

**CZECH UNIVERSITY OF LIFE SCIENCES
PRAGUE**

Faculty of Environmental Sciences

Department of Ecology



BACHELOR THESIS

Diatoms and their interactions with microorganisms in
aquatic ecosystems.

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Declaration

I declare that I have worked on my bachelor thesis titled "Diatoms and their interactions with microorganisms in aquatic environments" by myself and I have used only the sources mentioned at the end of the thesis. As the author of a bachelor thesis, I declare that the thesis does not break copyright of any third person.

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Abstract

The role of the diatoms in the ecosystem is considerable as they play a pivotal role in global oxygen production, carbon sequestration, and aquatic food chains. Yet, to fully understand their population dynamics and role in aquatic environments, it is important to first study interactions between diatoms and other aquatic microorganisms such as bacteria, viruses, and fungi. This bachelor thesis dives into this topic by investigating the importance of these interactions in ecology. The findings of this study in particular reveal the substantial control of diatom populations and diversity by viruses, which in turn influences biogeochemical cycling and aquatic food chains. The thesis also explores the relationships such as symbiosis, parasitism, competition or facilitation between diatoms and other microorganisms (notably bacteria and fungi) which is influential for organic matter decomposition and cycling of nutrients.

Abstrakt

Rozsivky hrají v ekosystému významnou roli, protože mají klíčový význam pro globální produkci kyslíku, vázání uhlíku a nepostradatelnou funkci v potravních řetězcích vodních ekosystémů. Pro úplné pochopení jejich populační dynamiky a úlohy ve vodním prostředí je však důležité nejprve studovat interakce mezi rozsivkami a dalšími vodními mikroorganismy jako jsou bakterie, viry či houby. Tato bakalářská práce se ponořuje do tohoto tématu a zkoumá význam těchto interakcí v ekologii. Výsledky této studie odhalují zejména podstatnou kontrolu populací a rozsivkové diverzity viry, což následně ovlivňuje biogeochemický cyklus a dále i potravní řetězce. Práce také zkoumá vztahy jako je symbióza, parazitismus, konkurence nebo facilitace mezi rozsivkami a dalšími mikroorganismy, které mají vliv na rozklad organické hmoty a koloběh živin.

Keywords

diatoms, ecological interactions, bacteria, virus, microbes, marine ecosystems, decomposition, ocean, diversity, fungi, pathogen

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1. Introduction

Diatoms, unicellular algae and photosynthetic eukaryotes, are primary producers which are essential for aquatic food webs. Due to their high productivity, and the fact they occur almost everywhere, they are key components of global carbon and nutrient cycles. For example, 20 % of oxygen on the Earth is made by diatoms through their photosynthesis (Falkowski, Barber, Smetacek, 1998). These organisms are also known for their cell walls made out of the silica (i.e. glass), and their uptake, coupled with their biomass, make them important considerations for the global silica cycle (Round et al. 1990). Diatoms also play a part in carbon sequestration, as when diatoms die in marine ecosystems, their silica shells cause them to sink to the sediments, which helps to bring the fixed carbon to the bottom of the sea (Amin, Parker, Armbrust 2012).

Diatoms live as members of ecological communities, which are characterized as a complex network of interactions between co-occurring species (Barnes, Mann 2009). Ecological interactions are effects that two organisms have on each other. The organisms can be the same species - as in the case of intraspecific interactions - or different species, in the case of interspecific interactions. These interactions may have various effects on each organism, and each organism can either experience positive (+), neutral (o), or negative (-) effects in the short or long-term (Raghukumar 2017). For example, mutualism (which is a ++ relationship, that means positive effects for both organisms) is a synergy, where the fitness of both organisms is improved by the other, for example by the exchange of resources. Another relationship is called competition, which is when fitness of one organism is reduced by another organism, and generally comes at a cost to the other organism as well (-/-). Parasitism, meaning when an organism (i.e. a parasite) lives on or inside the other organisms (host) and causes harm (+/-), herbivory is when an organism (i.e. a herbivore) eats autotrophs (such as algae and photosynthesizing bacteria) (+/-), and predation is a relationship when one organism (i.e. a predator) kills and eats another organism (its prey) (+/-) (Franzé et al. 2018).

However, the interactions that characterize communities can be difficult to observe, and may not be visible even though they are very important (such as the case for

competition, although exploitation interactions like herbivory or predation are very obvious). (Franzé et al. 2018). These interactions hold true for both terrestrial and aquatic ecosystems, though they have been arguably studied less in latter ecosystems. The largest biome on the Earth is the oceans, and marine microorganisms are crucial components for fulfilling global biogeochemical cycles. As such, there are various ecological factors influencing their diversity, communities, and interactions (Diner et al. 2016), all of which ultimately regulate these biogeochemical cycles.

Diatoms in particular form complex associations with other microorganisms (Amin, Parker, Armbrust 2012). Diatoms, bacteria, viruses and fungi all live together and interact, and this has implications for community structure and functioning. Therefore, the aim of this bachelor thesis is to investigate complicated connections in aquatic environments between diatoms, bacteria, viruses and fungi, explore their basic mechanisms, and evaluate their ecological importance. This study tries to clarify the dynamics of these interactions, dealing with fundamental questions such as: How important diatoms are for ecosystems? What are the consequences of their interactions? What is their impact on ecosystem functioning? Thus, this bachelor thesis aims to provide a better understanding of microbial ecology in aquatic ecosystems, the results of which can inform the management of these ecosystems, as well as conservation strategies in the context of challenges arising from global environmental change.

2. Diatoms

Diatoms are one of the most ecologically important groups of primary producers in the modern oceans, but they can be found in nearly every aquatic environment existing on the Earth, including freshwaters, soils, and hypersaline or thermal waters (Round et al. 1990). They can represent some of the greatest proportions of biomass (Benoiston et al. 2017), and typically occur in two types of habitats, the first one being submerged surfaces, which are called the benthos or phytobenthos, and here can form chain-like microcolonies and compose the biofilm, which are jungles of biodiversity with 'self-sufficient' carbon cycles due to exchange of the substances between heterotrophs and phototrophs (Battin et al. 2016). The second is open water, and these are called planktonic (i.e. phytoplankton) (Round et al. 1990). However, diatoms have also been found on the feathers of seabirds (i.e. epizoon), as well as on plants (epiphytes), rocks (epilithon), and other habitats (Round et al. 1990).

Diatoms are brown micro-algae belonging to the class *Bacillariophyceae* (Zecher et al. 2015), but their systematics are difficult to describe due to the fact that every scientist has their own opinion on how to define species and taxonomic categories (Round et al. 1990). Silicified frustules are the main physical feature of diatoms. These silicified frustules form the basis for their traditional morphological identification by looking at their patterned surfaces (Round et al. 1990). The majority of species found in the benthos or biofilm are characteristic for the presence of one or two slits going through the valve, which is called the raphe system (Round et al. 1990). Figure 1 shows some species of benthic pennate diatoms.

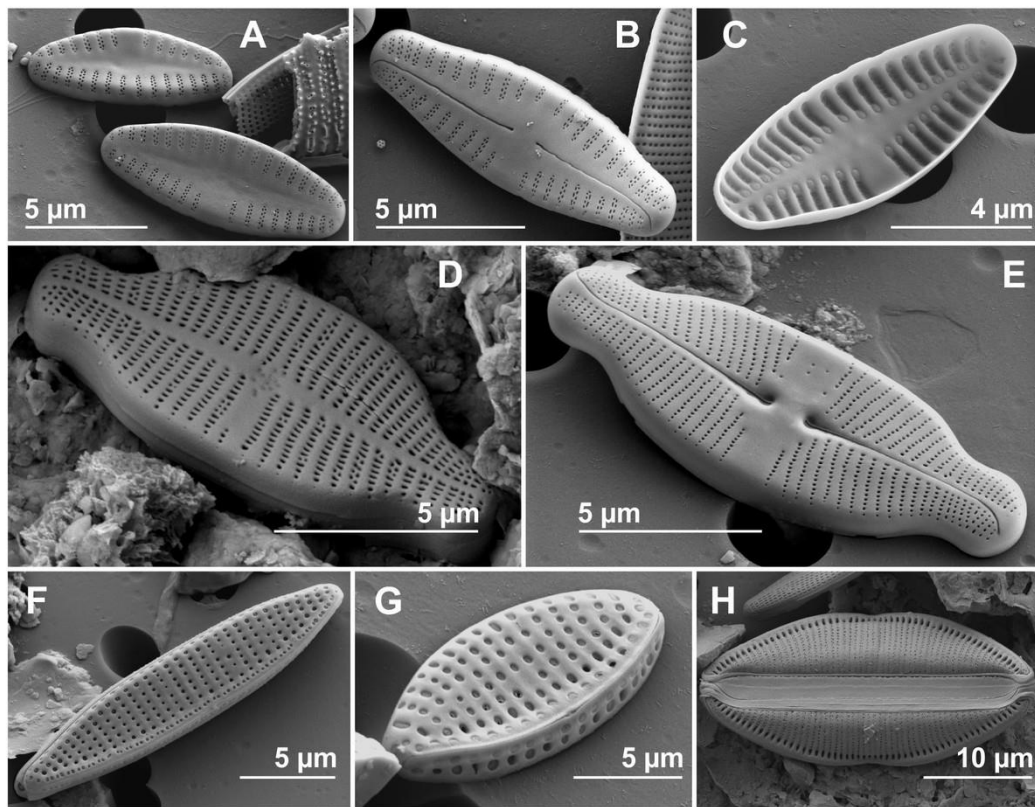


Figure 1. (A) *Crenotia thermalis*, external rafeless valve view. (B) *Crenotia thermalis*, external raphe valve view. (C) *Crenotia thermalis*, internal rafeless valve view. (D) *Lemnicola exigua*, external rafeless valve view. (E) *Lemnicola exigua*, external raphe valve view. (F) *Nitzschia amphibia*, external valve view. (G) *Nitzschia inconspicua*, external valve and mantle view. (H) *Rhopalodia operculata*, external frustule view (source: Lai et al. 2019).

But not all diatom species have this slit (Round et al. 1990), and Figure 2 shows some species of centric planktonic diatoms.

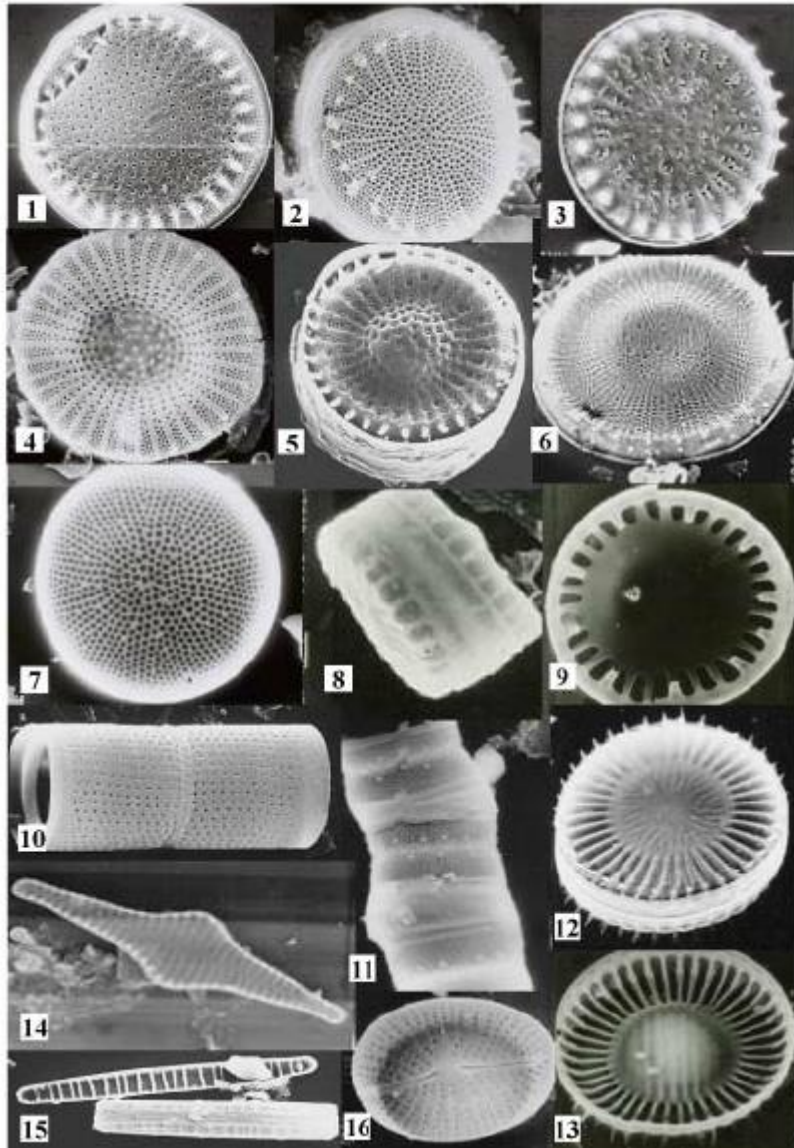


Figure 2. The most common centric planktonic diatoms species - 1. *Stephanodiscus hantzschii*, 2. *S. hantzschii* f. *tenuis*, 3. *S. parvus*, 4–5. *S. minutulus*, 6. *S. rotula*, 7. *Actinocyclus normanii* f. *subsalsa*, 8–9. *Cyclotella atomus*, 10. *Aulacoseira islandica*, 11. *Stephanodiscus binderanus*, 12–13. *Cyclotella meneghiniana*, 14. *Fragilaria inflata* var. *istvanffy*, 15. *Diatoma moniliformis*, 16. *Navicula scutelloides* (source: Kasperoviéienė, Vaikutienė 2007).

2.1 Function of diatoms

While they are found everywhere, diatoms in marine systems typically dominate at high latitudes and upwelling regions. They also contribute significantly to sporadic blooms that often come about in springtime, which makes them play an important role in biogeochemical cycles globally (Benoiston et al. 2017). They are often found in high abundance near the sea ice edge, where other organisms which photosynthesize are more rare. Notably, these other organisms include bacteria, fungi, and viruses - all of which play an important role in either positively or negatively regulating diatom populations, and in turn marine biogeochemical cycles. As a result, Arctic and Southern ocean ecosystems depend on them, and there are extensive deposits of siliceous mud and seeps (more than 1 km thick in some areas) which proves their importance to the biochemistry of these places over geological time periods (Benoiston et al. 2017).

Given that they are among the most abundant components of the plankton community, diatoms are therefore key functional components of the oceans thanks to their primary production (Andrew et al. 2022, Benoiston et al. 2017). Notwithstanding the fact that the size of these organisms is microscopic, the biochemistry of the planet is influenced by their abundant collective numbers supplying a significant part of oxygen on the Earth (Andrew et al. 2022).

Diatoms can survive long periods of limited nutrient and light supply because of their ability to go dormant, so when conditions are appropriate for them to grow, they usually dominate oceanic spring blooms, since they can divide faster compared to other phytoplankton, though depending on the silicon supply (Benoiston et al. 2017). Silicon is a basic nutrient for plenty of marine organisms, and it gets to the oceans from terrestrial weathering through rivers and groundwater and as a biogenic phase created by the silica secretion of primary producers, for example diatoms (Hatton et al. 2019).

Marine diatoms are essential for the biological ocean pump and fixation of the carbon in the atmosphere, and some of this is regulated by silicon availability (Hawkings et al. 2018). A larger source of silicon influences the drawdown of CO₂ and functioning of the ecosystem due to stimulating higher diatom productivity, this has an impact on

marine biogeochemical cycles, because when the silicon input is higher, diatoms grow more compared to other phytoplankton (Hawkings et al. 2018). This will probably have an impact on the export of the organic carbon, alkalinity of the surface and the “silica pump”, which controls the nutrients ratio reaching the deep ocean (Hawkings et al. 2018).

Biogeography

Diatoms can be found in all oceans throughout the world, as long as there is enough light and nutrients. Typically, diatoms occur in upwelling and well-mixed coastal areas (Benoiston et al. 2017), yet their importance in the oligotrophic open ocean is significantly smaller (Malviya et al. 2016). Coastal shallow areas are ecosystems with one of the highest levels of productivity globally. Planktonic and benthic cyanobacteria and diatoms are the main primary producers in such systems. Admiraal and Colijn & van Buurt say that the most important parts of a muddy estuary are the benthic diatoms (Colijn, Van Buurt 1975). However, there is still minimal knowledge about the ecology of the microphytobenthic communities, which includes the benthic microalgae (Watermann et al. 1999).

The *Tara* oceans project performed one of the most complete biogeographical studies of marine diatoms to date. They had collected samples from various types of oceanic regions using a standardized sampling procedure during the circumnavigation. This study revealed two diatom diversity choke points (a region of intense mixing among water masses, it is responsible for limiting the distribution and diversity of diatoms), the Drake Passage and the Agulhas retroflexion at different sides (Malviya et al. 2016), which correspond to choke points for oceanic circulation as well. According to previous studies, Agulhas choke point is not a plankton dispersal barrier (Malviya et al. 2016). In all, Tara Oceans found 79 genera worldwide, with *Chaetoceros* being the most abundant genus, representing 23.1% of total sequences assigned. *Fragilariopsis* accounted for 15.5% of total assigned sequences, then *Thalassiosira* (13.7%) *Corethron* (11%), *Leptocylindrus* (10.1%), *Actinocyclus* (8.7%), *Pseudo-nitzschia* (4.4%), and *Proboscia* (3.9%) (Malviya et al. 2016). Just a small number of sequences was attributed to genera known from freshwater or from benthic environments, with low similarity in most cases (Malviya et al. 2016).

3. Bacterial Associations with Diatoms

3.1 Bacteria

The bacteria are a large group of unicellular prokaryotic microorganisms which inhabit nearly every habitat on the Earth. Prokaryotes are single-cell organisms, their cells lack a nucleus and other membrane-bound organelles. They play a pivotal role in nutrient cycle and fixation of nitrogen (Stock et al. 2014). Bacteria have management implications as well.

Here is an example of how bacteria can interact with algae. Several studies with pure cultures of fecal coliforms (*Escherichia coli* was present also) and some other coliform bacteria (such as *Klebsiella* or *Enterobacter*) showed results that these bacteria might grow on filtrates from *Chlorella* cultures at surrounding stream temperatures, which is 13 °C, and might assimilate those organic compounds which *Chlorella* release, so these studies propose that the intestinal microflora can be highly disseminated in fresh water (Cole 1982). Not long ago, high densities of coliforms were found for unpolluted alpine streams in Wyoming, such a large presence of coliforms usually indicates input of sewage or animal waste and these sudden appearances of the coliforms correlate with *Chlorella* blooms (Cole 1982).

3.2 Archaeobacteria

Archaea are morphologically similar to bacteria in shape and size, and being prokaryotes, the cell nuclei are not present (Wommack, Colwell 2000). In some marine environments, archaeobacteria make up a significant proportion of the bacterioplankton community, Previously, it was believed that archaea are restricted to extreme environments characterized by high salinity, high temperature, or anaerobiosis (Wommack, Colwell 2000). In Antarctic coastal waters, archaea make up to 34% of bacterioplankton abundance, in temperate ocean midwaters it is 40 to 60% of total bacterial abundance. Consequently, it is probable that archaeal viruses constitute a significant proportion of the virioplankton in these environments. (Wommack, Colwell 2000).

3.3 Carbon fixation by Cyanobacteria

Cyanobacteria are a group of bacteria that use light energy for their photosynthesis (especially by chlorophyll-a) for the purpose of generating their carbon cellular material and producing oxygen, numerous species are able to grow heterotrophically as well if they use organic compounds as a source of carbon (Percival, Williams 2014). Cyanobacteria are the only recognized prokaryotes which exhibit photosynthesis with oxygen generation. The protein complexes within the thylakoid membranes of cyanobacteria play two important roles, they facilitate the electron transport chains important for photosynthesis, and those chains which are involved in respiration as well. In the end, the photosynthesis of cyanobacteria is very similar to the one seen in plants (Percival, Williams 2014).

If phosphorus and nitrogen-rich conditions are available, cyanobacteria absorb and intracellularly store these elements. This ability has evolved during their several billion years in existence, and allows them to survive under extreme environmental conditions. Some of the cyanobacteria create their own proteinaceous gas vacuoles which make them able to float in aquatic environments (Percival, Williams 2014). Some of them (for example *Nostoc*), can also fix their own nitrogen from the atmosphere, which gives them an advantage in nitrogen limited systems, this is a major reason to make symbiotic associations with cyanobacteria and marine *Epithemia* are believed to be closely related to *Crocospaera* (Schvarcz et al. 2022).

It is important to know that cyanobacteria are able to grow abundantly when the conditions are suitable, generating so-called “blooms” in eutrophic freshwater reservoirs and lakes. Cyanobacteria produce a number of potentially toxic secondary metabolites which might lead to harmful impacts to local ecology and the health of animals and humans as well (Percival, Williams 2014).

Cyanobacteria play an important role in ecology, when it comes to the supply of global oxygen, they are major components, same for sequestration of carbon dioxide (CO₂) and nitrogen fixation (Percival, Williams 2014). Symbiosis between *Rhopalodia/Epithemia* and a coccoid cyanobacterium has been long known, and recently, a new symbiosis between diatoms and cyanobacteria was brought to light,

with cyanobacteria living inside the cells of *Climacodium frauenfeldianum* (Janson 2002).

3.4 Mutualistic interactions between diatoms and heterotrophic bacteria

Diatoms provide organic matter necessary for bacterial proliferation. Interestingly, bacteria also have the potential to control diatom growth. The physicochemical properties of EPS, which stands for extracellular polymeric substances, are factors crucial for the formation of biofilms (Bruckner et al. 2011), and provide the matrix for organisms to live in, including diatoms.

Interactions between diatoms and bacteria can be considered as a key factor in biofilm formation, in addition to other biotic and abiotic factors that influence diatom EPS (extracellular polymeric substances) secretion, for example the stage of their cell cycle, surface material or accessible nutrients (Bruckner et al. 2011).

Bacteria are highly abundant in seawater and play crucial roles in assimilating and decomposing organic carbon fixed by diatoms. Phototrophic eukaryotes like diatoms and heterotrophic bacteria together form the "microbial loop", which significantly impacts the cycling of carbon and other essential nutrients in marine ecosystems (Andrew et al. 2022). The microbial loop is a process when aquatic bacterial populations return primary production lost to higher order consumers back into biomass. This is done by using the dissolved products of primary production that leak from cells through death and lysis (for example), with the result of making a bigger proportion of primary production available to the marine food web (Wommack, Colwell 2000). Figure 3 describes how the microbial loop works.

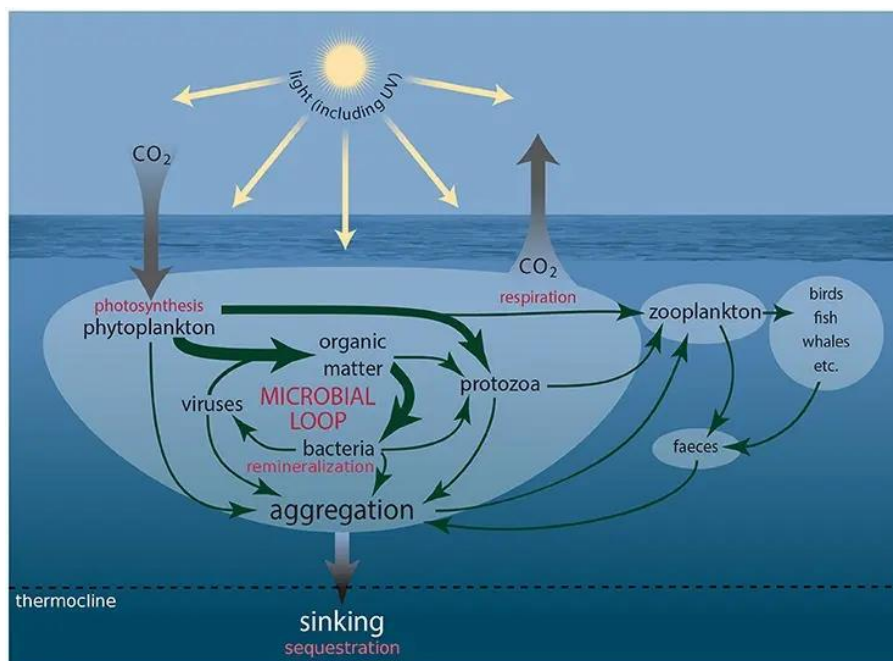


Figure 3. Carbon export toward the abyss, the microbial loop (Source: Stacy L. Deppeler and Andrew T. Davidson 2017).

Biofilms are microorganisms that stick to each other and work together on a surface. Under ideal conditions, a single diatom cell is enough to initiate a successful biofilm (Khandeparker 2013). Almost all or maybe even all bacteria can form a biofilm, the importance of the interactions between microbial organisms was highlighted by study, which also proved the role of the biofilm matrix as a place of activity of the extracellular enzymes and dissolved organic matter adsorption (Battin et al. 2016).

It is assumed interactions between algae and bacterias associated with diatoms such as *Proteobacteria* (which include *Alphaproteobacteria*, *Betaproteobacteria*, *Gammaproteobacteria*, *Deltaproteobacteria* and *Epsilonproteobacteria*) and *Bacteroidetes* (which include *Bacteroidetes*, *Flavobacteria* and *Sphingobacteria*) are based on microbial degradation and transformation of organic matter produced by the algae (Bruckner et al. 2011). Several experiments revealed various effects of extracellular polymeric substances (EPS), significantly present in the biofilm matrix, such as bacterial growth and DNA synthesis might be stimulated, also diatom growth can be suppressed or enhanced (Bruckner et al. 2011). The sticking strength of diatoms might be reduced, enhanced or even fluctuate depending on the cultivation parameters and the presence of microbial communities as well, it is probable interactions between diatoms and bacteria are key factors for the formation of cellular aggregates. For

example *Didymosphenia geminata* make a lot of EPS material and create a lot of habitat for other organisms, such as bacteria, to grow (Bruckner et al. 2011).

However, associated bacterial groups are difficult to generalize. For example, Schäfer and colleagues (2002), who studied the ‘satellite’ bacterial populations of various diatoms in batch cultures, did not find any gamma-Proteobacteria present, and concluded that this group of bacteria play a less important role in diatom-bacteria interactions (Grossart et al. 2005). The axenic diatoms were inoculated with natural assemblages of bacteria and observed by Grossart et al. to examine dynamics of bacteria in batch cultures of two axenic marine diatoms (*Thalassiosira rotula* and *Skeletonema costatum*) (Grossart et al. 2005).

Nevertheless, it is obvious from the results that gamma-Proteobacteria are an integrative part of bacterial communities in diatom cultures and might play an important, but not so specific, role in diatom-bacteria interactions and nutrient cycling compared to alpha-Proteobacteria (Grossart et al. 2005). Marine diatom growth was highly affected by bacteria and the opposite, species composition and the physiological state of the algae were directly linked to abundance and species composition of bacteria (Grossart et al. 2005).

There was a survey about incubating and illuminating diatom species, according to the results, algal growth showed pronounced differences in axenic treatments and when bacteria were present (Grossart et al. 2005). Bacterial abundance and structure of the community distinctly depended on species, growth and physiological status of even closely related algae, free-living and phytoplankton-associated bacteria were extremely different from each other and were dominated by different phylogenetic groups (Grossart et al. 2005).

The bacteria which were diatom-associated, mainly belonged to the *Flavobacteria-Sphingobacteria* group of the *Bacteroidetes* phylum considering free living bacteria, which were rather similar in both cultures, consisted mainly of members of the *Roseobacter* group of a *Proteobacteria* (Grossart et al. 2005). Significant differences in environmental conditions over time and selection of bacteria which are highly adapted to the changing conditions is indicated by presence and disappearance of specific bacteria during algal growth and it seems close interactions between marine

bacteria and diatoms apparently appear to be important for the decomposition of organic matter and nutrient cycling in the sea (Grossart et al. 2005).

Bacterial colonization of phytoplankton such as marine diatoms and *Phaeocystis* colonies is often observed to depend on the stage of the bloom. In early stages of bloom bacteria mostly are practically absent, considering late bloom stages are similar with increased colonization by attached bacteria (Grossart et al. 2005). Study shows that two diatom species which were incubated and illuminated, they are closely related (both belonging to *Coscinodiscophyceae*) and harbor different attached bacterial communities, which develop in a different way as a function of the physiological state of the algae (Grossart et al. 2005).

Although a few studies have already demonstrated that bacterial community composition varies with the algal species and its physiological state, Grossart's study demonstrates for the first time that free-living and phytoplankton-associated bacteria are markedly different from each other and are dominated by different phylogenetic groups (Grossart et al. 2005). As opposed to most other studies, Grossart used axenic algal cultures and the same natural bacterial inoculum for all experiments, which enable a detailed examination of the development of the bacterial communities under special conditions which are solely related to growth of the given diatom (Grossart et al. 2005).

Results of this study of incubation and illumination show that bacteria affected the growth of the two diatoms and that the effects were specific for each species and related to the physiological state (Grossart et al. 2005). The inclusion of natural marine bacteria to exponentially growing diatoms resulted in a moderate growth stimulation of *T. rotula* but a moderate growth inhibition of *S. costatum* both during exponential growth. Rapid degradation of algal cells and a powerful increase in bacterial numbers resulted in case of addition of bacteria to *T. rotula* in the stationary phase (Grossart et al. 2005).

3.5 Harmful interactions with bacteria

Interactions between bacteria and phytoplankton in aquatic systems range from symbiosis to parasitism and are very variable in space and time (Grossart et al. 2005).

It was found out that cyanobacteria resist nutrient stress quite well and they can be found in mud flats also (Watermann et al. 1999). Additionally, bacteria directly compete with phytoplankton for resources, for example iron (Fe) (Andrew et al. 2022).

In one experiment, three marine diatoms such as *Cylindrotheca fusiformis*, *Nitzschia laevis* and *Thalassiosira weissflogii*, were grown in axenic culture and incubated under controlled lab conditions with single bacterial isolates, mixed bacterial populations and seawater off Scripps Pier. Both bacteria and algae growth was considerably higher when incubated together in f/2 medium or artificial seawater, these conditions were rich in inorganic nutrients, vitamins and trace metals. On the other hand, growth of diatoms was reduced in vitamin and trace metal free medium or even negative when they were incubated together with bacterial isolates or seawater bacteria (Grossart et al. 2005).

Study shows that interactions between specific bacteria and a marine diatom (*Cylindrotheca fusiformis*, *Thalassiosira weissflogii*, or *Nitzschia laevis*) is heavily dependent on the changing environmental conditions, those media which were rich in inorganic but with no organic nutrients resulted in higher growth of both bacteria and algae compared to single bacterial or algal cultures and those media which were rich in organic nutrients, the bacterial abundance here was increased by 2 orders of magnitude compared to media with no organic nutrients (Grossart et al. 2005).

In media which were rich in organic nutrients, algal growth was also increased if the bacteria were present but bacterial and algal quantity never reached a stable state as observed for media with no organic nutrients, when phytoplankton was stressed by incubation in media with no vitamins and trace metals, the result was lower algal growth or even reduction in living cells when bacteria were present as well (Grossart et al. 2005). Figure 4 shows the presence of bacteria with species *S. costatum* and *T. rotula*.

Without bacteria

With bacteria

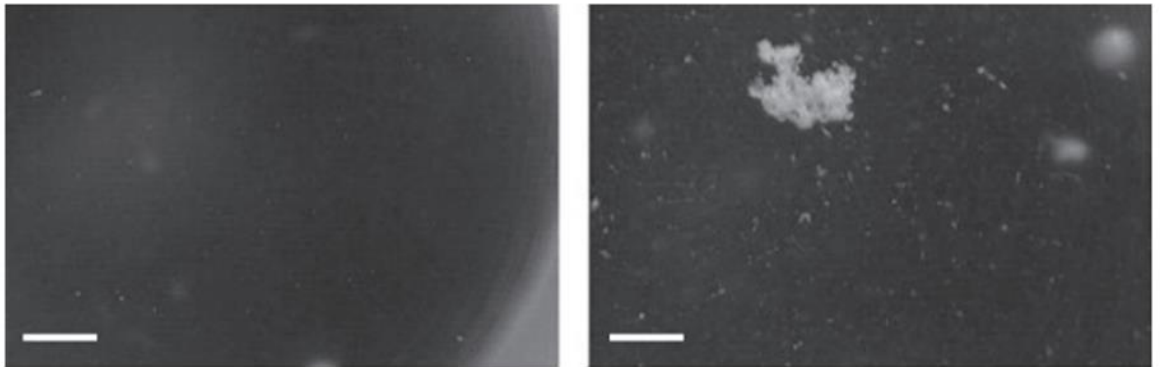


Figure 4. Grossart, G. Czub and M. Simon in their study about Algae-bacteria interactions and their effects on aggregation and organic matter flux in the sea show presence of bacteria with species *S. costatum* and *T. rotula* (Source: Grossart, Czub, Simon 2006).

4. Viral associations with diatoms

4.1 Physiology and morphology of viruses

Viruses are submicroscopic pathogens that replicate only inside living cells of another organism. They are probably present in every habitat on the Earth (Kranzler et al. 2019), and are able to infect every known life form including animals, plants, and microorganisms (Kranzler et al. 2019).

Recent studies show that marine viruses play crucial roles in shaping aquatic communities as well as determining ecosystem dynamics. In marine waters, viral abundance ranges from 10^7 to 10^{10} g of dry weight in marine sediments. That being the case, abundances in surface and subsurface sediments exceed those in the water column by 10 – 1000 times, on a volumetric basis. Several studies implemented in different pelagic systems throughout the world provided evidence that changes in physicochemical characteristics of the water masses have significant influence on viral abundance and distribution (Danovaro 2011).

Important covariates influencing viral dynamics in marine ecosystems are physical and chemical characteristics of surface waters, for example salinity, temperature, nutrient availability etc., because they have crucial effects on the abundance, distribution and metabolism of planktonic host cells. Several studies which were carried out at a regional scale show that virioplankton abundance decreases moving from productive coastal to oligotrophic off-shore surface waters. Also, the distribution of benthic viruses appears dependent upon pelagic primary production and vertical particle flux, which indicates a possible causal relationship between viriobenthos and trophic state (Danovaro 2011).

Furthermore, different studies provide evidence that viral abundance, and the importance of viruses in prokaryotic mortality, increases with the productivity of waterbodies, with the highest percentage of infected cells in highly eutrophic ecosystems. For example, the ‘Piggyback-the-Winner’ hypothesis says that lysogenic viruses are more abundant than lytic viruses when host density is high. However, the ‘Kill-the-Winner’ hypothesis, says that specialists of the competition are being

controlled by predation by phage, which allow slower growing "defensive specialists" access to resources (Danovaro 2011). Positive correlation between viral production and prokaryotic respiration, and between viral production and prokaryotic growth rate is observed, in various studies, and this supports the theory. Abundance of marine viruses is closely linked with the abundance of their hosts, so that any change in the abundance, metabolic state and doubling time of the prokaryotic host populations will affect viral abundance, this is evident from the analyses of available literature information (Danovaro 2011). Figure 5 describes the two different infect strategies.

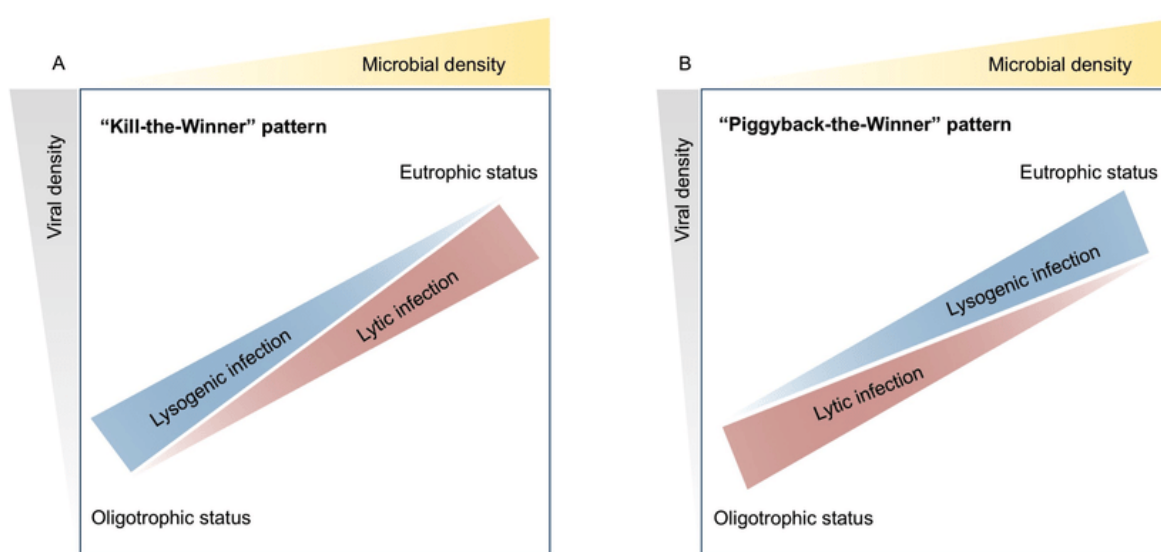


Figure 5. Two different strategies for who to infect (Source: Chen et al. 2021).

4.2 Harmful Interactions with viruses

Viruses which infect bacteria are called 'bacteriophages', and they have significant impacts on the diversity and activity of bacteria colonies in every biome globally (Peter et al. 2022). As a main source of marine microorganisms mortality represents viral infections, which are frequently followed by death of the host cells (Danovaro 2011). Even though viruses can cause spectacular epidemics within a wide range of organisms, the majority of marine viruses infect prokaryotes and microalgae, most common organisms in the ocean (Danovaro 2011).

It is distinctly possible that virioplankton is not only most abundant, but also the most diverse component of plankton, although various viruses infecting a wide range of

phyto- and bacterioplankton species have been isolated, still, these represent only a small portion of viroplankton diversity, as with aquatic bacteria (Wommack, Colwell 2000).

The discovery, that viruses in natural waters are highly abundant, initiated renewed interest on the impact of lysis and viral infection on aquatic microorganisms, about 10 years ago which gave importance to a previously underappreciated plankton class which is the viroplankton as well (Wommack, Colwell 2000). In the following years, several studies on a wide variety of aquatic environments have shown that viruses are generally 10 times more abundant than the following most abundant class, the bacterioplankton (Wommack, Colwell 2000).

Observed from long-term, it can be concluded that viroplankton abundance changes seasonally in accordance with cycles of primary and secondary productivity, over the course of seasonal algal bloom events, some of the most dramatic changes in viroplankton abundance have been noted, with peaks in viroplankton numbers following those of phytoplankton and bacterioplankton abundance, daily changes in viroplankton abundance have been observed as well (Wommack, Colwell 2000).

Nevertheless, consistent daily cycles of abundance have not been shown, it is interesting that significant changes in viral abundance have been noted for time intervals of as small as 20 minutes, which suggest that viral production may occur through a series of synchronous lysis events (Wommack, Colwell 2000).

Viruses play a very important role in the microbial food webs of both marine and freshwater ecosystems, trophic status seems to be a more important factor of batch size, rates of virus production and extensiveness of lysogeny/pseudolysogeny than salinity (Danovaro et al. 2011). In both systems, viruses are relevant controlling factors of microbial community structure, marine and freshwater viruses seem to be taxonomically clear (some of the viruses are shared across both systems as well) and host range plays a main role (Danovaro et al. 2011).

Nevertheless, little is known about the effects of modifications of salinity, osmotic stress and pH on marine viruses, the surveys of data from literature show that systems characterized by lower salinity represent higher viral abundance in general (Danovaro

et al. 2011). Even though the data set (of the flux of dimethylsulfide) is highly influenced by the access of data from just a few estuarine systems (like the Chesapeake Bay) and such results might mirror the more specific features of the sampling areas more so than a general trend which is valid to the benthic compartment as well, considering the fact that the data set which is available is still relatively limited (Danovaro et al. 2011).

Furthermore, it is probable that the positive effect on viral abundance is related to the different availability of nutrients and trophic state in estuarine systems which support metabolism and larger host abundance more than to a straight effect on the assemblages of viruses (Danovaro et al. 2011). The reaction of benthic viruses to changes in salinity is vague, so far the obvious increase of viral production with decreasing salinity is statistically poor, rates of viral disintegration are too reduced to show a complex view of any potential effects of changing salinity on dynamics of viruses (Danovaro et al. 2011).

5. Fungal interactions with diatoms

Fungi are eukaryotic organisms including microorganisms such as molds and yeasts. Their cell walls contain chitin, which is characteristic for them; they are also not capable of photosynthesis (Raghukumar 2017). Fungi play a key role in sustaining life on earth, they are the second most diverse eukaryotic organisms on earth behind insects, and together with bacteria, they are the main decomposers of dead organic material (Raghukumar 2017).

Terrestrial species mostly have spores which are dispersed by wind, freshwater and marine species of fungi produce spores which adapt to the habitat so they can be dispersed in aquatic conditions (Raghukumar 2017). There is a bit better knowledge about fungi in freshwater and terrestrial environments compared to fungi in marine environments, but both topics are still relatively unexplored. Thus, it is becoming more and more obvious that fungi inhabit nearly all marine habitats and play a few crucial ecological roles (Raghukumar 2017).

Fungi have special adaptation to living on or inside another thing which is alive, such as algae, sponges, corals or other fungi, primary producers such as dinoflagellates and diatoms are often infected by marine fungi, which can play an imponderable role in global carbon cycles, several diseases have been associated with fungal infection, for example in crustaceans, macroalgae or even marine mammals (Gladfelter, James, Amend, 2019). Fungi are also believed to be responsible for coral death in reefs, but they undergo a great deal of stress nowadays, for sure, fungi are related to healthy reefs, they inhabit the calcium skeleton and probably decompose senescent rubble (Gladfelter, James, Amend, 2019). Finally, fungal activity has also been observed in the sediments of the deep sea; they might play the same role in cycling of nutrients as in terrestrial environments, aquatic and marine fungi must tolerate many factors when compared to the terrestrial species, such as high salinity, limited access to substrates for growth, ultraviolet light and sometimes notable hydrostatic pressure and moreover, dispersing is much more complicated while being in water (Gladfelter, James, Amend, 2019).

Fungi and bacteria are able to coexist, fungi are eukaryotic microorganisms, their nutrition is osmoheterotrophic, which is heterotrophy (acquisition of external energy in the form of food) by osmosis, reproduction and dispersion is carried out by producing spores (Raghukumar 2017). Bacteria and fungi together play an important role in global C and N cycling and they are responsible for almost 90 % of all organic matter decomposition. (McGuire, Treseder 2010). Decomposing of organic matter is a series of special processes, when the organic matter is changing into other components either physically or chemically and can be even both, the size of the material changes so it may be positive when it comes to water transport (Findlay 2021). Freshwater ‘priming’ is a process of organic matter degradation, defined by Kuzyakov et al. (2000) as “strong short-term changes in the turnover of soil organic matter caused by comparatively moderate treatments of soil” (Bianchi et al. 2015). Primary producers, such as diatoms, can stimulate decomposition rates from bacteria and fungi due to producing high quality leachates (Bianchi et al. 2015). Diatoms can have a strong effect on the speed at which decomposition takes place. Figure 6 describes the ecological role and habitats of marine fungi.

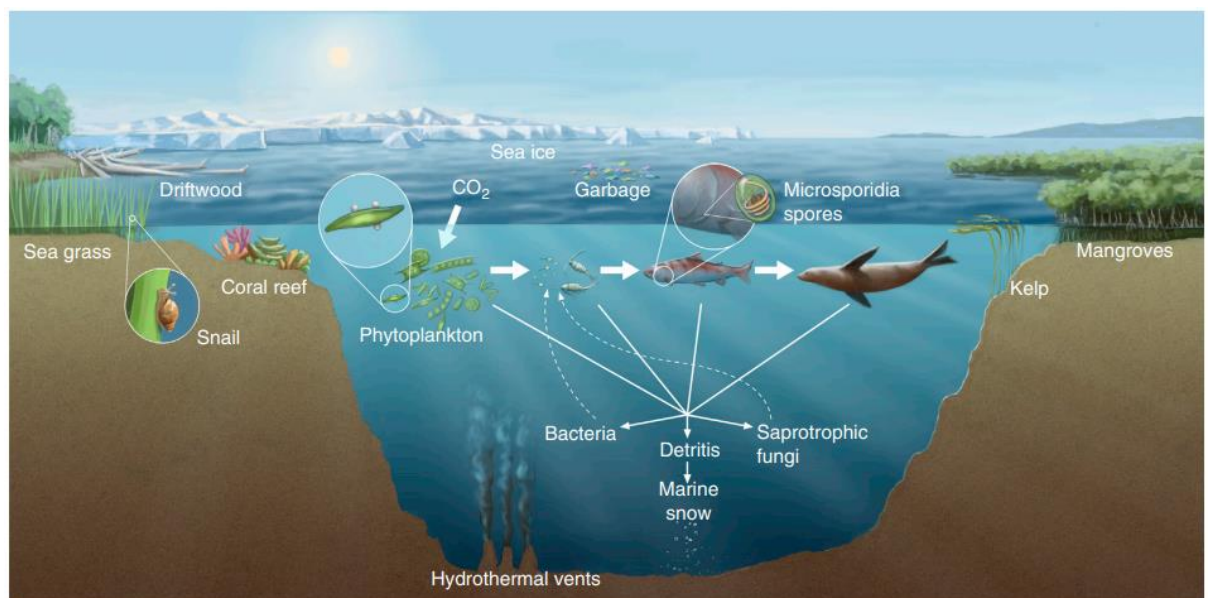


Figure 6. This picture shows the habitats of marine fungi and their ecological role (Source: Gladfelter, James, Amend 2019).

5.1 Pathogenic relationships

Parasites of large phytoplankton cells in freshwater bodies are members of phylum *Chytridiomycota*, they are believed to be responsible for the changes in phytoplankton community composition and massive diatom mortality (Gutiérrez, Jara, Pantoja 2016). Chytrids are adapted to planktonic lifestyle and they infect a large number of hosts such as algae, but their primary goal is freshwater phytoplankton (Sime-Ngando 2012). The implications of chytrids in ecology are various, they might kill the host, release substrates for microbial processes and produce zoospores and fragments of inedible host for the food chain of the grazers (Sime-Ngando 2012). Also, epidemics of chytrids is an essential driving factor in seasonal successions of the phytoplankton (Sime-Ngando 2012).

According to Sparrow (1969) a phycomycetous fungus, *Ectrogella* species parasite on diatoms and *Ectrogella pegorans* might cause infection of the marine pennate diatom species of *Licmophora* to epidemic levels, apart from *Licmophora* it causes infection of species *Vorticella*, *Synedra* and *Striatella* as well (Raghukumar 2006). When the diatom cells become infected, they happen to be hypertrophied (size increased) and chlorotic (abnormal condition, green parts might turn yellow), experiments in the lab with *Licmophora hyalina* from the North Sea proved that zoospores which adhere to the surface of the host cells initiate multiple infections (Raghukumar 2006). Studies on such host-parasite interactions revealed that the pathogen enters inside the host cell by piercing the narrow areolae of the diatom wall which is silicified, the chromoplasts of the host start to lose their usual color, disintegrate and finally break down when the fungal sporangium matures inside the host, the vacuolated cytoplasm of the host appears and a few fungal sporangia evolve inside the host cell and the valves of the diatom cells are pushed when the fungal zoosporangium matures (Raghukumar 2006).

The top-down control of diatoms includes herbivory and parasitism (Franzé et al. 2018). Herbivory of microzooplankton serves as a main factor which controls the primary production in the ocean, dinoflagellates and ciliates have the ability to feed on diatoms (Franzé et al. 2018). Also, grazing of the microzooplankton might change the phytoplankton communities structure with effects of ecosystem level (Franzé et al. 2018).

Diatoms are parasitized by zoosporic fungi such as chytridiomycota in freshwater and some marine ecosystems. It was also proved that oomycetes protist parasites serve as a considerable source of top-down control of toxic diatom bloom species. Nevertheless, there is still a lot unknown about the abundance and diversity of fungi and their influence on the food webs in most of the marine ecosystems. (Chambouvet et al. 2019). Diatoms are also prone to chytrid fungal parasitism, abiotic factors are the ones to determine if the fungal infection becomes epidemic or not, there is not enough knowledge about how biotic factors, especially interactions with zooplankton, affect the process of fungal infection (Kagami et al. 2004).

Various experiments show that *Daphnia* considerably decreases fungal parasitism by foraging on the fungal zoospores, also, *Daphnia* had a little positive influence on fungal infection, possibly because it increases the encounter rate between fungi and host phytoplankton cells (Kagami et al. 2004). Results of the studies indicate that *Daphnia* might affect the seasonal succession of chytrids and their host phytoplankton and furthermore, zoospore-producing fungi might probably play an important ecological role in aquatic food webs for *Daphnia* as a food source (Kagami et al. 2004).

The Mycoloop is a relatively newly conceptualized pathway playing an important role in shaping aquatic ecosystems. For example, chytrids infect large inedible phytoplankton species, zoospores of plastic chytrids transfer nutrients within host cells to zooplankton (Kagami, Miki, Takimoto 2014). Mycoflux in aquatic environments presents a part of capturing the carbon, fungi break down the organic matter (Grossart et al. 2019). Mycoplankton are lower trophic level organisms which direct the energy and nutrient flow, such a process is called benthic shunt (Grossart et al. 2019). Figure 7 describes the processes such as mycoloop, mycoflux and benthic shunt.

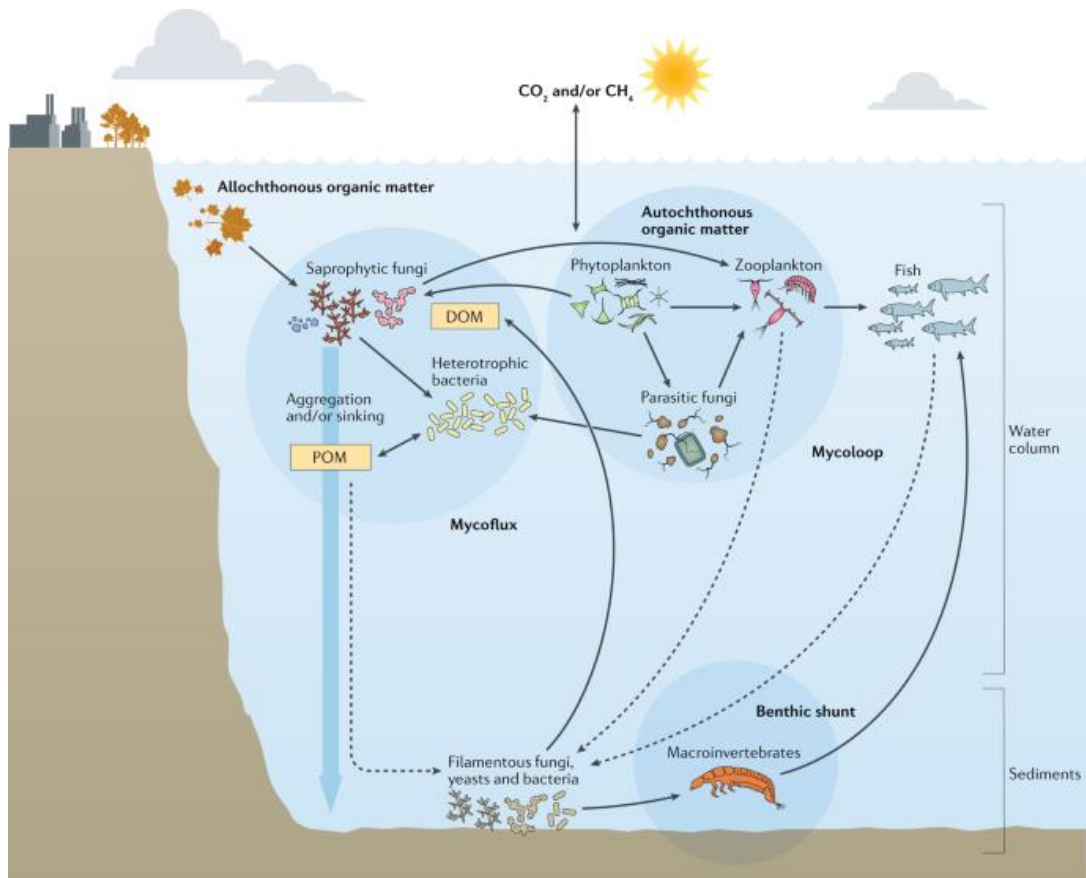


Figure 7. Ecological role of aquatic fungi, three major processes are highlighted - mycocoop, mycoflux and benthic shunt (Source: Grossart et al. 2019).

6. Discussion

As discussed above, primary production, especially in the world's oceans, is a complex dance of interactions taking place between the diatoms, bacteria, fungi, and viruses. However, as if this were not enough, taking place at the same time as all of these interactions are indirect interactions with humans, which are similarly important and influential. As human populations continue to expand and industrial activities escalate, the impact of our actions on marine ecosystems become increasingly evident.

Each year, we are currently burning the equivalent of around 1 million years of buried carbon derived from diatoms and other plankton, which shows the serious overprint of human activities on Earth's biogeochemical cycles (Benoit et al. 2017). It is estimated that since the beginning of the 19th century, the oceans have absorbed 50 % of fossil fuel emissions and 30 % of anthropogenic emissions completely (those from land-use modifications are included also) and by that the build-up of CO₂ in the atmosphere is reduced, air is in balance with the CO₂ at the surface of the ocean and moves freely over the interface (Danovaro et al. 2011). When it is chemically transformed into dissolved and particulate forms of carbon, it is transported to the depth of the ocean by exporting of the shelf, by mixing or using an active biological system followed by the sinking of particulate carbon from the plankton that has a key role in the cycle of carbon (Danovaro et al. 2011).

On the other hand, global climate change affects the oceans, because it influences temperature, ocean circulation, sea level and the frequency and intensity of storms, if the storms are stronger, it affects wave regimes and vertical mixing (Danovaro et al. 2011). This might influence marine ecosystems and habitats and it will also result in more variable precipitation, more frequent intense rainfall which leads to comprehensive floods. (Danovaro et al. 2011).

Another serious topic of concern is acidification, the decrease in the pH of seawater has various effects on the productivity, functioning, survival and growth of marine organisms (Danovaro et al. 2011). A great deal of attention has been paid to the hypothetical consequences for calcifying organisms, especially coral reefs, *coccoliths*, *foraminifera* and *bivalves* (Danovaro et al. 2011). Acidification of the ocean decreases

concentrations of carbonate and therefore lowers the saturation state of CaCO₃ in the seawater and many of these organisms calcify less, their growth is reduced or they even disappear completely even at small changes in pH or CaCO₃ saturation states (Danovaro et al. 2011). There are several other consequences of acidification of marine waters for noncalcifying organisms like diatoms, nitrifiers and heterotrophic bacteria, including also the sound penetration in seawater which affect the bioacoustics of marine mammals (Danovaro et al. 2011). In general, at this time there is a higher acknowledgement that ocean acidification has cardinal effects on the survival and performance of marine communities, even though marine biota might be more resistant to gradual changes than quick perturbation within experimentation. (Danovaro et al. 2011).

The interconnection between present climate change and consequences on marine ecosystems and their function is considerably interesting, because in the old days, prokaryotes and viruses have been considered as a 'black box' in big-scale global oceanic models (Danovaro et al. 2011). Nowadays, it is known that viruses play a key role in the functioning of both benthic and pelagic ecosystems, which influence microbial food webs, control prokaryotic diversity and have an impact on biogeochemical cycles. It is obvious a better understanding of their reaction to actual climate change would upgrade our ability to predict and adapt to the consequences of changes such as these (Danovaro et al. 2011).

Usually, the assessment of the effects of climate change on natural ecosystems is performed by the paleoecological and stratigraphic records analysis or by the long term data sets analysis that allow the identification of the relationships between spreading or decline of specific biological components and climatic conditions. (Danovaro et al. 2011). Already before the genome sequencing method, biochemical and ultrastructural data had provided persuasive evidence that diatoms were derived from a secondary endosymbiotic event which involved a red alga that had occurred sometime between 1200 and 700 Ma and that was common to all stramenopiles, the phylum in which diatoms sit, same as the *chromalveolata* supergroup of eukaryotes that includes *dinoflagellates* and *coccolithophores* (Benoiston et al. 2017).

The diatom genome sequences analyzed until the present time do provide support for a red algal endosymbiont, but the abundance of genes apparently derived from a green algal source has led to the controversial hypothesis that a green algal endosymbiont preceded the red alga and that many of its genes were retained before the arrival of the red alga, while on the contrary the red algal genes that were acquired later were not (Benoiston et al. 2017). In a case such as this one, diatoms (and other photosynthetic *chromalveolates*) bear red algal derived chloroplasts driven to a significant extent by green algal genes encoded in the nucleus, which could have possibly provided a selective advantage in ocean environments and this explains why such organisms have come to dominate in the ocean although photosynthetic organisms harboring green algal-derived plastids dominate terrestrial habitats (Benoiston et al. 2017).

Another characteristic is the presence of several hundreds of bacterial genes dispersed throughout diatom genomes, which represents around 5% of total gene content, numerous genes such as these appear to have ancient origins because they participate among several diatoms, and encode functions essential for diatom biology, so it seems diatom-specific transposable elements have been instrumental in generating the rich diversity of species found nowadays (Benoiston et al. 2017).

Unique combinations of genes that collectively encode non-canonical pathways of nutrient assimilation and metabolite management have been put together due to the chimeric nature of diatom genomes, together with a urea cycle that is integral to a nitrogen metabolism, and new configuration coupling photosynthesis and respiration between diatom chloroplasts and mitochondria (Benoiston et al. 2017). These various discoveries have deep and unexpected implications for human understanding of the diatom's role in biogeochemical cycles, calling attention to the utility of genome sequences for revealing an organism's metabolic potential (Benoiston et al. 2017).

7. Conclusion

Diatoms are one of the most abundant and ecologically essential parts of phytoplankton and biofilms, this unicellular algae play a crucial role in aquatic ecosystems. They are primary producers, significantly contributing to the production of oxygen and sequestration of carbon globally. They are also an important provider of food for various marine organisms. Interactions between diatoms, bacteria and viruses also are necessary for nutrients cycling in the oceans and for diatom population dynamics. The result of this bachelor thesis is a better understanding of the interconnectivity and complexity of such relationships.

One of the pivotal findings in this thesis is the complicated diatom-viruses relationship. Viruses affect the diatom populations and diversity by infecting and controlling them, such viral controlling might have cascade effects on biogeochemical cycles and marine food webs. Gaining an understanding of the dynamics of these interactions with viruses is essential for forecasting and managing marine ecosystem changes in the context of environmental pressures for example climate changes or acidification of the oceans.

Additionally, this thesis also clarifies the interactions between diatoms and bacteria, and the relevance of microbial communities in aquatic environments. Bacteria play a crucial role when it comes to nutrient cycling, symbiosis with diatoms and organic matter degradation, the metabolites and signaling molecules exchange affect the productivity, growth and resistance of diatom populations. Fungi parasites produce zoospores and infect the algae, which cause hypertrophy and chloroticity of the algae cells. There is a need to study interactions between diatoms and archaea, because this relationship is still not explored enough.

Understanding these interactions offers important information about the way marine ecosystems function and the possible consequences of environmental disturbances. The effects of interactions between diatoms, bacteria and viruses reaches further than ecological research and include applied sciences and environmental protection activities. By clarifying the mechanisms that underlie these interactions, the scientists

might potentially create new and innovative pathways for biotechnological applications for example discoveries in pharmaceuticals.

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