

Viruses and prokaryotes in the deep-sea

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In the last decades the development of new technological and methodological tools has allowed demonstrating that microbes dominates both in terms of abundance and biomass the world oceans. Microbes are of size ranging from 0.02 to a few micrometres and include a wide diversity of viruses, prokaryotes (Bacteria and Archaea), and eukaryotes (either phototrophic and heterotrophic). These tiny particles, either suspended in the water column or attached to the sediments play crucially important functions and control the global biogeochemical cycles. More recently it has been also demonstrated that viruses are by far more important than previously thought. In particular we now know that viruses are the most abundant biological entities of the biosphere, with current estimates of the global viral abundance in the order of 10^{30} - 10^{31} . They outnumber prokaryotes by at least one order of magnitude. This huge numerical abundance suggests that viruses can account also for the vast majority of the genetic diversity of the Earth (figure 1). Being not able to self-replicate, viruses invade other organisms and use their cell's machinery to propagate. They can infect all the known life forms of the oceans, from the largest mammals to the smallest marine microbes. Indeed, also tiny viruses inside larger viruses have been recently discovered.

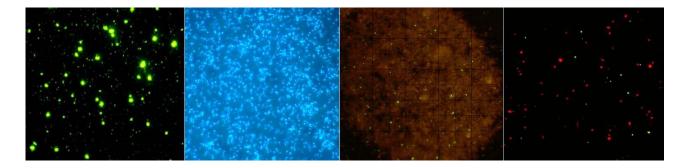


Figure 1. Some examples of Viruses and Prokaryotes (i.e., Bacteria and Archaea) from seawater and sediments as revealed by microscopic analysis using different epifluorescence techniques.

From left to right: green fluorescence produced by staining with SYBR Green I, blue fluorescence obtained by staining with DAPI (both on seawater samples), and examples from sediments where bacteria appear as green dots attached to a yellow-orange organic detritus particles by using SYBR Green I and Bacteria appearing as red fluorescent dots and Archaea appearing as green dots in sediment samples, based on a CARD-fish analysis).

Viruses can be distinguished from the prokaryotes from their dimensions as they are in the dimensional range of 0.02-0.2 μ m, while prokaryotes (i.e., Bacteria and Archaea) display a cell size ranging from 0.2 to 2 μ m.



In oceans the prevalent hosts of viruses are Bacteria and Archaea (i.e., the prokaryotes), due to their huge abundance, but also microalgae and all multi-cellular organisms can be subjected to viral infections (figure 2). Viral infections have a profound impact also on microbial and possibly also other biological components, and in some cases are able to control population sizes, biodiversity and horizontal transfer of genetic materials. Since autotrophic and heterotrophic prokaryotes and protists play pivotal roles in biogeochemical cycles and global ocean functioning, viral infections, by controlling the abundance and activity of these groups of organisms, have important ecological consequences. For instance, by killing the hosts after the completion of their replication cycle, viruses can transform living biomass into organic detritus (mostly dissolved organic matter), which can then be used again by other microbes stimulating their growth.

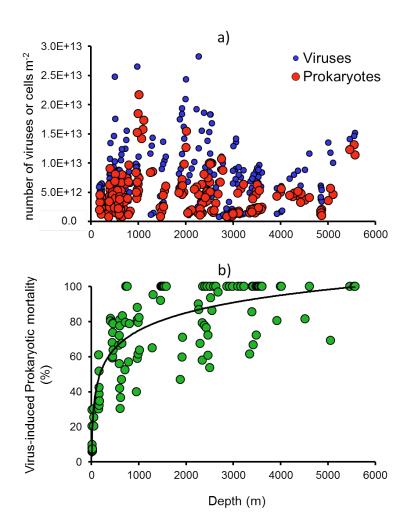


Figure 2. Bathymetric patterns of viruses and prokaryotes (abundance per m² of sediment) (a) and of the virusinduced prokaryotic mortality (b) in the deep ocean interior worldwide. Microbial abundance inhabiting surface marine sediments do not show clear decreasing trends, with constantly high numbers of viruses and prokaryotes at all depths (a), and virus-induced prokaryotic mortality, calculated as the percent ratio between the number of cells killed by viruses, and the total number of prokaryotes produced, per hour, increases with water depth (b).



This process, called "viral shunt", fuels prokaryotic heterotrophic production by releasing dissolved organic compounds and/or support autotrophic production by enhancing nutrient regeneration pathways, but it can also decrease the efficiency of the carbon transfer to higher trophic levels.

The ocean interior (the "Deep Sea") includes the waters and sediments beneath 200 m depth, representing more than 65% of the Earth's surface. The deep oceans include more than 95% of the global biosphere, thus representing the world's largest biome. Despite their huge dimensions and ecological importance, the knowledge of the deep-sea microbial diversity is still in its infancy. With high concern, the general knowledge of deep-sea benthic ecosystems is very limited.

It is now evident that these ecosystems play a key role in biomass production and biogeochemical cycles on a global scale, and it is now equally evident that these processes are largely mediated by benthic prokaryotes. These prokaryotes account for most of the microbial biomass of the oceans and play a key role in biogeochemical cycles, organic matter remineralisation and the transfer of energy to higher trophic levels. Deep-sea ecosystems are dark, extreme environments and lack photosynthetic primary production, thus depending on carbon export from the surface oceans. The availability of food and resources, and consequently the biomass of all faunal components, decreases exponentially with increasing water depth, but this does not apply to benthic prokaryotic biomass. This was estimated to be approximately 160 Pg of organic carbon, equivalent to almost half of the total microbial biomass on Earth. In the benthic compartment, organic matter, nutrients, DNA concentrations and prokaryotic cell abundance are typically 10-1000 times higher than in the water column, and the production of new viruses by infected microbes is 1-2 orders of magnitude higher, thus being potentially responsible for higher rates of microbial cell death, subsequent lysis and final release of intracellular material. Recent studies on deep-sea sediments worldwide demonstrated that viral-induced prokaryote mortality is a key mechanism controlling prokaryotes' dynamics, and that the release of DNA by viral lysis may sustain an important fraction of prokaryotic metabolism. Notably, it was estimated that extracellular DNA released by viral lysis of infected prokaryotes accounts for 65-100% of N and P requirements in the water column and 2-15% of N and P requirements in the sediments. Increasing evidences highlight the important role of viral infections in marine sediments, which is likely to be far more relevant than in pelagic systems. The "benthic viral shunt" represents an important mechanism of trophic supply and transformation in quantity and quality of the food resources available for prokaryotes, especially in the Deep Sea, typically characterized by reduced availability of external trophic inputs. Controlling benthic prokaryotic biomass (top down, predatory control), supporting prokaryotic metabolism (bottom-up control), and accelerating biogeochemical processes, viral infection is now recognized as a fundamental driver of the functioning of the largest ecosystem of our biosphere.

All of these processes have the potential to change the biogeochemical cycles of carbon, nitrogen and phosphorus. In addition, prokaryotes have the potential to alter the transfer of sinking particles from the surface waters towards the ocean floor by determining their dissolution during sinking. In turn this process can be modified by viral infections of the prokaryotes colonizing detrital particles during sinking. Thus, marine viruses can influence directly and indirectly biogeochemical cycles, and the carbon sequestration capacity of the oceans. Moreover, by infecting and killing the phytoplankton, they can influence also the gas exchange between the ocean surface and the atmosphere (figure 3).



Viruses are indeed able to influence the present climate changes on marine ecosystems by interacting actively or passively with the biotic components able to control CO₂ emissions or storage or to release climate-altering gases.

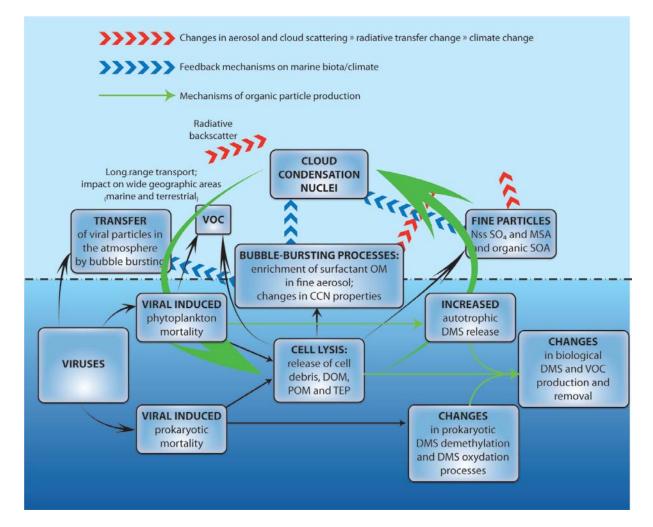


Figure 3. A schematic example of the complex processes in which viruses are involved, from the influence of viral infections on the functioning of the pelagic food web, to the regulation of climatic processes and response of the

Oceans to the climate change. CCN: cloud condensation nuclei DMS: dimethylsulfate DOM: dissolved organic matter MSA: methylsulfonic acid Nss: non-sea-salt OM: organic matter POM: particulate organic matter SOA: secondary organic aerosol TEP: transparent exopolymeric particles VOC : Volatile organic compound

Viruses and prokaryotes are now well recognized as important drivers of biomass production, metabolism and energetic budgets of all oceanic systems. Deepening the knowledge on the role of the viral component



into the major trophodynamic and biogeochemical cycles is crucially important for improving our understanding of the marine ecology and of the function of the world's oceans.

Further readings:

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