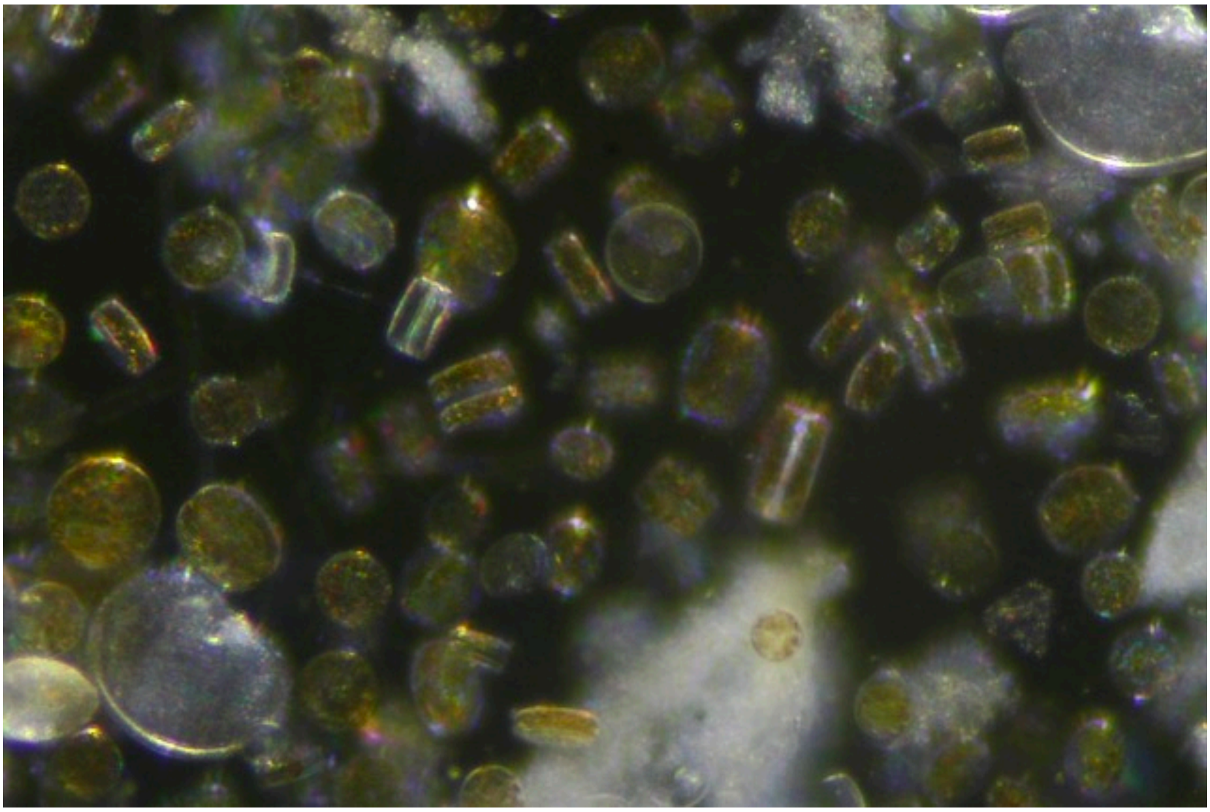
The amazing biomass and diversity of microbial marine life

Mommy, Are there microbes in the ocean?



Diatoms from a drop of water, net 20-200um, taken with curiosity microscope

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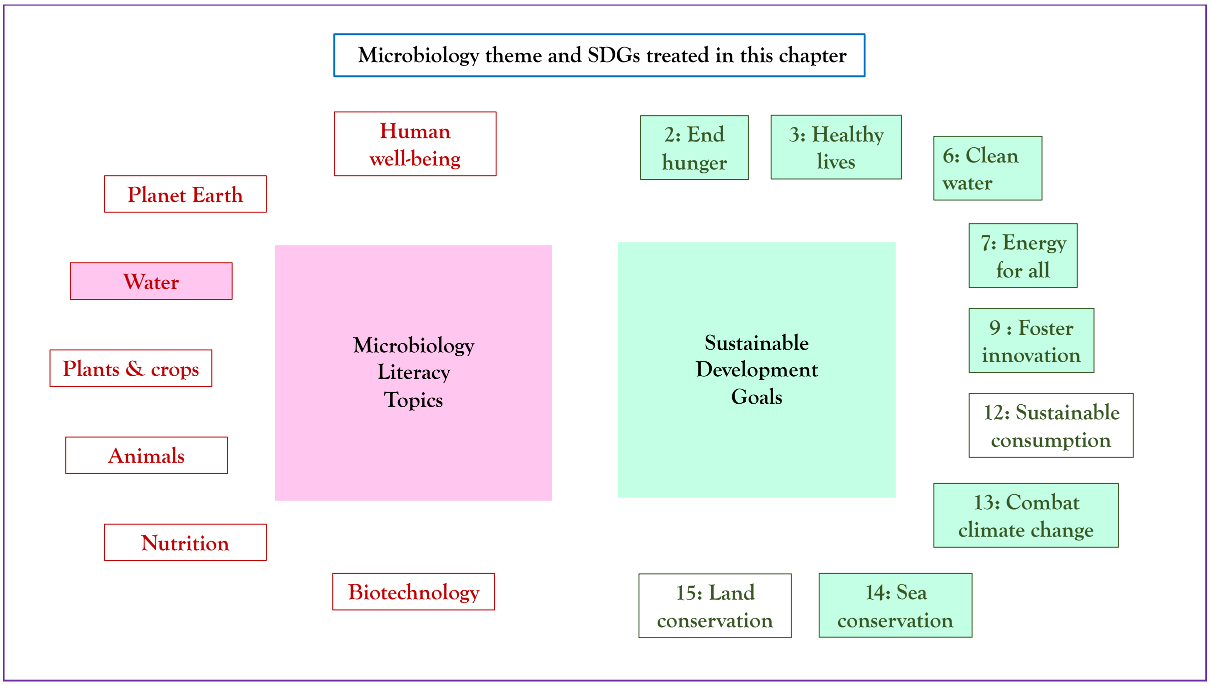
The amazing biomass and diversity of microbial marine life

Storyline

The general public is usually aware of bewitching animals living in the oceans. However, the most numerous, diverse and often strange inhabitants of the seas are actually microbes. All groups of microorganisms, be it bacteria, archaea, protists and viruses, are represented in the oceans. Marine microbes were able to adapt to all marine environments, from the most ubiquitous to the most extreme, thanks to a fascinating array of lifestyles. These invisible ocean inhabitants are the cornerstone of marine ecosystems: they constitute the base of the marine food web, produce half of Earth's oxygen through photosynthesis, recycle organic carbon in the ocean, and are pioneers in colonizing new environments and establishing ecosystems there. Humans profit from valuable ecosystem and economic services rendered by ocean microbes. They regulate climate via the storing of atmospheric CO_2 in the ocean interior and sustain the food webs from which fisheries depend. Moreover, marine microorganisms represent a largely unexplored reservoir for the discovery of new molecules and technologies and could represent the future of food and energy production. Human activities and climate change are significantly destabilizing current ocean microbial ecosystems and jeopardize the ecological and economic services they have been providing us, invisibly, until now.

The Microbiology and Societal Context

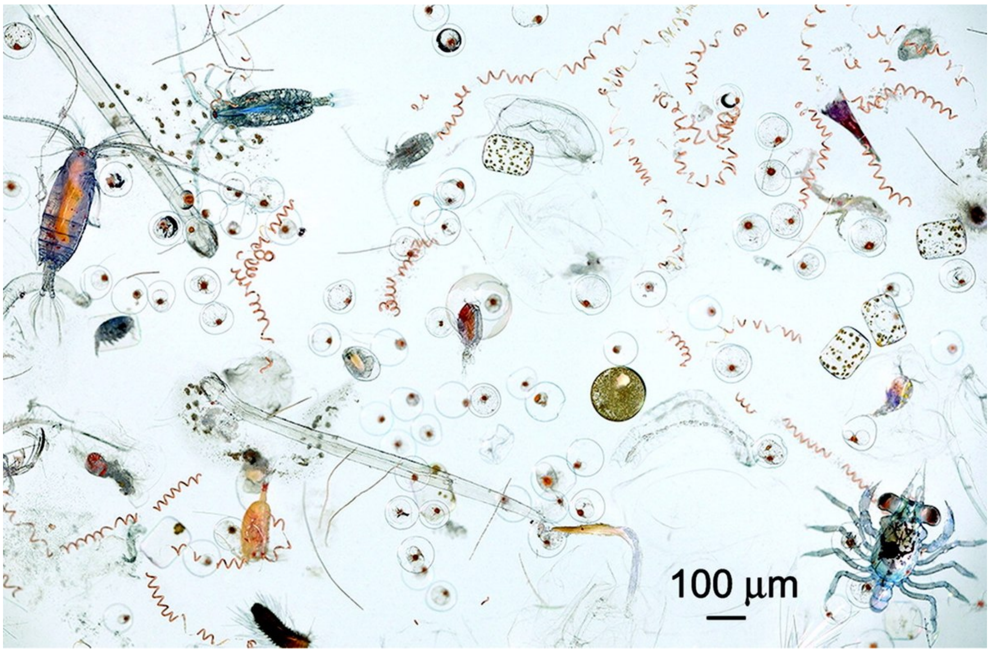
The microbiology: marine microbe diversity and habitats; photosynthesis and ocean food webs; carbon recycling; symbiosis; ocean diseases; climate regulation; economic and industrial avenues; climate change and ocean health. *Sustainability issues:* nutrient cycling; ocean health; carbon sequestration; food and energy; global warming; ocean acidification; invasive species.



The amazing biomass and diversity of microbial marine life: the Microbiology

Discovering the diversity of the microscopic inhabitants of Earth's seas and oceans

1. A large majority of organisms living in marine habitats are invisible microbes



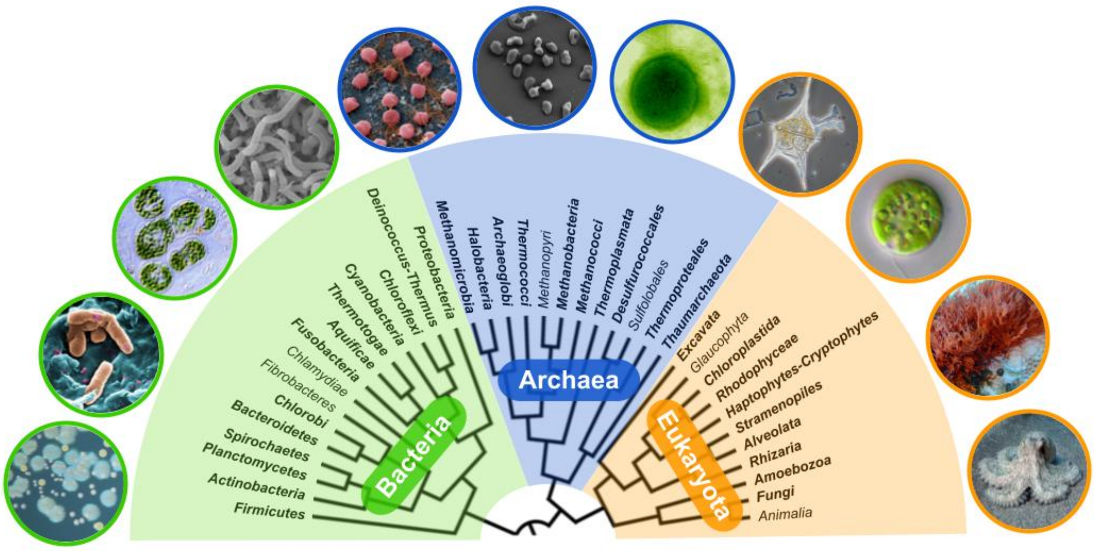
Marine microplankton (drifting-floating microscopic life) found in a hand net after one dip in ocean water under the lens of a magnifier, including cyanobacteria, diatoms, zooplankton, worm and crab larvae and fish eggs. Image credit : Photograph by David Liittschwager, published in Nadeau et al. (2016) Astrobiology (CC BY-SA 4.0).

Although macroscopic (visible to our eyes) animals and algae are the most visual and talked about marine inhabitants, they are just the tip of the iceberg: the majority of organisms living in the ocean are in fact invisible to the naked eye. There are millions of microbes in a glass of marine water but, due to their very small size (from a few dozen nanometres to a few hundred micrometres), they can only be seen through the lens of a microscope. If we weighed all living organisms in marine habitats, around 70% of that biomass would be microbes.

However, little is still known about the microbial biodiversity of the oceans (i.e., the number of species of microbes living in oceans), despite a dramatic increase in our understanding of ocean microbes in the last decades with the increase in ocean exploration expeditions like *Tara* Oceans. Indeed, more than 80% of the oceans remain to be explored, the least well studied areas being the deep seas. The ocean diversity we know is estimated to represent only 9% of the predicted total marine species around the globe, meaning most of the ocean microbial diversity is still to be discovered.

2. ***Marine microbes span all domains of life.*** Marine microbes are very diverse and belong to all groups of the tree of life, all quite distinct and distantly related in terms of evolution. Note: strictly speaking, microplankton also includes microscopic multicellular eukaryotes, as well as

fish, arthropod or worm larvae and eggs. However, here we will focus on single cell microorganisms and viruses.



Simplified tree of life. Groups containing marine microbes are highlighted in bold. Credit: Juliette Laude.

a. Prokaryotes

Prokaryotes are bacteria and archaea: simple, mostly single-celled forms of life lacking a nucleus containing the chromosome(s). The chromosome of prokaryotes is located in the cytoplasm – the contents of the cell – without a membrane that encloses it. They differ from mostly multicellular Eukaryotes, like plants, animals, and fungi, which have larger, more complex cells containing numerous organelles, such as a nucleus, in which distinct cellular activities are carried out.

i. Bacteria

One of the most important groups of ocean microbes are **Bacteria**, which constitute one of the three domains of life. They are small unicellular organisms, ranging from 0.2 to a few micrometers long. Bacteria can be found almost everywhere imaginable on Earth, including the most inhospitable places: they are present on most surfaces we see on a daily basis, on our skin and in our gut, in the ice at the poles, at 10,000m depths in the oceans, or even around hot springs in contact with hot water (70°C-80°C).

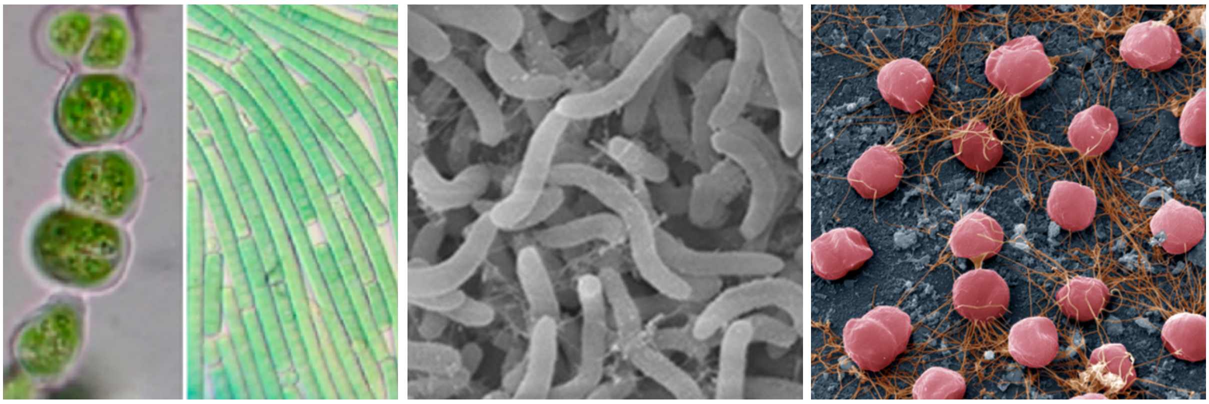
We mostly think of bacteria as vectors of disease. However, the large majority of bacteria are not pathogens of any sort and are key players of ecosystems and the services they provide. They actually embrace almost all existing biological lifestyles, from photosynthesis, hunting other bacteria, to feeding on decaying matter or methane and sulphur sources. There are a hundred million more bacteria in the ocean (currently estimated at 10^{29}) than there are stars in the universe (10^{23} estimated stars).

ii. Archaea

Another major group of ocean microbes are the **Archaea**. Although they were long mistaken for bacteria due to their visual resemblance, archaea constitute their own separate domain of life and are actually closer to eukaryotes (the third domain of life, which contains plants, animals and fungi, for instance) in terms of evolution and biology.

The first described archaea were discovered in extreme environments (for example highly salty, hot, acidic, or radioactive habitats), which gave them a reputation of being "extremophiles". It is now recognized that they are present in almost all environments on Earth, including marine ones. Still, archaea currently hold the record for the highest tolerated temperature at 122°C/266°F for *Methanopyrus kandleri*, an archaeon living at a depth of 2000m on hydrothermal vents. Archaea are still an understudied group, despite a growing scientific interest and the recent realization of their importance in the oceans.

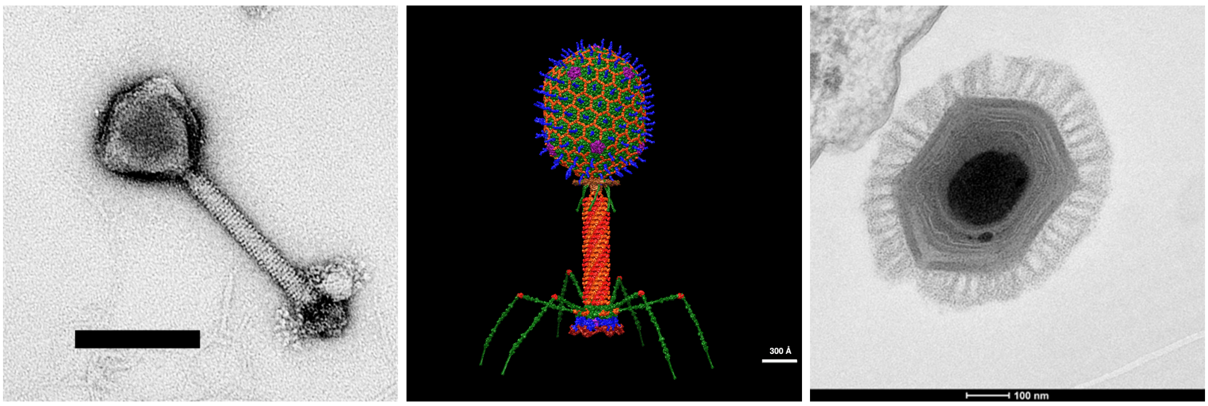
Both Archaea and Bacteria have a relatively simple cellular structure. Their DNA is not in a nucleus but directly in the cytoplasm, which is why they are called prokaryotes.



Examples of marine bacteria and archaea. From left to right: two cyanobacteria, *Hyella gigas* and *Kamptonema okenii*. The green color reflects the presence of chlorophyll, a pigment essential to harvest light energy for photosynthesis. Image credit: Published in Shiels et al. (2019) Biology (CC BY 4.0). *Pelagibacter ubique*, the most abundant bacterium in the ocean, a consumer of free organic matter. Image credit: NOAA: Ocean Exploration and Research. *Pyrococcus furiosus*, an extremophile archaeon which can survive temperatures above 100°C (colors were computer added for visualisation). Image credit: Published in Kengen et al. (2017) Microbial Biotechnology (CC BY 4.0).

b. Viruses

Viruses are tiny cellular parasites capable of infecting all forms of life from bacteria, archaea and eukaryotes, and even other viruses. They depend entirely on the molecular machinery of the infected host to reproduce themselves. To that end, they are able to hijack and reprogram major cellular processes of the host to suit their needs.



Different marine viruses. From left to right: A cyanophage (virus infecting cyanobacteria). The scale bar represents 100 nm. Image credit : Bin Ni, Chisholm Lab, MIT. Computer-generated model of a bacteriophage. The scale bar represents 30 nm (300 ångströms). Image credit: Victor Padilla-Sanchez (CC BY-SA 4.0). The giant virus *Megavirus chilensis*. Image credit: Chantal Abergel (CC BY-SA 3.0)

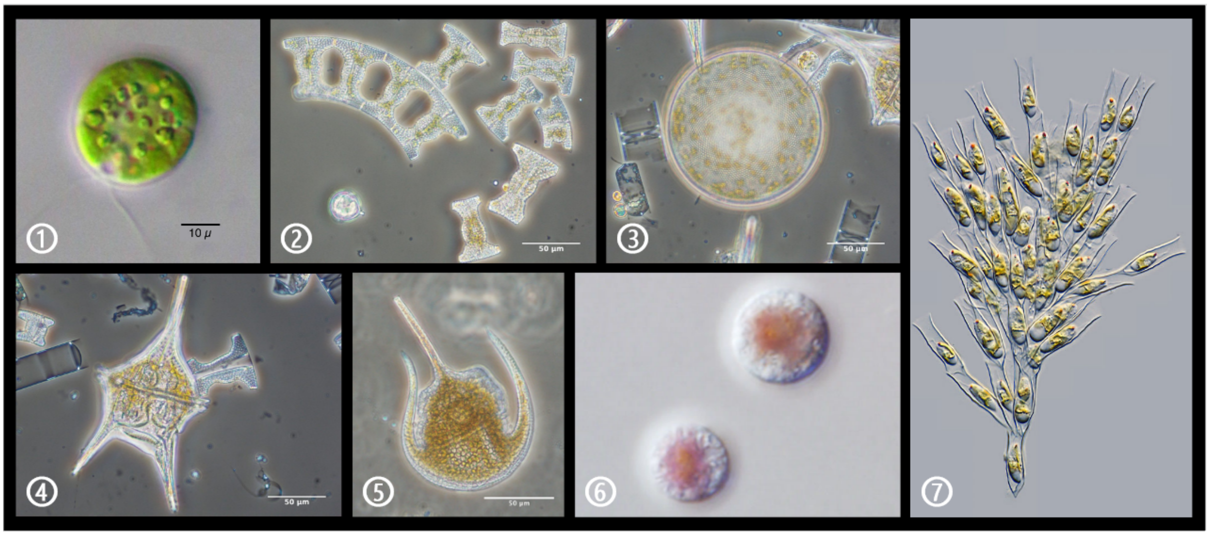
Marine viruses have an average size of 50 nm, although sizes can range from a few nanometres to a few hundred nanometres. There are more than 10^{30} viruses in the ocean, making it the most abundant group in the ocean in terms of sheer number. Yet viruses are so tiny that they actually represent less than 1% of total marine biomass.

The rate of viral infection in the ocean is colossal, estimated to be 10^{23} infections per second. As such, viral infections are responsible for killing around 20% of total microbial biomass each day.

c. Protists

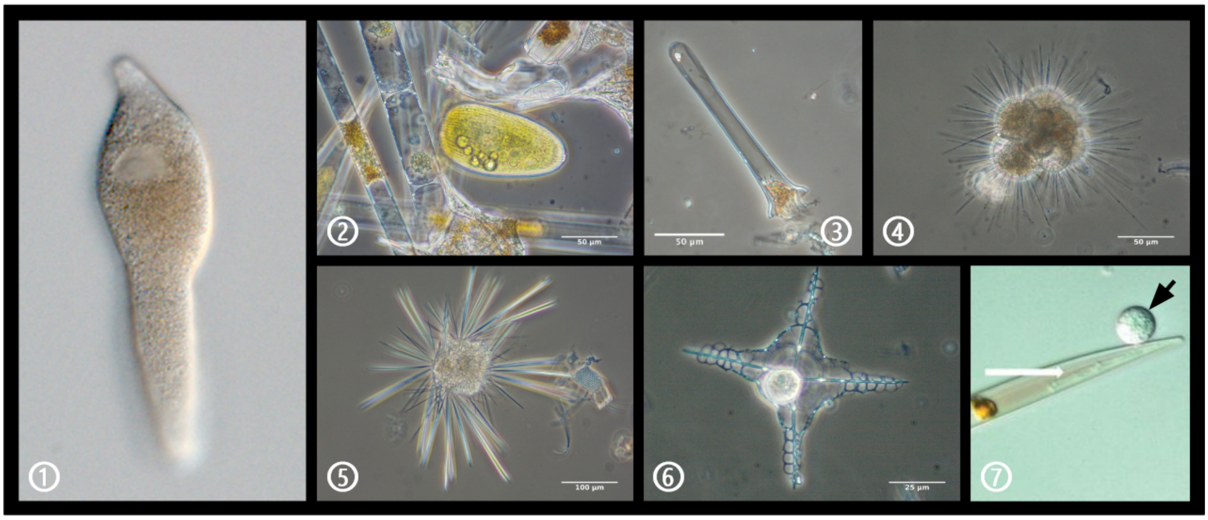
In addition to Bacteria and Archaea, the ocean also hosts a huge diversity of eukaryotic microbes, called Protists, belonging to the third domain of life which contains animals, plants and fungi, whose genetic information is compartmentalized in a nucleus.

Protists are composed of one or only a few cells and yet share the same core cellular machinery and biology as some of their more complex multicellular cousins, be it plants, animals and fungi. Protists derive from several different eukaryote families, in various shapes, forms and lifestyles. Akin to multicellular plants and algae, some protist families are photosynthetic. They are called microalgae and come in many colours, such as green, red, golden or brown depending on their light-absorbing pigments. Other protists, constituting the microzooplankton, consume organic matter to power themselves, in a way similar to animals and fungi. Indeed, some protists hunt and consume prokaryotes or other protists, some "graze" on photosynthetic microalgae, while others feed on the decaying remains of other organisms.



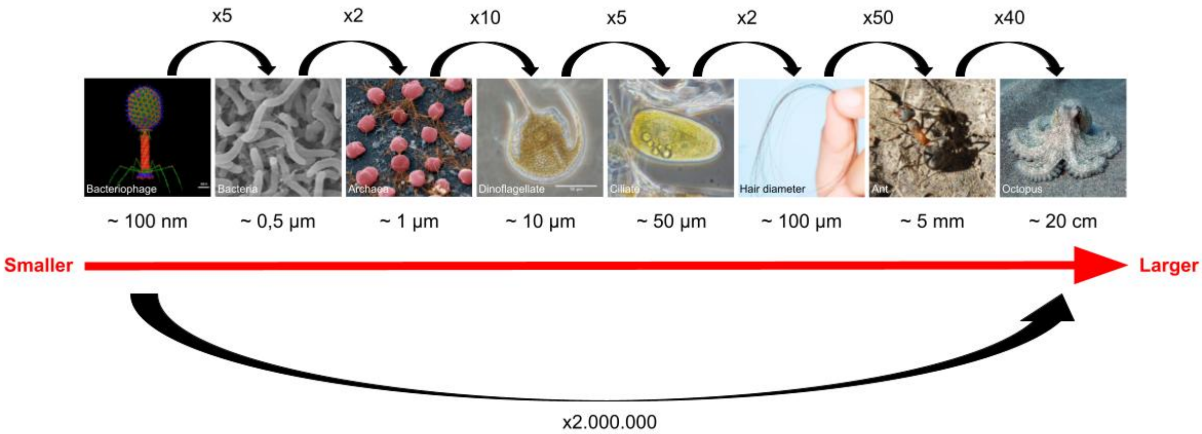
Examples of photosynthetic protists (microalgae). ① Green microalgae *Chlamydomonas globosa*. Image credit: Picturepest (CC BY 2.0). ② The diatom (brown microalgae) *Eucampia antarctica*. Image credit: Mediterranean Institute of Oceanography. ③ A diatom of the genus *Coscinodiscus*. Image credit: Mediterranean Institute of Oceanography. ④ and ⑤ the dinoflagellates (brown microalgae) *Ceratium lineatum* and *Ceratium paradoxides*. Image credit: Mediterranean Institute of Oceanography. ⑥ The red microalgae *Porphyridium purpureum*. Image credit: Neobodo (CC BY-SA 4.0). ⑦ A Chrysophyte (golden microalgae) of the *Dinobryon* genus. The tree-like structure is actually composed of dozens of individual cells. Image credit: Frank Fox, www.mikro-foto.de (CC BY-SA 3.0 DE).

Marine microbes often display beautiful and intricate cell designs, such as the external glass shells of Diatoms and Radiolaria. Sometimes looking at ocean microbial life under the microscope feels like discovering the fauna of an alien planet.



Microzooplankton protists. ① The apicomplexan *Lankesteria cystodytae*. Image credit: Sonja I. Rueckert (CC BY 3.0). ② A ciliate, surrounded by microalgae. Image credit: Mediterranean Institute of Oceanography. ③ The ciliate *Steenstrupiella sp*. Image credit: Mediterranean Institute of Oceanography. ④ A foraminifera. Image credit: Mediterranean Institute of Oceanography. ⑤ The radiolarian *Sticholonche-zanclea*. Image credit: Mediterranean Institute of Oceanography. ⑥ The radiolarian *Plectagonidium-deflandrei*. Image credit: Mediterranean Institute of Oceanography. ⑦ A single celled Chytrid fungi (black arrow) infecting a diatom cell. The white arrow shows the fungi growing into the host cell. Image credit: Published in Hassett et al. (2016) Environmental Microbiology (CC BY 4.0).

Size comparison between viruses, bacteria, archaea, protists and animals. Images from Wikipedia Commons.



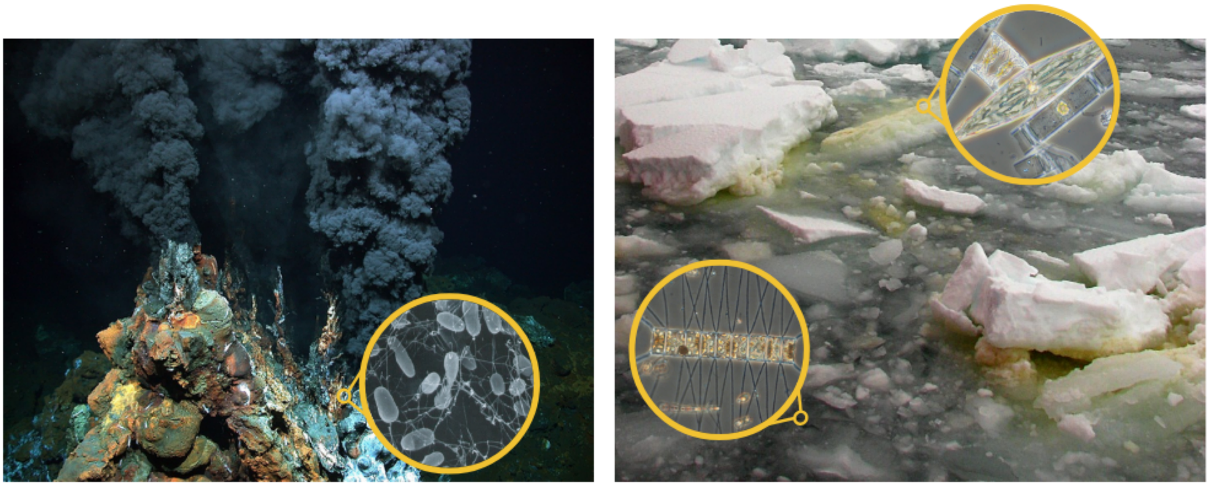
3. ***Microbes dominate and are adapted to all marine habitats on Earth.*** 71% of the Earth's surface is covered by oceans. As such, most habitats on our planet are actually marine and span the entire globe. In the ocean, environmental conditions such as temperature, salinity, acidity or light and nutrient availability, vary on a global scale as a function of latitude, longitude and depth. Moreover, environmental conditions also vary locally on a seasonal and daily basis as the ocean is constantly in motion and in constant transformation, and coastal regions are affected by inputs from land and rivers.

To be able to thrive in their respective habitats, marine microbes have undergone multiple rounds of adaptation driven by natural selection over millions of years. Consequently, two marine environments located at different places in the world ocean are very dissimilar: each possesses its specific physical and biological conditions and its own set of adapted microbial species.

Microbes have colonized and adapted to "classic" temperate and tropical regions, as well as extreme ones. For example, polar oceans actually host diverse and productive microbial communities in open waters and underneath sea ice, despite the water temperature being very cold and reaching freezing point during winter. Arctic and Antarctic species have developed strategies to thrive at temperatures normally inhibiting biochemical reactions and to resist freezing.

Similarly, microbes have been able to adapt to the unique and extreme conditions associated with hydrothermal vents. These are cracks in the Earth's crust/seafloor releasing boiling hot waters charged with minerals and metals, commonly present around geologically active zones at the bottom of the ocean. Microbes there evolved to survive high water temperatures. As no sunlight can reach this depth, microbes have invented new ways of utilizing dissolved minerals and metals as energy sources and have thus become the base of the entire food webs of hydrothermal ecosystems.

Ocean microbes were the first forms of life to appear on our planet around 4 billion years ago, after the formation of the oceans 4.4 billion years ago, and were the sole inhabitants of Earth until multicellular organisms appeared around 2.1 billion years ago. Microbes also invented key biological processes still powering most organisms to this day, such as photosynthesis and cellular respiration. In our modern oceans, microbes still dominate all forms of life in terms of sheer number, biomass and biological diversity.

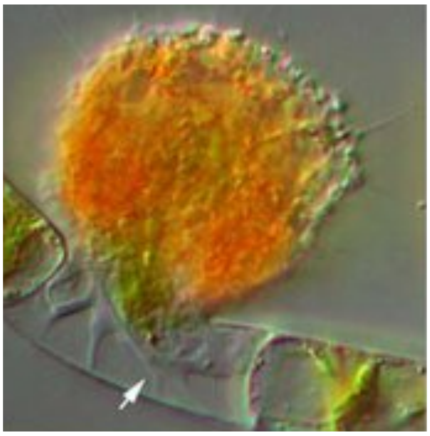


Microbes living in extreme marine environments. Left: A hydrothermal vent at 2980 meters deep in the Mid-Atlantic Ridge and the mineral- and metal-using bacteria living there. Image credits : MARUM – Zentrum für Marine Umweltwissenschaften, Universität Bremen (CC-BY 4.0) ; Mark Amend, NOAA Photo Library. Right: Packs of sea ice in the Ross Sea, Antarctica. Microalgae grow in the cold open waters and form communities (green-brown) at the bottom of sea ice, at the interface between ice and water. Image credits : GeSHaFish (CC BY-SA 3.0) ; Mediterranean Institute of Oceanography.

Diversity of microbial lifestyles in the ocean

Ocean microbes can be of very different origins. When it comes to feeding and producing their energy and organic matter, microbes also display a wide variety of lifestyles and food regimes.

1. ***Plant-like microbes are at the base of the food chain.*** Just like plants on land, some bacteria and protists capture light energy and carbon dioxide through a process called photosynthesis to generate their own energy and organic matter. Light energy is absorbed by the green pigment chlorophyll inside intracellular machineries and is used to convert carbon dioxide into sugars and forms of chemical energy usable by the cell. Organisms able to create their own energy and organic matter from mineral sources in the environment, such as photosynthetic ones, are called autotrophs. Photosynthetic microbes are grazed by other microbes or bigger organisms such as the tiny arthropod copepods, which in turn are eaten to sustain the higher levels of the food chain. These organisms that need to consume organic matter to produce their own energy and organic matter are called heterotrophs.



A protist of the *Vampyrella* genus (Amoebozoa) ingesting the content of an algal cell (white arrow). Image credit: Published in Hess et al (2012) PLoS ONE (CC BY 4.0). More examples of zooplankton feeding are provided in the videos "Vampyrella feeding on algae" and "How Microscopic Hunters Get Their Lunch" (see Photo and Video resources).

Since heterotrophs are dependent on already existing organic matter to power themselves, autotrophs creating organic matter from mineral sources are needed at the base of all food chains to sustain all other species. As such, photosynthetic microbes often constitute the first level of the food chain in environments where light is available and are the basal engines fuelling organic nutrients into higher levels of the aquatic food web.

Other modes of autotrophy exist in addition to photosynthesis. Certain groups of bacteria and archaea utilize sulfur, ammonium, ferrous oxide, hydrogen sulfide and other compounds as energy sources to produce organic matter. Many of these live in hostile environments deprived of sunlight, such as the ocean floor, and sustain the entire ecosystem as without light, photosynthesis cannot take place.

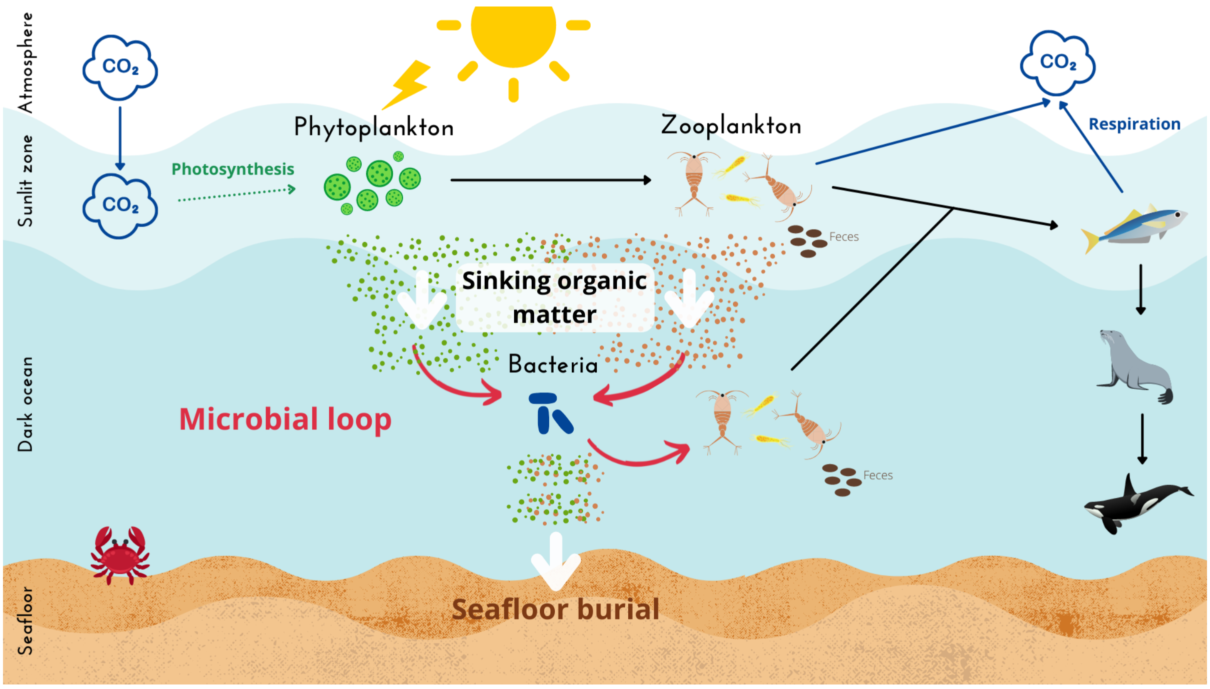
2. ***The microbial loop, or how marine microbes recycle wasted organic matter into the food web.*** Most heterotrophic microbes, especially those living in the dark part of the ocean where photosynthetic microbes are unavailable as a direct food source (photosynthesis is only possible in the sunlit top layers of the water column, and most of it takes place in the upper 100

meters), actually feed on a source of organic matter that is readily available in their environment. Indeed, microscopic fragments of organic matter – the remains of cells and dead organisms and faeces – drift in significant quantities in ocean waters, either dissolved or as particles and aggregates.

How does this organic matter get released into the ocean in the first place? There are multiple sources. First, a large portion of a meal is wasted while eating, leaving behind remains of dead organisms. Ocean creatures actually eat "sloppily" and consume only a small chunk of the organism they are feeding on. For example, when a copepod is grazing, its munching jaws will rip apart microalgae cells so that only a small portion of them will actually end up in its mouth. The rest of the cell content is released in the water. Secondly, ocean inhabitants excrete their waste directly into the surrounding waters after feeding. The consumed organic matter they did not use to power themselves, and thus that was excreted, can be an excellent source of energy for others, especially microbes. Finally, organic matter is released after the death of microbes caused by viruses and other pathogens.

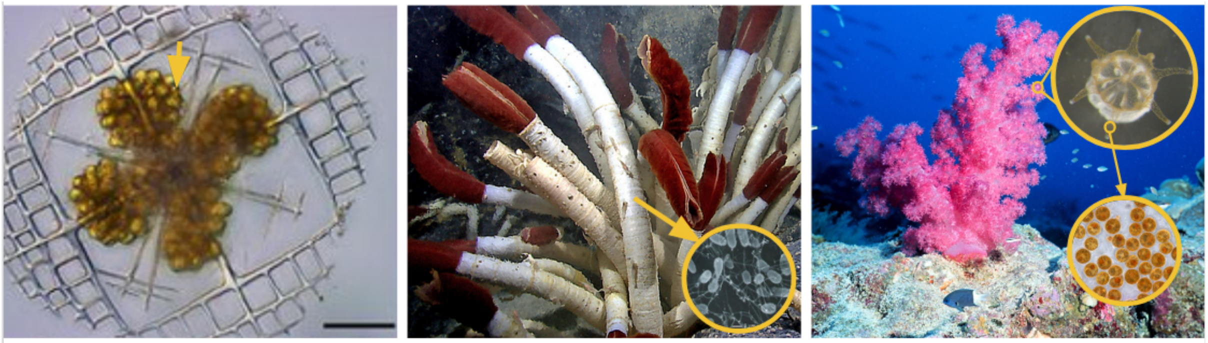
Organic matter particles and aggregates slowly sink from the very productive upper layers of the ocean to the seafloor in a continuous shower called *marine snow*. Therefore, even if heterotrophic microbes do not live directly in the rich and productive sunlit zone where photosynthetic microbes are abundant, they indirectly benefit from its richness via the consumption of marine snow.

The heterotrophic microbes feeding on this free organic matter are in turn eaten by other organisms and fuel the higher levels of the food chain. Thus, they recycle the waste of other organisms and loop these resources back into the food chain, a process called the **microbial loop**. Without the action of microbes, those waste products would accumulate and pollute the water, making the ocean a wasteland. Therefore, microbes represent an essential link fuelling the entire marine food web while keeping the ocean clean.



Role of the ocean microorganisms in the food chains in the ocean. Microorganisms play a great role from carbon storage to feeding larger organisms, while degrading the organic matter. Credit: Juliette Laude & Mathilde Bourreau

3. ***Symbiosis.*** Ocean inhabitants do not always live by themselves in isolation. On the contrary, many develop in local communities where they are surrounded by other species with whom they interact and rely on to survive. Sometimes two organisms develop an even stronger bond over the course of their common evolution: a symbiosis, a close, long-term and mutually beneficial association between the two partners. For an organism, the benefits gained from forming a symbiotic association can for example range from protection, a more hospitable living place, partner supplied food or a boost in disease immunity.



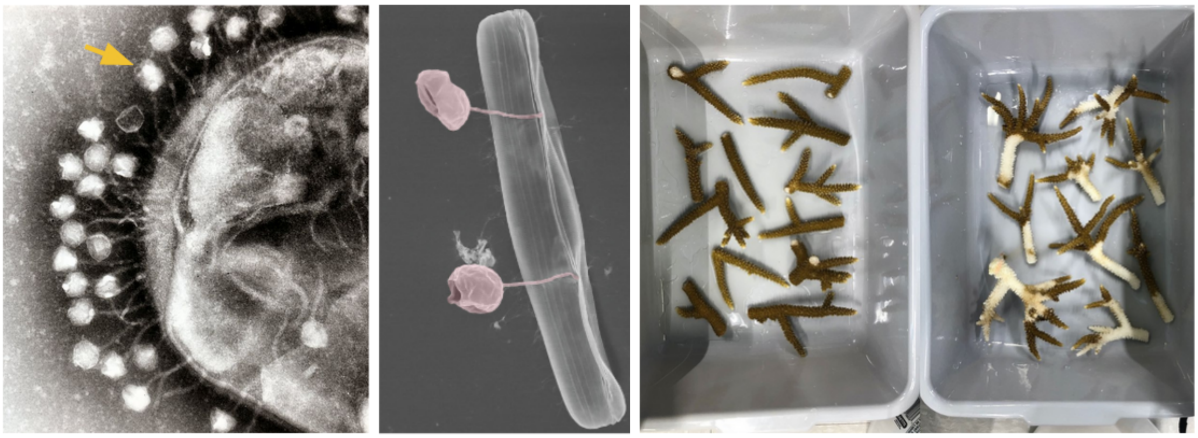
Different examples of symbiosis involving marine microbes. From left to right: A protist (Radiolaria) carrying dozens of symbiotic microalgae of the *Phaeocystis* genus (Haptophytes, yellow arrow). The scale bar represents 20 µm. Image credit: Published in Decelle et al (2015) Communicative & Integrative Biology (CC BY-NC 3.0). The giant tube worm *Riftia pachyptila* and its symbiotic bacteria. Image credits: NOAA. A coral, with close-ups of a polyp and the symbiotic zooxanthellae it contains. Image credits: Linda Wade, NOAA ; Narrissa Spies (CC BY-SA 4.0) ;Todd C. LaJeunesse (CC BY-SA 2.0), respectively.

In the ocean, the majority of symbioses are between microbes. For example, some Radiolarians (heterotrophic protists) inhabiting the sunlit surface waters live in symbiosis with microalgae of the genus *Phaeocystis* (Haptophytes). Microbes also occasionally associate with larger organisms, such as plants and animals.

One striking example is that of corals, a group of invertebrate animals forming reefs in tropical waters. For a long time, scientists wondered how corals were able to survive in the quite nutrient-poor marine habitats they tended to colonize. We now know that corals shelter microalgae called zooxanthellae (protists belonging to the *genus Symbiodinium*) inside their body. Zooxanthellae directly benefit corals by supplying photosynthesis-made food and energy including sugars and amino acids. Therefore, symbiotic associations often allow both partners to thrive in habitats they would barely survive in on their own.

A number of astounding examples of symbiosis can also be found in hydrothermal vent ecosystems. As photosynthesis cannot be performed in the deep dark waters of hydrothermal vent fields, many animal species, like the giant tube worm *Riftia pachyptila,* developed a symbiosis with local autotrophic bacteria that use minerals and metals as energy sources. While the animals usually host their microbial partners inside their own body, providing them with a protected environment, a shelter, the bacteria supply the worms with food and energy and detoxify harmful chemicals present in high amounts around the vents, like hydrogen sulfide which would otherwise kill the animal. Hydrothermal vent ecosystems are powered from the base by such autotrophic microbes, and largely depend on symbioses to function. Here, symbioses made life possible in an inhospitable environment and are the base on which the entire ecosystem and food web rely on.

4. ***The microbial world is riddled with diseases too.*** Much like us on land, ocean microbes, be it bacteria, fungi, archaea or protists, are constantly exposed and infected by parasites and pathogens. Those infectious agents are themselves microbes and belong to bacteria, virus, fungi and protists groups.



Ocean pathogens in action. From left to right: Multiple bacteriophages (yellow arrow) infecting a bacterium. Image credit: Dr Graham Beards (CC BY-SA 3.0). A diatom (grey) attacked by two parasitic fungi (pink). Image credit: Published in Kilias et al (2020) Communications Biology (CC BY 4.0). Healthy (left) and diseased (right) corals. Coral diseases can be caused by pathogen bacteria, fungi or protists. Image credit: Oregon State University (CC BY-SA 2.0).

Viruses are the most abundant group of infectious agents in the ocean. As mentioned earlier, viral infections alone are responsible for killing around 20% of total microbial biomass each day. As they are dependent on the host cell molecular machinery to reproduce themselves, viruses are necessarily cellular parasites. For instance, bacteriophages are viruses that specifically infect bacteria. They consist of a multi-protein structure that resembles a syringe and that is capable of piercing the bacterial cell wall and injecting their viral genetic information directly into the host cytoplasm to hijack the cell. Most marine viruses end up bursting the host cell once they are done replicating inside, expelling the cellular contents, including the newly grown viruses, into the ocean.

Despite the fact that only a very small portion of marine bacteria, fungi and protists are pathogens, this does not prevent them from being responsible for a significant part of daily infections. Ocean microbes also infect bigger organisms such as seaweed, fishes or corals.

Although it is a dramatic and final event at the level of the individual cell, death caused by diseases actually plays an essential role in marine life at the level of the ecosystem. Indeed, diseases are constantly shaping and regulating the populations of the different ocean inhabitants. For example, viruses counteract the over-proliferation of microalgae during seasonal or accidental blooms, which could be harmful to the entire ecosystem by consuming all the resources, blocking sunlight access or driving away other organisms. Moreover, diseases directly contribute to releasing free organic matter in the ocean, fuelling the microbial loop.

Ocean microbial life and humankind

1. ***Ecosystem services rendered by microbes.*** Ocean microbes render huge services to both marine ecosystems and humans, from food production to climate regulation. Indeed, marine photosynthetic microbes are responsible for more than half of Earth's oxygen production. This

oxygen sustains all ocean creatures requiring oxygen to function (i.e., most eukaryotes, including animals, plants and algae, as well as some bacteria and archaea). Microbes are also at the base of marine food webs and constantly recycle wasted organic matter back into the food chain through the microbial loop, thus playing a critical role for fish and seafood production.

Furthermore, ocean microbes allow atmospheric carbon to be stored in the ocean interior. Atmospheric CO_2 is fixed by microbes during photosynthesis and thus enters the ocean food web. Dead cells and other organic remains, containing this fixed carbon, sink from the surface to the bottom of the ocean (part of it is recycled back into the food chain through the microbial loop). Carbon reaching the bottom of the ocean is sequestered into its interior and seafloor from several hundreds to millions of years. This mechanism, called the biological pump, is essential to regulate global temperatures. Less than 1% of organic carbon gets buried into the seafloor; however, over geological times, it has been transformed into the oil and gas fossil fuels our societies currently depends on.

2. ***Industrial and economic services rendered by microbes.*** Microorganisms also render a large range of industrial and economic services to humankind. As explained above, marine microbes sustain food webs, providing us with a healthy and productive ocean from which the fish and seafood industry prosper.

Due to their huge diversity (most of which is still to be discovered), marine microbes represent a largely untapped reservoir of "natural products" for the discovery of new drugs and chemicals[1]. These include bioactive molecules (antibiotic, antiviral, antifungal, antioxidant and anti-cancer drugs) to cure diseases, such as **Brentuximab vedotin**, an anti-cancer molecule derived from the cyanobacterium *Caldora penicillata* and commercialized under the name Adcetris®.

Microorganism-derived molecules can also be used in a broad range of potential applications, ranging from biocatalysts to speed up reactions in the chemical industry, to more environmentally friendly antifouling compounds. Antifouling agents aim to prevent the accumulation of microorganisms, plants, algae, and/or animals on wetted surfaces. Microbial antifouling agents are promising candidates to replace the toxic and polluting coatings currently used to cover ship hulls to reduce the colonisation and growth of organisms on the hull surface and the "drag" that they cause as the ship moves through the water. Microbial antifouling agents

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[1] [1] "Natural products" are mostly so-called secondary metabolites, compounds made by the cell that are not vital for its central metabolic activities and that serve, for example, to increase its ecological competitivity. But they are vital to us, because they often possess powerful activities that we can use in medicine and other enterprises. Mostly, useful natural products that are discovered are „drug leads", because drugs that finally enter the clinic are usually made chemically, not biologically. The way things usually work is that microbiologist discovers the new natural product made by a microbe, shows it has a useful activity, such as anti-cancer activity, figures out how it works (mode of action), and then produces it in large amounts for chemical characterization. The chemist then makes a large number of chemical variants of the natural product in order to improve its activity, or reduce its toxicity, or make it better for formulation as a medicine. So, once a new medicine enters the clinic, it is often rather different from the natural product originally discovered in a microbe. For this reason, we often speak of "natural product-inspired medicines".

could also be used in food packaging and storage, water purification systems, marine and industrial equipment, and medical devices.

Moreover, marine microorganisms are studied with the aim of developing new industrial processes related to pigment, food ingredients and supplements, lipid and biofuel production. For instance, the diatom *Odontella aurita*, a microalga rich in the omega-3 fatty acid EPA, shows promise as a food supplement to reduce cardiovascular disease and is already available on the market.

Marine water represents a highly available and abundant resource which does not compete with potable water and cultivated land, while most highly populated areas are located close to coasts. Thus, being able to cultivate marine microalgae has a great potential in food and biofuel production.

Finally, new biotechnologies could be developed from mimicking natural processes happening in marine microorganisms. For instance, diatoms are studied for their ability to make glass at low temperature and to encapsulate drugs and/or organisms in glass nano shells for drug delivery.

A demonstration plant for marine microalgae industrial cultivation in Kona, Hawaii, operated by Cellana LLC. Published in Greene et al (2016) Oceanography.

A better understanding of the ocean's microscopic inhabitants will ultimately benefit the development of marine microbe-derived drugs and technologies. The ocean microbial world is still largely a black box and research is needed to explore it. To that end, several scientific projects, such as *Tara* Oceans, aim to describe the diversity of the microbial world across Earth's oceans. The *Tara* schooner carries an onboard lab all over the globe to study microbes in open and coastal waters.

Of note, it is imperative to have an international legal framework to regulate the usage of data yielded from international research projects involving biodiversity and genetic resources. Hence the Nagoya protocol was adopted in 2010 to ensure access and fair and equitable share of genetic resources and positive research outcomes.

3. ***Impact of human activities on the marine microorganisms and consequences for us.***

Since the industrial revolution at the beginning of the 19th century, combustion of fossil fuels for energy production is responsible for the accumulation of greenhouse gases such as CO_2 in the atmosphere and increased worldwide temperatures. This manmade climate change negatively impacts overall microbial community structure and diversity and disturbs the productive food webs we are profiting from. Warmer and more acidic conditions could impact ecosystem community composition, favouring cyanobacteria over eukaryotic phytoplankton, leading to higher detritus production instead of conversion at higher trophic levels.

Global warming increases the concentration of CO_2 in marine waters which in turn leads to acidification of our oceans. Acidification has major consequences on many marine microorganisms: those that cannot sustain this habitat change will be driven away. Calcareous microbes such as coccolithophores or foraminifera are particularly sensitive to pH changes as acidic conditions inhibit the formation of their calcareous tests.

Similarly, ocean warming significantly changes habitats marine microorganisms were once adapted to. Some species are favoured by these new environmental conditions while others are disadvantaged. Since cold ecological niches tend to disappear, we observe a shift towards warmer water-adapted species as their habitats expand.

Most tropical invasive species are favoured by these warming temperatures as high latitudes are progressively becoming more hospitable to them. Such species are often transported to new ocean regions over large distances in the ballast waters of ships. Thank to metabolic advantages and absence of pathogens and predators, invasive species can become highly dominant over the local species and unbalance the entire microbial food web, thus further contributing to local biodiversity erosion. Of note, global warming works in concert with eutrophication to favour invasive species development in newly colonized habitats.

Warmer temperatures also favour the development and spread of diseases in oceans as pathogens of warm-blooded animals (like us) often thrive in warmer temperatures: development cycles are shortened while their habitats are expanding into new areas where new hosts lack the necessary defence mechanisms that are acquired by continuous exposure and co-evolution.

Additionally, species stressed by warming waters can be more susceptible to infections. These situations are similar to the arrival of the Europeans in America between the 15th and 18th century, bringing several new diseases to the continent, which had a deadly impact on indigenous populations that didn't have any acquired immune defences against these illnesses.

Warmer temperatures also impact important microbial symbioses. A famous example is coral bleaching. In fact, most coral reefs are affected dramatically by the rise in temperature. Such a stress causes the corals to release their zooxanthellae symbionts as it has to relocate more of its nutrients and energy towards itself. Less is translocated to its symbionts which in turn share less of their photosynthetic products, destabilizing the symbiotic relationship. This result in corals being less resilient and more vulnerable to future stresses and diseases.

Relevance for Sustainable Development Goals and Grand Challenges

Through their importance both on climate and food chain regulation, marine microorganisms influence the United Nations' agenda towards achieving the Sustainable Development Goals at several levels:

- **Goal 2. End hunger.** Microorganisms are at the base of ocean food webs and thus ensure food provision for people around the globe. For example, around 3 billion people rely on fish as their primary source of protein. This fish comes either from wild stocks or aquaculture.
- **Goal 3: Ensure healthy lives and promote well-being for all at all ages.** Phytoplankton is known to produce the equivalent of one out of two oxygen molecules on Earth. This oxygen primarily benefits to the ocean's ecosystem and wildlife. Phytoplankton also helps to store carbon

dioxide into the oceans. It is estimated that of the 1300 gigatons of carbon dioxide emitted by human activities over the last 200 years, 38% is stored in the oceans.

- **Goal 6: Ensure access to water and sanitation for all.** Microorganisms help keep the ocean clean through the microbial loop. Moreover, some, in particular bacteria and fungi, have the ability to degrade some plastics and some hydrocarbons. Thus, microorganisms can be of great help in bioremediation. A good example is the use of hydrocarbon-degrading microbes to combat oil spills.
- **Goal 7: Ensure access to affordable, reliable, sustainable and modern energy; Goal 9: Build resilient infrastructure, promote sustainable industrialization and foster innovation.** Several industrial projects are working towards using algae in either autonomous buildings (waste water purification, heating) or towards energy production. On the other hand, microalgae are used in bioreactors as alternative ways of producing fuel.

BIQ (Bio Intelligent Quotient), a building powered entirely by algae in Hamburg. Credit: NordNordWest (CC BY-SA 3.0).

Innovative companies are currently developing more sustainable ocean microbe derived products (alternative food sources for humans and livestock, pigments and lipid production, …). For instance, diatoms are used in plant-based alternatives such as a vegan salmon brand. The diatom *Odontella* gives its "fishy" taste to the "salmon".

- **Goal 13: Take urgent action to combat climate change and its impacts; Goal 14: Conserve and sustainably use the oceans, seas and marine resources for sustainable**

development._Climate change is strongly affecting the microbial life of the ocean. We have reached a tipping point where phytoplankton biomass decreases by 1% every year. Considering all the ecosystem services rendered by marine microorganisms, it is now crucial to put considerable effort into education, sensibilisation and conservation around marine life, including its essential marine microbes.

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Pupil Participation

1. ***Class discussion of the importance of marine microbes*** (e.g. recycling of organic matter, creating oxygen for us, feeding the fish, etc.)

2. ***Pupil stakeholder awareness***

a. Medicines are chemical compounds and the diverse range of different medicines currently in use reflects chemical diversity. Many of these are derived from world of microbes: microbial diversity provides the chemical diversity needed to discover new medicines. Marine microbes constitute an amazing diversity, so there is currently much effort to discover new medicines by screening marine microbes. It is to be expected that a number of these will enter medical use over the coming years.

b. Similarly, marine microbes produce a number of compounds that are important for our nutrition and wellbeing, and some are edible themselves. We can expect an increasing involvement of marine microbes in our daily diet in future.

c. The fish we eat itself feeds on smaller organisms that in turn feed on microbes. Fertiliser run-off from coastal farms promotes the growth of microbes that produce toxins which may then contaminate the fish. When this happens, the fishing industry is prohibited from harvesting fish in the region, so we have to source our fish from other regions, which may make it less fresh and cost more.

d. The seas are major transportation routes and ships bring us food and other important things from distant lands. However, when they have light loads or are returning empty, they load ballast water at the point of departure of the journey to provide stability when on the high seas. This ballast water is then discharged at the destination, including any organisms in it. If any of the organisms are not the normal inhabitants of the destination waters, there is a low but real risk that may become invasive species or new pathogens.

3. ***Exercises***

a. Travel with *Tara* Oceans

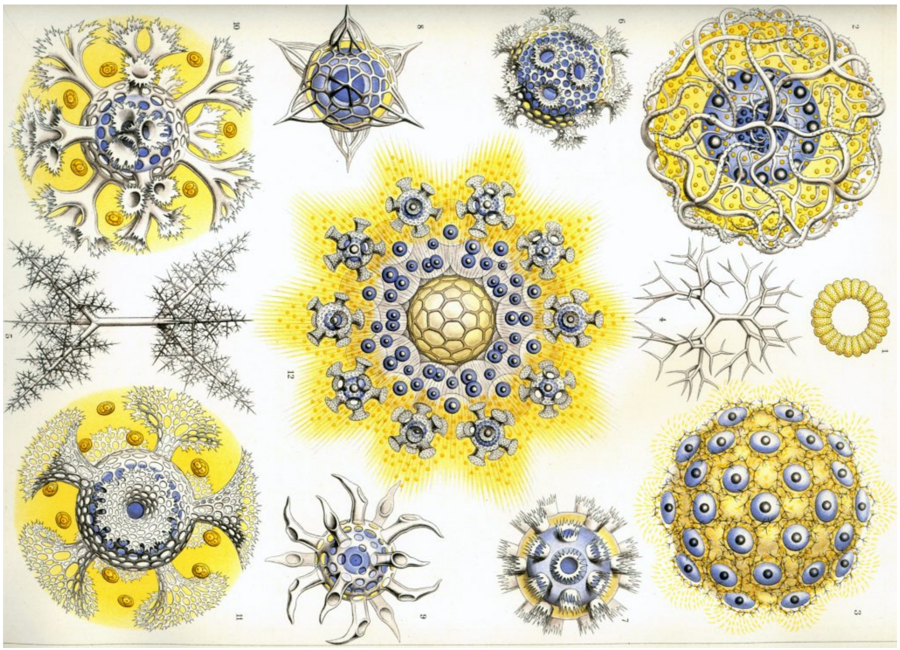
Objective: approach the different biomes of the planet and understand the different microbial communities across the ocean. For instance, understand the patterns in distribution, abundance and diversity of the phytoplankton at the global scale.

Activity: travel around the globe following the *Tara* Oceans project and the microorganisms which are key to regional ecosystems. For that you can access the freely available Tara oceans educational material. They are organised according to target age. https://oceans.taraexpeditions.org/en/m/education/educational-resources/

b. Drawing activities

Objectives: enhance contact with marine microorganisms. It also trains patience and helps with relaxing and concentration, such as colouring mandalas. It can work as a calming activity.

Activity: For small kids, it will be a colouring activity with black and white printed illustrations from Ernst Haeckel for instance. The illustrations can be selected from any microorganisms' forms. It is recommended to print them in big format to facilitate the colouring. For schools equipped with tablets the colouring can occur on the tablet with the adequate app.

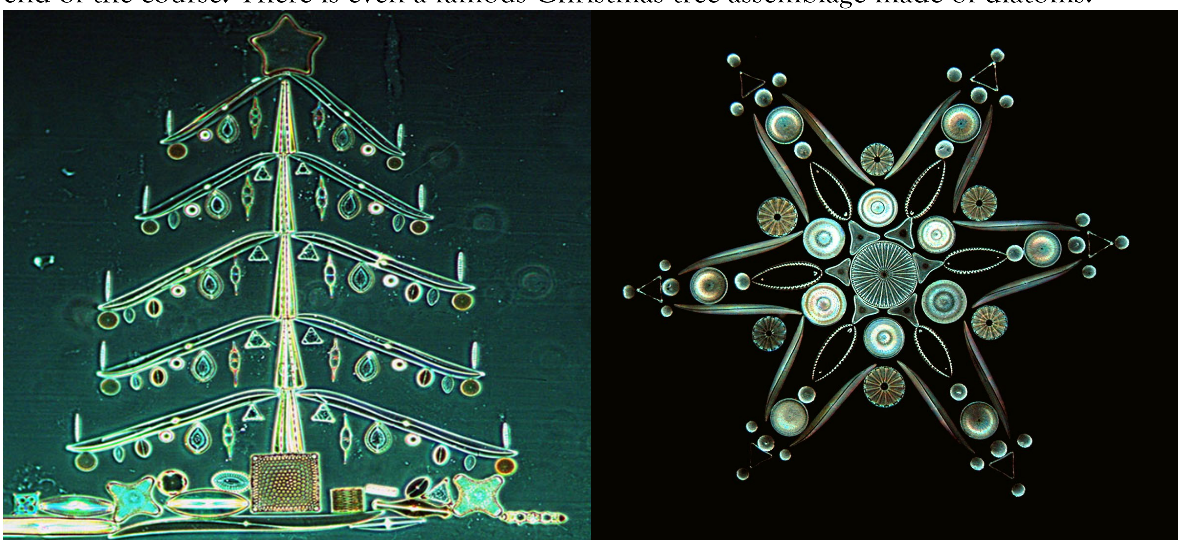


Radiolarians, by Ernst Haeckel, Kunst von Nature, 1904.

c. Create your own diatom assemblage:

Objectives: Apprehend the diversity and beauty of the ocean microorganisms.

Activity: As did UK aristocrats at the end of the 19th century, use your creativity and the (printed) microorganisms you have at your disposal to create your own diatom/microorganism assemblage. It can be abstract (the student will justify the choice in the shapes) or figurative (the student will explain why this particular topic). For didactic purposes you can print microorganisms as diverse as you want (Eukaryotes: diatoms, dinoflagellates..., Prokaryotes, Archaea). You can provide the students with examples of previous diatoms or microscopic assemblages for inspiration or at the end of the course. There is even a famous Christmas tree assemblage made of diatoms!



Example of antique Victorian diatom assemblages (observed with a microscope).

The Evidence Base, Further Reading and Teaching Aids

Photo and Video resources

Discovering the diversity of the microscopic inhabitants of Earth's seas and oceans

"The secret life of Plankton" (protist microbes from 2:41 to 3:32) https://www.youtube.com/watch?v=xFQ_fO2D7f0&t=196s
"Diatoms: Tiny Factories You Can See From Space"
https://www.youtube.com/watch?v=Ygty9HxhFK4
"How Cyanobacteria Took Over The World" https://www.youtube.com/watch?v=ps2GlGs8oso
Images of marine cyanobacteria and viruses from the Chisholm lab:
https://www.flickr.com/photos/prochlorococcus/
A collection of ocean protist images from Mediterranean Institute of Oceanography: https://plankton.mio.osupytheas.fr/

Diversity of microbial lifestyles in the ocean

"Vampyrella feeding on algae"
https://www.sciencephoto.com/media/688150/view/vampyrella-feeding-on-algae-time-lapse
"How Microscopic Hunters Get Their Lunch"
https://www.youtube.com/watch?v=io731XY8fH8
"The Microbial loop" https://www.youtube.com/watch?v=KtxUp2s_HIU
"Hydrothermal vents: Explore a bizarre deep ocean habitat"
https://www.youtube.com/watch?v=JtV-FP212Uc
"How Giant Tube Worms Survive at Hydrothermal Vents | I Contain Multitudes"
https://www.youtube.com/watch?v=8W_ywzhkR90
"Nature's Cutest Symbiosis: The Bobtail Squid | I Contain Multitudes"
https://www.youtube.com/watch?v=3ivMSCi-Y2Q
"The Coral and the Algae"
https://oceantoday.noaa.gov/fullmoon-coralandalgae/welcome.html

Ocean microbial life and humankind

"Sinking marine snow - the biological pump in action"
https://www.youtube.com/watch?v=rr_pEP_Bvww
"Oceans Part 4: Ocean Carbon & The Biological Pump"
https://www.youtube.com/watch?v=oUwfhLOlvX8
Numerous video courses for students (all levels) available on the Tara Oceans Youtube channel (French):
https://www.youtube.com/watch?v=Yhwoycktpwo&list=PLkeVMgFz3heDE_TT920AwNsfLfWVS7cpL&index=23 ; https://www.youtube.com/watch?v=YLCv8k-Zqlc&list=PLkeVMgFz3heDntqggcHOpv2DoTHRPC9wj

Scientific references

Discovering the diversity of the microscopic inhabitants of Earth seas and oceans

1. ***A large majority of organisms living in marine habitats are invisible microbes***

Marine microplankton in a hand net: Nadeau et al (2016) Microbial Morphology and Motility as Biosignatures for Outer Planet Missions. *Astrobiology* 16(10): 755–774

Marine microbe biomass estimates: Bar-On et al (2018) The biomass distribution on Earth. *Proceedings of the National Academy of Sciences of the United States of America* 115(25): 6506–6511 ; Census of Marine Life

Estimate of the proportion of undiscovered species in the ocean: Mora et al (2011) How many species are there on earth and in the ocean? *PLoS Biology* 9(8): 1–8

2. ***Marine microbes span all of the domains of life***

Estimation of bacteria abundance in the ocean: Whitman et al (1998) Prokaryotes: The unseen majority. *Proceedings of the National Academy of Sciences of the United States of America* 95(12): 6578–6583
Virus biomass in the ocean: Bar-On et al (2019) The Biomass Composition of the Oceans: A Blueprint of Our Blue Planet. *Cell* 179(7): 1451–1454
Virus statistics: Suttle CA (2007) Marine viruses - Major players in the global ecosystem. *Nature Reviews Microbiology* 5(10): 801–812

Diversity of their lifestyles/food regimes

https://ocean.si.edu/ocean-life/microbes/marine-microbes

Ocean microbial life and humankind

1. ***Ecosystem services rendered by microbes***

Ecosystem services rendered by marine phytoplankton: Naselli-Flores et al (2022) Ecosystem services provided by marine and freshwater phytoplankton. *Hydrobiologia*.
Organic carbon buried in the seafloor: Atwood et al (2020) Global Patterns in Marine Sediment Carbon Stocks. *Frontiers in Marine Science* 7

2. ***Industrial and economic services rendered by microbes***

Biocatalysts: Birolli et al (2019) Applications of marine-derived microorganisms and their enzymes in biocatalysis and biotransformation, the underexplored potentials. *Frontiers in Microbiology* 10: 1453
Antifouling compounds: Adnan et al (2018) Significance and potential of marine microbial natural bioactive compounds against biofilms/biofouling: Necessity for green chemistry. *PeerJ* 2018(6)
Pigment production and use: Nawaz et al (2021) An overview on industrial and medical applications of bio-pigments synthesized by marine bacteria. In *Microorganisms* 9(1): 1–24
Food ingredients and supplements: Dewapriya et al (2014) Marine microorganisms: An emerging avenue in modern nutraceuticals and functional foods. In *Food Research International* 56: 115–125
Hydrocarbon-degrading bacteria: https://www.frontiersin.org/articles/10.3389/fmicb.2018.02885/full

Large-scale industrial cultivation of microalgae for biofuel production: Greene et al (2016) Marine microalgae: Climate, energy, and food security from the sea. In *Oceanography* 29(4): 10–15
Industrial applications of diatom glass making capacities: https://news.cnrs.fr/articles/soft-chemistry-naturally-creative

3. Impact of human activities on the marine microorganisms and consequences for us

Exhaustive review of climate change impact on oceans and associated organisms, from the Intergovernmental Panel on Climate Change (IPCC, United Nations body): https://www.ipcc.ch/srocc/chapter/chapter-5/
Climate change and invasive species: Sacca A (2015) Invasive Aquatic Microorganisms: Patterns of Introduction and Impacts. Chapter in *Biological invasions: patterns, management, and economic impacts* ; https://earthobservatory.nasa.gov/images/91591/bacteria-thrive-as-ocean-warms
Impact of climate change on coral-microalgae symbiosis: Rädecker et al (2021) Heat stress destabilizes symbiotic nutrient cycling in corals. *Proceedings of the National Academy of Sciences of the United States of America* 118(5): e2022653118

Relevance for Sustainable Development Goals and Grand Challenges

BIQ: the Algae-Powered Building in Germany:
https://www.labroots.com/trending/videos/11463/biq-the-alga-powered-building-in-germany
Vegan salmon brand using Odontella for "salmon" flavor: https://www.odontella.com/fr/odontella-accueil/
Global phytoplankton biomass decline: https://www.nature.com/articles/nature09268
Carbon dioxide storage in the oceans: Rackley SA (2010) Chapter 12 - Ocean Storage. Chapter in *Carbon Capture and Storage.*

Pupil participation

Antique Victorian era diatom assemblages:
http://www.victorianmicroscopeslides.com/slideexb.htm

Books

Christian Sardet, Plankton – Wonders of the Drifting World, Univ. Chicago Press (2015)

Marc-André Selosse, Jamais seul – Ces microbes qui construisent les plantes, les animaux et les civilisations, Actes Sud (2017, French only)

Drew Harvell, Ocean Outbreak – Confronting the Rising Tide of Marine Disease, Univ. California Press (2021)

Glossary

Adaptation	Adaptation is the dynamic evolutionary process by which organisms become better suited to the conditions in their environment, increasing their reproductive success. Natural selection is a phenomenon by which inside a population better adjusted individuals tend to survive and reproduce more, and therefore are able to transmit and perpetuate their essential genotypic qualities to succeeding generations. Natural selection is one of the key drivers of adaptation.
Autotroph	An organism capable of producing its energy and organic matter from mineral sources of energy (light, CO_2, methane, ferrous oxide, hydrogen sulfide, …) available in the environment.
Bacteriophage	Virus infecting bacteria.
Ballast waters	Waters stored in the ballast reservoir of a ship to increase its stability at sea. Ballast waters are usually collected by a ship in the coastal region of a port and later discharged at the next port of call, therefore transplanting a variety of organisms into non-native ecosystems.
Biodiversity	Variety of living forms in a given ecosystem.
Biofouling Antifouling	Biofouling is the (undesirable) accumulation of microorganisms, plants, algae and animals on wetted surfaces such as pipes, cables, ships, medical equipment etc., reducing the item's performance. Antifouling agents are used to prevent biofouling.
Biofuel	A fuel produced directly from a living biomass, in contrast with fossil fuels which arise from the decomposition of buried plant and animal remains over millions of years.
Biological pump	A process allowing the sequestration of carbon from the atmosphere to the bottom of the ocean and its seafloor sediments thanks to marine microbial activity.
Bioluminescence	Production of light by a living organism.
Biomass	Mass of biological organisms in a given area or ecosystem.
Biotechnology	Use of living systems and organisms or their derived molecular tools to develop knowledge, products and services.
Bloom	Rapid growth of a microorganism population over a short period of time due to favorable conditions.
Calciferous test	A test is the hard external shell made by certain marine animals (seaorchins) and microorganisms. Tests produced from calcium salts, such those of the Foraminifera and coccolithophore protists are called calciferous.
Cellular respiration	Major biochemical process by which organisms obtain chemical energy usable by the cell from breaking down nutrients such as glucose.
Coccolithophores	A group of unicellular photosynthetic eukaryotes belonging to the Haptophyta division, distinguishable for their tests formed of calcium carbonate scales.

Cyanobacteria	A large family of photosynthetic bacteria found in all terrestrial and aquatic environments.
Cytoplasm	The internal content of a cell.
Diatoms	A group of unicellular photosynthetic eukaryotes belonging to the Heterokonta group. Their most defining feature is their ornamented glass (silica) cell wall called frustule.
Dinoflagellates	A group of unicellular eukaryotes belonging to the Alveolata group. Dinoflagellates are primarily photosynthetic but some species also consume other microorganisms.
Ecosystem services	All the benefits and support provided to humankind by healthy ecosystems.
Ecosystem services	Ecosystem services consist of all the advantages and support provided to the humankind by healthy ecosystems.
EPA	Eicosapentaenoic acid, a polyunsaturated fatty acid. Omega-3 fatty acids docosahexaenoic acid (DHA) and eicosapentaenoic acid (EPA) are essential parts of the human diet and have a protective role against cardiovascular diseases.
Eukaryotes	Organisms whose genetic information is enclosed in a nucleus. They constitute a separate domain of life including protists, plants, algae, animals and fungi.
Eutrophication	Process by which a body of water becomes progressively enriched in minerals and nutrients. This nutrient increases often causes algae blooms harmful to the local ecosystem. Anthropogenic eutrophication has become a wide-spread phenomenon due to nutrient pollution from agriculture and industry.
Extremophile	An organism able to live in extreme environments (for example highly salty, hot, acidic, or radioactive habitats).
Food chain - Food web	The sequence of transfers of matter and energy from organism to organism in the form of food in a given ecosystem.
Foraminifera	A group of unicellular heterotrophic eukaryotes belonging to the Rhizaria supergroup. Their external test is often made of calcium carbonate.
Heterotroph	An organism that needs to consume organic matter (from other living organisms) to produce its own energy and organic matter.
Hydrothermal vent	A crack in the seafloor releasing geothermally heated water, commonly found near volcanically active places, areas where tectonic plates are diverging or hotspots. Water discharged is usually rich in minerals, leading to mineral ore deposits around the vent.
Invasive species	A non-native species introduced in a new environment where it becomes overpopulated, ultimately impacting negatively the local habitat and ecosystem.
Microalgae	Microscopic algae, often unicellular and powering themselves through photosynthesis.
Microbial loop	The process by which heterotrophic microorganisms recycle unconsumed organic matter, reintroducing that energy back into the food web.

Organic matter	Matter constituting of all living organisms, fabricated by themselves. It is mostly composed of proteins, carbohydrates, lipids and nucleic acids (DNA and RNA).
Photosynthesis	Biochemical process by which some organisms can convert light energy and atmospheric carbon dioxide into chemical energy usable by the cell to power its activity.
Plankton Microplankton Phytoplankton Zooplankton	The organisms drifting and/or floating in fresh or ocean waters are collectively referred to as plankton, in contrast to organisms fully controlling their mobility such as fishes. The microplankton is the microscopic fraction of plankton. The phytoplankton is the fraction of plankton performing photosynthesis (microalgae and photosynthetic bacteria). The zooplankton is the heterotrophic fraction of plankton.
Prokaryotes	Unicellular organisms whose genetic information is not enclosed in a nucleus, corresponding to bacteria and archaea.
Radiolaria	A group of unicellular eukaryotes belonging to the Rhizaria group. Radiolarians are primarily heterotrophic but many species have microalgae symbionts. They produce an intricate skeleton, usually made of silica.
Symbiosis	A close, long-term and mutually beneficial association between the two organisms of different species.
Tree of life Domains of life	The tree of life is a scientific model describing the evolutionary relationships between all organisms, both living and extinct. Non-cellular life (viruses) is not included in this system. The tree of life first divides into three separated domains: bacteria, archaea and eukaryotes.
Unicellular/multicellular organism	An organism formed of a single cell is unicellular, whereas multicellular organisms consist of at least two cells.