



An Introduction to Planktology

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Table of Contents

Chapter 1 - Plankton

Chapter 2 - Aeroplankton and Bacterioplankton

Chapter 3 - Chaetognatha and *Emiliana Huxleyi*

Chapter 4 - Diatom

Chapter 5 - Frustule and Nanophytoplankton

Chapter 6 - *Ostreococcus* and *Ostreococcus Tauri*

Chapter 7 - Photosynthetic Picoplankton

Chapter 8 - Phytoplankton

Chapter 9 - Picoeukaryote and Raphidophyte

Chapter 10 - Spring Bloom and Zooplankton

Chapter 11 - Diel Vertical Migration and Thin Layers (Oceanography)

Chapter 12 - *Chaetoceros* and *Bacteriastrum*

Chapter 1

Plankton

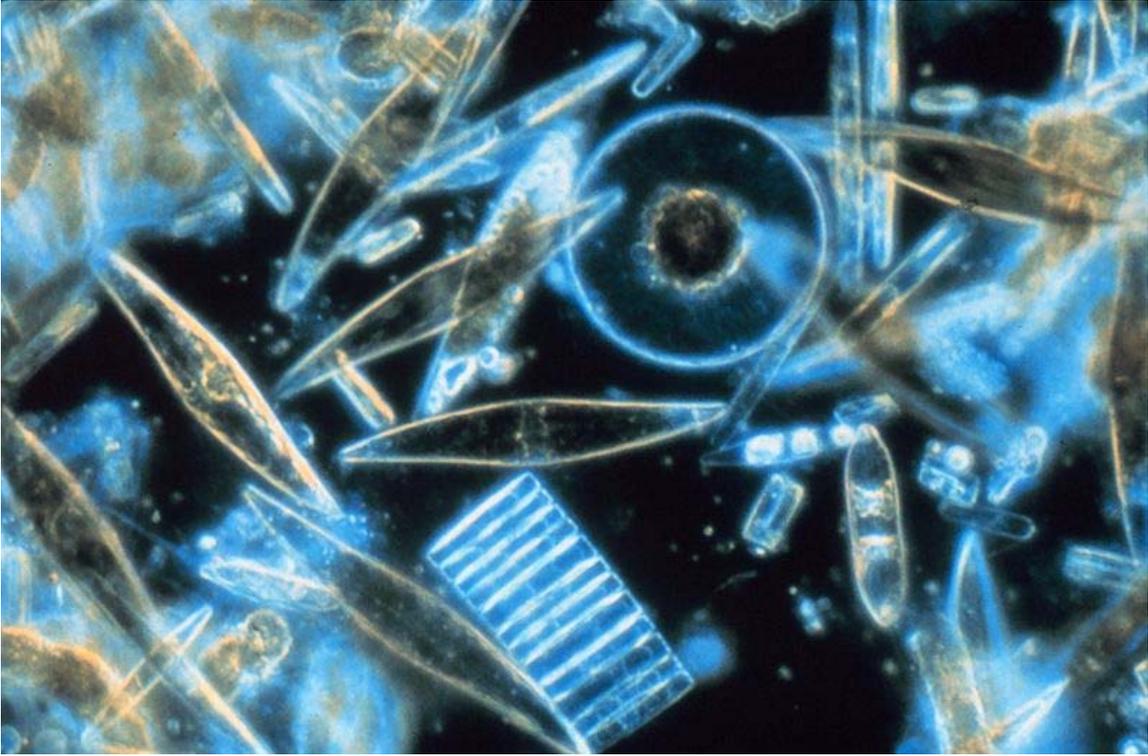


Photomontage of planktonic organisms

Plankton (singular **plankter**) are any drifting organisms (animals, plants, archaea, or bacteria) that inhabit the pelagic zone of oceans, seas, or bodies of fresh water. Plankton are defined by their ecological niche rather than phylogenetic or taxonomic classification. They provide a crucial source of food to larger, more familiar aquatic organisms such as fish and cetacea.

Though many **planktic** species are microscopic in size, *plankton* includes organisms covering a wide range of sizes, including large organisms such as jellyfish.

Terminology



Some marine diatoms - a key phytoplankton group

The name **plankton** is derived from the Greek adjective *πλαγκτός* - *planktos*, meaning "errant", and by extension "wanderer" or "drifter". Plankton typically flow with ocean currents. While some forms are capable of independent movement and can swim hundreds of meters vertically in a single day (a behavior called diel vertical migration), their horizontal position is primarily determined by the surrounding currents. This is in contrast to **nekton** organisms that can swim against the ambient flow and control their position (e.g. squid, fish, and marine mammals).

Within the plankton, **holoplankton** spend their entire life cycle as plankton (e.g. most algae, copepods, salps, and some jellyfish). By contrast, **meroplankton** are only planktic for part of their lives (usually the larval stage), and then graduate to either a nektic or benthic (sea floor) existence. Examples of meroplankton include the larvae of sea urchins, starfish, crustaceans, marine worms, and most fish.

Plankton abundance and distribution are strongly dependent on factors such as ambient nutrients concentrations, the physical state of the water column, and the abundance of other plankton.

The study of plankton is termed planktology and a planktonic individual is referred to as a plankter.

The widespread use of **planktonic** in both scientific and popular literature is grammatically incorrect because of the Greek roots of **plankton**. When deriving English words from their Greek or Latin roots the gender specific ending (in this case "-on," which indicates the word is neuter) is dropped, using only the root of the word in the derivation. The less commonly used **planktic** is the correct adjective.

Trophic groups



An amphipod (*Hyperia macrocephala*)

Plankton are primarily divided into broad functional (or trophic level) groups:

- **Phytoplankton** (from Greek *phyton*, or plant), autotrophic, prokaryotic or eukaryotic algae that live near the water surface where there is sufficient light to support photosynthesis. Among the more important groups are the diatoms, cyanobacteria, dinoflagellates and coccolithophores.

- **Zooplankton** (from Greek *zoon*, or animal), small protozoans or metazoans (e.g. crustaceans and other animals) that feed on other plankton and telonemia. Some of the eggs and larvae of larger animals, such as fish, crustaceans, and annelids, are included here.
- **Bacterioplankton**, bacteria and archaea, which play an important role in remineralising organic material down the water column (note that the prokaryotic phytoplankton are also bacterioplankton).

This scheme divides the plankton community into broad **producer**, **consumer** and **recycler** groups. However, determining the trophic level of some plankton is not straightforward. For example, although most dinoflagellates are either photosynthetic producers or heterotrophic consumers, many species are mixotrophic depending upon circumstances.

Size groups

Plankton are also often described in terms of size. Usually the following divisions are used:

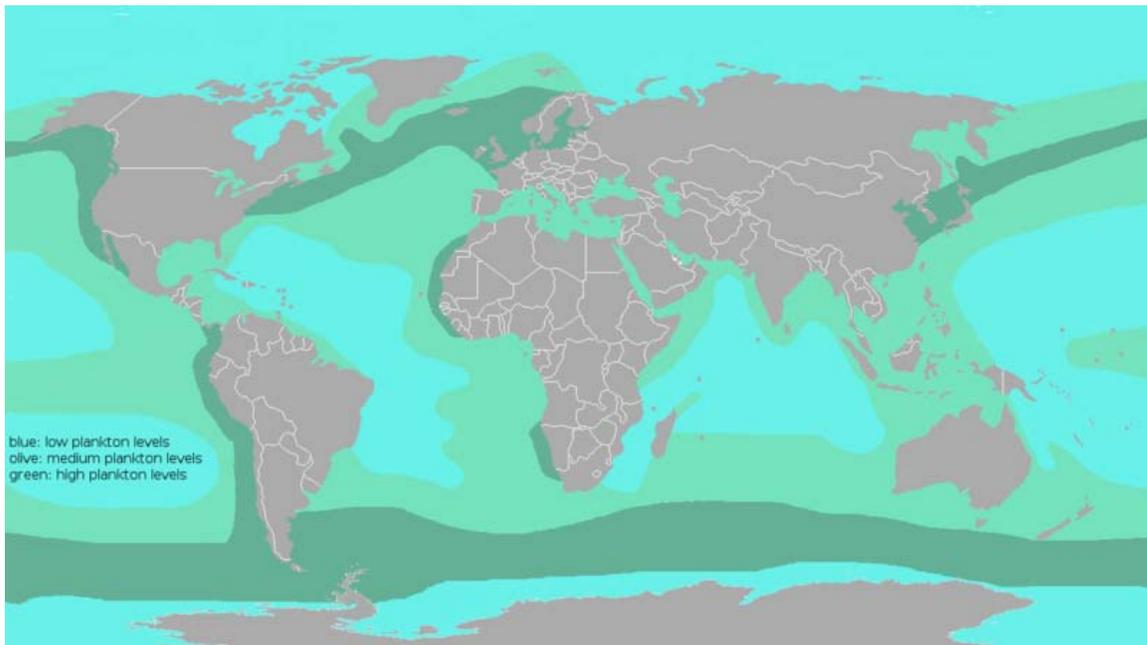
Group	Size range (ESD)	
Megaplankton	$> 2 \times 10^{-2}$ m (20+ mm)	metazoans; e.g. jellyfish; ctenophores; salps and pyrosomes (pelagic Tunicata); Cephalopoda
Macroplankton	$2 \times 10^{-3} \rightarrow 2 \times 10^{-2}$ m (2–20 mm)	metazoans; e.g. Pteropods; Chaetognaths; Euphausiacea (krill); Medusae; ctenophores; salps, doliolids and pyrosomes (pelagic Tunicata); Cephalopoda
Mesoplankton	$2 \times 10^{-4} \rightarrow 2 \times 10^{-3}$ m (0.2 mm–2 mm)	metazoans; e.g. copepods; Medusae; Cladocera; Ostracoda; Chaetognaths; Pteropods; Tunicata; Heteropoda
Microplankton	$2 \times 10^{-5} \rightarrow 2 \times 10^{-4}$ m (20–200 μ m)	large eukaryotic protists; most phytoplankton; Protozoa (Foraminifera); ciliates; Rotifera; juvenile metazoans - Crustacea (copepod nauplii)
Nanoplankton	$2 \times 10^{-6} \rightarrow 2 \times 10^{-5}$ m (2–20 μ m)	small eukaryotic protists; Small Diatoms; Small Flagellates; Pyrrophyta; Chrysophyta; Chlorophyta; Xanthophyta
Picoplankton	$2 \times 10^{-7} \rightarrow 2 \times 10^{-6}$ m (0.2–2 μ m)	small eukaryotic protists; bacteria; Chrysophyta
Femtoplankton	$< 2 \times 10^{-7}$ m (< 0.2 μ m)	marine viruses

However, some of these terms may be used with very different boundaries, especially on the larger end of the scale.

The existence and importance of nano- and even smaller plankton was only discovered during the 1980s, but they are thought to make up the largest proportion of all plankton in number and diversity.

The microplankton and smaller groups are microorganisms and operate at low Reynolds numbers, where the viscosity of water is much more important than its mass or inertia.

Distribution



World distribution of plankton

Plankton inhabit oceans, seas and lakes. Local abundance varies horizontally, vertically and seasonally. The primary cause of this variability is the availability of light. All plankton ecosystems are driven by the input of solar energy, confining primary production to surface waters, and to geographical regions and seasons having abundant light.

A secondary variable is nutrient availability. Although large areas of the tropical and subtropical oceans have abundant light, they experience relatively low primary production because they offer limited nutrients such as nitrate, phosphate and silicate. This results from large-scale ocean circulation and water column stratification. In such regions, primary production usually occurs at greater depth, although at a reduced level (because of reduced light).

Despite significant macronutrient concentrations, some ocean regions are unproductive (so-called HNLC regions). The micronutrient iron is deficient in these regions, and adding it can lead to the formation of blooms of many kinds of phytoplankton. Iron primarily reaches the ocean through the deposition of dust on the sea surface. Paradoxically, oceanic areas adjacent to unproductive, arid land thus typically have abundant phytoplankton (e.g., the western Atlantic Ocean, where trade winds bring dust from the Sahara Desert in north Africa). While plankton are most abundant in surface waters, they live throughout the water column. At depths where no primary production occurs, zooplankton and bacterioplankton instead consume organic material sinking from more productive surface waters above. This flux of sinking material, so-called marine snow, can be especially high following the termination of spring blooms.

Biogeochemical significance

Aside from representing the bottom few levels of a food chain that supports commercially important fisheries, plankton ecosystems play a role in the biogeochemical cycles of many important chemical elements, including the ocean's carbon cycle.

Primarily by grazing on phytoplankton, zooplankton provide carbon to the planktic foodweb, either respiring it to provide metabolic energy, or upon death as biomass or detritus. Typically more dense than seawater, organic material tends to sink. In open ocean ecosystems away from the coasts this transports carbon from surface waters to the deep. This process is known as the **biological pump**, and is one reason that oceans constitute the largest carbon sink on Earth.

It might be possible to increase the ocean's uptake of carbon dioxide generated through human activities by increasing plankton production through "seeding", primarily with the micronutrient iron. However, this technique may not be practical at a large scale. Ocean oxygen depletion and resultant methane production (caused by the excess production remineralising at depth) is one potential drawback.

Biomass variability

The growth of phytoplankton populations is dependent on light levels and nutrient availability. The chief factor limiting growth varies from region to region in the world's ocean. On a broad scale, growth of phytoplankton in the oligotrophic tropical and subtropical gyres is generally limited by nutrient supply, while light often limits phytoplankton growth in subarctic gyres. Environmental variability at multiple scales influences the nutrient and light available for phytoplankton, and as these organisms form the base of the marine food web, this variability in phytoplankton growth influences higher trophic levels. For example, at interannual scales phytoplankton levels temporarily plummet during El Nino periods, influencing populations of zooplankton, fishes, sea birds, and marine mammals.

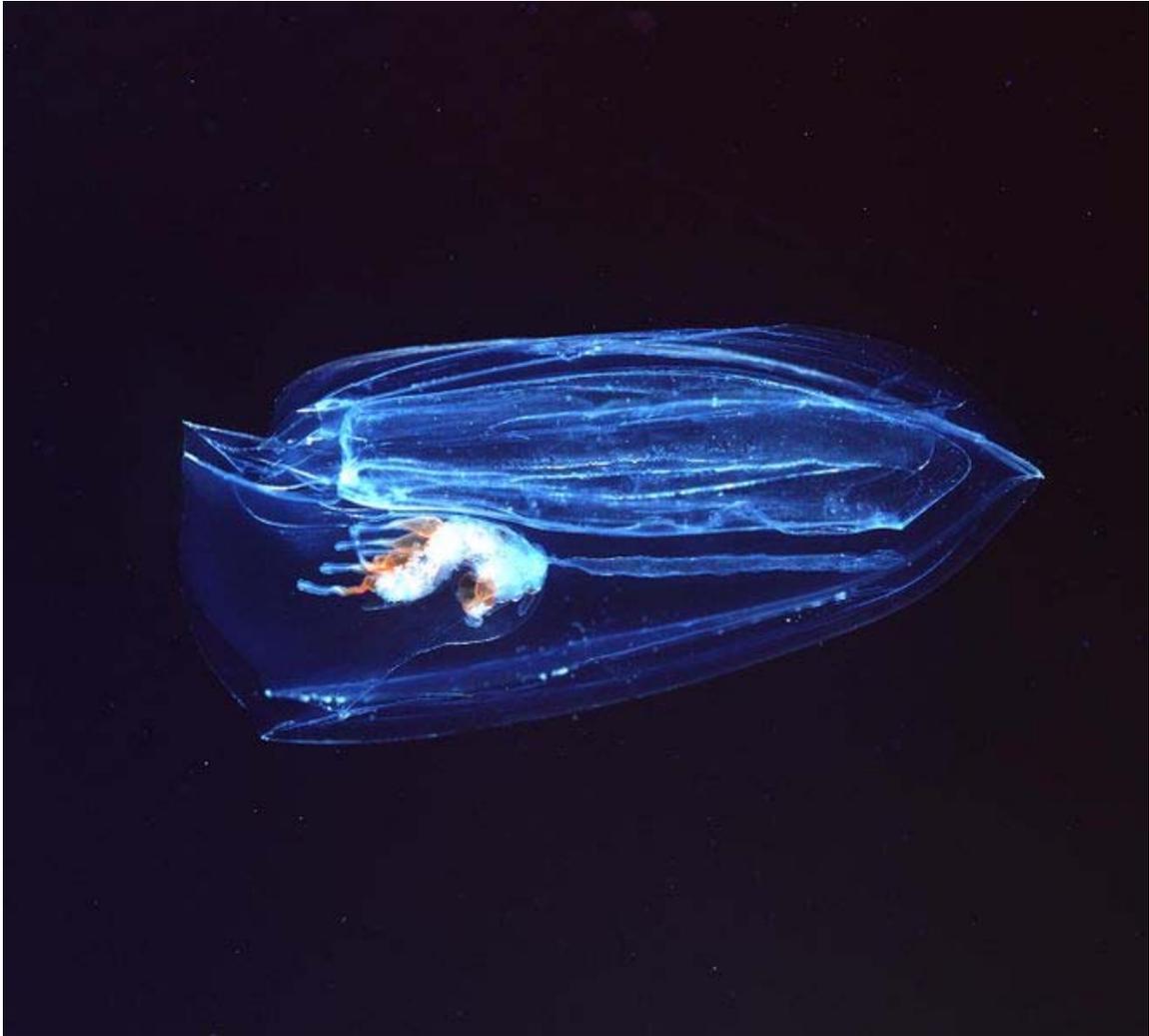
The effects of anthropogenic warming on the global population of phytoplankton is an area of active research. Changes in the vertical stratification of the water column, the rate of temperature-dependent biological reactions, and the atmospheric supply of nutrients are expected to have important impacts of future phytoplankton productivity. Additionally, changes in the mortality of phytoplankton due to rates of zooplankton grazing may be significant.



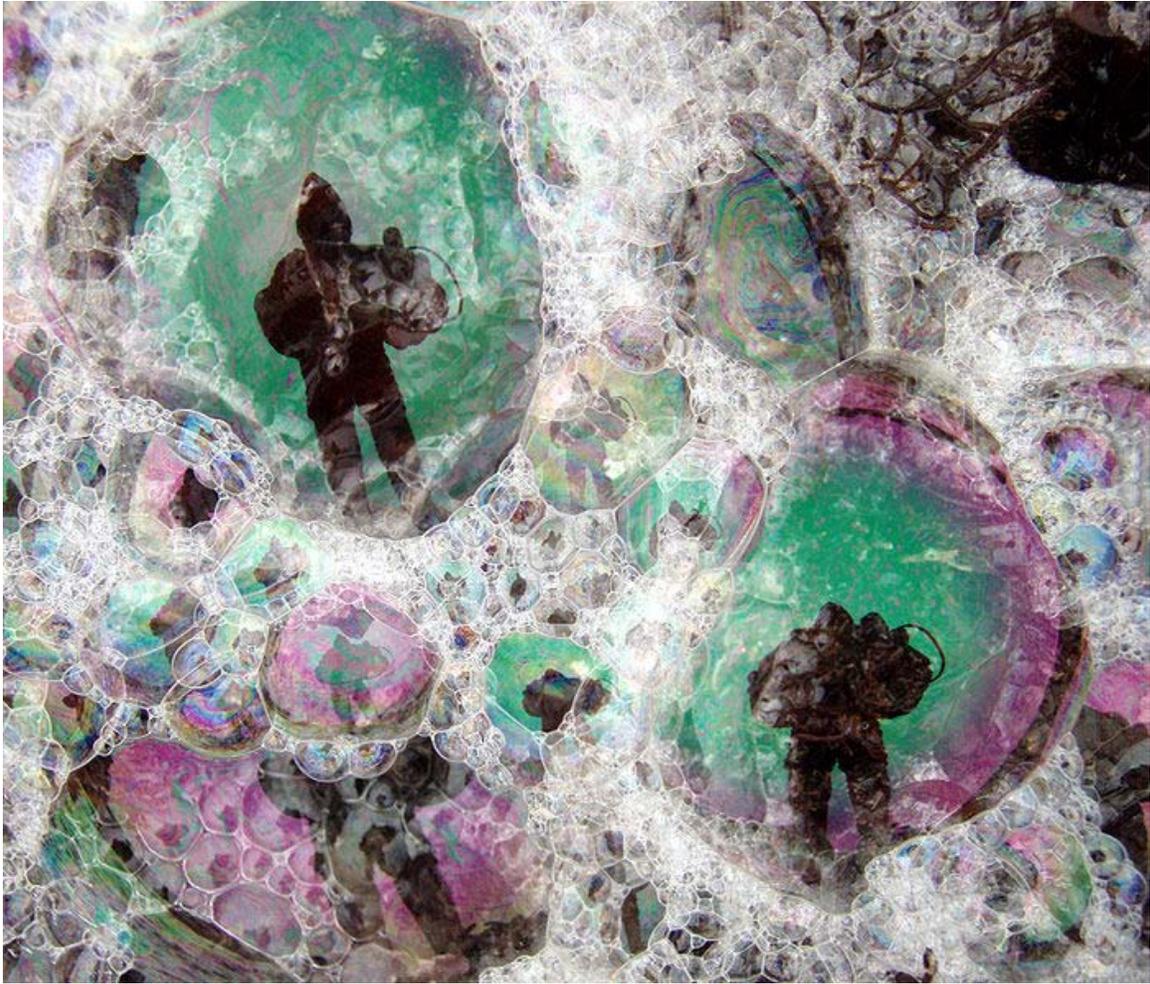
An amphipod, photo of exoskeletoned animal with curved body, with two long and two short antenna.



A copepod (*Calanoida* sp.) ca. 1-2 mm long, photo of translucent ovoid animal with two long antennae



Siphonophora – the "conveyor belt" of the upgrowing larvae and the ovary can be seen



Sea foam is produced by plankton, photo of many, differently sized bubbles with image of man

Importance to fish

Zooplankton are the initial prey item for almost all fish larvae as they switch from their yolk sacs to external feeding. Fish rely on the density and distribution of zooplankton to match that of new larvae, which can otherwise starve. Natural factors (e.g., current variations) and man-made factors (e.g. river dams) can strongly affect zooplankton, which can in turn strongly affect larval survival, and therefore breeding success.

Chapter 2

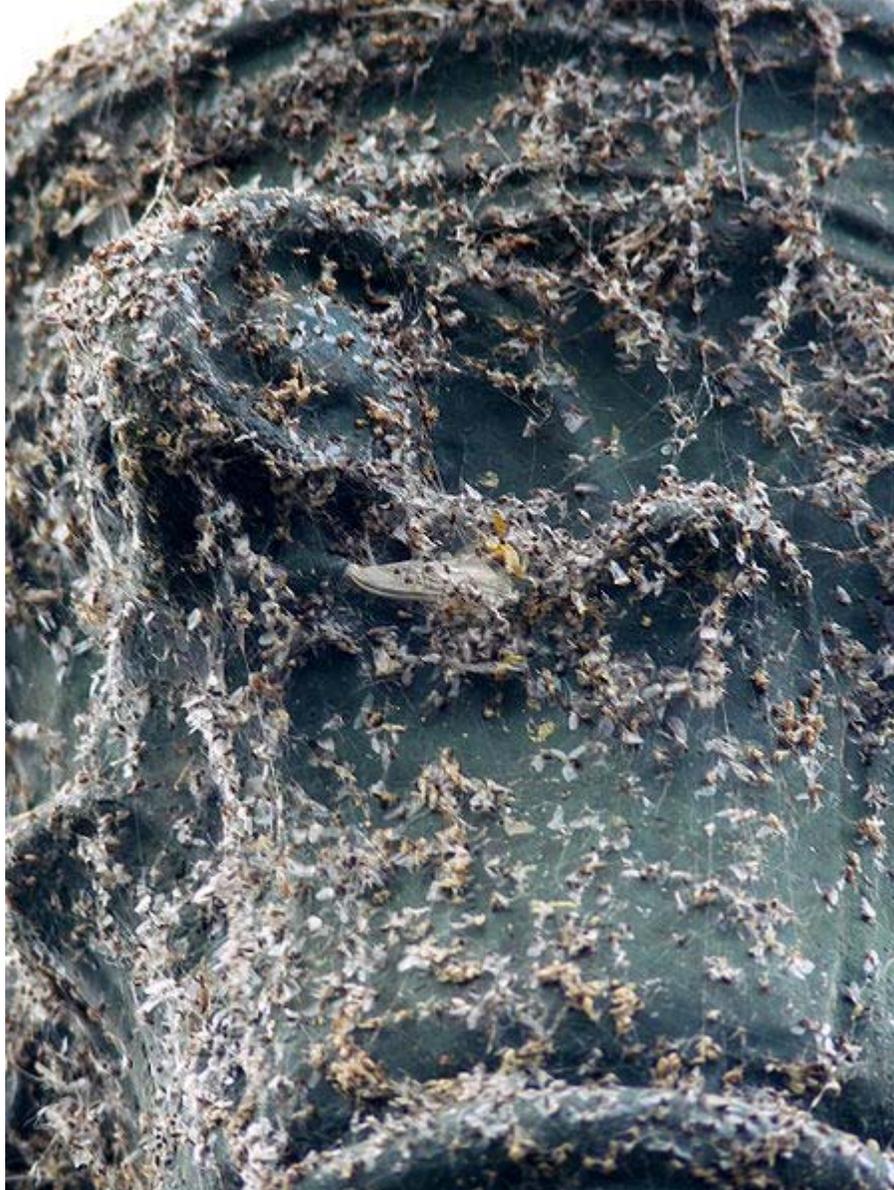
Aeroplankton and Bacterioplankton

Aeroplankton

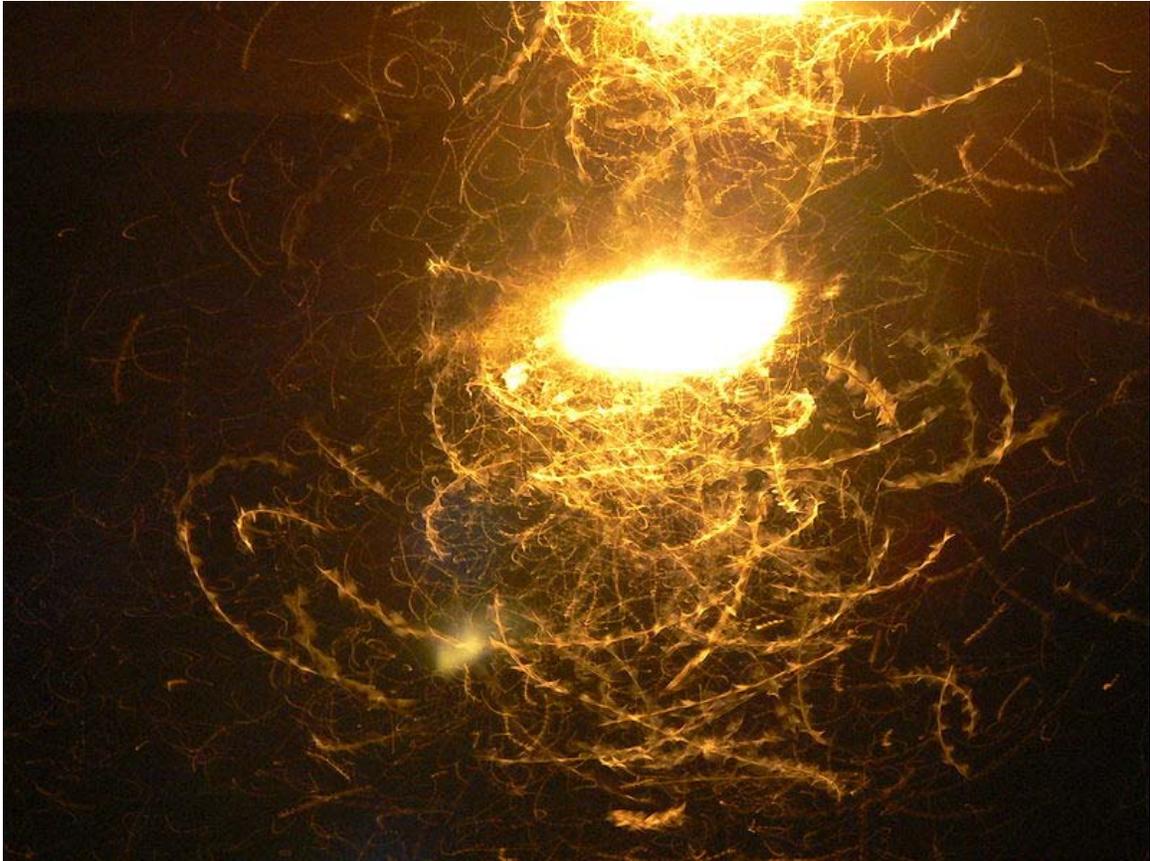
Aeroplankton (or **aerial plankton**) is the term used to describe the tiny lifeforms which float and drift in the air, carried by the current of the wind; it is the atmospheric analogue to oceanic plankton.



Detail of the formation of a dense but absolutely normal aeroplankton cloud at sunset, over the Loire river in France (early August 2010)



On the banks of the Loire, the luminaries of the lighting (by the bridge of Briare) trap a large number of individuals of key species of insects comprising the air plankton. It is one of the problems posed by the Light pollution



Effect of ecological fragmentation of nighttime environment caused by light pollution, which attracts and trap aeroplankton (easily trapped by bats and spiders) here in one of the 6 lamps illuminating the bridge Meun-sur-Loire (August 2010). The break allows to distinguish the path and speed of insects (and the number of beats of wings for the largest of them)



Snapshot (with flash) showing better on the same site as above, and at the same time the different sizes of insects attracted by the light

Most of the living things that make up aeroplankton are very small to microscopic in size, and many can be difficult to identify because of their tiny size. Scientists can collect them for study in traps and sweep nets from airplanes, kites or balloons.

The aeroplankton comprises numerous microbes, including viruses, about 1000 different species of bacteria, around 40,000 varieties of fungi, and hundreds of species of protists, algae, mosses and liverworts that live some part of their life cycle as aeroplankton, often as spores, pollen, and wind-scattered seeds.

A large number of small animals, mainly arthropods (such as insects and spiders), are also carried upwards into the atmosphere by air currents and may be found floating several thousand feet up.

Aphids, for example, are frequently found at high altitudes.

Many species of spiders deliberately use the wind to propel themselves around an area. The spider will find a vantage point (such as a branch, fence or surface) and, pointing its abdomen upward, eject fine threads of silk from the spinnerets. At some point, the friction of the air upon the silk thread(s) is great enough to get the spider lifted into the air and carried off by the breeze. This is called ballooning. Ballooning spiders are capable of

drifting many miles away from where they started. The flexibility of their silk draglines can aid the aerodynamics of their flight, causing the spiders to drift an unpredictable and sometimes long distance.

Bacterioplankton

Bacterioplankton refers to the bacterial component of the plankton that drifts in the water column. The name comes from the Ancient Greek word *πλανκτος* (*planktos*), meaning "wanderer" or "drifter" (Thurman, 1997), and *bacterium*, a Latin neologism coined in the 19th century by Christian Gottfried Ehrenberg. They are found in both seawater and freshwater.

Bacterioplankton occupy a range of ecological niches in aquatic systems. Many are saprotrophic, and obtain energy by consuming organic material produced by other organisms. This material may be dissolved in the medium and taken directly from there, or bacteria may live and grow in association with particulate material such as marine snow. Many other bacterioplankton species are autotrophic, and derive energy from either photosynthesis or chemosynthesis. The former are often categorised as picophytoplankton, and include cyanobacterial groups such as *Prochlorococcus* and *Synechococcus*. Bacterioplankton also play roles in ecological pathways such as nitrogen fixation, nitrification, denitrification, remineralisation and methanogenesis.

Like other small plankton, the bacterioplankton are preyed upon by zooplankton (usually protozoans), and their numbers are also controlled through infection by bacteriophages.

Chapter 3

Chaetognatha and Emiliaenia Huxleyi

Chaetognatha

Arrow worms
Temporal range: Lower
Cambrian–Recent



Spadella cephaloptera

Scientific classification [e]

Kingdom: Animalia

Subkingdom: Eumetazoa

(unranked): Bilateria

Phylum: **Chaetognatha**
Leuckart, 1854

Classes

Archisagittoidea

Sagittoidea

Chaetognatha, meaning *hair-jaws*, and commonly known as **arrow worms**, are a phylum of predatory marine worms that are a major component of plankton worldwide. About 20% of the known species are benthic, that is belonging to the lowest zone of the ocean, or benthic zone, and can attach to algae and rocks. They are found in all marine waters, from surface tropical waters and shallow tide pools to the deep sea and polar regions. Most chaetognaths are transparent and are torpedo shaped, but some deep-sea species are orange. They range in size from 2 to 120 millimetres (0.079 to 4.7 in).

There are more than 120 modern species assigned to over 20 genera. Despite the limited diversity of species, the number of individuals is large.

Anatomy

Chaetognaths are transparent or translucent dart-shaped animals covered by a cuticle. The body is divided into a distinct head, trunk, and tail. There are between four and fourteen hooked, grasping spines on each side of their head, flanking a hollow vestibule containing the mouth. The spines are used in hunting, and covered with a flexible hood arising from the neck region when the animal is swimming. All chaetognaths are carnivorous, preying on other planktonic animals.

The trunk bears one or two pairs of lateral fins incorporating structures superficially similar to the fin rays of fish. Unlike those of vertebrates, however, these are composed of a thickened basement membrane extending from the epidermis, and they are not homologous. An additional caudal fin covers the post-anal tail. Two chaetognath species, *Caecosagitta macrocephala* and *Eukrohnia fowleri*, have bioluminescent organs their fins.,

Chaetognaths swim in short bursts using a dorso-ventral undulating body motion, where their tail fin assists with propulsion and the body fins for stabilization and steering. Some species are known to use the neurotoxin tetrodotoxin to subdue prey.

The body cavity lacks a peritoneum, and therefore resembles the pseudocoel of animals such as nematodes, but is divided into one compartment on each side of the trunk, and additional compartments inside the head and tail. Although they have a mouth with one or two rows of tiny teeth, compound eyes, and a nervous system, they have no respiratory or circulatory systems.

The mouth opens into a muscular pharynx which contains glands to lubricate the passage of food. From here, a straight intestine runs the length of the trunk to an anus just in front of the tail. The intestine is the primary site of digestion and includes a pair of diverticula near the anterior end.

The nervous system is reasonably simple, consisting of a ganglionated nerve ring surrounding the pharynx. The dorsal ganglion is the largest, but nerves extend from all the ganglia along the length of the body. Chaetognaths have two compound eyes, each consisting of a number of pigment-cup ocelli fused together. In addition, there is a number of sensory bristles arranged in rows along the side of the body, where they probably perform a function similar to that of the lateral line in fish. An additional, curved, band of sensory bristles lies over the head and neck.

Materials are moved about the body cavity by cilia. Waste materials are simply excreted through the skin and anus.

The arrow worm rhabdomeres are derived from microtubules, which in turn form conical bodies, which contain granules and thread structures. The cone body is derived from a cilium, and the microtubules of the rhabdomeres are 20 nm long and 50 nm wide.

Reproduction

All species are hermaphroditic, carrying both eggs and sperm. They have some developmental similarities to nematodes.

Each animal possesses a pair of testes within the tail, and a pair of ovaries in the posterior region of the main body cavity. Immature sperm are released from the testes to mature inside the cavity of the tail, and then swim through a short duct to a seminal vesicle where they are packaged into a spermatophore.

During mating, each individual places a spermatophore onto the neck of its partner after rupture of the seminal vesicle. The sperm rapidly escape from the spermatophore and swim along the midline of the animal until they reach a pair of small pores just in front of the tail. These pores connect to the oviducts, into which the developed eggs have already passed from the ovaries, and it is here that fertilisation takes place.

The eggs are planktonic, or attached to nearby algae, and hatch into miniature versions of the adult, without a well-defined larval stage.

Classification

Chaetognaths are traditionally classed as deuterostomes by embryologists. Lynn Margulis and K. V. Schwartz place chaetognaths in the deuterostomes in their *Five Kingdom* classification. Molecular phylogenists, however, consider them to be protostomes. Thomas Cavalier-Smith places them in the protostomes in his *Six Kingdom* classification. The similarities between chaetognaths and nematodes mentioned above may support the

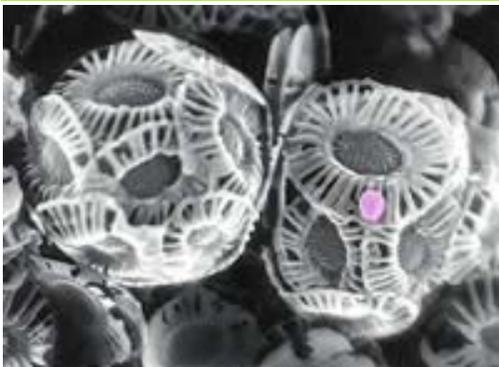
protostome thesis - in fact, chaetognaths are sometimes regarded as a basal ecdysozoan or lophotrochozoan. Chaetognatha appears close to the base of the protostome tree in most studies of their molecular phylogeny. This may explain their deuterostome embryonic characters. If chaetognaths branched off from the protostomes before they evolved their distinctive protostome embryonic characters, they may have retained deuterostome characters inherited from early bilaterian ancestors. Thus chaetognaths may be a useful model for the ancestral bilaterian. Studies of arrow worms' nervous systems suggests they should be placed within the protostomes.

Fossil record

Due to their soft bodies, chaetognaths fossilize poorly. Even so, several fossil chaetognath species have been described. Chaetognaths appear to have originated in the Cambrian Period. Complete body fossils have been formally described from the Lower Cambrian Maotianshan shales of Yunnan, China (*Eognathacantha ercainella* Chen & Huang and *Protosagitta spinosa* Hu) and the Middle Cambrian Burgess Shale of British Columbia (*Oesia disjuncta* Walcott). A more recent chaetognath, *Paucijaculum samamithion* Schram, has been described from the Mazon Creek biota from the Pennsylvanian of Illinois. Chaetognaths were thought possibly to be related to some of the animals grouped with the conodonts. The conodonts themselves, however, are thought to be related to the vertebrates. It is now thought that protoconodont elements (e.g., *Protohertzina anabarica* Missarzhevsky, 1973), are probably grasping spines of chaetognaths rather than teeth of conodonts. Previously chaetognaths in the Early Cambrian were only suspected from these protoconodont elements, but the more recent discoveries of body fossils have confirmed their presence then.

Emiliana huxleyi

Emiliana huxleyi



Emiliana huxleyi

Scientific classification

Domain: Eukaryota
Kingdom: Chromalveolata
Phylum: Haptophyta
Class: Prymnesiophyceae
Order: Isochrysidales
Family: Noelaerhabdaceae
Genus: *Emiliana*
Species: *E. huxleyi*

Binomial name

Emiliana huxleyi
(Lohm.) Hay and Mohler

Emiliana huxleyi, often abbreviated to simply "EHUX", is a species of coccolithophore with a global distribution from the tropics to subarctic waters. It is studied for the extensive blooms it forms in nutrient depleted waters after the reformation of the summer thermocline. Like other coccolithophores, *E. huxleyi* is a single-celled phytoplankton covered with uniquely ornamented calcite disks, coccoliths (also informally known as liths or scales). Individual coccoliths are abundant in marine sediments although complete coccospheres are more unusual. In the case of *E. huxleyi*, not only the shell, but also the soft part of the organism may be recorded in sediments. It produces a group of chemical compounds that are very resistant to decomposition. These chemical compounds, known as alkenones, can be found in marine sediments long after other soft parts of the organisms have decomposed. Alkenones are used by earth scientists as a clue to past sea surface temperatures.



Landsat image from 24th July 1999 of an *Emiliana huxleyi* bloom

Named after Thomas Huxley and Cesare Emiliani, it is the most numerically abundant and widespread coccolithophore species. Its coccoliths are transparent and commonly colourless, but they are formed of calcite which refracts light very efficiently in the water column. This, and the high concentrations caused by continual shedding of their coccoliths makes *E. huxleyi* blooms easily visible from space. Satellite images show that blooms can cover large areas (possibly >100,000 square kilometers), with complementary shipboard measurements indicating that *E. huxleyi* is by far the dominant phytoplankton species under these conditions.

This species has been the inspiration for James Lovelock's Gaia hypothesis which claims that living organisms somehow may be able to self regulate their own conditions of chemistry and climate at a state favourable for life.

Chapter 4

Diatom

Diatoms



Marine diatoms.

Scientific classification

Domain: Eukaryota

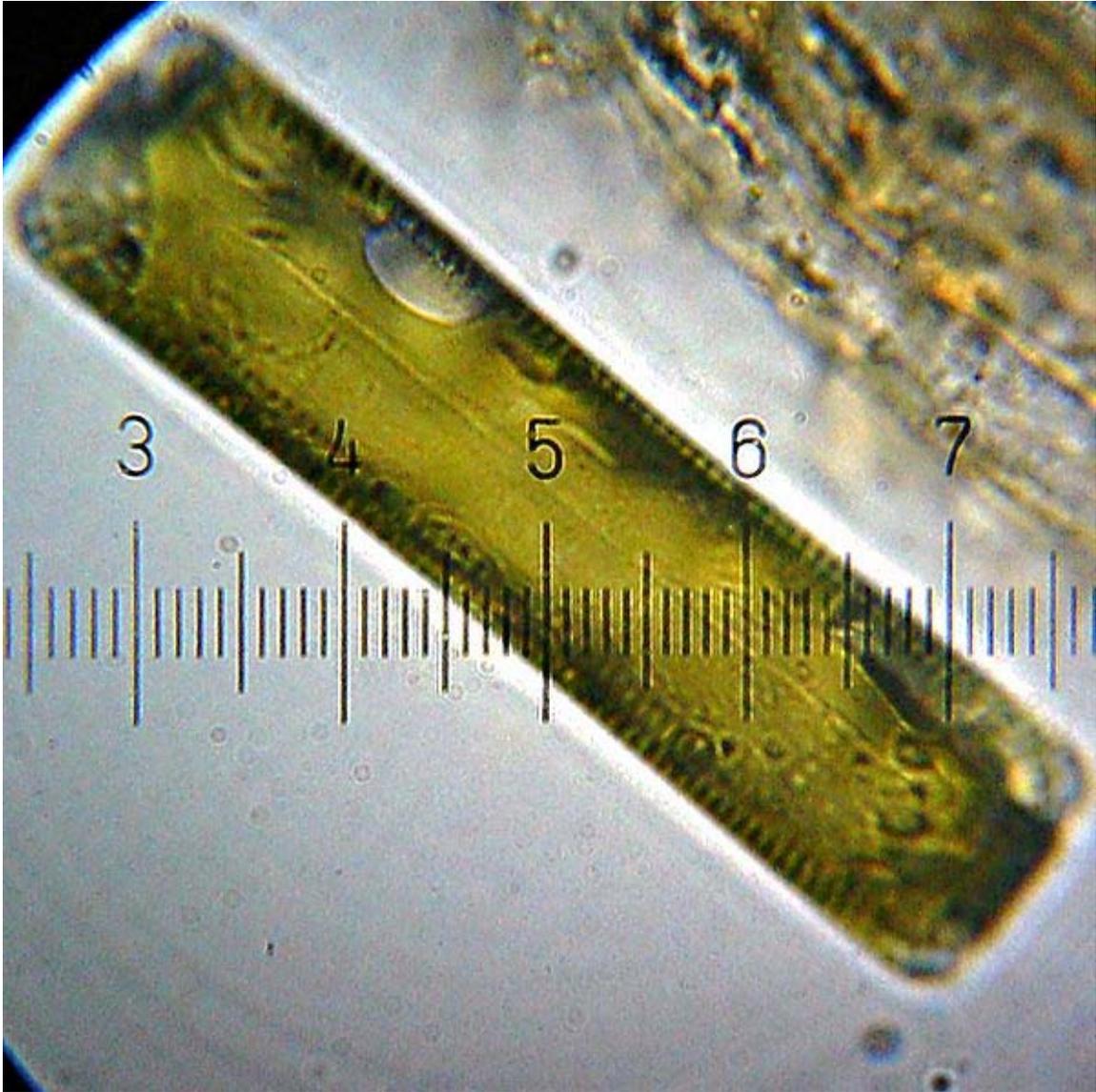
Kingdom: Chromalveolata

Phylum: Heterokontophyta

Class: **Bacillariophyceae**
Haeckel 1878

Orders

- Centrales
- Pennales



A diatom. Numbered ticks are 11 microns apart.

Diatoms are a major group of algae, and are one of the most common types of phytoplankton. Most diatoms are unicellular, although they can exist as colonies in the shape of filaments or ribbons (e.g. *Fragillaria*), fans (e.g. *Meridion*), zigzags (e.g. *Tabellaria*), or stellate colonies (e.g. *Asterionella*). Diatoms are producers within the food chain. A characteristic feature of diatom cells is that they are encased within a unique cell wall made of silica (hydrated silicon dioxide) called a frustule. These frustules show a wide diversity in form, but usually consist of two asymmetrical sides with a split between them, hence the group name. Fossil evidence suggests that they originated during, or before, the early Jurassic Period. Diatom communities are a popular tool for monitoring environmental conditions, past and present, and are commonly used in studies of water quality.

General biology

There are more than 200 genera of living diatoms, and it is estimated that there are approximately 100,000 extant species. Diatoms are a widespread group and can be found in the oceans, in freshwater, in soils and on damp surfaces. Most live pelagically in open water, although some live as surface films at the water-sediment interface (benthic), or even under damp atmospheric conditions. They are especially important in oceans, where they are estimated to contribute up to 45% of the total oceanic primary production. Spatial distribution of marine phytoplankton species is restricted both horizontally and vertically. Diatoms occur in all oceans from the poles to the tropics; polar and subpolar regions contain relatively few species compared with temperate biota. Although tropical regions exhibit the greatest number of species, more abundant populations are found in polar to temperate regions. Usually microscopic, some species of diatoms can reach up to 2 millimetres in length.



Several species of fresh-water diatoms.

Diatoms belong to a large group called the heterokonts, including both autotrophs (e.g. golden algae, kelp) and heterotrophs (e.g. water moulds). Their yellowish-brown chloroplasts are typical of heterokonts, with four membranes and containing pigments such as the carotenoid fucoxanthin. Individuals usually lack flagella, but they are present in gametes and have the usual heterokont structure, except they lack the hairs

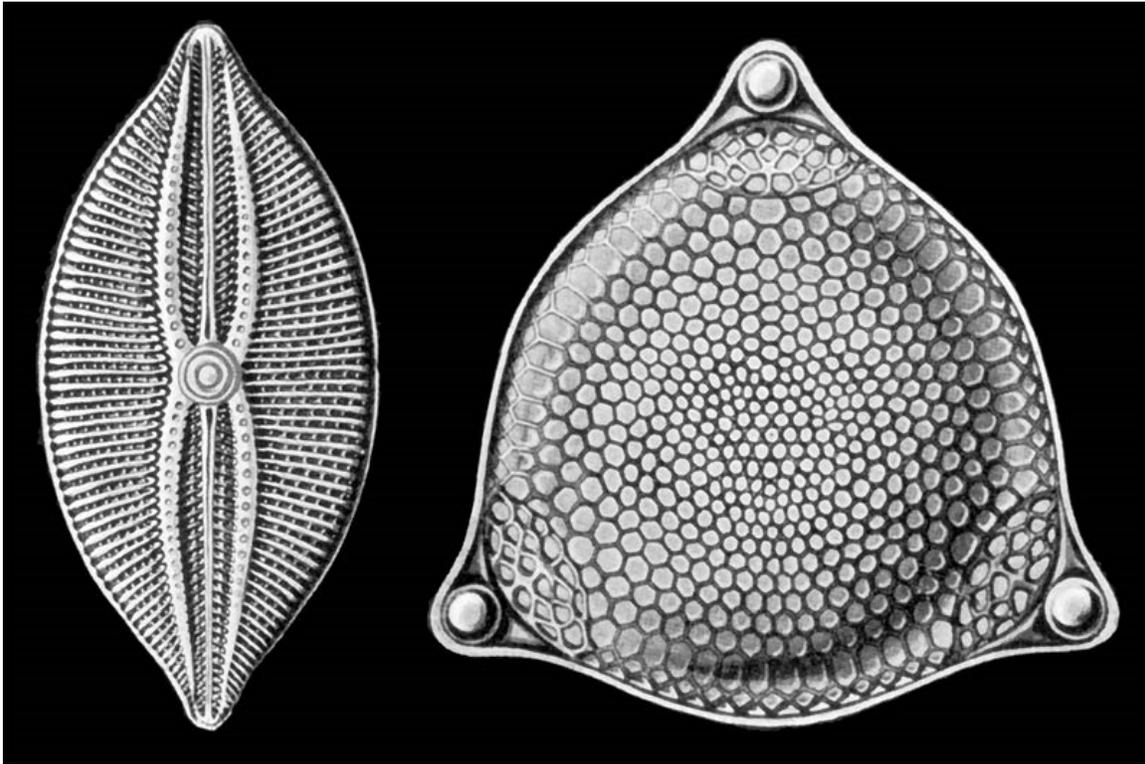
(mastigonemes) characteristic in other groups. Most diatoms are non-motile, although some move via flagellation. As their relatively dense cell walls cause them to readily sink, planktonic forms in open water usually rely on turbulent mixing of the upper layers by the wind to keep them suspended in sunlit surface waters. Some species actively regulate their buoyancy with intracellular lipids to counter sinking.

Diatom cells are contained within a unique silicate (silicic acid) cell wall comprising two separate valves (or shells). The biogenic silica that the cell wall is composed of is synthesised intracellularly by the polymerisation of silicic acid monomers. This material is then extruded to the cell exterior and added to the wall. Diatom cell walls are also called **frustules** or **tests**, and their two valves typically overlap one over the other like the two halves of a petri dish. In most species, when a diatom divides to produce two daughter cells, each cell keeps one of the two halves and grows a smaller half within it. As a result, after each division cycle the average size of diatom cells in the population gets smaller. Once such cells reach a certain minimum size, rather than simply divide vegetatively, they reverse this decline by forming an auxospore. This expands in size to give rise to a much larger cell, which then returns to size-diminishing divisions. Auxospore production is almost always linked to meiosis and sexual reproduction.

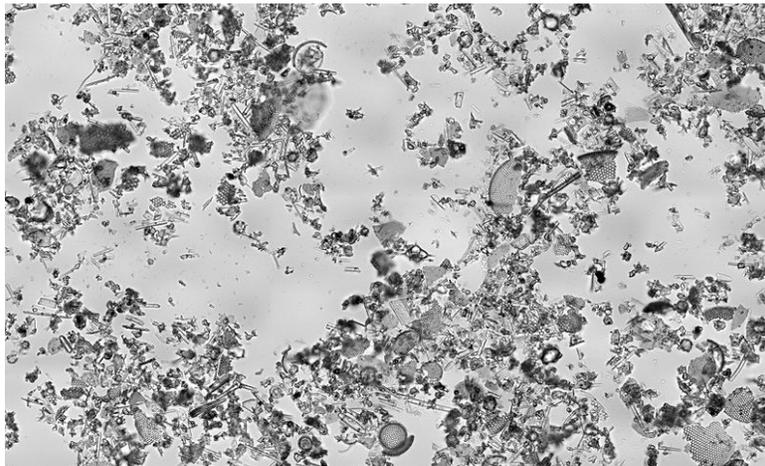
Decomposition and decay of diatoms leads to organic and inorganic (in the form of silicates) sediment, the inorganic component of which can lead to a method of analyzing past marine environments by corings of ocean floors or bay muds, since the inorganic matter is embedded in deposition of clays and silts and forms a permanent geological record of such marine strata.

The study of diatoms is a branch of phycology, and phycologists specializing in diatoms are called diatomists.

Classification



Selections from Ernst Haeckel's 1904 *Kunstformen der Natur* (Artforms of Nature), showing pennate (left) and centric (right) frustules.



Diatomaceous earth as viewed under bright field illumination on a light microscope. Diatomaceous earth is a soft, siliceous, sedimentary rock made up of the cell walls of diatoms and readily crumbles to a fine powder. This sample consists of a mixture of centric (radially symmetric) and pennate (bilaterally symmetric) diatoms. This image of diatomaceous earth particles in water is at a scale of 6.236 pixels/ μm , the entire image covers a region of approximately 1.13 by 0.69 mm.

The classification of heterokonts is still unsettled, and they may be treated as a division (or phylum), kingdom, or something in-between. Accordingly, groups like the diatoms may be ranked anywhere from class (usually called **Diatomophyceae**) to division (usually called **Bacillariophyta**), with corresponding changes in the ranks of their subgroups.

Diatoms are traditionally divided into two orders:

- **centric** diatoms (Centrales), which are radially symmetric
- **pennate** diatoms (Pennales), which are bilaterally symmetric. The former are paraphyletic to the latter.

A more recent classification divides the diatoms into three classes:

- centric diatoms (Coscinodiscophyceae)
- pennate diatoms
 - without a raphe (Fragilariophyceae)
 - with a raphe (Bacillariophyceae)

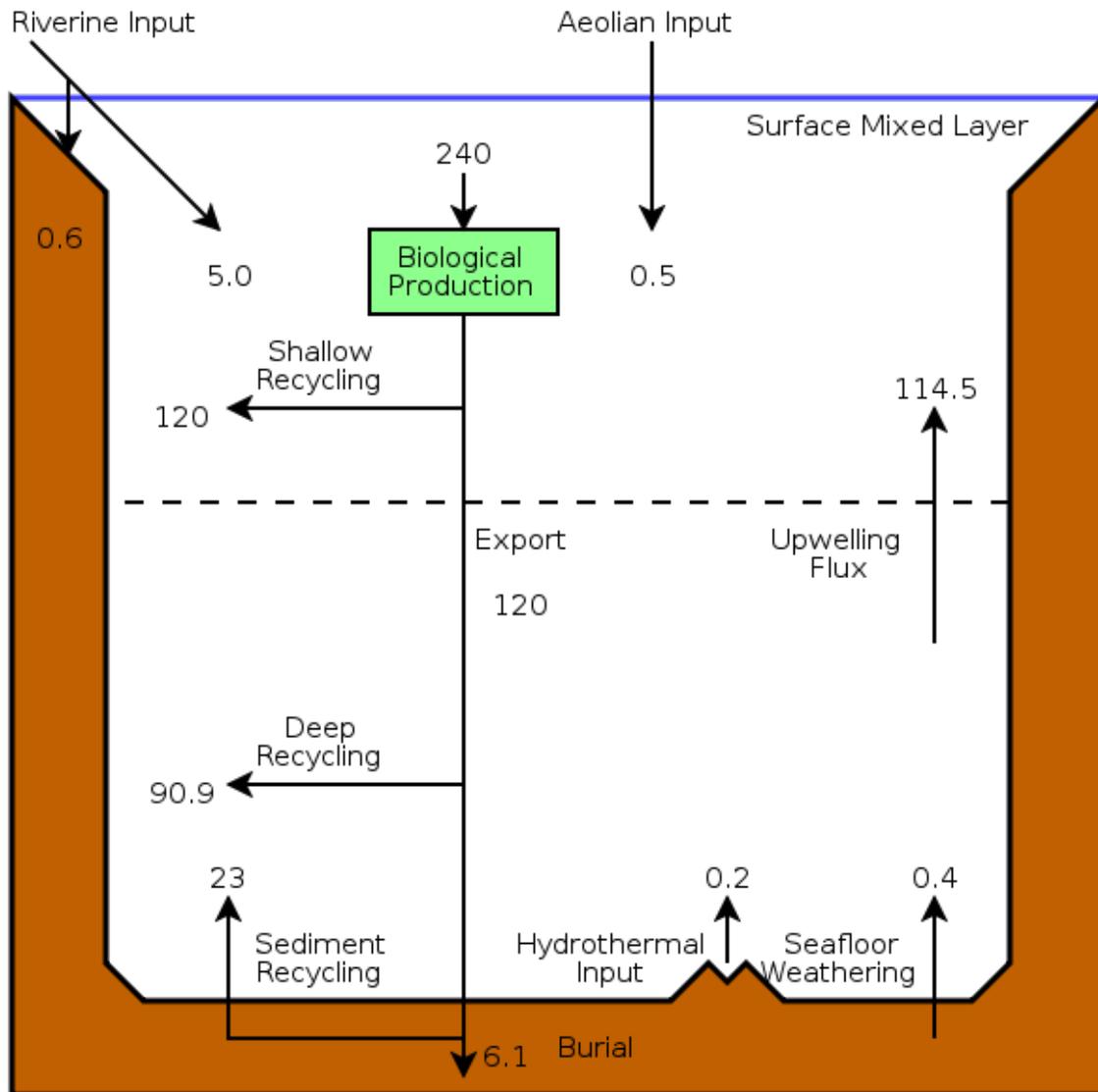
It is probable there will be further revisions as understanding of their relationships increases.

Diatoms generally range in size from ca. 2-200 μ m, and are composed of a cell wall comprising silica. This siliceous wall can be highly patterned with a variety of pores, ribs, minute spines, marginal ridges and elevations; all of which can be utilised to delineate genera and species. The cell itself consists of two halves, each containing an essentially flat plate, or valve and marginal connecting, or girdle band. One half, the hypotheca, is slightly smaller than the other half, the epitheca. Diatom morphology varies, typically though the shape of the cell is circular, although, some cells may be triangular, square, or elliptical.

Cells are solitary or united into colonies of various kinds, which may be linked by siliceous structures; mucilage pads, or stalks; mucilage tubes; amorphous masses of mucilage and threads of polysaccharide (chitin), which are secreted through strutted processes. Major pigments of diatoms are chlorophylls a and c, beta-carotene, fucoxanthin, diatoxanthin and diadinoxanthin. Diatoms are primarily photosynthetic. A few, however, are obligate heterotrophs, while others can live heterotrophically in the absence of light, provided an appropriate organic carbon source is available. Storage products are chrysolaminarin and lipids.

Round & Crawford (1990) and Hoek *et al.* (1995) provide more comprehensive coverage of diatom taxonomy.

Ecology



A budget of the ocean's silicon cycle

Planktonic diatoms in freshwater and marine environments typically exhibit a "boom and bust" (or "**bloom** and bust") lifestyle. When conditions in the upper mixed layer (nutrients and light) are favourable (*e.g.* at the start of spring) their competitive edge allows them to quickly dominate phytoplankton communities ("boom" or "bloom"). As such they are often classed as opportunistic *r*-strategists (*i.e.* those organisms whose ecology is defined by a high growth rate, *r*).

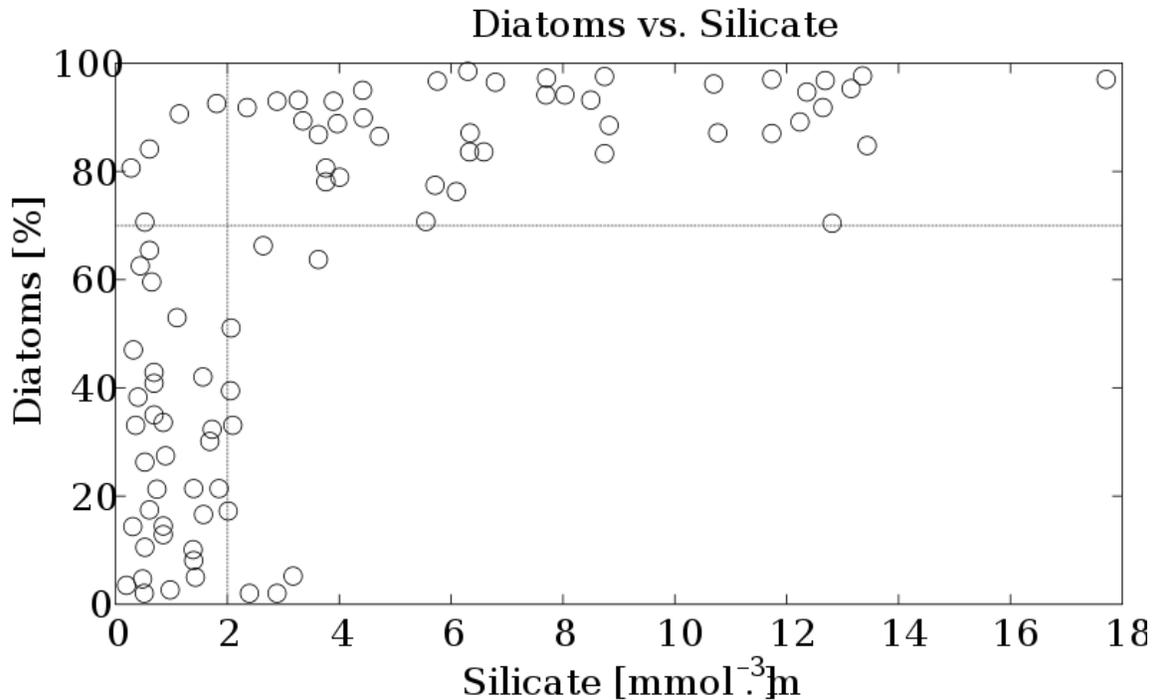
When conditions turn unfavourable, usually upon depletion of nutrients, diatom cells typically increase in sinking rate and exit the upper mixed layer ("bust"). This sinking is induced by either a loss of buoyancy control, the synthesis of mucilage that sticks diatoms cells together, or the production of heavy **resting spores**. Sinking out of the

upper mixed layer removes diatoms from conditions unfavourable to growth, including grazer populations and higher temperatures (which would otherwise increase cell metabolism). Cells reaching deeper water or the shallow seafloor can then rest until conditions become more favourable again. In the open ocean, many sinking cells are lost to the deep, but refuge populations can persist near the thermocline.

Ultimately, diatom cells in these resting populations re-enter the upper mixed layer when vertical mixing entrains them. In most circumstances, this mixing also replenishes nutrients in the upper mixed layer, setting the scene for the next round of diatom blooms. In the open ocean (away from areas of continuous upwelling), this cycle of bloom, bust, then return to pre-bloom conditions typically occurs over an annual cycle, with diatoms only being prevalent during the spring and early summer. In some locations, however, an autumn bloom may occur, caused by the breakdown of summer stratification and the entrainment of nutrients while light levels are still sufficient for growth. Since vertical mixing is increasing, and light levels are falling as winter approaches, these blooms are smaller and shorter-lived than their spring equivalents.

In the open ocean, the condition that typically causes diatom (spring) blooms to end is a lack of silicon. Unlike other nutrients, this is only a major requirement of diatoms so it is not regenerated in the plankton ecosystem as efficiently as, for instance, nitrogen or phosphorus nutrients. This can be seen in maps of surface nutrient concentrations - as nutrients decline along gradients, silicon is usually the first to be exhausted (followed normally by nitrogen then phosphorus).

Because of this bloom-and-bust cycle, diatoms are believed to play a disproportionately important role in the export of carbon from oceanic surface waters. Significantly, they also play a key role in the regulation of the biogeochemical cycle of silicon in the modern ocean.

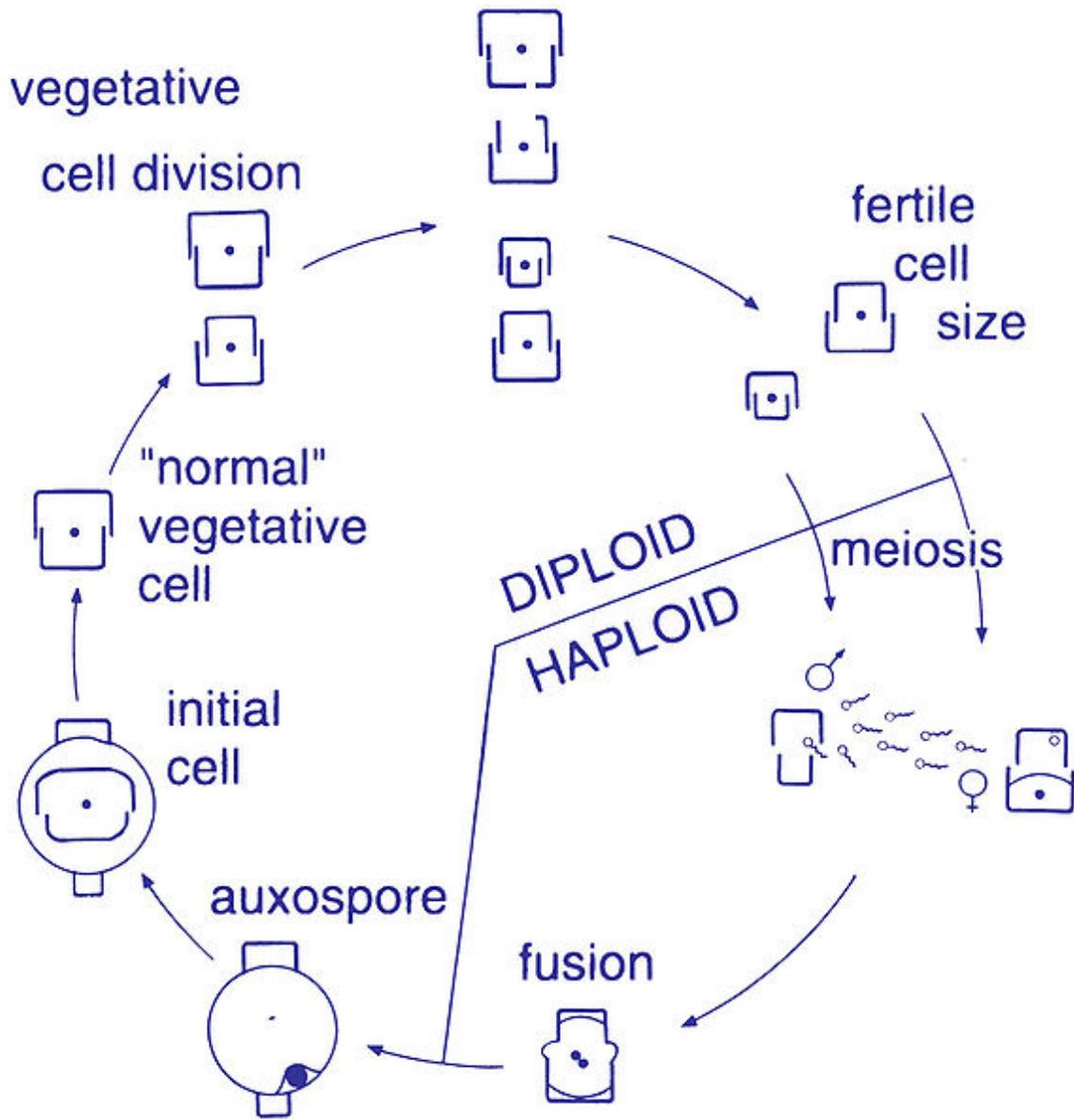


Egge & Aksnes (1992) figure.

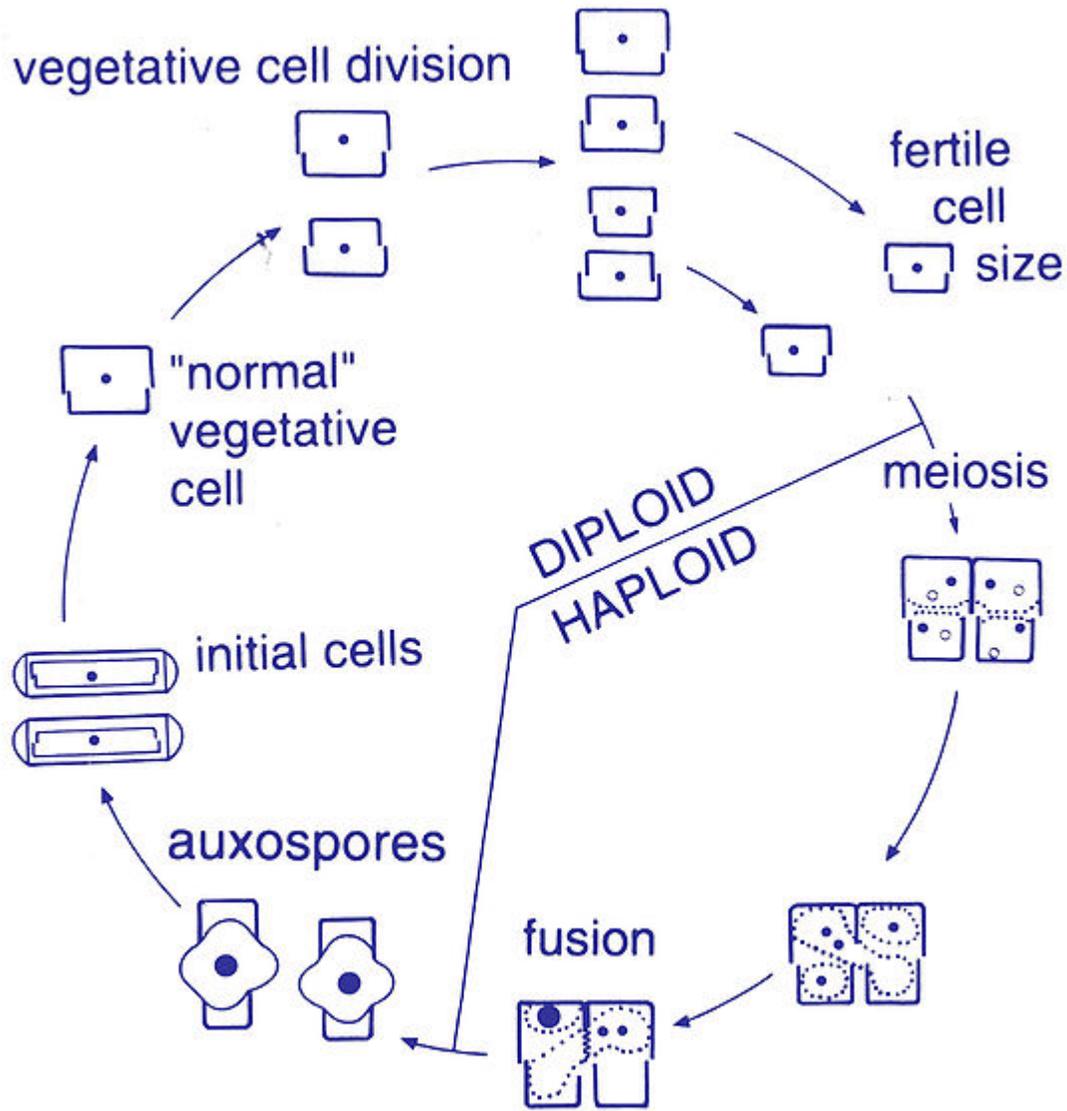
The use of silicon by diatoms is believed by many researchers to be the key to their ecological success. In a now classic study, Egge & Aksnes (1992) found that diatom dominance of mesocosm communities was directly related to the availability of silicic acid — when concentrations were greater than 2 mmol m⁻³, they found that diatoms typically represented more than 70% of the phytoplankton community. Raven (1983) noted that, relative to organic cell walls, silica frustules require less energy to synthesize (approximately 8% of a comparable organic wall), potentially a significant saving on the overall cell energy budget. Other researchers have suggested that the biogenic silica in diatom cell walls acts as an effective pH buffering agent, facilitating the conversion of bicarbonate to dissolved CO₂ (which is more readily assimilated). Notwithstanding the possible advantages conferred by silicon, diatoms typically have higher growth rates than other algae of a corresponding size.

Diatoms occur in virtually every environment that contains water. This includes not only oceans, seas, lakes and streams, but also soil.

Life-Cycle



Sexual reproduction of a centric diatom (oogamy)



Sexual reproduction of a pinnate diatom (morphological isogamy, physiological anisogamy)

Diatoms are non-motile; however, sperm found in some species can be flagellated, though motility is usually limited to a gliding motion. Reproduction among these organisms is primarily asexual by binary fission, with each daughter cell receiving one of the parent cell's two frustules (or theca). This is used by each daughter cell as the larger frustule (or epitheca) into which a second, small frustule (or hypotheca) is constructed.

This form of division results in a size reduction of the offspring and therefore the average cell size of a diatom population decreases, until the cells are about one-third their maximum size. It has been observed, however, the ability of certain taxa to divide without causing a reduction in cell size. Nonetheless, in order to restore the cell size of a

diatom population for those that do endure size reduction, sexual reproduction and auxospore formation must occur. Vegetative cells of diatoms are diploid (2N) and so meiosis can take place, producing male and female gametes which then fuse to form the zygote. The zygote sheds its silica theca and grows into a large sphere covered by an organic membrane, the auxospore. A new diatom cell of maximum size, the initial cell, forms within the auxospore thus beginning a new generation. Resting spores may also be formed as a response to unfavourable environmental conditions with germination occurring when conditions improve.

In centric diatoms, the small male gametes have one flagellum while the female gametes are large and non-motile (oogamous). Conversely, in pinnate diatoms both gametes lack flagella (isoogamous). Certain araphid species have been documented as anisogamous and are, therefore, considered to represent a transitional stage between centric and pinnate diatoms.

Evolutionary history

Heterokont chloroplasts appear to be derived from those of red algae, rather than directly from prokaryotes as occurred in plants. This suggests they had a more recent origin than many other algae. However, fossil evidence is scant, and it is really only with the evolution of the diatoms themselves that the heterokonts make a serious impression on the fossil record.

The earliest known fossil diatoms date from the early Jurassic (~185 Ma), although molecular clock and sedimentary evidence suggests an earlier origin. It has been suggested that their origin may be related to the end-Permian mass extinction (~250 Ma), after which many marine niches were opened. The gap between this event and the time that fossil diatoms first appear may indicate a period when diatoms were unsilicified and their evolution was cryptic. Since the advent of silicification, diatoms have made a significant impression on the fossil record, with major deposits of fossil diatoms found as far back as the early Cretaceous, and some rocks (diatomaceous earth, diatomite, kieselguhr) being composed almost entirely of them.

Although the diatoms may have existed since the Triassic, the timing of their ascendancy and "take-over" of the silicon cycle is more recent. Prior to the Phanerozoic (before 544 Ma), it is believed that microbial or inorganic processes weakly regulated the ocean's silicon cycle. Subsequently, the cycle appears dominated (and more strongly regulated) by the radiolarians and siliceous sponges, the former as zooplankton, the latter as sedentary filter feeders primarily on the continental shelves. Within the last 100 My, it is thought that the silicon cycle has come under even tighter control, and that this derives from the ecological ascendancy of the diatoms.

However, the precise timing of the "take-over" is unclear, and different authors have conflicting interpretations of the fossil record. Some evidence, such as the displacement of siliceous sponges from the shelves, suggests that this takeover began in the Cretaceous (146 Ma to 65 Ma), while evidence from radiolarians suggests "take-over" did not begin

until the Cenozoic (65 Ma to present). The expansion of grassland biomes and the evolutionary radiation of grasses during the Miocene is believed to have increased the flux of soluble silicon to the oceans, and it has been argued that this has promoted the diatoms during the Cenozoic era. However, work on the variation of diatom diversity during the Cenozoic suggests instead that diatom success is decoupled from the evolution of grasses, and that diatoms were most diverse prior to the diversification of grasses. Nevertheless, regardless of the details of the "take-over" timing, it is clear that this most recent revolution has installed much tighter biological control over the biogeochemical cycle of silicon.

Fossil record

The fossil record of diatoms has largely been established through the recovery of their siliceous frustules in marine and non-marine sediments. Although diatoms have both a marine and non-marine stratigraphic record, diatom biostratigraphy, which is based on time-constrained evolutionary originations and extinctions of unique taxa, is only well developed and widely applicable in marine systems. The duration of diatom species ranges have been documented through the study of ocean cores and rock sequences exposed on land. Where diatom biozones are well established and calibrated to the geomagnetic polarity time scale (e.g., Southern Ocean, North Pacific, eastern equatorial Pacific), diatom-based age estimates may be resolved to within <100,000 years, although typical age resolution for Cenozoic diatom assemblages is several hundred thousand years.

The Cretaceous record of diatoms is limited, but recent studies reveal a progressive diversification of diatom types. The Cretaceous-Tertiary extinction event, which in the oceans dramatically affected organisms with calcareous skeletons, appears to have had relatively little impact on diatom evolution.

Although no mass extinctions of marine diatoms have been observed during the Cenozoic, times of relatively rapid evolutionary turnover in marine diatom assemblages occurred near the Paleocene–Eocene boundary and at the Eocene–Oligocene boundary. Further turnover of assemblages took place at various times between the middle Miocene and late Pliocene, in response to progressive cooling of polar regions and the development of more endemic diatom assemblages. A global trend toward more delicate diatom frustules has been noted from the Oligocene to the Quaternary. This coincides with an increasingly more vigorous circulation of the ocean's surface and deep waters brought about by increasing latitudinal thermal gradients at the onset of major ice sheet expansion on Antarctica and progressive cooling through the Neogene and Quaternary towards a bipolar glaciated world. This drove the diatoms into uptaking silica more competitively (i.e., to use less silica in formation of their frustules). Increased mixing of the oceans renews silica and other nutrients necessary for diatom growth in surface waters, especially in regions of coastal and oceanic upwelling.

Collection

Living diatoms are often found clinging in great numbers to filamentous algae, or forming gelatinous masses on various submerged plants. *Cladophora* is frequently covered with *Cocconeis*, an elliptically shaped diatom; *Vaucheria* is often covered with small forms. Diatoms are frequently present as a brown, slippery coating on submerged stones and sticks, and may be seen to "stream" with river current.

The surface mud of a pond, ditch, or lagoon will almost always yield some diatoms. They can be made to emerge by filling a jar with water and mud, wrapping it in black paper and letting direct sunlight fall on the surface of the water. Within a day, the diatoms will come to the top in a scum and can be isolated.

Since diatoms form an important part of the food of molluscs, tunicates, and fishes, the alimentary tracts of these animals often yield forms that are not easily secured in other ways. Marine diatoms can be collected by direct water sampling, though benthic forms can be secured by scraping barnacles, oyster shells, and other shells.

EST sequencing

The first insights into the properties of the *P. tricornutum* gene repertoire was described using 1,000 ESTs. Subsequently, the number of ESTs was extended to 12,000 and the Diatom EST Database was constructed for functional analyses. These sequences have been used to make a comparative analysis between *P. tricornutum* and the putative complete proteomes from the green alga *Chlamydomonas reinhardtii*, the red alga *Cyanidioschyzon merolae*, and *T. pseudonana*. The diatom EST database now consists in over 200,000 ESTs from *P. tricornutum* (16 libraries) and *T. pseudonana* (7 libraries) cells grown in a range of different conditions, many of which corresponding to different abiotic stresses.

Genome sequencing

The entire genomes of the centric diatom, *Thalassiosira pseudonana* (32.4 Mb), and the pennate diatom, *Phaeodactylum tricornutum* (27.4 Mb), have been sequenced. Comparisons of the two fully sequenced diatom genomes finds that the *P. tricornutum* genome includes fewer genes (10,402 opposed to 11,776) than *T. pseudonana* and no major synteny (gene order) could be detected between the two genomes. *T. pseudonana* genes show an average of ~1.52 introns per gene as opposed to 0.79 in *P. tricornutum*, suggesting recent widespread intron gain in the centric diatom. Despite relatively recent evolutionary divergence (90 million years), the extent of molecular divergence between centrics and pennates indicates rapid evolutionary rates within the Bacillariophyceae compared to other eukaryotic groups. Comparative genomics also established that a specific class of transposable elements, the Diatom Copia-like retrotransposons (or CoDis), has been significantly amplified in the *P. tricornutum* genome with respect to *T. pseudonana*, constituting 5.8 and 1% of the respective genomes.

Importantly, diatom genomics brought much information about the extent and dynamics of the endosymbiotic gene transfer (EGT) process. Comparison of the *T. pseudonana* proteins with homologs in other organisms suggested that hundreds have their closest homologs in the Plantae lineage. EGT towards diatom genomes can be illustrated by the fact that the *T. pseudonana* genome encodes six proteins which are most closely related to genes encoded by the *Guillardia theta* (cryptomonad) nucleomorph genome. Four of these genes are also found in red algal plastid genomes, thus demonstrating successive EGT from red algal plastid to red algal nucleus (nucleomorph) to heterokont host nucleus. More recent phylogenomic analyses of diatom proteomes provided evidence for a prasinophyte-like endosymbiont in the common ancestor of chromalveolates as supported by the fact the 70% of diatom genes of Plantae origin are of green lineage provenance and that such genes are also found in the genome of other stramenopiles. Therefore, it was proposed that chromalveolates are the product of serial secondary endosymbiosis first with a green algae, followed by a second one with a red algae that conserved the genomic footprints of the previous but displaced the green plastid. However, phylogenomic analyses of diatom proteomes and chromalveolate evolutionary history will likely take advantage of complementary genomic data from under-sequenced lineages such as red algae.

In addition to EGT, horizontal gene transfer (HGT) can occur independently of an endosymbiotic event. The publication of the *P. tricornutum* genome reported that at least 587 *P. tricornutum* genes appear to be most closely related to bacterial genes, accounting for more than 5% of the *P. tricornutum* proteome. About half of these are also found in the *T. pseudonana* genome, attesting their ancient incorporation in the diatom lineage.

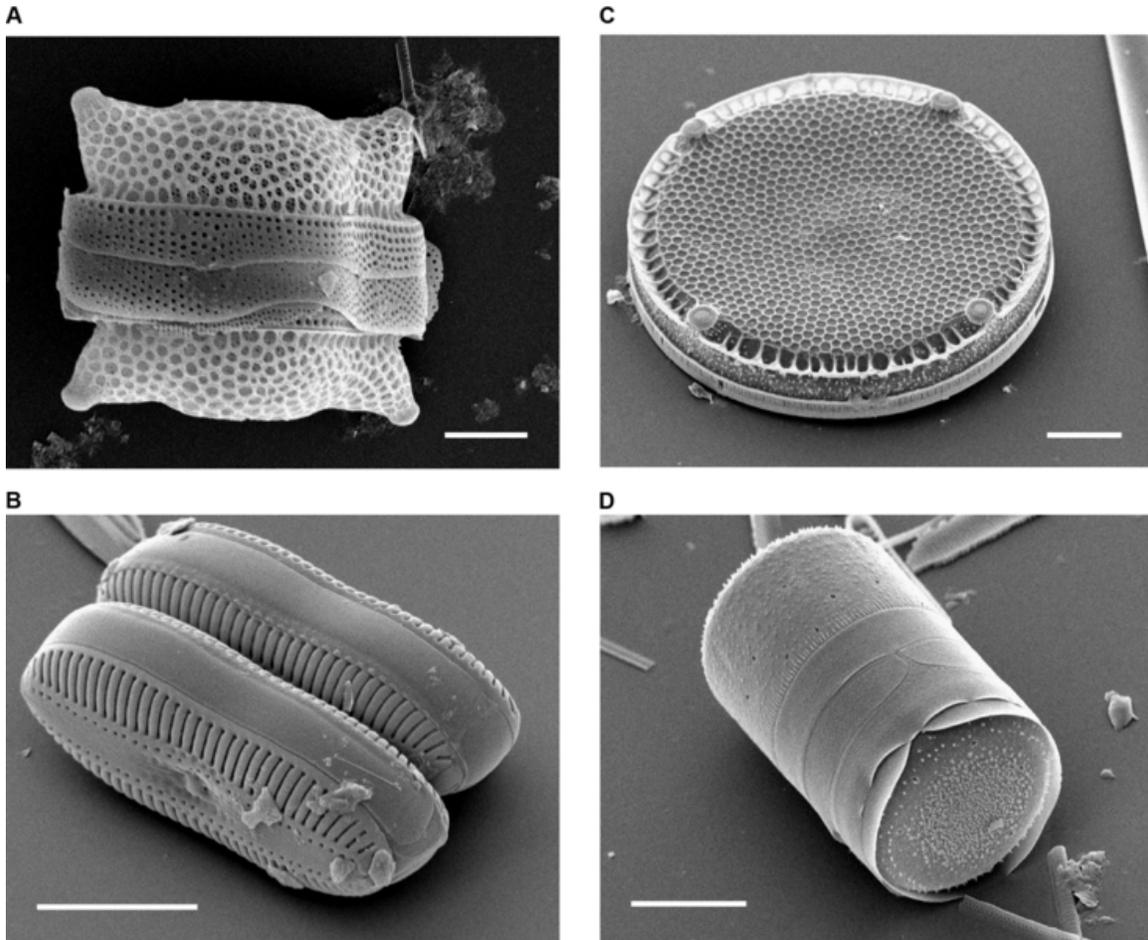
Nanotechnology research

The deposition of silica by diatoms may also prove to be of utility to nanotechnology. Diatom cells repeatedly and reliably manufacture valves of various shapes and sizes, potentially allowing diatoms to manufacture micro- or nano-scale structures which may be of use in a range of devices, including: optical systems; semiconductor nanolithography; and even using diatom valves as vehicles for drug delivery. Using an appropriate artificial selection procedure, diatoms that produce valves of particular shapes and sizes could be evolved in the laboratory, and then used in chemostat cultures to mass produce nanoscale components. It has also been proposed that diatoms could be used as a component of solar cells, by substituting photosensitive titanium dioxide for the silicon dioxide normally used in the creation of cell walls.

Chapter 5

Frustule and Nanophytoplankton

Frustule



Frustules from some algae species

A **frustule** is the hard and porous cell wall or external layer of diatoms. The frustule is composed almost purely of silica, made from silicic acid, and is coated with a layer of organic substance, which was referred to in the early literature on diatoms as pectin, a fiber most commonly found in cell walls of plants. This layer is actually composed of several types of polysaccharides.

The frustule's structure is usually composed of two overlapping sections (known as valves). The upper valve is termed the epitheca and is slightly larger and overlaps the lower valve, the hypotheca. The join between the two valves is supported by bands of silica (girdle bands) that hold the two valves together. The overlapping allows for some additional internal expansion room and is essential during the reproduction process when the cell expands to allow for the formation of two new valves as the mother cell divides. As the cell divides each new cell retains one valve of the original frustule and one new valve. Interestingly this means that one "daughter" cell is the same size as the parental cell (epitheca and new hypotheca) while in the other the old hypotheca becomes the new epitheca in the smaller daughter cell. The frustule also contains many pores and slits that provide the diatom access to the external environment for processes such as waste removal and mucilage secretion.

Diatoms

Diatoms have varied life strategies including floating in the water column (phytoplankton), colonising submerged surfaces and living within the surface of deposited sediments. Some cells are essentially cylindrical (centric) while other have an elongated "boat-like" shape. Since they are algae belonging to the division Bacillariophyta they require light for photosynthesis. Perhaps the most studied group of diatoms belong to the phytoplankton. Phytoplanktonic diatoms rely on ocean currents and wind to keep them in the upper oceanic levels as their cell wall is denser than water around them. They would naturally sink otherwise.

Diatom skeletons and their uses

When diatoms die and their organic material decomposes, the frustules sink to the bottom of the aquatic environment. This left over material is called diatomite and used is commercially as filters, mineral fillers, in insulation material, anti-caking agents and as a fine abrasive. There is also research underway regarding the use of diatom frustules and their properties for the field of optics, along with other cells, such as those in butterfly scales.

Frustule formation

As the diatom prepares to separate it undergoes several processes in order to start the production of either a new hypotheca or new epitheca. Once each cell is completely separate they then have similar protection and the ability to continue frustule production.

A brief and extremely simplified version can be explained as:

1. The newly formed nucleus and the pre-existing nucleus each move to the side of the diatom where the new hypotheca will be formed.
2. A vesicle known as the silica deposition vesicle forms near the plasma membrane.
3. This forms the center of the pattern and silica deposition can continue outward from that point, till the frustule is produced.

Nanophytoplankton

Nanophytoplankton are free-floating, aquatic plant; contains algae, protists, and cyanobacteria; photosynthetic, autotrophic plankton. They have chlorophyll in their cells. The main difference between nanophytoplankton and plankton is its smaller size (2-20 μm versus $>50 \mu\text{m}$). Nanophytoplankton fix large amounts of carbon, which would otherwise be released as carbon dioxide.

Antarctic Nanophytoplankton

In the Southern Ocean in the Antarctic zone, nanophytoplankton are the most abundant type of plankton in terms of number, but not volume. Antarctic marine flora consists almost entirely of algae, with phytoplankton, and therefore nanophytoplankton, being the most numerous type, as having great importance. Nanophytoplankton growth has been seen in pack-ice, covering nearly 73% of the Southern Ocean by the end of the winter. They even grow on icebergs. Nanophytoplankton production is affected by light intensity and duration, ice, surface water stability, and currents. Also, availability of silicates, a nutrient for the organism, can affect photosynthetic efficiency and cell composition. Nanophytoplankton also require vitamins. They thrive in areas of shallow water where there is upwelling and mixing. Although optimal growth for the species occurs in water 5-7 $^{\circ}\text{C}$, growth still occurs in Antarctic waters, which can reach as low as -2 $^{\circ}\text{C}$. Limitation of light intensity and duration is another factor for survival. In Antarctica, the sun's lower position above the horizon reduces light due to increased reflection, and the stormy seas reduce transmission of light due to bubble formations. However, some Antarctic nanophytoplankton seem to be adapted to low light levels. Most phytoplankton exist in warmer, equatorial waters. For example, in the northwestern Philippine Sea, the average number of nanophytoplankton was $1 \times 10^4/l$. It is the nanophytoplankton in particular that seem to survive better under the conditions provided by the oceans of the Antarctic. A physiological change in the cells must have occurred to allow this phenomenon. Low salinity is desirable for survival, as well.

Nanophytoplankton in the ecosystem

Phytoplankton form the beginning of the food chain for aquatic animals. Microzooplankton and krill feed on nanophytoplankton, which are then eaten by whales, seals, birds, fish, squid, and other organisms.

Life cycle

Populations are low in the winter, when nutrients are high, and then the populations increase as the nanophytoplankton consume nearly all of the nutrients, reach their carrying capacity, and decline in number at the end of the summer, beginning the cycle again in the winter. However, nanophytoplankton have different seasonal cycles depending on which oceanic biome of the world they live in.

Nutrient uptake

Phytoplanktons' density (1.02 g/cm^3) is higher than that of sea water (1.00 g/cm^3). Therefore, they sink in the ocean, unless there is an upward movement of water. However, nanophytoplankton, with as small as a $1 \text{ }\mu\text{m}$ radius, can swim in the ocean, but at a very slow rate, like "a human swimming in molasses." In either case, movement of water past the organism is created, allowing it to grab nutrients passing by. To supply nutrients through their boundary layer, nanophytoplankton employ diffusion more effectively than swimming, however.

Effect on global warming

Continued global warming will significantly alter the food chain on Earth. With nanophytoplankton and phytoplankton at the base of the food chain, their decreased productivity from increased UV-B radiation from ozone depletion will provide less food for krill and subsequent organisms in the food chain. Antarctica has experienced up to 50% ozone depletion, harming nanophytoplankton located here the most. Through carbon fixation, nanophytoplankton absorb carbon from the atmosphere, and with depleting populations, more carbon is left in the air, contributing to more global warming and ozone depletion. The cycle then continues. However, some scientists believe that existence of nanophytoplankton contributes to further progression of global warming, because they absorb the sun's radiation that would otherwise be reflected back into space. Despite the controversy, it is evident that nanophytoplankton, albeit their minimal size and apparent irrelevance because they are hardly visible, are an integral part of sustaining life on Earth.

Chapter 6

Ostreococcus and Ostreococcus Tauri

Ostreococcus

Ostreococcus



Transmission electron micrograph of an *O. tauri* cell

Scientific classification

Domain: Eukaryota

Kingdom: Plantae

Division: Chlorophyta

Class: Prasinophyceae

Order: Mamiellales

Family: Mamiellaceae

Ostreococcus

Genus: C. Courties & M.-J. Chrétiennot-Dinet (1995)

Species

- *O. tauri*

- *O. lucimarinus*

Ostreococcus is a genus of unicellular coccoid or spherically shaped green alga belonging to the class Prasinophyceae. It includes prominent members of the global picoplankton community, which plays a central role in the oceanic carbon cycle.

History

The first member of the genus, *O. tauri*, was discovered in 1994 in an investigation of the picoplankton in the Thau lagoon by Courties and Chretiennot-Dinet using flow cytometry. Unicellular photosynthetic organisms are generally amenable to study using flow cytometry because of the autofluorescence provided by chlorophyll and other fluorophores used by the cells for the harvesting and control of sunlight, which allows such pigments to be studied without any staining of the cells. The different pigments present can be distinguished and identified on a cell-by-cell basis using flow cytometry, allowing researchers to deduce the different species present in the sample and help classify any new species found. *O. tauri* was immediately placed in the class Prasinophyceae based on the presence of characteristic chlorophyll pigments and Chlorophyceae-related carotenoids as well as cell ultrastructure, and its position was later confirmed by analysis of its 18S rDNA. Other members of the genus have since been found in many oceanic regions.

Anatomy

The genus contains the smallest known free-living eukaryotic species, with an average size of 0.8 μm . The ultrastructure of cells in this genus have so far been characterised by remarkable simplicity, being coccoid cells lacking a cell wall and containing a single chloroplast, a single mitochondrion, and a single Golgi body as well as its nucleus. The genome sequence of three members of this genus have been published: the 12.56 Mb nuclear genome of *O. tauri* in 2006, and the sequences of *O. lucimarinus* and strain RCC141 have followed.

Ostreococcus tauri

Ostreococcus tauri



Transmission electron micrograph of an *O. tauri* cell

Scientific classification

Kingdom:	Plantae
Division:	Chlorophyta
Class:	Prasinophyceae
Order:	Mamiellales
Family:	Mamiellaceae
Genus:	<i>Ostreococcus</i>
Species:	<i>O. tauri</i>

Binomial name

Ostreococcus tauri

C. Courties & M.-J. Chrétiennot-Dinet (1995)

Ostreococcus tauri is a unicellular species of green alga about 0.8 micrometres (μm) in diameter, the smallest free-living eukaryote yet described. It has a very simple ultrastructure, and a compact genome.

As a common member of global oceanic picoplankton populations, this organism has a major role in the carbon cycle in many areas. Recently, *O. tauri* has been the subject of studies using comparative genomics and functional genomics due to its compact genome and green lineage.

History

O. tauri was discovered in 1994 in the Thau lagoon, France, in an year-long study of the picoplankton population of the lagoon using flow cytometry. *O. tauri* was found to be the main component of the picoplankton population in the lagoon, and images of cells produced by transmission electron microscopy revealed the smallest yet described free-living eukaryotic cells. *O. tauri* was immediately placed in the class Prasinophyceae based on the presence of characteristic chlorophyll pigments and Chlorophyceae-related carotenoids, and this classification was confirmed by further work.

Anatomy

Cells are roughly spherical (coccioid), averaging about 1 μm long by 0.7 μm wide. The cell's ultrastructure is very simple, lacking a cell wall and consisting of a nucleus, a single mitochondrion, a single chloroplast, and a single Golgi apparatus. Cells also lack flagella.

Initially described as containing 14 chromosomes, it is now known that the nucleus contains 20 chromosomes, in all about 33 fg of DNA.

Ecology

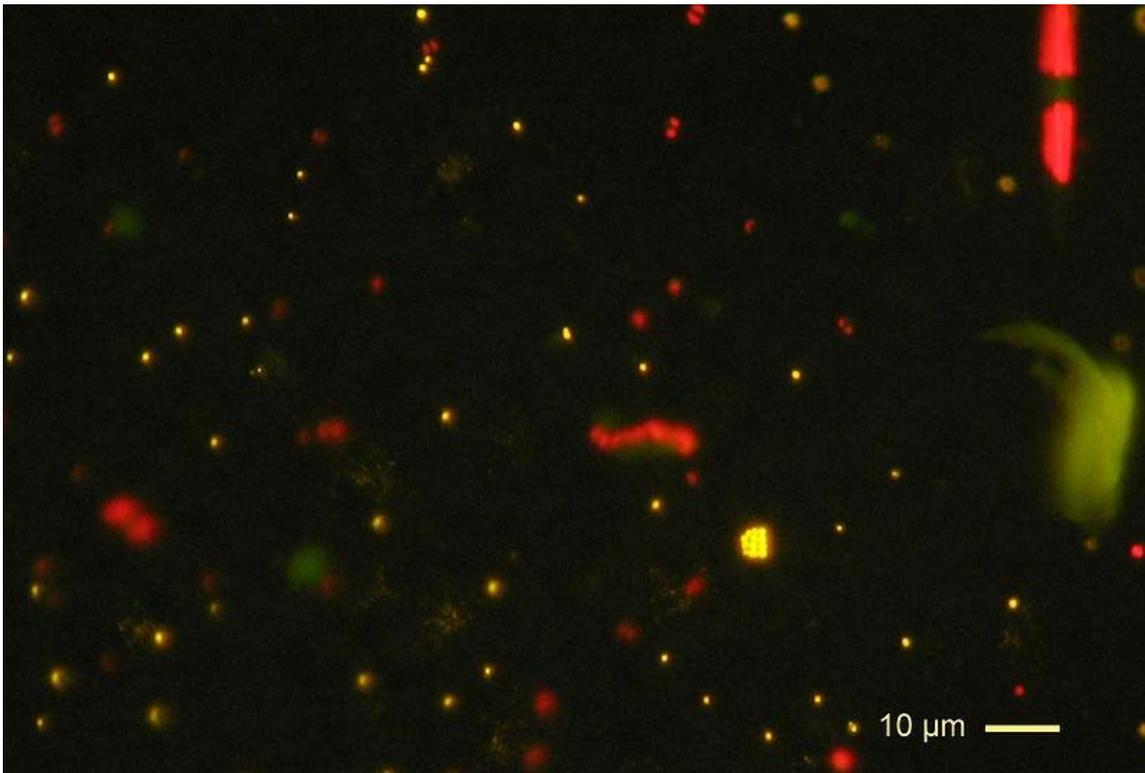
O. tauri is the dominant algal species, by cell abundance, in the Thau Lagoon in the south of France. The conditions that are thought to lead to this dominance are firstly that the Lagoon is used for intensive mollusc cultivation, and secondly that copper levels in the Lagoon are high. The first consideration selects for smaller cells (picoplankton); larger eukaryotic species of alga and many predators of smaller algae are preferentially consumed by the molluscs, which are filter feeders. The second consideration selects against cyanobacteria, as *O. tauri* is thought to cope better with "adverse conditions". The excess copper in the lagoon is thought to originate from agricultural chemicals used by surrounding vineyards.

Use as a Model Organism

As early as 1998, *O. tauri* was identified as "a good candidate for biological models such as cell division and/or genome sequencing studies".

Chapter 7

Photosynthetic Picoplankton



Picoplankton observed by epifluorescence

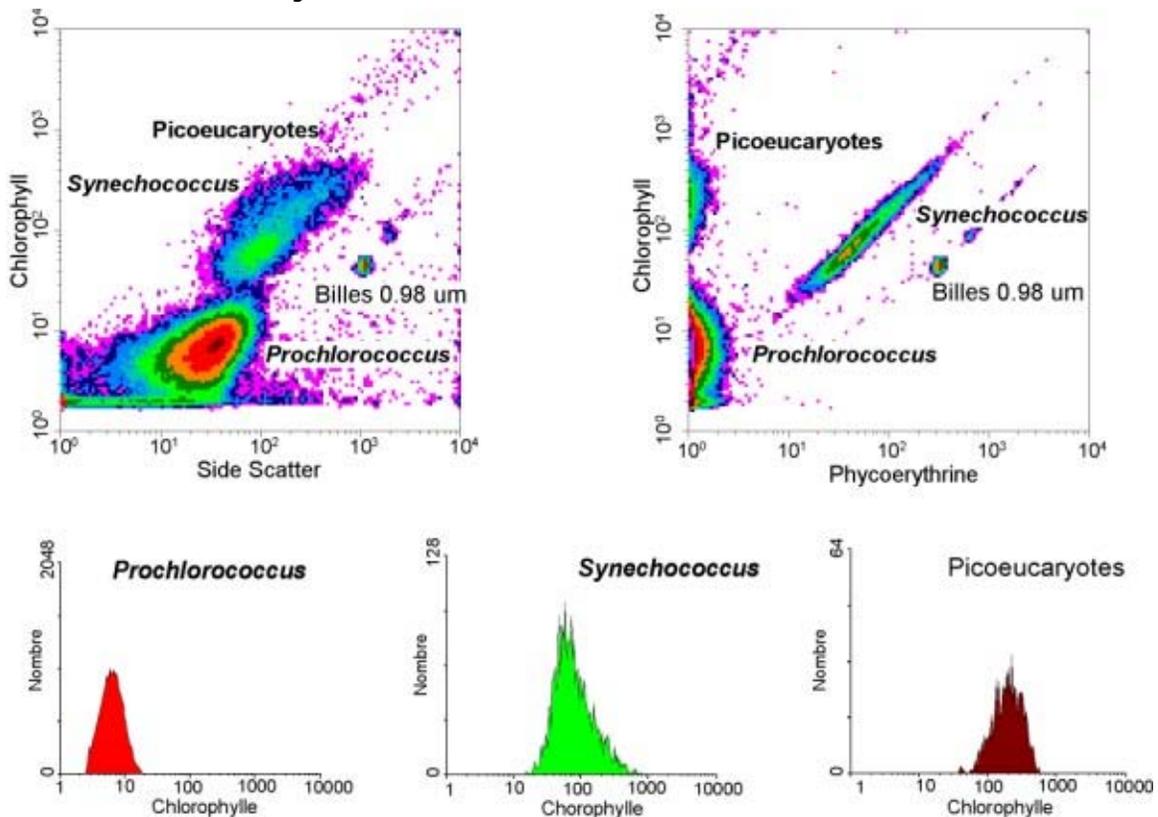
Photosynthetic picoplankton is the fraction of the plankton performing photosynthesis composed by cells between 0.2 and 2 μm (picoplankton). It is especially important in the central oligotrophic regions of the world oceans that have very low concentration of nutrients.

History

- 1952: Description of the first truly picoplanktonic species, *Chromulina pusilla*, by Butcher. This species was renamed in 1960 to *Micromonas pusilla* and is now known as one of the most abundant in temperate oceanic waters.

- 1979 : Discovery of marine *Synechococcus* by Waterbury and confirmation with electron microscopy by Johnson and Sieburth.
- 1982 : The same Johnson and Sieburth demonstrate the importance of small eukaryotes by electron microscopy.
- 1983 : W.K. Li and Platt show that a large fraction of marine primary production is due to organisms smaller than 2 μm .
- 1986 : Discovery of "prochlorophytes" by Chisholm and Olson in the Sargasso Sea, named in 1992 as *Prochlorococcus marinus*.
- 1994 : Discovery in the Thau lagoon in France of the smallest photosynthetic eukaryote known to date, *Ostreococcus tauri*, by Courties.
- 2001 : Through sequencing of the ribosomal RNA gene extracted from marine samples, several European teams discover that eukaryotic picoplankton are highly diverse.

Methods of study



Analysis of picoplankton by flow cytometry

Because of its very small size, picoplankton is difficult to study by classic methods such as optical microscopy. More sophisticated methods are needed.

- Epifluorescence microscopy allows to detect certain groups of cells possessing fluorescent pigments such as *Synechococcus* which possess phycoerythrin.

- Flow cytometry measures the size (" forward scatter ") and fluorescence of 1,000 in 10,000 cells per second. It allows one to determine very easily the concentration of the various picoplankton populations on marine samples. Three groups of cells (*Prochlorococcus*, *Synechococcus* and picoeukaryotes) can be distinguished. For example *Synechococcus* is characterized by the double fluorescence of its pigments: orange for phycoerythrin and red for chlorophyll. Flow cytometry also allows to sort out specific populations (for example *Synechococcus*) in order put them in culture, or to make more detailed analyses.
- Analysis of photosynthetic pigments such as chlorophyll or carotenoids by high precision chromatography (HPLC) allows to determine the various groups of algae present in a sample.
- Molecular biology techniques:
 - Cloning and sequencing of genes such as that of ribosomal RNA, which allows to determine total diversity within a sample.
 - DGGE (Denaturing Gel Electrophoresis), that is faster than the previous approach allows to have an idea of the global diversity within a sample.
 - In situ hybridization (FISH) uses fluorescent probes recognizing specific taxon, for example a species, a genus or a class.
 - Real-time PCR can be used, as FISH, to determine, the abundance of specific groups. It has the main advantage to allow the rapid analysis of a large number of samples simultaneously, but requires more sophisticated controls and calibrations.

Composition

Three major groups of organisms constitute photosynthetic picoplankton.

- Cyanobacteria belonging to the genus *Synechococcus* of a size of 1 μm (micrometer) were first discovered in 1979 by J. Waterbury (Woods Hole Oceanographic Institution). They are quite ubiquitous, but most abundant in relatively mesotrophic waters.
- Cyanobacteria belonging to the genus *Prochlorococcus* are particularly remarkable. With a typical size of 0.6 μm , *Prochlorococcus* was discovered only in 1988 by two American researchers, Sallie W. (Penny) Chisholm (Massachusetts Institute of Technology) and R.J. Olson (Woods Hole Oceanographic Institution). In spite of its small size, this photosynthetic organism is undoubtedly the most abundant of the planet: indeed its density can reach up to 100 million cells per liter and it can be found down to a depth of 150 m in all the intertropical belt.
- Picoplanktonic eukaryotes are the least well known, as demonstrated by the recent discovery of major groups. Andersen created in 1993 a new class of brown algae, the Pelagophyceae. More surprising still, the discovery in 1994 of a eukaryote of very small size, *Ostreococcus tauri*, dominating the phytoplanktonic biomass of a French brackish lagoon (étang de Thau), shows that these organisms can also play a major ecological role in coastal environments. In 1999, yet a new class of alga

was discovered, the Bolidophyceae, very close genetically of diatoms, but quite different morphologically. At the present time, about 50 species are known belonging to several classes.

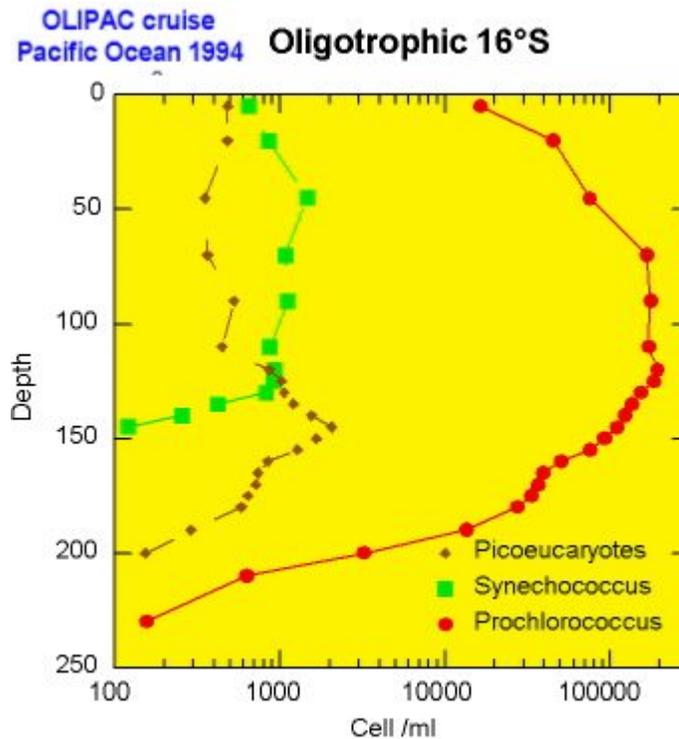
Algal classes containing picoplankton species	
Classes	Picoplanktonic genera
Chlorophyceae	<i>Nannochloris</i>
Prasinophyceae	<i>Micromonas</i> , <i>Ostreococcus</i> , <i>Pycnococcus</i>
Prymnesiophyceae	<i>Imantonia</i>
Pelagophyceae	<i>Pelagomonas</i>
Bolidophyceae	<i>Bolidomonas</i>
Dictyochophyceae	<i>Florenciella</i>

The use of molecular approaches implemented since the 1990s for bacteria, were applied to the photosynthetic picoeukaryotes only 10 years later around 2000. They revealed a very wide diversity and brought to light the importance of the following groups in the picoplankton :

- Prasinophyceae
- Haptophyta
- Cryptophyta

In temperate coastal environment, the genus *Micromonas* (Prasinophyceae) seems dominant. However, in numerous oceanic environments, the dominant species of eukaryotic picoplankton remain still unknown.

Ecology



Vertical distribution of picoplankton in the Pacific Ocean

Each picoplanktonic population occupies a specific ecological niche in the oceanic environment.

- The *Synechococcus* cyanobacterium is generally abundant in mesotrophic environments, for example in the vicinity of the equatorial upwelling or in coastal regions.
- The *Prochlorococcus* cyanobacterium replaces it when the waters becomes impoverished in nutrients (i.e. oligotrophic). On the other hand in temperate region (for example in the North Atlantic Ocean), *Prochlorococcus* is absent because the cold waters prevent its development.
- The diversity of eukaryotes, corresponds undoubtedly to a big variety of environments. In oceanic regions, they are often observed at depth at the base of the well-lit layer (the "euphotic" layer). In coastal regions, certain sorts of picoeukaryotes such as "Micromonas" dominate. Their abundance follows a seasonal cycle, as the plankton of bigger size, with a maximum in summer.

Thirty years ago, it was hypothesized that the speed of division for micro-organisms in central oceanic ecosystems was very slow, of the order of one week or one month. This hypothesis was consolidated by the fact that the biomass (estimated for example by the contents of chlorophyll) was very stable over time. However with the discovery of the picoplankton, it was found that the system was much more dynamic than previously thought. In particular, small predators of a size of a few micrometres which ingest

picoplanktonic algae as quickly as they were produced, were found to be ubiquitous. This extremely sophisticated predator-prey system is practically always at equilibrium and results in a quasi-constant picoplankton biomass. This perfect equivalence between production and consumption makes it however extremely difficult to measure precisely the speed at which the system turns over.

In 1988, two American researchers, Carpenter and Chang, had suggested estimating the speed of cell division of phytoplankton by following the course of DNA replication by microscopy. By replacing the microscope by a flow cytometer, it is possible to follow the DNA content of picoplankton cells over time. This allowed to establish that picoplankton cells are extremely synchronous: they replicate their DNA and then divide all at the same time at the end of the day. This synchronization could be due to the presence of an internal biological clock.

Genomics

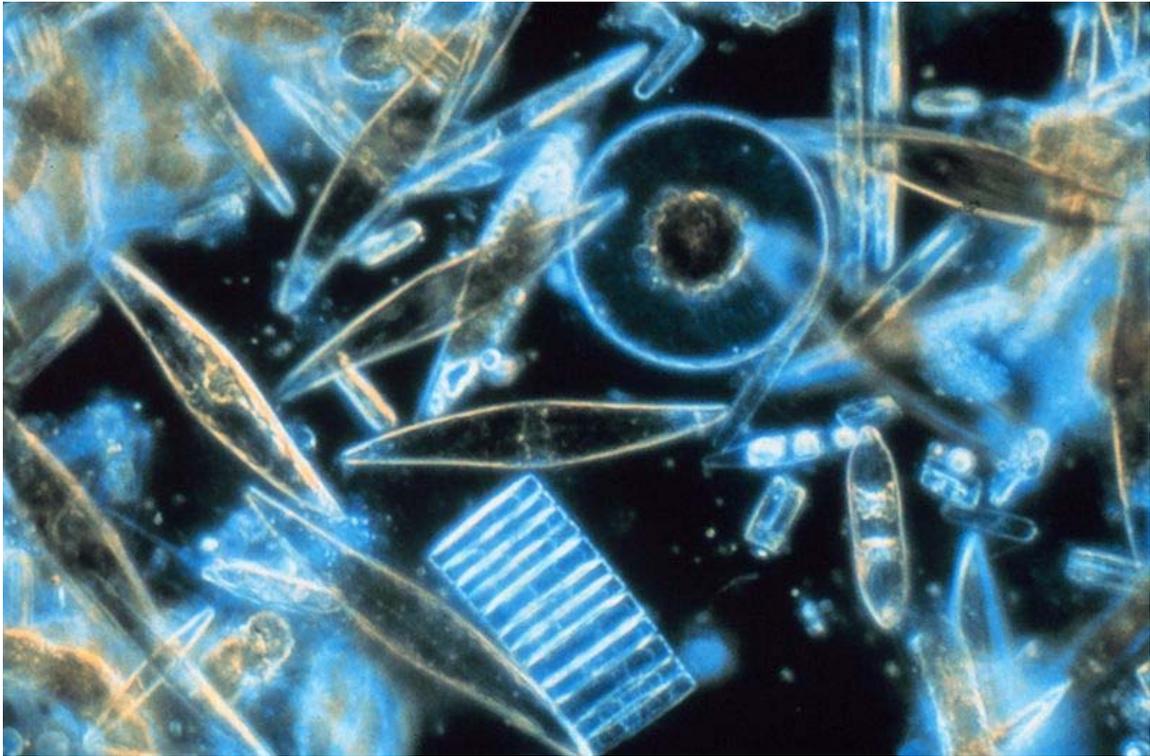
In the 2000s, genomics allowed to cross a supplementary stage. Genomics consists in determining the complete sequence of genome of an organism and to list every gene present. It is then possible to get an idea of the metabolic capacities of the targeted organisms and understand how it adapts to its environment. To date, the genomes of several types of *Prochlorococcus* and *Synechococcus*, and of a strain of *Ostreococcus* have been determined, while those of several other cyanobacteria and of small eukaryotes (*Bathycoccus*, *Micromonas*) are under sequencing. In parallel, genome analyses begin to be done directly from oceanic samples (ecogenomics or métagenomics), allowing us to access to large sets of gene for uncultivated organisms.

Genomes of photosynthetic picoplankton strains
that have been sequenced to date

Genus	Strain	Sequencing center	Remark
<i>Prochlorococcus</i>	MED4	JGI	
	SS120	Genoscope	
	MIT9312	JGI	
	MIT9313	JGI	
	NATL2A	JGI	
	CC9605	JGI	
	CC9901	JGI	
<i>Synechococcus</i>	WH8102	JGI	
	WH7803	Genoscope	
	RCC307	Genoscope	
	CC9311	TIGR	
<i>Ostreococcus</i>	OTTH95	Genoscope	

Chapter 8

Phytoplankton

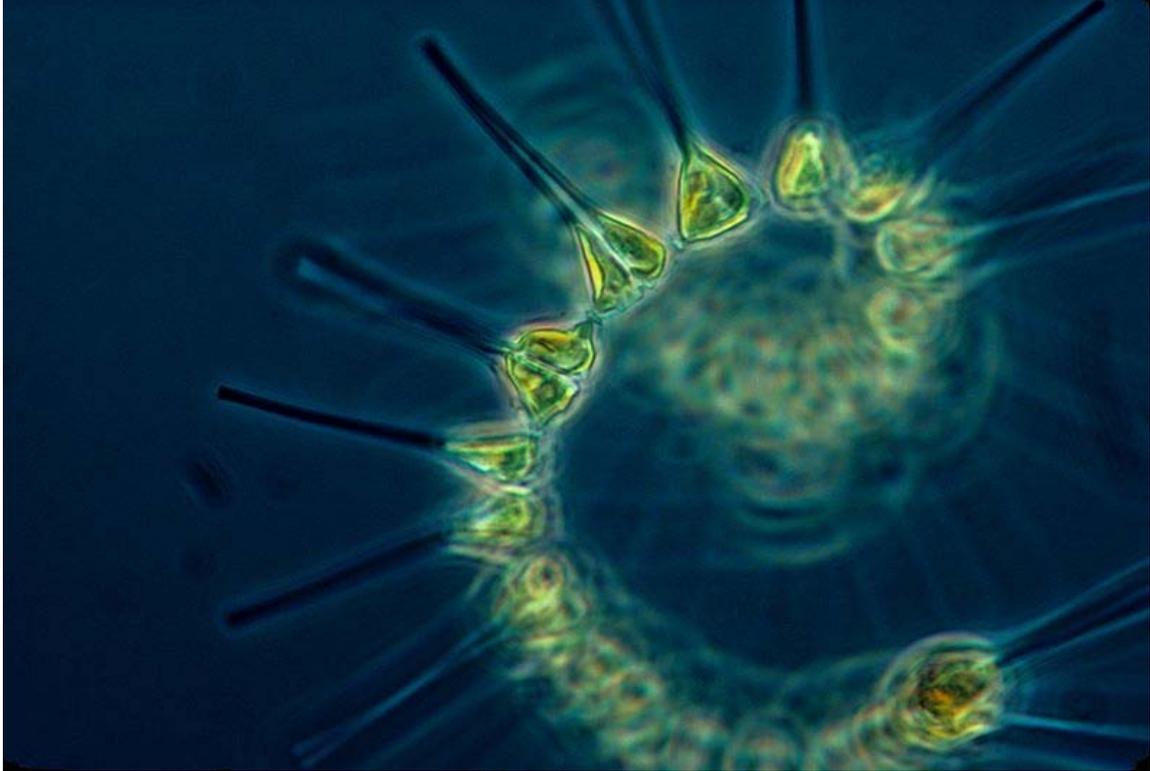


Diatoms are one of the most common types of phytoplankton.

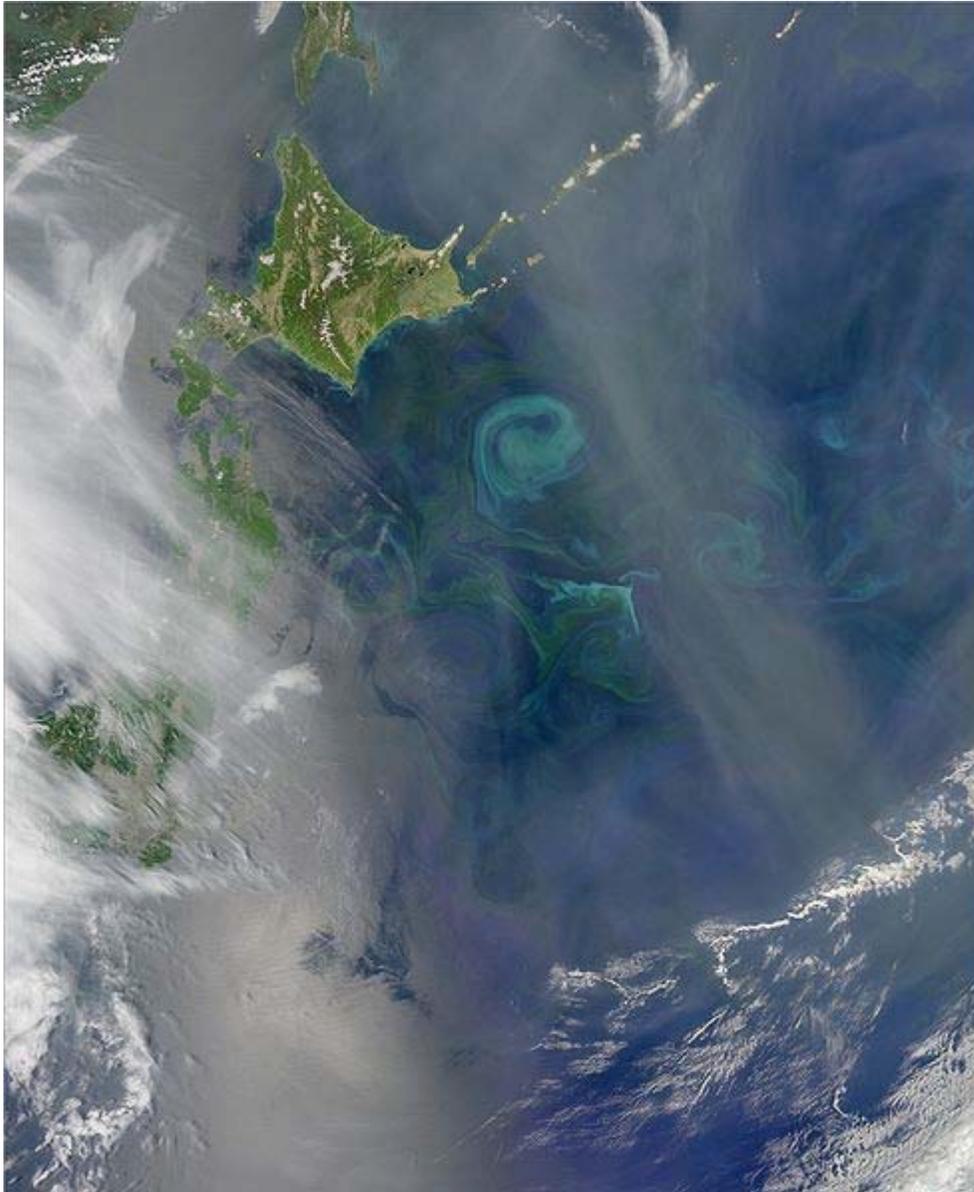
Phytoplankton are the autotrophic component of the plankton community. The name comes from the Greek words *φυτόν* (*phyton*), meaning "plant", and *πλαγκτός* (*planktos*), meaning "wanderer" or "drifter". Most phytoplankton are too small to be individually seen with the unaided eye. However, when present in high enough numbers, they may appear as a green discoloration of the water due to the presence of chlorophyll within their cells (although the actual color may vary with the species of phytoplankton present

due to varying levels of chlorophyll or the presence of accessory pigments such as phycobiliproteins, xanthophylls, etc.).

Ecology



Phytoplankton are the foundation of the oceanic food chain.



When two currents (in this case the Oyashio and Kuroshio currents) collide, they create eddies. Phytoplankton become concentrated along the boundaries of these eddies, tracing out the motions of the water.

Phytoplankton obtain energy through the process of photosynthesis and must therefore live in the well-lit surface layer (termed the euphotic zone) of an ocean, sea, lake, or other body of water. Phytoplankton account for half of all photosynthetic activity on Earth. Thus phytoplankton are responsible for much of the oxygen present in the Earth's atmosphere – half of the total amount produced by all plant life. Their cumulative energy fixation in carbon compounds (primary production) is the basis for the vast majority of oceanic and also many freshwater food webs (chemosynthesis is a notable exception). Since the 20th century, phytoplankton has declined by roughly 1% yearly, possibly linked to warming oceanic temperatures - as of 2010 this means a decline of 40% relative to

1950. As a side note, one of the more remarkable food chains in the ocean – remarkable because of the small number of links – is that of phytoplankton feeding krill (a type of shrimp) feeding baleen whales.

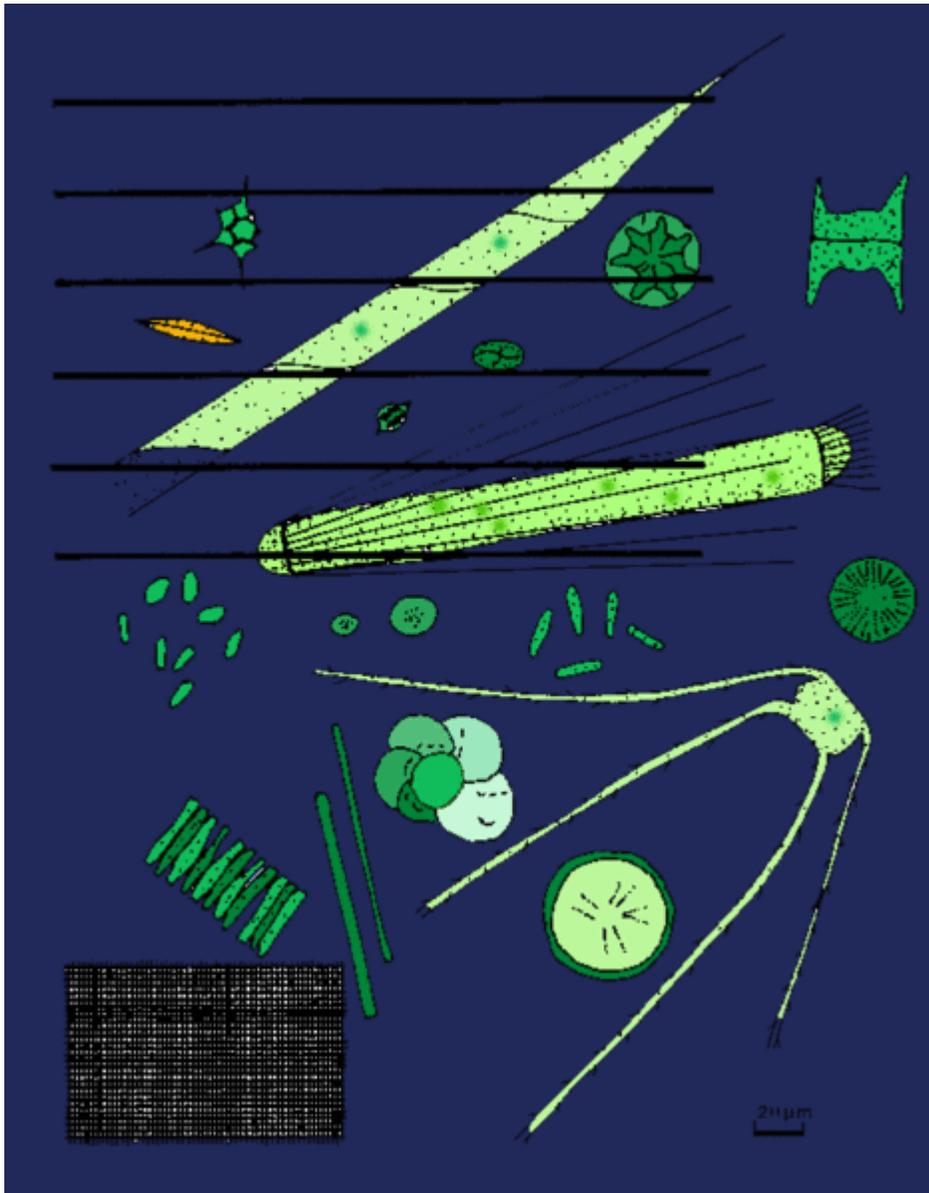
Phytoplankton are also crucially dependent on minerals. These are primarily macronutrients such as nitrate, phosphate or silicic acid, whose availability is governed by the balance between the so-called biological pump and upwelling of deep, nutrient-rich waters. However, across large regions of the World Ocean such as the Southern Ocean, phytoplankton are also limited by the lack of the micronutrient iron. This has led to some scientists advocating iron fertilization as a means to counteract the accumulation of human-produced carbon dioxide (CO₂) in the atmosphere. Large-scale experiments have added iron (usually as salts such as iron sulphate) to the oceans to promote phytoplankton growth and draw atmospheric CO₂ into the ocean. However, controversy about manipulating the ecosystem and the efficiency of iron fertilization has slowed such experiments.

While almost all phytoplankton species are obligate photoautotrophs, there are some that are mixotrophic and other, non-pigmented species that are actually heterotrophic (the latter are often viewed as zooplankton). Of these, the best known are dinoflagellate genera such as *Noctiluca* and *Dinophysis*, that obtain organic carbon by ingesting other organisms or detrital material.

The term phytoplankton encompasses all photoautotrophic microorganisms in aquatic food webs. Phytoplankton serve as the base of the aquatic food web, providing an essential ecological function for all aquatic life. However, unlike terrestrial communities, where most autotrophs are plants, phytoplankton are a diverse group, incorporating protistan eukaryotes and both eubacterial and archaeobacterial prokaryotes. There are about 5,000 known species of marine phytoplankton. There is uncertainty in how such diversity has evolved in an environment where competition for only a few resources would suggest limited potential for niche differentiation.

In terms of numbers, the most important groups of phytoplankton include the diatoms, cyanobacteria and dinoflagellates, although many other groups of algae are represented. One group, the coccolithophorids, is responsible (in part) for the release of significant amounts of dimethyl sulfide (DMS) into the atmosphere. DMS is converted to sulfate and these sulfate molecules act as cloud condensation nuclei, increasing general cloud cover. In oligotrophic oceanic regions such as the Sargasso Sea or the South Pacific Gyre, phytoplankton is dominated by the small sized cells, called picoplankton, mostly composed of cyanobacteria (*Prochlorococcus*, *Synechococcus*) and picoeucaryotes such as *Micromonas*.

Aquaculture

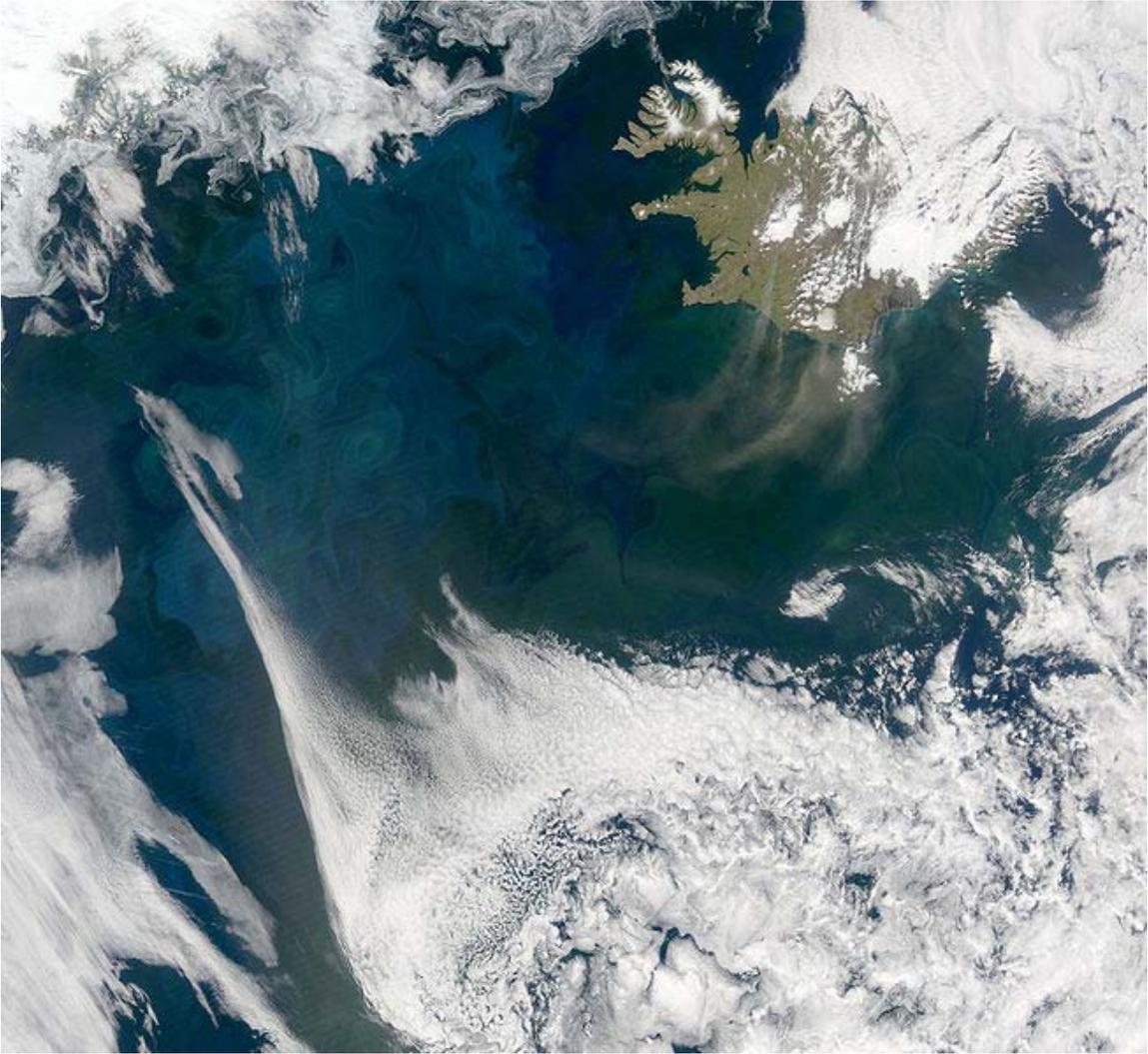


Diagrams of some typical phytoplankton

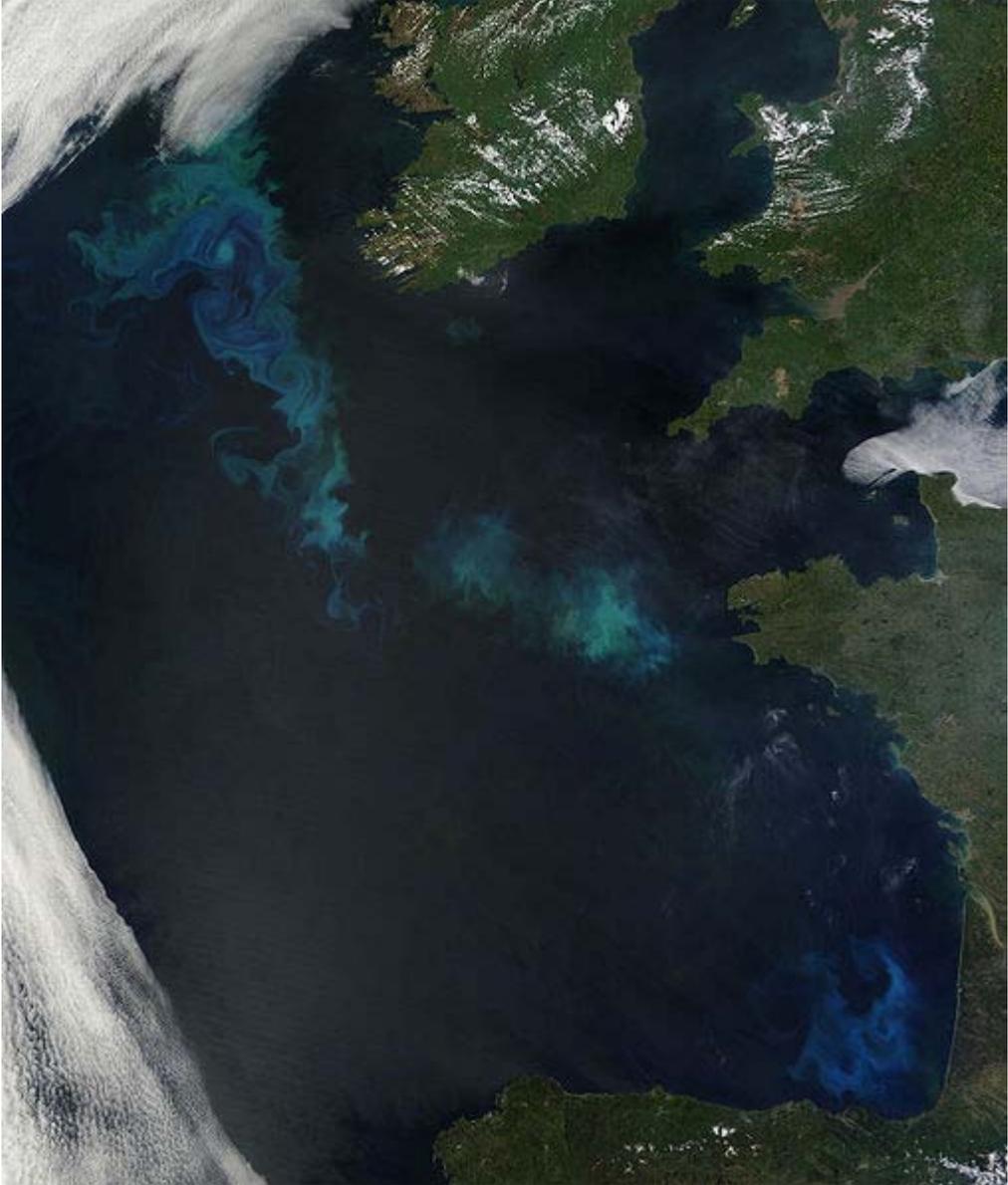
Phytoplankton are a key food item in both aquaculture and mariculture. Both utilize phytoplankton as food for the animals being farmed. In mariculture, the phytoplankton is naturally occurring and is introduced into enclosures with the normal circulation of seawater. In aquaculture, phytoplankton must be obtained and introduced directly. The plankton can either be collected from a body of water or cultured, though the former method is seldom used. Phytoplankton is used as a foodstock for the production of rotifers, which are in turn used to feed other organisms. Phytoplankton is also used to feed many varieties of aquacultured molluscs, including pearl oysters and giant clams.

The production of phytoplankton under artificial conditions is itself a form of aquaculture. Phytoplankton is cultured for a variety of purposes, including foodstock for other aquacultured organisms, a nutritional supplement for captive invertebrates in aquaria. Culture sizes range from small-scale laboratory cultures of less than 1L to several tens of thousands of liters for commercial aquaculture. Regardless of the size of the culture, certain conditions must be provided for efficient growth of plankton. The majority of cultured plankton is marine, and seawater of a specific gravity of 1.010 to 1.026 may be used as a culture medium. This water must be sterilized, usually by either high temperatures in an autoclave or by exposure to ultraviolet radiation, to prevent biological contamination of the culture. Various fertilizers are added to the culture medium to facilitate the growth of plankton. A culture must be aerated or agitated in some way to keep plankton suspended, as well as to provide dissolved carbon dioxide for photosynthesis. In addition to constant aeration, most cultures are manually mixed or stirred on a regular basis. Light must be provided for the growth of phytoplankton. The colour temperature of illumination should be approximately 6,500 K, but values from 4,000 K to upwards of 20,000 K have been used successfully. The duration of light exposure should be approximately 16 hours daily; this is the most efficient artificial day length.

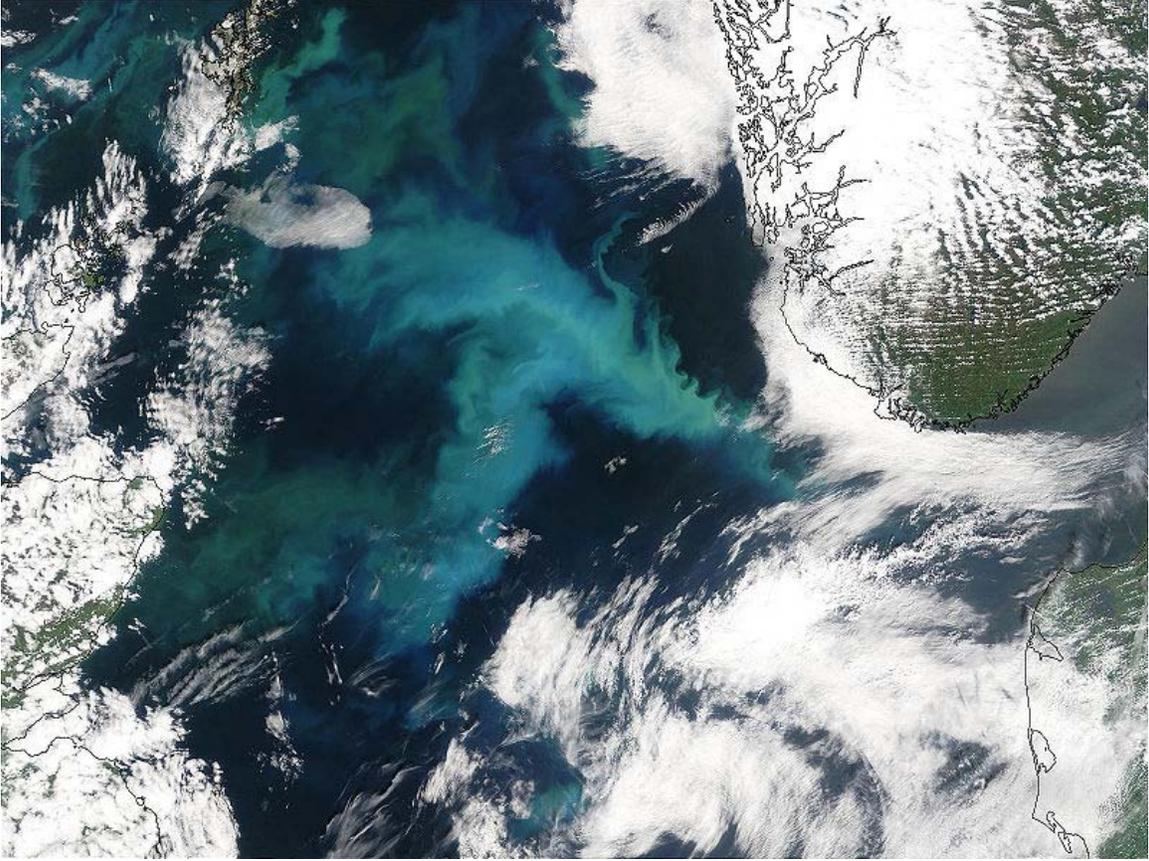
Blooms



West of Iceland



West of France



North Sea



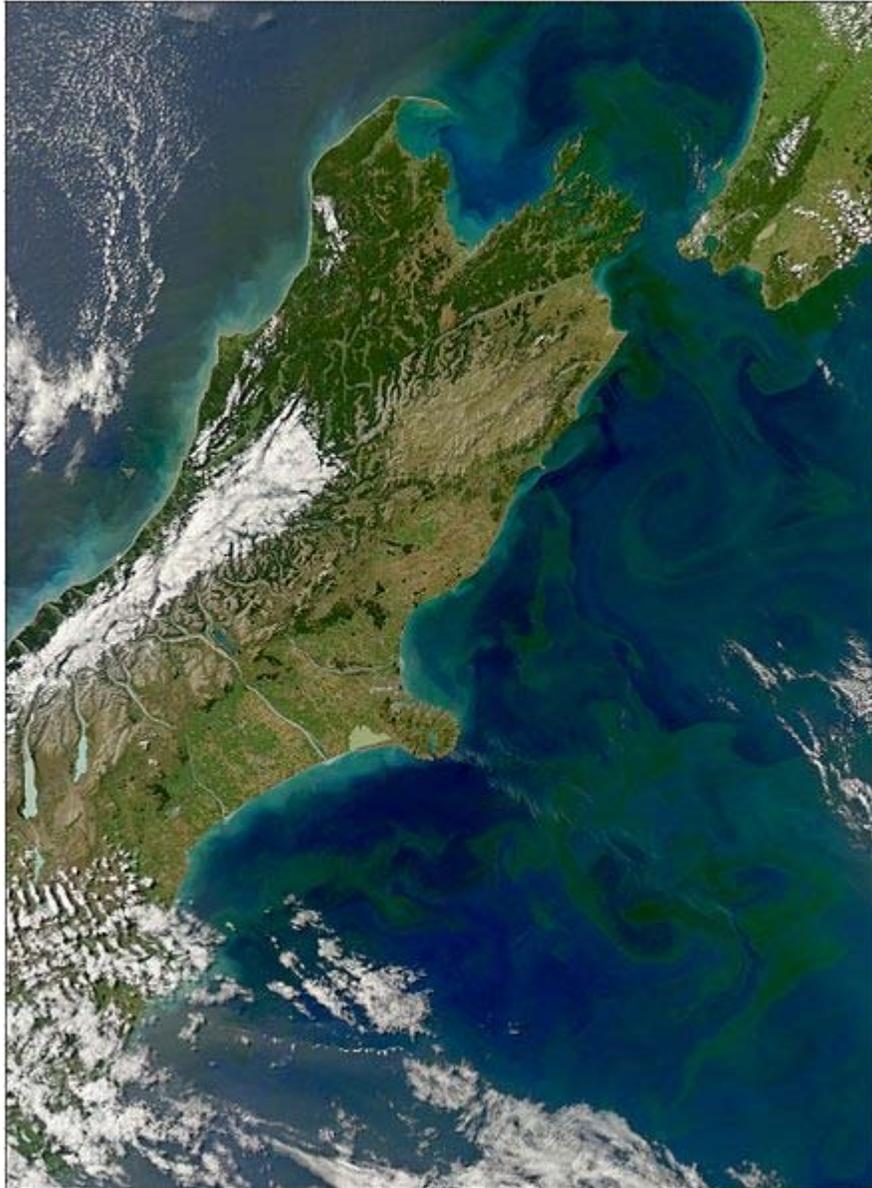
Norwegian Sea



Barents Sea



Off the east coast of New Zealand



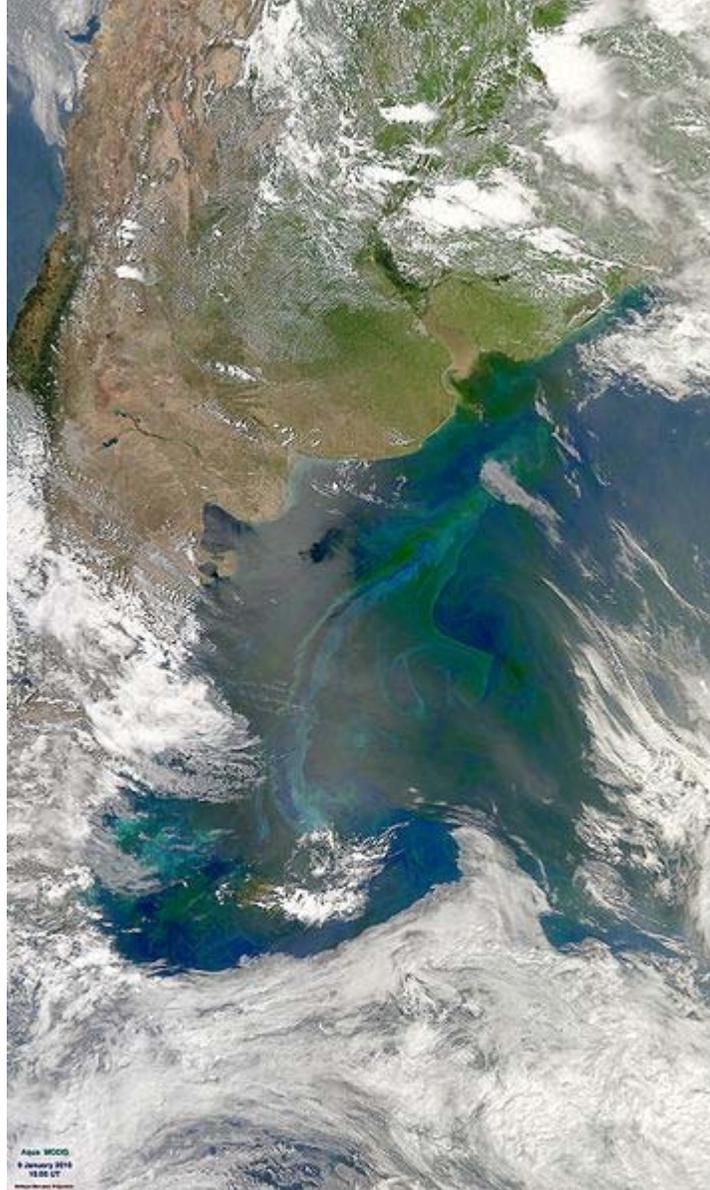
Along the shores of New Zealand's South Island



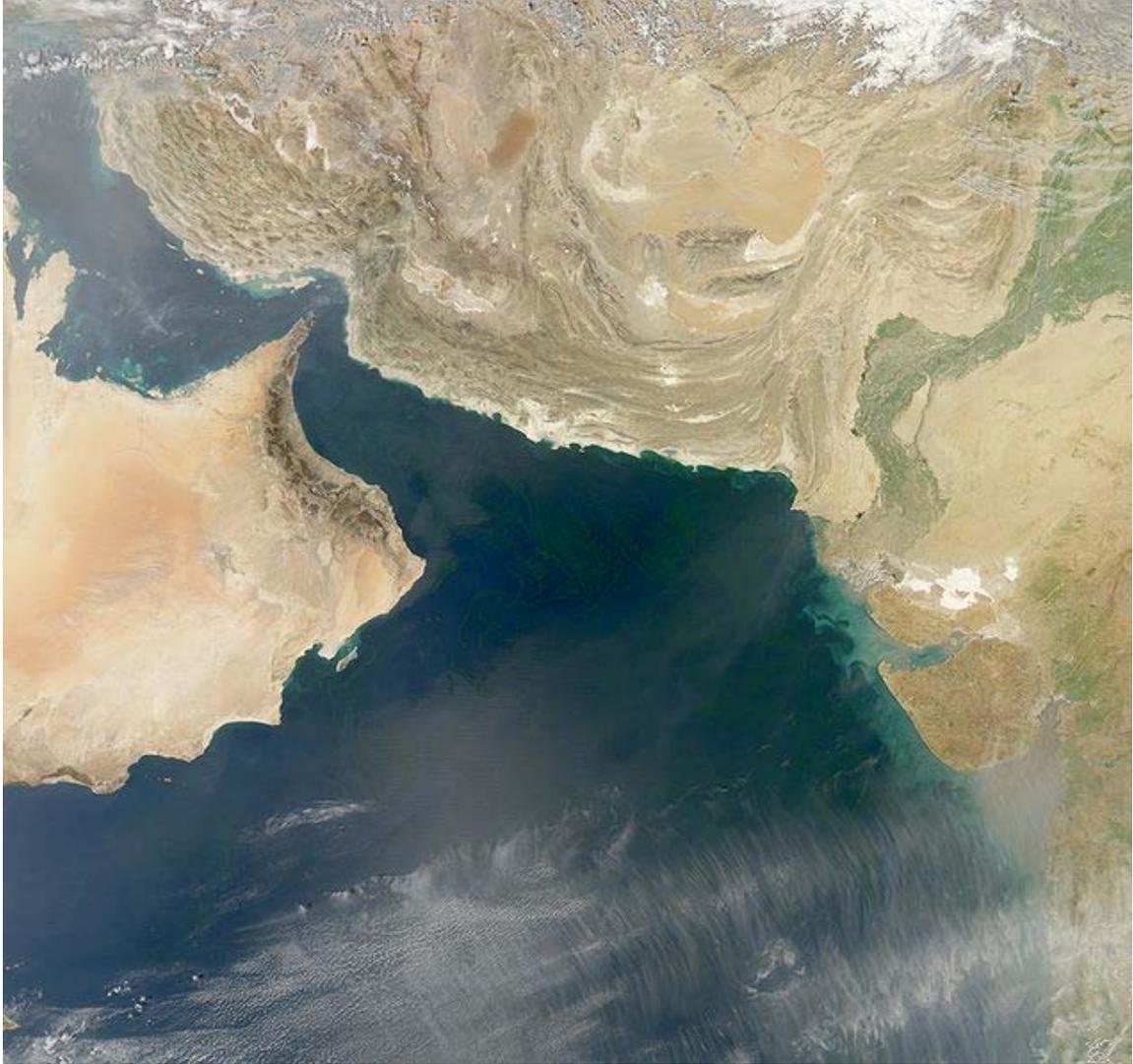
Off the coast of Argentina



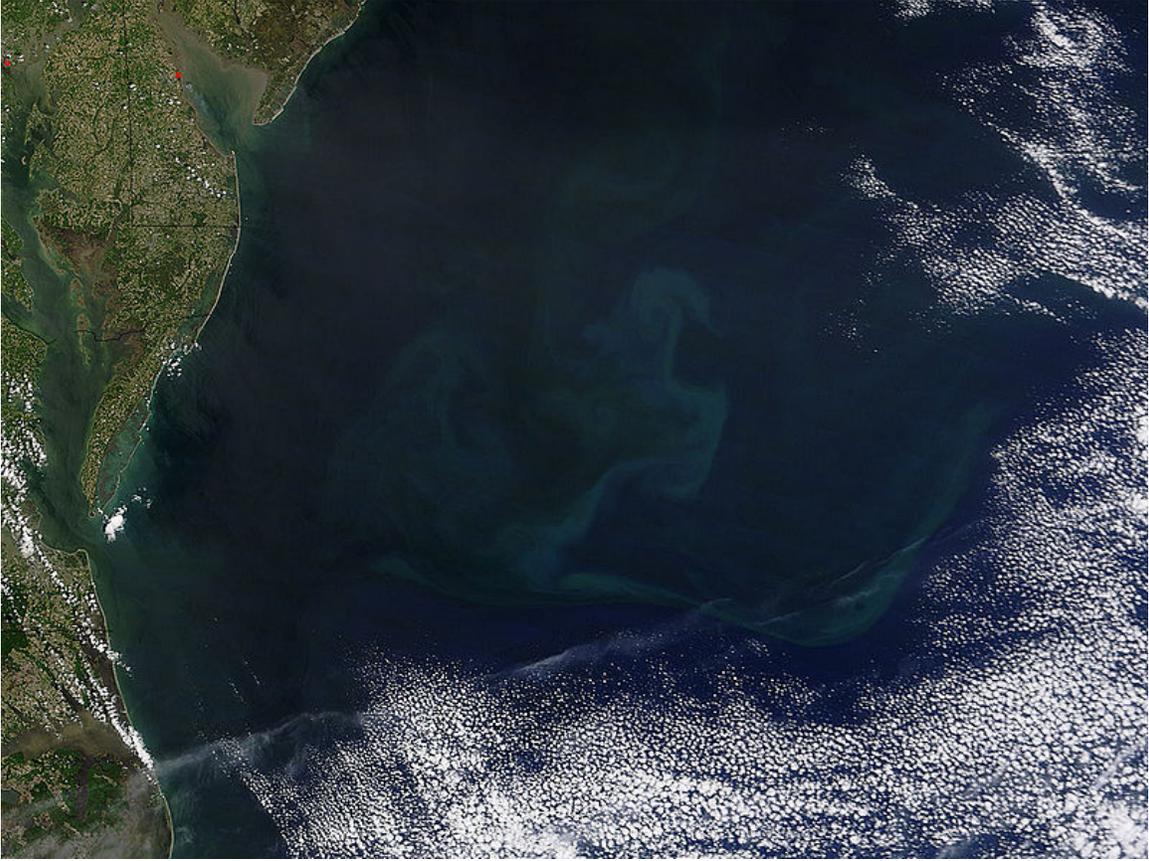
South Atlantic



Patagonia



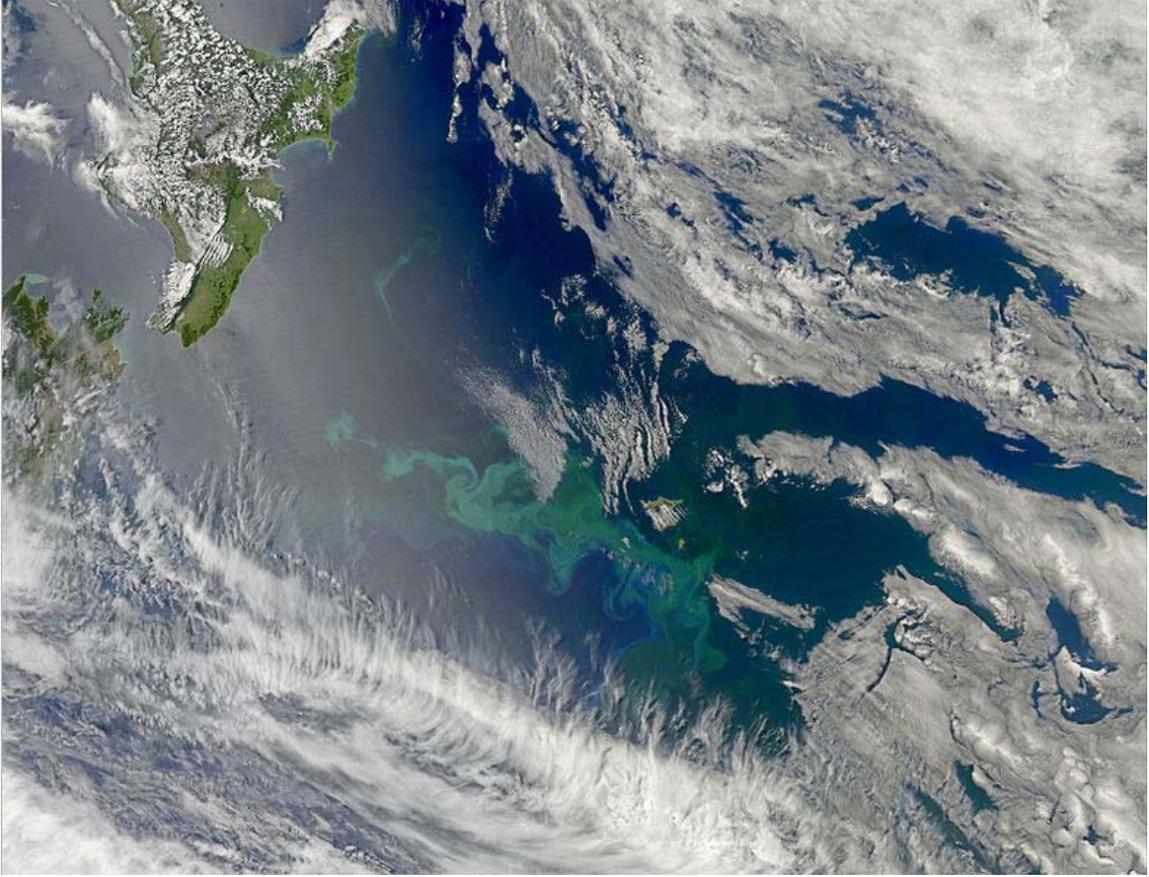
Arabian Sea



Gulf stream



Off the east coast of Greenland



Around the Chatham Islands



In the Ross Sea

Chapter 9

Picoeukaryote and Raphidophyte

Picoeukaryote

Picoeukaryotes are picoplanktonic eukaryotic organisms that range in size from 0.2 – 2.0 μm . They are distributed throughout the world's marine and freshwater ecosystems and constitute a significant contribution to autotrophic communities. Though the SI prefix pico- might imply an organism smaller than atomic size, the term was likely used to avoid confusion with existing size classifications of plankton.



Ostreococcus, the smallest known eukaryote.

Characteristics

Cell structure

Picoeukaryotes can be either autotrophic and heterotrophic, and usually contain a minimal number of organelles. For example, *Ostreococcus tauri*, an autotrophic picoeukaryote belonging to the class Prasinophyceae, contains only the nucleus, one mitochondrion and one chloroplast, tightly packed within a cell membrane. Members of a heterotrophic class, the Bicosoecida, similarly contain only two mitochondria, one food vacuole and a nucleus.

Distributions

These organisms are found throughout the water columns. Autotrophic picoeukaryotes are restricted to the upper 100-200 m (the layer that receives light) and are often characterized by a sharp cell maximum near the Deep Chlorophyll Maximum Layer (DCML) and decrease significantly below. Heterotrophic groups are found at greater depths and for example, in the Pacific Ocean, they have been found in the vicinity of hydrothermal vents at depths up to 2000-2550 m. Some heterotrophic lineages are found, unstratified, at all depths from the surface down to 3000 m. They show high phylogenetic diversity and high variability in global cell concentrations, ranging from 10^7 to 10^5 liter⁻¹.

Diversity

Autotrophic picoeukaryotes are members of groups such as the Prasinophyceae (a kind of green algae) and the Haptophyceae. Regardless of their small size, these organisms have been found to contribute at least 10% of the total global aquatic net primary productivity. In more oligotrophic environments, such around the Hawaiian station of ALOHA, researchers believe that approximately 80% of the chlorophyll α biomass is due to cells in the pico-size range. Analysis of rDNA sequences indicate that heterotrophic oceanic picoeukaryotes belong to lineages such as the Alveolata, stramenopiles, choanoflagellates, and Acantharea. In these lineages, many groups do not have cultured representatives yet. Grazing experiments have demonstrated that novel stramenopile picoeukaryotes are bacterivorous.

Ecology

Since the size of these organisms determines how they interact with their environment, it is no surprise that they are not known to form significant sinking organic aggregates. Their contribution to carbon cycling is difficult to assess because they are difficult to separate by techniques such as filtration. Recent fluorescent in situ hybridization (FISH) experiments have shown that picoeukaryotes are fairly abundant in the deep sea. Increased resolution with the development of better FISH techniques indicates that study and detection should become easier. Research has also shown that picoeukaryotes have a strong correlation with chlorophyll concentrations in both meso-autotrophic reservoirs

and hypereutrophic reservoirs. Moreover, nitrogen enrichment experiments suggest that picoeukaryotes have an advantage over larger cells when it comes to acquiring nutrients because of their large surface area per unit volume. They have exhibited more effectiveness in the uptake of photons and nutrient from low-resource environments.

Biological characteristics

Picoeukaryotes, much like other planktonic species, are exposed to light variations during the diel cycle and due to vertical displacement in the mixed layer of the water column. They have specialized biological reactions to help them deal with excessive densities of light, such as the Xanthophyll cycle.

Raphidophyte

Raphidophytes



Gonyostomum semen

Scientific classification

Domain: Eukaryota
Kingdom: Chromalveolata
Phylum: Heterokontophyta
Class: **Raphidophyceae**
Chadefaud, 1950

Raphidophytes (formerly referred to as **Chloromonadophyceae** and **Chloromonadineae**) are a small group of eukaryotic algae that includes both marine and freshwater species. All raphidophytes are unicellular, with large cells (50 → 100 μm) but no cell walls. Raphidophytes possess a pair of flagella, organised such that both originate from the same invagination (or gullet). One flagellum points forwards, while the other, covered in hair-like mastigonemes, points backwards across the cell surface, lying within a ventral groove. Raphidophytes contain numerous ellipsoid chloroplasts, which contain chlorophylls a, c₁ and c₂. They also make use of accessory pigments including β-carotene and diadinoxanthin. Unlike other heterokontophytes, raphidophytes do not possess the photoreceptive organelle (or eyespot) typical of this group.

In terms of ecology, raphidophytes occur as photosynthetic autotrophs across a range of aquatic systems. Freshwater species are more common in acidic waters, such as pools in bogs. Marine species often produce large blooms in summer, particularly in coastal waters. Off the Japanese coast, the resulting red tides often cause disruption to fish farms, although raphidophytes are not usually responsible for toxic blooms.

Chapter 10

Spring Bloom and Zooplankton

Spring bloom

The **spring bloom** is a strong increase in phytoplankton abundance (i.e. stock) that typically occurs in the early spring and lasts until late spring or early summer. This seasonal event is characteristic of temperate North Atlantic, sub-polar, and coastal waters. The magnitude, spatial extent and duration of a bloom depends on a variety of environmental conditions, such as light availability, nutrients, temperature, and stratification of the water column. The initial phytoplankton stock size is also important.

The standard spring bloom mechanism

While other mechanisms have been described (see below), the standard explanation is that during winter, wind-driven turbulence (often derived from storms) and cooling water temperatures break down the stratified water column formed during the summer. This breakdown allows vertical mixing of the water column. This mixing replenishes nutrients from depth to the surface waters and the rest of the euphotic zone. Phytoplankton use these nutrients to perform photosynthesis. However, vertical mixing also causes high losses, as phytoplankton are carried below the euphotic zone (so their respiration exceeds primary production). In addition, reduced illumination (intensity and daily duration) during winter limits growth rates .

In the spring, more light becomes available and stratification of the water column occurs as increasing temperatures warming the surface waters (referred to as thermal stratification). As a result, vertical mixing is inhibited and phytoplankton and nutrients are held at the surface . This coupling of nutrients and phytoplankton promotes exponential increases in photosynthetic activity, and, thus, primary production .

Along with thermal stratification, spring blooms can be triggered by salinity stratification due to freshwater input, from sources such as high river runoff. This type of stratification is normally limited to coastal areas and estuaries, including Chesapeake Bay . Freshwater influences primary productivity in two ways. First, because freshwater is less dense, it

rests on top of seawater and creates a stratified water column . Second, freshwater often carries nutrients that phytoplankton need to carry out processes, including photosynthesis.

Drastic increases in phytoplankton growth, such as that which occurs during the spring bloom, take place because phytoplankton can reproduce rapidly under optimal growth conditions (i.e. high nutrients, ideal illumination and temperature, and minimal losses due to grazing and vertical mixing). In terms of reproduction, many species of phytoplankton can double at least once per day, allowing for exponential increases in phytoplankton stock size. For example, the stock size of a population that doubles once per day will increase 1000-fold in just 10 days . In addition, there is a lag in the grazing response of herbivorous zooplankton at the start of blooms, which further promotes rapid growth of phytoplankton. This lag occurs because there is lower zooplankton abundance coming out of winter and many zooplankton, such as copepods, require weeks to reproduce rather than the hours or days it takes phytoplankton .

Spring blooms typically last until late spring or early summer, at which time the bloom collapses due to nutrient depletion in the stratified water column and increased grazing pressure by zooplankton . The most limiting nutrient in the marine environment is typically nitrogen (N). This is because most organisms are unable to fix atmospheric nitrogen into usable forms (i.e. ammonium, nitrite, or nitrate). However, with the exception of coastal waters, it can be argued, that iron (Fe) is the most limiting nutrient because it is required to fix nitrogen, but is only available in small quantities in the marine environment, coming from dust storms and leaching from rocks . Phosphorus can also be limiting, particularly in freshwater environments and tropical coastal regions .

Alternative mechanisms of spring blooms

Historically, blooms have been explained by Sverdrup's Critical Depth Hypothesis, which says blooms are caused by shoaling of the mixed layer. Similarly, Winder and Cloern (2010) described spring blooms as a response to increasing temperature and light availability . However, new explanations have been offered recently, including that blooms occur due to:

- Coupling between phytoplankton growth and zooplankton grazing. In this scenario, blooms occur when physical processes (seasonally variable) influence this balance and favor phytoplankton growth .
- Mixing of the water column, rather than stratification
- Low turbulence
- Increasing light intensity (in shallow water environments).

Northward progression of spring blooms

At greater latitudes, spring blooms take place later in the year. This northward progression is due to the fact that spring occurs later, delaying thermal stratification and increases in illumination that promotes blooms. A study by Wolf and Woods (1988)

showed evidence that spring blooms follow the northward migration of the 12°C isotherm, suggesting that blooms may be controlled by temperature limitations, in addition to stratification .

At high latitudes, the shorter warm season commonly results in one mid-summer bloom. These blooms tend to be more intense than spring blooms of temperate areas because there is a longer duration of daylight for photosynthesis to take place. Also, grazing pressure tends to be lower because the generally cooler temperatures at higher latitudes slow zooplankton metabolism .

Species succession during spring blooms

The spring bloom often consists of a series of sequential blooms of different phytoplankton species. Succession occurs because different species have optimal nutrient uptake at different ambient concentrations and reach their growth peaks at different times. Shifts in the dominant phytoplankton species are likely caused by biological and physical (i.e. environmental) factors . For instance, diatom growth rate becomes limited when the supply of silicate is depleted . Since silicate is not required by other phytoplankton, such as dinoflagellates, their growth rates continue to increase.

For example, in oceanic environments, diatoms (cells diameter >10 to 70 µm or larger) typically dominate first because they are capable of growing faster. Once silicate is depleted in the environment, diatoms are succeeded by smaller dinoflagellates . This scenario has been observed in Rhode Island , as well as Massachusetts and Cape Cod Bay . By the end of a spring bloom, when most nutrients have been depleted, the majority of the total phytoplankton biomass is very small phytoplankton, known as ultraphytoplankton (cell diameter <5 to 10 µm) . Ultraphytoplankton can sustain low, but constant stocks, in nutrient depleted environments because they have a larger surface area to volume ratio, which offers a much more effective rate of diffusion . The types of phytoplankton comprising a bloom can be determined by examination of the varying photosynthetic pigments found in chloroplasts of each species .

Spring bloom variability and the influence of climate change

Variability in the patterns (e.g. timing of onset, duration, magnitude, position, and spatial extent) of annual spring bloom events has been well documented . These variations occur due to fluctuations in environmental conditions, such as wind intensity, temperature, freshwater input, and light. Consequently, spring bloom patterns are likely sensitive to global climate change.

Links have been found between temperature and spring bloom patterns. For example, several studies have reported the earlier onset of the spring bloom to be correlated with temperature increases over time . Furthermore, in Long Island Sound and the Gulf of Maine, blooms begin later in the year, are more productive, and last longer during colder years, while years that are warmer exhibit earlier, shorter blooms of greater magnitude .

Temperature may also regulate bloom sizes. In Narragansett Bay, Rhode Island, a study by Durbin et al. (1992) indicated that a 2°C increase in water temperature resulted in a three week shift in the maturation of the copepod, *Acartia hudsonica*, which could significantly increase zooplankton grazing intensity. Oviatt et al. (2002) noted a reduction in spring bloom intensity and duration in years when winter water temperatures were warmer. Oviatt et al. suggested that the reduction was due to increased grazing pressure, which could potentially become intense enough to prevent spring blooms from occurring altogether.

Miller and Harding (2007) suggested climate change (influencing winter weather patterns and freshwater influxes) was responsible for shifts in spring bloom patterns in the Chesapeake Bay. They found that during warm, wet years (as opposed to cool, dry years) the spatial extent of blooms were larger and were positioned more seaward. Also, during these same years, biomass was higher and peak biomass occurred later in the spring.

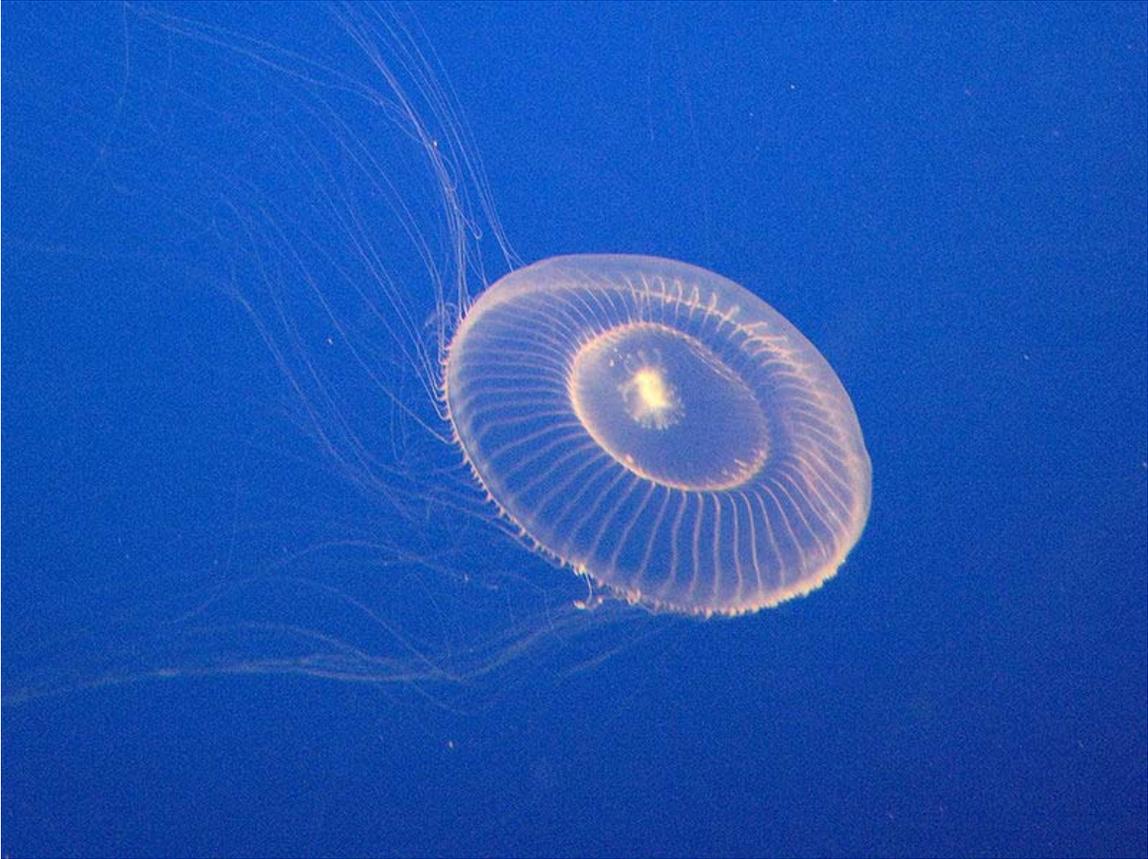
Zooplankton



A copepod (*Calanoida* sp.)

Zooplankton are heterotrophic (sometimes detritivorous) plankton. Plankton are organisms drifting in oceans, seas, and bodies of fresh water. The word "zooplankton" is derived from the Greek *zoon* (ζῷον), meaning "animal", and *planktos* (πλανκτος), meaning "wanderer" or "drifter". Individual zooplankton are usually too small to be seen with the naked eye.

Ecology



A jellyfish (*Aequorea victoria*)



Krill (*Meganyctiphanes norvegica*)

Zooplankton is a categorisation spanning a range of organism sizes including small protozoans and large metazoans. It includes holoplanktonic organisms whose complete life cycle lies within the plankton, as well as meroplanktonic organisms that spend part of their lives in the plankton before graduating to either the nekton or a sessile, benthic existence. Although zooplankton are primarily transported by ambient water currents, many have locomotion, used to avoid predators (as in diel vertical migration) or to increase prey encounter rate.

Ecologically important protozoan zooplankton groups include the foraminiferans, radiolarians and dinoflagellates (the latter are often mixotrophic). Important metazoan zooplankton include cnidarians such as jellyfish and the Portuguese Man o' War; crustaceans such as copepods and krill; chaetognaths (arrow worms); molluscs such as pteropods; and chordates such as salps and juvenile fish. This wide phylogenetic range includes a similarly wide range in feeding behavior: filter feeding, predation and symbiosis with autotrophic phytoplankton as seen in corals. Zooplankton feed on bacterioplankton, phytoplankton, other zooplankton (sometimes cannibalistically), detritus (or marine snow) and even nektonic organisms. As a result, zooplankton are primarily found in surface waters where food resources (phytoplankton or other zooplankton) are abundant.

Through their consumption and processing of phytoplankton and other food sources, zooplankton play a role in aquatic food webs, as a resource for consumers on higher trophic levels (including fish), and as a conduit for packaging the organic material in the biological pump. Since they are typically small, zooplankton can respond rapidly to increases in phytoplankton abundance, for instance, during the spring bloom.

Zooplankton can also act as a disease reservoir. They have been found to house the bacterium *Vibrio cholerae*, which causes cholera, by allowing the cholera vibrios to attach to their chitinous exoskeletons. This symbiotic relationship enhances the bacterium's ability to survive in an aquatic environment, as the exoskeleton provides the bacterium with carbon and nitrogen.

Chapter 11

Diel Vertical Migration and Thin Layers (Oceanography)

Diel vertical migration

Diel vertical migration, also known as **diurnal vertical migration**, is a pattern of movement that some organisms living in the ocean and in lakes undertake each day. Usually organisms move up to the epipelagic zone at night and return to the mesopelagic zone of the oceans or to the hypolimnion zone of lakes during the day. The word diel comes from the Latin dies day, and means a 24-hour period.

Discovery

During World War II the Navy was taking sonar readings of the ocean when they discovered the deep scattering layer. The DSL was caused by large groupings of organisms that scattered the sonar to create a false or second bottom. The false bottom was shallower during the day and deeper during the night, this was the first recording of diel vertical migration.

Once scientists started to do more research on what was causing the DSL it was discovered that a large range of organisms were vertically migrating. Most types of plankton and some types of nekton (fish) have exhibited some type of vertical migration, although it is not always diel.

Types and stimuli of vertical migration

There are two different factors that are known to play a role in vertical migration, endogenous and exogenous. Endogenous factors originate from the organism itself; sex, age, biological rhythms, etc. Exogenous factors are environmental factors acting on the organism such as light, gravity, oxygen, temperature, predator-prey interactions, etc.

Endogenous factors

- **Endogenous rhythm**- An experiment was done at the Scripps Oceanographic Research Institute which kept organisms in column tanks with light/dark cycles. A few days later the light was changed to a constant low light and the organisms still displayed diel vertical migration. Thus suggestions that some type of internal response was causing the migration.

Exogenous factors

- **Light** - An organisms wants to find an optimum light intensity (isolume). Whether it is no light or a large amount of light, an organism will travel to where it is most comfortable. Studies have shown that during a full moon organisms will not migrate up as far or during an eclipse they will start to migrate.
- **Temperature** - sometimes thermoclines can act as a barrier that an organism will not cross.
- **Salinity** - in areas such as the Arctic melting ice was cause a layer of freshwater which organisms cannot cross.
- **Predator kairomones** - a predator might release a chemical cue which could cause its prey to vertically migrate away.

Types of vertical migration

- **Diel** - This has already been mentioned and is the most common form. Organisms migrate daily, usually up to shallow waters at night and deep waters during the day. But there are other forms of vertical migration worth mentioning.
- **Seasonal** - Organisms are found at different depths depending on what season it is.
- **Ontogenic** - Organisms spend different stages of their life cycle at different depths.

Reasons to vertically migrate

There are a lot of hypotheses on why organisms would vertically migrate. Each of these hypotheses are equally valid and most of the time more than one of the hypothesis account for a reason a species would vertical migrate.

- **Predator avoidance** - Organisms come up to shallow waters at night to feed while it's dark out because their predators cannot see them as easily.
- **Metabolic Advantages** - By feeding in the warm surface waters at night and residing in the cooler deep waters during the day they can conserve energy. Alternatively, organisms feeding on the bottom in cold water during the day may migrate to surface waters at night in order to digest their meal at warmer temperatures.
- **Dispersal and Transport** - Organisms can use deep and shallow currents to find food patches or to maintain a geographical location.

- **Avoid UV Damage** - The sunlight can penetrate into the water column. If an organism, especially something small like a microbe, is too close to the surface the UV can actually damage them. So they would want to avoid getting too close to the surface, especially during daylight.

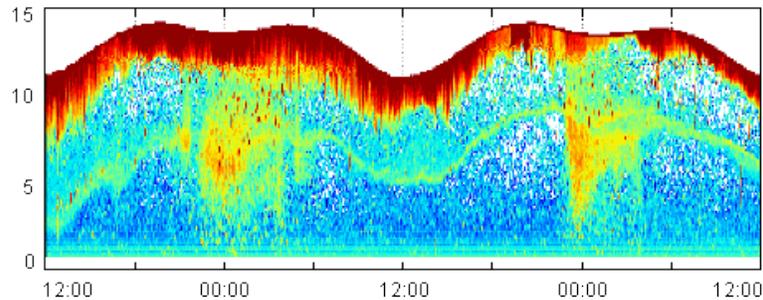
Importance with the biological pump

The biological pump is the conversion of CO₂ and inorganic nutrients by plant photosynthesis into particulate organic matter in the euphotic zone and transferred to the deeper ocean. This is a major process in the ocean and without vertical migration it wouldn't be nearly as efficient. The deep ocean gets most of its nutrients from higher up in the water column and it sinks down in the form of marine snow. Marine snow is made up of dead or dying animals and microbes, fecal matter, sand, and other inorganic material. Fecal matter is what vertical migration helps get to depth much faster.

Organisms migrate up to feed at night so when they migrate back to depth during the day they defecate large sinking fecal pellets. Whilst some larger fecal pellets can sink quite fast, the speed that organisms move back to depth is still faster. At night organisms are in the top 100 metres of the water column but during the day they move down to between 800-1000 meters. If organisms were to defecate at the surface it would take the fecal pellets days to reach the depth that they reach in a matter of hours. Therefore by releasing fecal pellets at depth they have almost 1000 metres less to travel to get to the deep ocean. This is something known as active transport. The organisms are playing a more active role in moving organic matter down to depths. Because a large majority of the deep sea, especially marine microbes, depends on nutrients falling down, the quicker they can reach the ocean floor the better.

Zooplankton and salps are to play a large role in the active transport of fecal pellets. 15-50% of zooplankton biomass above 15-50% is estimated to vertically migrate and this can account for the transport of 5-45% of Particulate Organic Nitrogen to depth. As for salps, they are large gelatinous plankton that can vertically migrate 800 meters and eat large amounts of food at the surface. They also have a very long gut retention time so fecal pellets usually are released at maximum depth. Salps are also known for having some of the largest fecal pellets. Because of this they have a very fast sinking rate and small detritus particles are known to aggregate on them. This makes them sink that much faster. So while currently there is still a lot of research being done on why organisms vertically migrate, it is very clear that vertical migration plays a large role in the active transport of dissolved organic matter to depth.

Thin layers (oceanography)



The figure shows the persistence of a thin layer of zooplankton (green line, between 10 and 15 meters) over a 48 hour period

Thin layers are congregations of phytoplankton and zooplankton in the water column which were discovered with advances in instrumentation and deployment technologies allowed samples at the temporal and spatial scales where patterns were revealed. Although they may extend for kilometers, thin layers are only a few tens of centimeters in vertical thickness. They have distinct physical, biological, chemical, optical and acoustical signatures. Thin layers of phytoplankton or zooplankton may contain densities of organisms ranging up to 1000 times those found just above, or below the structure. These extraordinary concentrations of living material must have important implications for many aspects of marine ecology (e.g., phytoplankton growth dynamics, micro- and macrozooplankton grazing, behaviour, life histories, predation, harmful algal blooms), as well as for ocean optics and acoustics.

Chapter 12

Chaetoceros and Bacteriastrum

Chaetoceros

Chaetoceros



Chaetoceros furcellatus

Scientific classification

Domain: Eukaryota
Kingdom: Chromalveolata
Phylum: Heterokontophyta
Class: Bacillariophyceae
Order: Centrales
Suborder: Biddulphiineae
Family: Chaetocerotaceae
Genus: *Chaetoceros*
(Ehrenberg, 1844)

Chaetoceros is probably the largest genus of marine planktonic diatoms with approximately 400 species described. Although a large number of these descriptions are

no longer valid. It is often very difficult to distinguish between different *Chaetoceros* species. Several attempts have been made to restructure this large genus into subgenera and this work is still in progress. However, most of the effort to describe species have been focused in boreal areas, and the genus is cosmopolitan, so there are probably a large number of tropical species still undescribed.

Description

The genus *Chaetoceros* were first described by Ehrenberg in 1844.

Cells are more or less rectangular in girdle view.

Cells are usually elliptical in valve view.

Opposite setae of adjacent cells touch near their origin.

Some currently accepted *Chaetoceros* species

- *Chaetoceros abnormis* A.I. Proshkina-Lavrenko
- *Chaetoceros aculeatus* I.V. Makarova
- *Chaetoceros adelianus* E.E. Manguin
- *Chaetoceros aduncus* I.N. Sukhanova
- *Chaetoceros aequatorialis* var. *antarcticus* Manguin
- *Chaetoceros aequatorialis* Cleve
- *Chaetoceros affinis* f. *pseudosymmetricus* (E. Steemann Nielsen) M. Thorrington-Smith
- *Chaetoceros affinis* f. *parallelus* M. Thorrington-Smith
- *Chaetoceros affinis* f. *inaequalis* M. Thorrington-Smith
- *Chaetoceros affinis* Lauder
- *Chaetoceros amanita* A. Cleve-Euler
- *Chaetoceros anastomosans* Grunow
- *Chaetoceros angularis* Schütt
- *Chaetoceros angulatus* F. Schütt
- *Chaetoceros anostomosans* var. *speciosus* F. Schütt
- *Chaetoceros armatus* T. West
- *Chaetoceros astrabadicus* A. Henckel
- *Chaetoceros atlanticus* var. *compactus* (F. Schütt) P.T. Cleve
- *Chaetoceros atlanticus* var. *neapolitanus* (Schroeder) Hustedt
- *Chaetoceros atlanticus* var. *tumescens* A. Grunow
- *Chaetoceros atlanticus* Cleve
- *Chaetoceros atlanticus* f. *audax* (F. Schütt) H.H. Gran
- *Chaetoceros atlanticus* var. *cruciatus* (G. Karsten) M. Thorrington-Smith
- *Chaetoceros audax* F. Schütt
- *Chaetoceros bacteriastris* G.C. Wallich
- *Chaetoceros bacteriastroides* f. *imbricatus* (L.A. Mangin) M. Thorrington-Smith
- *Chaetoceros bacteriastroides* G.H.H. Karsten
- *Chaetoceros bermejense* D. U. Hernández-Becerril
- *Chaetoceros bisetaceus* J. Schumann
- *Chaetoceros borealis* J.W. Bailey

- *Chaetoceros borealoides* H.L. Honigmann
- *Chaetoceros breve* F. Schütt
- *Chaetoceros brevis* Schütt
- *Chaetoceros brussilowi* A. Henckel
- *Chaetoceros buceros* G.H.H. Karsten
- *Chaetoceros buceros* Karsten
- *Chaetoceros bulbosus* (Ehrenberg) Heiden
- *Chaetoceros bulbosus* f. *cruciatus* (G. Karsten) H. Heiden
- *Chaetoceros bulbosus* f. *schimperana* (G. Karsten) H. Heiden
- *Chaetoceros bungei* Honigmann
- *Chaetoceros calcitrans* f. *pumilus* Takano
- *Chaetoceros californicus* A. Grunow
- *Chaetoceros capense* G.H.H. Karsten
- *Chaetoceros caspicus* C.E.H. Ostefeld
- *Chaetoceros caspicus* var. *karianus* A. Henckel
- *Chaetoceros caspicus* f. *pinguichaetus* A. Henckel & P. Henckel
- *Chaetoceros castracanei* Karsten
- *Chaetoceros castracanei* G.H.H. Karsten
- *Chaetoceros ceratospermus* var. *minor* A.F. Meunier
- *Chaetoceros ceratosporus* var. *brachysetus* Rines & Hargraves
- *Chaetoceros ceratosporus* Ostefeld
- *Chaetoceros chunii* G.H.H. Karsten
- *Chaetoceros cinctus* Gran
- *Chaetoceros clavigera* C.E.H. Ostefeld
- *Chaetoceros clavigerus* A. Grunow
- *Chaetoceros clevei* F. Schütt
- *Chaetoceros coarctatus* Lauder
- *Chaetoceros cochleus* F. Schütt
- *Chaetoceros compactus* F. Schütt
- *Chaetoceros compressus* var. *gracilis* F. Hustedt
- *Chaetoceros compressus* var. *hirtisetus* J.E.B. Rines & P.E. Hargraves
- *Chaetoceros concavicornis* Mangin
- *Chaetoceros confervoides* J. Ralfs
- *Chaetoceros confusus* S.L. VanLandingham
- *Chaetoceros constrictus* Gran
- *Chaetoceros convolutus* Castracane
- *Chaetoceros convolutus* f. *trisetosus* Brunel
- *Chaetoceros convolutus* f. *volans* L.I. Smirnova
- *Chaetoceros cornutus* G. Leuduger-Fortmorel
- *Chaetoceros coronatus* Gran
- *Chaetoceros costatus* Pavillard
- *Chaetoceros crenatus* (C.G. Ehrenberg) T. Brightwell
- *Chaetoceros crinitus* Schütt
- *Chaetoceros criophilus* Castracane
- *Chaetoceros cruciatus* G.H.H. Karsten
- *Chaetoceros curvatus* Castracane

- *Chaetoceros curvisetus* Cleve
- *Chaetoceros dadayi* Pavillard
- *Chaetoceros danicus* Cleve
- *Chaetoceros debilis* Cleve
- *Chaetoceros decipiens* f. *singularis* H.H. Gran
- *Chaetoceros decipiens* Cleve
- *Chaetoceros delicatulus* C.E.H. Ostefeld
- *Chaetoceros densus* Cleve
- *Chaetoceros diadema* (Ehrenberg) Gran
- *Chaetoceros dictya* f. *unicellularis* H. Heiden
- *Chaetoceros dictya* Ehrenberg
- *Chaetoceros dictya* var. *polygonus* (F. Schütt) H. Heiden
- *Chaetoceros didymus* var. *praelongus* E.J. Lemmermann
- *Chaetoceros didymus* f. *aestivus* H.H. Gran
- *Chaetoceros didymus* f. *autumnalis* H.H. Gran
- *Chaetoceros didymus* C.G. Ehrenberg
- *Chaetoceros difficilis* Cleve
- *Chaetoceros distichus* F. Schütt
- *Chaetoceros distinguendus* E.J. Lemmermann
- *Chaetoceros diversicurvatus* Van Goor
- *Chaetoceros diversus* var. *mediterraneus* J.L.B. Schröder
- *Chaetoceros diversus* Cleve
- *Chaetoceros eibenii* (Grunow) Meunier
- *Chaetoceros elmorei* Boyer
- *Chaetoceros elongatus* Honigmann
- *Chaetoceros exospermus* Meunier
- *Chaetoceros externus* Gran
- *Chaetoceros fallax* Proskina-Lavrenko
- *Chaetoceros femur* F. Schütt
- *Chaetoceros filiferus* G.H.H. Karsten
- *Chaetoceros filiforme* Meunier
- *Chaetoceros flexuosus* Mangin
- *Chaetoceros fragilis* Meunier
- *Chaetoceros furca* var. *macroceras* J.L.B. Schröder
- *Chaetoceros furcellatus* J.W. Bailey
- *Chaetoceros fusus* F. Schütt
- *Chaetoceros galvestonense* Collier & Murphy
- *Chaetoceros gastridius* (C.G. Ehrenberg) T. Brightwell
- *Chaetoceros gausii* Heiden & Kolbe
- *Chaetoceros glacialis* A. Henckel
- *Chaetoceros glandazii* Mangin
- *Chaetoceros gobii* A. Henckel
- *Chaetoceros gracilis* Pantocsek
- *Chaetoceros grunowii* F. Schütt
- *Chaetoceros hendeyi* Manguin
- *Chaetoceros hispidus* var. *monicae* A. Grunow

- *Chaetoceros hohnii* Graebn. & Wujek
- *Chaetoceros holsaticus* Schütt
- *Chaetoceros ikari* B.V. Skvortzov
- *Chaetoceros imbricatus* Mangin
- *Chaetoceros incurvus* var. *umbonatus* Castracane
- *Chaetoceros incurvus* Bailey
- *Chaetoceros indicus* Karsten
- *Chaetoceros ingolfianus* Ostenfeld
- *Chaetoceros intermedius* A. Henckel
- *Chaetoceros karianus* Grunow
- *Chaetoceros karyanus* A. Henckel
- *Chaetoceros knipowitschii* A. Henckel
- *Chaetoceros lacinosus* Schüt
- *Chaetoceros lacinosus* f. *protuberans* M. Thorrington-Smith
- *Chaetoceros lacinosus* f. *pelagicus* H.H. Gran
- *Chaetoceros lauderi* Ralfs
- *Chaetoceros leve* F. Schütt
- *Chaetoceros littorale littorale* E.J. Lemmermann
- *Chaetoceros lorenzianus* var. *forceps* A.F. Meunier
- *Chaetoceros lorenzianus* Grunow
- *Chaetoceros malygini* A. Henckel
- *Chaetoceros medius* F. Schütt C
- *Chaetoceros meridiana* (F. Schütt) G. Karsten
- *Chaetoceros mertensii* H.L. Honigmann
- *Chaetoceros messanense* Castracane C
- *Chaetoceros minimus* (Levander) D. Marino, G. Giuffre, M. Montresor & A. Zingone
- *Chaetoceros misumensis* H.H. Gran & K. Yendo
- *Chaetoceros mitra* (J.W. Bailey) Cleve
- *Chaetoceros muelleri* var. *duplex* E.J. Lemmermann
- *Chaetoceros muelleri* var. *subsalsum* J.R. Johansen & S. Rushforth
- *Chaetoceros muelleri* E.J. Lemmermann
- *Chaetoceros muellerii* var. *subsalsus* J.R. Johansen & Rushforth
- *Chaetoceros nansenii* A. Henckel
- *Chaetoceros natatus* E.E. Manguin
- *Chaetoceros neglectus* Karsten
- *Chaetoceros neobulbosus* T.V. Desikachary, S. Gowthaman & Y. Latha
- *Chaetoceros neocompactus* S.L. VanLandingham
- *Chaetoceros neogracile* S.L. VanLandingham
- *Chaetoceros neupokojewii* A. Henckel
- *Chaetoceros nipponicus* J. Ikari
- *Chaetoceros odontella* (C.G. Ehrenberg) G.L. Rabenhorst
- *Chaetoceros okamurae* var. *tetrasetus* J. Ikari
- *Chaetoceros okamurae* J. Ikari
- *Chaetoceros ostenfeldii* P.T. Cleve
- *Chaetoceros pachtussowii* A. Henckel

- *Chaetoceros pachyceros* R. Margalef
- *Chaetoceros pacificus* J. Ikari
- *Chaetoceros paradoxus* Cleve
- *Chaetoceros paradoxus* var. *luedersii* Engler
- *Chaetoceros parvus* F. Schütt
- *Chaetoceros paulsenii* f. *robustus* A. Henckel
- *Chaetoceros pavillardii* J. Ikari
- *Chaetoceros pelagicus*
- *Chaetoceros pendulus* Karsten
- *Chaetoceros perpusillus* Cleve
- *Chaetoceros peruvianus* var. *victoriae* Karsten
- *Chaetoceros peruvianus* var. *gracilis* J.L.B. Schröder
- *Chaetoceros peruvianus* Brightwell
- *Chaetoceros peruvianus* var. *robustum* P.T. Cleve
- *Chaetoceros peruvianus* var. *suadivae* Karsten
- *Chaetoceros peruvianus* f. *volans* (F. Schütt) C.E.H. Ostensfeld
- *Chaetoceros peruvianus* f. *robustus* (P.T. Cleve) C.E.H. Ostensfeld
- *Chaetoceros phuketensis* J.E.B. Rines, P. Boonruang & E.C. Theriot
- *Chaetoceros pingue* A. Henckel
- *Chaetoceros pinguichaetus* A. Henckel & P. Henckel
- *Chaetoceros pliocenens* J.-J. Brun
- *Chaetoceros protuberans* H.S. Lauder
- *Chaetoceros pseudoaurivillii* J. Ikari
- *Chaetoceros pseudocrinitus* Ostensfeld
- *Chaetoceros pseudocurvisetus* Mangin
- *Chaetoceros pseudodichaeta* J. Ikari
- *Chaetoceros pundulus* G.H.H. Karsten
- *Chaetoceros radians* F. Schütt
- *Chaetoceros radicans* F. Schütt
- *Chaetoceros recurvatus* f. *robustus* Henckel
- *Chaetoceros recurvatus* Henckel
- *Chaetoceros robustus* (P.T. Cleve) C.E.H. Ostensfeld
- *Chaetoceros rostratus* Lauder
- *Chaetoceros rusanowi* A. Henckel
- *Chaetoceros salsugineus* Takano
- *Chaetoceros saltans* P.T. Cleve
- *Chaetoceros schmidtii* C.E.H. Ostensfeld
- *Chaetoceros schuettii* f. *oceanicus* H.H. Gran
- *Chaetoceros secundus* P.T. Cleve
- *Chaetoceros seiracanthus* Gran
- *Chaetoceros sessile* Grøntved
- *Chaetoceros setoense* J. Ikari
- *Chaetoceros seychellarus* G.H.H. Karsten
- *Chaetoceros seychellarus* var. *austral* E.E. Manguin
- *Chaetoceros siamense* C.E.H. Ostensfeld
- *Chaetoceros similis* Cleve

- *Chaetoceros simplex* C.E.H. Ostenfeld C
- *Chaetoceros skeleton* F. Schütt
- *Chaetoceros socialis* f. *radians* (F. Schütt) A.I. Proshkina-Lavrenko
- *Chaetoceros socialis* Lauder
- *Chaetoceros socialis* var. *autumnalis* Proshkina-Lavrenko
- *Chaetoceros sedowii* A. Henckel
- *Chaetoceros strictus* G.H.H. Karsten
- *Chaetoceros subcompressus* J.L.B. Schröder
- *Chaetoceros subsalsus* Lemmermann
- *Chaetoceros subsecundus* (Grunow ex Van Heurck) Hustedt
- *Chaetoceros subtilis* Cleve
- *Chaetoceros sumatranus* Karsten
- *Chaetoceros tenuissimus* A.F. Meunier
- *Chaetoceros teres* f. *spinulosus* H.H. Gran
- *Chaetoceros teres* Cleve
- *Chaetoceros tetrachaeta* Ehrenberg
- *Chaetoceros tetras* G.H.H. Karsten
- *Chaetoceros tetrastichon* Cleve
- *Chaetoceros thienemannii* Hustedt
- *Chaetoceros thronsdensei* var. *trisetosus* Zingone
- *Chaetoceros thronsdensei* var. *thronsdensei* D. Marino, M. Montresor & A. Zingone
- *Chaetoceros thronsdensei* (Marino, Montresor, & Zingone) Marino, Montresor & Zingone
- *Chaetoceros tortissimus* H.H. Gran
- *Chaetoceros transisetus* J.R. Johansen & J.S. Boyer
- *Chaetoceros vanheurckii* H.H. Gran
- *Chaetoceros vermiculus* F. Schütt
- *Chaetoceros villosus* Kützing
- *Chaetoceros vistulae* C. Apstein
- *Chaetoceros volans* F. Schütt
- *Chaetoceros weissflogii* F. Schütt
- *Chaetoceros wighamii* Brightwell
- *Chaetoceros willei* Grunow
- *Chaetoceros zachariasii* var. *longus* H.L. Honigmann
- *Chaetoceros zachariasii* var. *variatus* H.L. Honigmann
- *Chaetoceros zachariasii* var. *latus* H.L. Honigmann
- *Chaetoceros zachariasii* Honigmann
- *Chaetoceros ziwolkii* A. Henckel

Bacteriastrum

Bacteriastrum



Bacteriastrum delicatulum

Scientific classification

Domain: Eukaryota
Kingdom: Chromalveolata
Phylum: Heterokontophyta
Class: Bacillariophyceae
Order: Centrales
Suborder: Biddulphiineae
Family: Chaetocerotaceae
Genus: *Bacteriastrum*

Bacteriastrum is a genus of diatoms in family Chaetocerotaceae. There are more than 30 described species in genus *Bacteriastrum*, but many of these are not currently accepted, and new species are still added to the genus.

Description

Bacteriastrum is a widely distributed marine, planktonic genus. This genus is often associated with *Chaetoceros* but differs in radial symmetry and fenestration of setae. The colonies tend to lie in girdle view, and the cells are separated by the curvature of the basal part of the setae, leaving a small gap between the cells. The cells are cylindrical and linked to form filaments. Each cell has several long, radiating setae which may be simple or bifurcate (branched), the setae from adjacent cells are fused. The plastids are discoid. At least one species, *B. solitarium*, exists as single cells.

Species

- *Bacteriastrum biconicum*
- *Bacteriastrum comosum* Pavilliard

- *Bacteriastrum delicatulum* Cleve
- *Bacteriastrum elegans*
- *Bacteriastrum elongatum* Cleve
- *Bacteriastrum furcatum* Shadbolt
- *Bacteriastrum hyalinum* Lauder
- *Bacteriastrum mediterraneum*
- *Bacteriastrum parallelum* D. Sarno, A. Zingone & D. Marino
- *Bacteriastrum solitarium* Mangin
- *Bacteriastrum varians*