse set of organisms that include the prokaryotic cyanobacteria and many eukaryotic groups (Hackett et al. 2007; Simon et al. 2009).

Overview

Evolutionary History

Microfossil and molecular clock evidence indicates that prokaryotes originated in the Archean and eukaryotes in the Proterozoic (Betts et al. 2018). Determining when these groups first became photosynthetic, first became planktonic, and whether they originally inhabited fresh or marine environments is extremely challenging. Analyses of extant cyanobacterial genomes indicate that photosynthesis may have been acquired relatively late in the evolution of cyanobacteria, perhaps not long before the rise of oxygen ~2.3 billion years ago (Soo et al. 2017), and the currently dominant oceanic picocyanobacteria, *Prochlorococcus* and *Synechococcus*, did not emerge until the Cryogenian, ~850 to 635 million years ago (Sánchez-Baracaldo 2015). While the photosynthetic eukaryotic lineages trace their origins to the Proterozoic, the dominant eukaryotic phytoplankton groups in the ocean today, namely, the diatoms, dinoflagellates, and coccolithophores, arose in the Mesozoic (Falkowski et al. 2004; Katz et al. 2004). Dinoflagellates and coccolithophores exhibit their highest levels of morphological diversity in the Mesozoic, while the diatoms reach their highest diversity in the later part of the Cenozoic.

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Diversity

The global estimate of marine phytoplankton richness based on microscopy ranges from 3444 to 4375 species in marine waters to about 14,000 in freshwaters (Sournia et al. 1991). A majority of the described marine species are dinoflagellates and diatoms, with a smaller number of haptophytes and green algae (Sournia et al. 1991; Simon et al. 2009). Recent molecular analyses are providing new insight into the diversity of phytoplankton. A study based on the DNA sequence of the V9 region of the 18S ribosome estimates the diversity of marine eukaryotic plankton (both photosynthetic and non-photosynthetic members) at ~150,000 operational taxonomic units (OTUs) (de Vargas et al. 2015). The highest levels of diversity are associated with the smallest size fraction examined, cells with diameters between 0.8 and 5 μm. The picoplankton include photosynthetic, mixotrophic, and heterotrophic members such as parasites and symbiotic hosts. While some taxonomic groups of phytoplankton are strictly photoautotrophs (depending strictly on light for energy), many of the eukaryotic groups are mixotrophic (meaning they acquire energy through a combination of photosynthesis and heterotrophic nutrition) (Stoecker et al. 2017).

Phytoplankton Functional Groupings and Their Biogeography

Phytoplankton species are often grouped into a modest number of clusters based on their ecological or biogeochemical role, termed phytoplankton functional types. The major marine phytoplankton groupings are described below. In some cases, there is overlap between evolutionary history (taxonomic group), cell size, and ecological and biogeochemical function. Biogeochemically, while all phytoplankton species use N and P, only some use Si (primarily the diatoms), and only a few can fix N_2 into reduced nitrogen (cyanobacteria). The stoichiometry of both the macro- and trace elements requirements (especially Fe) and ability to acquire resources vary across many of these groups. Differences in elemental requirements and ability to acquire resources are important determinants of the biogeography of phytoplankton functional groups.

Cell Size

Phytoplankton cell size influences competitive ability for resources, sinking rate, grazing susceptibility, and ecological and biogeochemical function (Finkel et al. 2010). Traditionally ecological and biogeochemical studies have divided the phytoplankton into three size classes (Sieburth et al. 1978): the picoplankton (0.2 to about 2–3 μm (10^{-6} m) in cell diameter), the nanoplankton (2–20 μm), and the microplankton (20–200 μm). Commonly, picophytoplankton communities are dominated by picocyanobacteria, while diatoms and dinoflagellates often constitute the largest fraction of the microplankton communities. Generally small cells thrive in stable and lower nutrient conditions, and larger cells predominate in environments with episodic and higher nutrient concentrations. Furthermore, larger phytoplankton are associated with higher trophic (fish yield) and carbon export efficiency (but see Richardson and Jackson (2007)).

Cyanobacteria

Cyanobacteria are often divided into two functional groupings: the (1) non-nitrogen-fixing picocyanobacteria and (2) nitrogen-fixing cyanobacteria. The dominant non-nitrogen-fixing picocyanobacteria in the ocean are dominated by two genera: *Prochlorococcus* and *Synechococcus* (see Partensky et al. 1999). Both are solitary coccoid species, but they differ in size and pigment composition. *Prochlorococcus* is smaller than *Synechococcus*, 0.6 versus 0.9 μm in diameter, and uses divinyl chlorophyll a/b versus phycobilisomes. These differences in cell size and pigment composition influence their competitive ability under different nutrient and light regimes. *Prochlorococcus* often dominates phytoplankton biomass in much of the oligotrophic open ocean and can be found both in surface waters and deeper in the euphotic zone. *Synechococcus* is common in the surface of the oligotrophic ocean and increases in abundance and biomass in areas with episodic and higher nutrient inputs. *Prochlorococcus* has a more restricted geographic distribution and is found at a narrower range of salinities and warmer temperature than *Synechococcus*.

Nitrogen-fixing cyanobacteria convert N_2 into ammonia, providing a biologically useful source of fixed nitrogen to aquatic ecosystems that stimulates photosynthetic carbon fixation and export into the deep sea. Nitrogen fixation is catalyzed by the enzyme nitrogenase that is inactivated by oxygen. Many photosynthetic nitrogen-fixing organisms isolate nitrogenase in a specialized cell, termed a heterocyst, which isolates nitrogenase from oxygen. There are several single-celled, nitrogen-fixing cyanobacteria and non-heterocystous colonial species that segregate nitrogen fixation and oxygenic photosynthesis over time or across the cell or colony. Common open-ocean marine nitrogen-fixing cyanobacteria include the non-heterocystous colonial *Trichodesmium*, the single-celled *Crocosphaera watsonii*, and the photoheterotrophic (does not use CO_2 as a C source) haptophyte symbiont UCYN-A (Martínez-Pérez et al. 2016). Common heterocystous forms include the free-living genera *Nodularia* and *Anabaena* and the diatom symbiont *Richelia intracellularis* (Sohm et al. 2011). *Nodularia* and *Anabaena* are typically found in cooler, more brackish, coastal regions, such as the Baltic Sea. In oligotrophic oceans, diatom diazotroph (can grow without external source of fixed N) associations (DDAs) provide biologically available nitrogen to diatom hosts (Villareal 1994). Common diatom hosts include *Hemiaulus* and *Rhizosolenia* with the nitrogen-fixing symbiont *Richelia*. DDAs are especially well documented in the western tropical North Atlantic near the Amazon river plume but may be much more widely distributed (Subramaniam et al. 2008).

Picoeukaryotes

The photosynthetic picoeukaryotes are taxonomically diverse, many (but not all) species are flagellated (phytoflagellates), and many are mixotrophs. Many of the picoeukaryotes contain only a single mitochondrion, Golgi apparatus, and chloroplast. Photosynthetic picoeukaryotes can reach densities between 10^3 and 10^5 cells per milliliter in surface waters (see Massana 2011) and tend to reach their largest relative abundances in moderately oligotrophic to mesotrophic conditions. Traditionally the picoeukaryotes are difficult to identify by light microscope, but molecular methods provide new insight into their spatial and temporal controls. Prasinophyceae, Pelagophyceae, Bolidophyceae, and Pinguiophyceae are common groups of photosynthetic picoeukaryotes found in the ocean.

Calcifying Coccolithophores

Coccolithophores, most notably the nanoplankter *Emiliania huxleyi*, which forms large blooms, produce inorganic carbon as well as organic carbon. Coccolithophores are covered in calcite scales (termed liths), which may affect predation rates and light harvesting. Their production (Monteiro et al. 2016) has a direct effect on alkalinity, dissolved inorganic carbon, and pH. Some species of coccolithophores are particularly sensitive to changes in pH and may be strongly affected by ocean acidification (Riebesell et al. 1993). The downward flux of liths made of $CaCO_3$ removes carbon from the surface ocean and augments the biological pump of organic carbon.

Silicifying Phytoplankton

Diatoms are a dominant group of phytoplankton, responsible for almost half of all marine primary production. They range in size from 2 to several 1000s of micrometers in diameter (Finkel et al. 2005). Despite this diversity, they are best known for their species, which grow rapidly, are strong competitors for nutrients, and form large, intense blooms. Diatoms play an important role in supporting fish production and in the export of carbon into the deep sea (Tréguer et al. 2017). Notably, diatoms have an obligate requirement for silicon to form a rigid frustule as part of their cell wall. Small differences in frustule structure are diagnostic of individual species. Although diatoms are the ecologically dominant silicifying phytoplankton group, several other phytoplankton groups incorporate Si, for example, silicoflagellates construct a skeleton of fused Si bars and rods. Some of the cyanobacteria have been shown to have a requirement for a trace amount of Si.

Dinoflagellates

Dinoflagellates are a diverse group with intermediate- to large-sized species and incorporate autotrophs, heterotrophs, and a large number of mixotrophs. Morphologically, they are characterized by two flagella and, for many species, the presence of an armored cell wall composed of chemically resistant organic plates called theca. Dinoflagellates generally have slower growth rates than diatoms (Tang 1996) and tend to be found in higher abundance in warmer, stratified waters.

Biogeochemical and Ecological Significance of the Phytoplankton

Phytoplankton perform approximately half of the photosynthesis on Earth: 45–50 Pg C per year (Falkowski et al. 1998). Photosynthesis splits water molecules, releasing O_2 into the atmosphere, and converts inorganic dissolved carbon and nutrients into biomass. As a consequence, phytoplankton influence the biogeochemistry of the Earth and fuel aquatic and marine food webs. Although total phytoplankton productivity is approximately the same as land plants, the total biomass of phytoplankton is a tiny fraction of land plant biomass, so carbon flows from inorganic forms through phytoplankton and into other pools relatively quickly. Most of the organic carbon fixed and oxygen evolved by phytoplankton is quickly respired by grazers or the microbial decomposers, reversing the process of photosynthesis. A small fraction of the organic carbon is transferred to long-lived organisms such as fish and marine mammals. Another small fraction is exported from the pelagic (surface sunlit) zone into the deep ocean and sediments. Carbon exported to the deep ocean and sediments is effectively removed from interactions with the atmosphere for thousands to many millions of years, respectively. It is this long-term export of carbon into the deep ocean and sediment that regulates atmospheric CO_2 and O_2 content.

Phytoplankton community composition and primary production vary in space and time (Finkel 2014). Generally, biomass and production are highest in regions where light and nutrients in the upper mixed layer of the ocean are sufficient to support high rates of photosynthesis, for example, in coastal and upwelling systems. In contrast, biomass and primary production becomes diminished and less variable in regions with deep surface mixed layers where average light experienced by phytoplankton is low, as occurs over much of the high-latitude oceans in winter and in low-nutrient regions, such as the subtropical central oceanic gyres. Inorganic nitrogen and iron and, to a lesser extent, phosphate are the most common elements limiting marine phytoplankton production. Other factors that influence the primary production include inorganic carbon concentration and pH, light dose, period, quality, turbulent mixing, and species interactions, as well as loss due to grazing by zooplankton and infection by parasites and viruses. The taxonomic and size structure of phytoplankton communities is shaped by environmental conditions and biotic interactions and, in turn, influences the structure of the food web and fraction of primary production that is ultimately exported out of the ocean surface to the sediments.

Basic Methodology

Traditionally phytoplankton have been collected via nets and water samples and identified using light microscopy (Mills 1989). Molecular analyses are increasingly being used to characterize phytoplankton community diversity (de Vargas et al. 2015). Chlorophyll-*a* is often used to estimate phytoplankton biomass in the field, and satellite remote-sensed chlorophyll is used to generate global estimates of both biomass and net primary production (Falkowski et al. 1998).

Key Research Findings

Warming ocean temperatures over the coming century will lead to wide-ranging changes in the physical, chemical, and biological state of the ocean. The amount of phytoplankton biomass, their rate of production, and the species present will be modified as much of the surface ocean becomes warmer and lower in nutrients. There is evidence that increasing warming and water-column stratification will reduce phytoplankton primary production (Behrenfeld et al. 2006) and that increasing CO_2 concentrations could fundamentally alter rates of nitrogen fixation by key cyanobacteria such as *Trichodesmium* (Hutchins et al. 2007) and calcification by coccolithophores (Riebesell et al. 1993). Taken all together, these effects are expected to lead to widespread changes in phytoplankton community structure and the global biogeochemical cycles of carbon and nitrogen.

Future Directions

Wider application of molecular tools, culture work, and statistical analyses will further improve our understanding of phytoplankton and how these species respond to different chemical and physical stimuli. A better knowledge of how environmental conditions influence functional types will enable improved models of production, export of carbon to the deep ocean, and changes in trophic transfer efficiency through the food web.

Cross-References

► Algae
► Biogeochemical Cycles
► Carbon Cycle, Biological
► Cyanobacteria
► Cyanobacteria, Diversity and Evolution of
► Nitrogen Fixation
► Photosynthesis

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