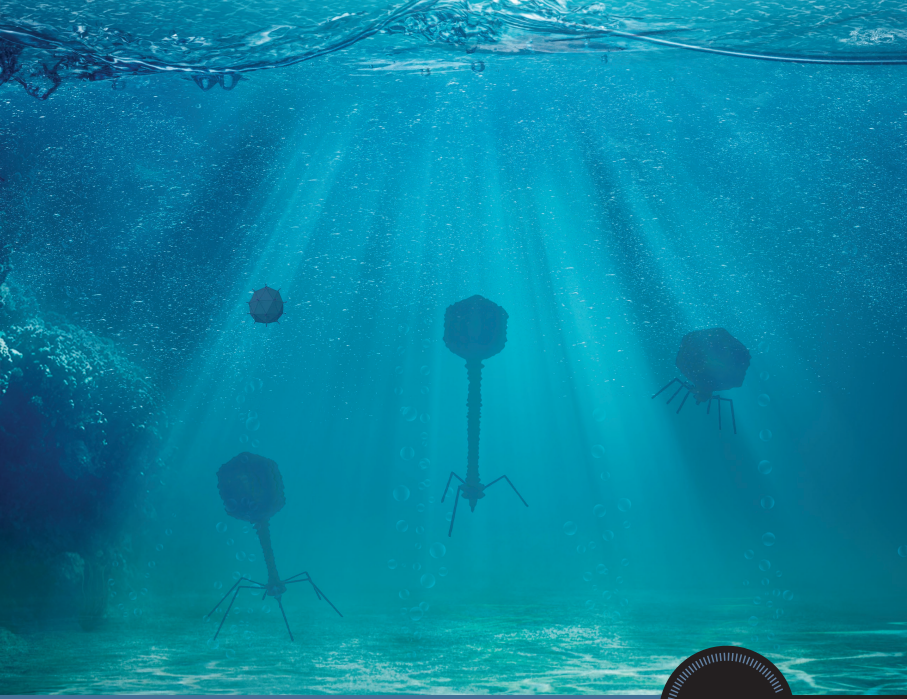

ENJEUX SCIENCES

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Table of contents

In memory of Markus Weinbauer

This book, published in 2026 as a translation of its French edition released in 2023, is dedicated to the memory of our colleague Markus Weinbauer, whose work profoundly shaped aquatic microbial ecology and opened new perspectives on the role of viruses in the oceans. Through a scientific outlook that was both rigorous and deeply curious, Markus helped reveal the immense importance of marine viruses in the functioning of ecosystems. At a time when these invisible entities were still largely overlooked, he demonstrated that they play an intimate role in the cycling of matter, the dynamics of microbial communities, and, more broadly, the balance of the oceanic biosphere. Beyond his major scientific contributions, those who had the privilege of working alongside him remember a generous and enthusiastic researcher who trained a great number of young scientists. The pages of our book devoted to marine viruses owe much to the path he helped chart. His influence can be seen in the questions we ask today, in the methods we employ, and in the ever-renewed sense of wonder inspired by the study of the microbial world. May this work, in its own way, extend the scientific momentum he helped inspire and remind us how curiosity, rigor, and generosity can shape a discipline in lasting ways.

WHAT IS A VIRUS, PARTICULARLY A MARINE VIRUS?

The study of viruses is relatively recent. It is less than 100 years since viruses were detected and characterized using the first electron microscopes (1937). As the word virus comes from the same Latin word meaning "poison", they were first, and for a long time, considered and studied as pathogens, in plants, animals and, particularly, humans. A virus is an obligate intracellular parasite that requires another living organism to replicate.

The study of viral diversity in ecosystems, including aquatic ecosystems, as components of microbial communities appeared much later. Indeed, it was not until the 1980s that this type of research began. To understand viral diversity, new methods had to be developed to identify and, when possible, quantify non-observable and mostly non-cultivable entities. Initially, microscopy highlighted the numerical predominance of viruses in aquatic environments, but these approaches remained limited in their capacity to describe viral diversity, as the shapes and sizes of different viruses are often very similar. Awareness of the enormous diversity of viruses is quite recent, especially due to developments in molecular biology and high-throughput sequencing from the 2000s onwards. Over the past two decades, metagenomic analyses (see box: *"Omics" in a nutshell*) of the non-cellular fraction of marine environments that contains viruses have significantly expanded our knowledge and revealed a vast genetic diversity of both DNA (deoxyribonucleic acid) and RNA (ribonucleic acid) viruses.

Marine viruses are not fundamentally different from terrestrial viruses, but the global ocean is incredibly vast and difficult to access, containing a potentially enormous diversity of viruses that remain largely unknown. In addition, in extreme marine environments, such as hydrothermal sources, a wide variety of unique viruses has been shown to exist, as synthesized in the publications of Lossouarn *et al.* (2015) or Gil *et al.* (2021).

Extremophilic microorganisms (e.g. those living in very hot or very acidic environments), such as archaea, are associated with viruses with totally unusual forms and unique genetic signatures. In the ocean, viral genes code for functions not typically found in terrestrial viruses. It is now estimated that 50–70% of the genetic information contained in the genomes of marine viruses encodes unknown functions, with some of these genes never having been recorded in the databases. Therefore, there may be differences between aquatic and terrestrial viruses. However, it is important to note that there is no strict dichotomy between marine (or more generally aquatic) and terrestrial viruses.

METAGENOMICS

It is now possible to determine the incredible diversity of microorganisms in a seawater sample on the basis of their DNA, whereas so-called conventional techniques (typically microscopy) only allowed a glimpse. Combining genetics, ecology, and computer science, metagenomics is a high-throughput sequencing approach coupled with bioinformatics analysis that, unlike genomics (which focuses on complete genomes from single or limited organisms), enables the study of genomes from multiple individuals across different species. It is thus possible to obtain the composition of a microbial assemblage, i.e. which species are present, their abundances and diversity, in a given sample.

Technical reasons and economic or public health interests have led terrestrial viruses of vertebrates to be given much more attention than aquatic viruses. However, our knowledge of the diversity and evolution of viruses of vertebrates is most often limited to those found in mammals or birds and associated with pathologies. The study of RNA viruses, known for their rapid evolution and very wide diversity of hosts, has quite logically shown a strong link between viruses and the evolution of their hosts. The history of these hosts most often began in the oceans, where they evolved over millions of years. The viruses associated with them have followed their evolution. Palaeovirology (the science that studies ancient viruses and the co-evolutionary

history of viruses and their hosts) shows that most RNA viruses infecting vertebrates have a marine origin. It therefore emphasizes the value of continuing studies to describe taxonomic diversity in the marine environment to help us understand the history of viral evolution. Such approaches challenge the conventional view that a single virus or viral type is associated with a single, specific host, especially since these hosts may share a common evolutionary ancestor. To advance understanding in this field, it is important to acquire more data on viral diversity within hosts, but also over time.

DEFINITION AND LIFE CYCLE

A virus is defined as a biological entity consisting of a single- or double-stranded DNA or RNA molecule surrounded by a protein shell (called a capsid) and, in some cases, a lipid envelope or layer. The definition also states that a virus does not breathe, divide or actively move. Viruses come in a wide variety of sizes and shapes, ranging from just a few hundredths of a micron to over one micron (µm), and take forms as diverse as filaments, bottle shapes, or the lunar-lander-like structures typical of bacteriophages. They also do not have their own metabolism, making them obligate parasites that rely entirely on the intracellular machinery of a living host to replicate and produce progeny. The first step of the infection of a host cell by a virus is quite universal: it consists of passive contact, recognition of the host targeted by the virus, then fixation of the virus to specific receptors, such as membrane transport proteins, and injection of genetic material into the cell. Subsequently, there are different replication methods: true lytic cycle, ineffective lytic cycle (where the virus does not lyse the cell), chronic cycle (production of virions[1] without lysis), lysogenic cycle or pseudo-lysogenic cycle (Figure 1).

1. Virion: The "free" form of a virus, therefore consisting of the capsid and the viral genome it contains.

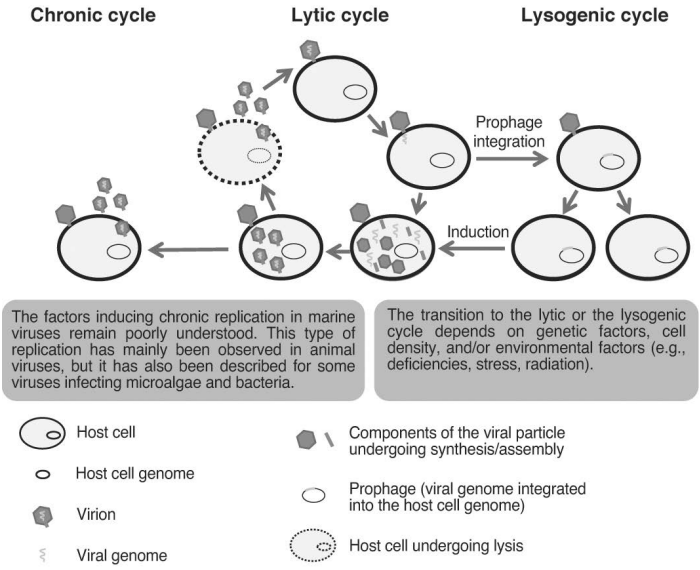

Figure 1. Major viral cycles or strategies.

Lytic and lysogenic cycles predominate in marine viruses. As shown in this diagram, there is no strict barrier between cycles, as the transition from one to the other can take place depending on the physiology of the host cell and environmental conditions.

The lytic cycle has been the most extensively studied in the marine environment, as it is quickly recognized for its significant and possibly measurable functional role: that of cell mortality and the redistribution of matter in the surrounding environment of infected organisms. Indeed, during the lytic cycle, the viral genome induces the synthesis of viral constituents, including the replication of viral genetic material. A certain number of viruses are then produced inside the host cell (this number, called the burst size, varies from a few to several thousand units) and their release takes place through the burst and hence the death of the cell that housed them. It is presently estimated that mortality induced by viruses affects at least 10% of microalgae (excluding mortality at the

termination[2] of blooms[3], where this estimate can almost reach 100%) and 40% of bacteria (again, the percentages are variable, depending on a multitude of environmental factors, or the physiological state and the resistance capacity of the host). It is more difficult to estimate virus-induced mortality for metazoan organisms (typically zooplankton), for which there is still very little information. Note that the lytic cycle may be ineffective when blocked at one or more of its stages (e.g. adsorption to the receptor, entry of the viral genome, synthesis of the viral progeny or their release). This type of cycle, which does not lead to the production of infectious offspring, could correspond to a cul-de-sac or, more simply, to the abortion of a lytic cycle.

The second most well-known mode of replication is the lysogenic cycle, in which the viral genome integrates into the host genome. This is called a provirus or prophage that reproduces and persists in this state until an environmental event (stress, shock, thermal or nutrient limitation) induces the transition to a lytic cycle. Lysogeny can provide the virus with a means of maintenance, a refuge to survive in when conditions are unfavourable to the host's metabolism, but only up to a certain point. If the host cell is about to die, then the virus is forced to abandon ship! This mode of replication could benefit the virus if the host is weakly abundant. The host cell may also find it "advantageous" to be occupied by a lysogenic virus, since the latter may offer it some resistance or immunity to a new viral infection (which is known as immunity to superinfection), or new functions brought about by the viral genome, such as virulence factors (toxins) or factors enabling the adaptation to environmental fluctuation.

A variant of the lysogenic cycle that has been reported for the marine environment is pseudolysogeny, which refers to when a virus infects a host cell, but its genome does not integrate into the cellular genome and remains in what appears to be an inactive

2. Termination: when a bloom disappears, which can have various causes, including viral lysis.

3. Bloom: rapid increase in the concentration of generally phytoplanktonic microorganisms (microalgae or cyanobacteria) in an aquatic environment. This proliferation often causes water coloration (green, red, etc.) due to the pigment of the species concerned.

state inside the cell. This type of viral persistence would appear when the host cell is in a very slowed down physiological state, for example under very limiting nutrient conditions, so that no viral replication occurs. To our knowledge, the question of whether a true lysogenic cycle can be re-established if the host cell finds itself in a more favourable environment has not yet been answered.

Another mode of replication that has been shown in some viruses is the chronic cycle, especially in some phytoplankton genus or species (e.g. *Ostreococcus tauri*, *Emiliania huxleyi, Micromonas* spp.). In this case, the newly formed viruses inside the host cell are released in a constant or episodic manner without bursting the cell and thus without its death. This release takes place by extrusion or budding of part of the cell membrane. Two scenarios have been reported in the literature depending on the type of host, some of which lead after several cycles to the classical lytic cycle and the death of the host, while others seem to establish a stable coexistence between host and virus (but with very low viral production, i.e. less than three viruses released per cell per day).

In the marine environment, habitats are diverse and environmental conditions vary spatially and temporally. These variations profoundly alter organism physiology and it is now known that the physiological state of the host influences the kinetics and/or alternation of viral replication cycles, as synthesized in the review of Mojica and Brussaard (2014). Thus, it is easy to understand that viruses can shift from one cycle to another. This has been repeatedly shown for the bacterium-bacteriophage pair, in which host abundance and cell physiology are critical and involved in the establishment of the lysogenic cycle in relation to the lytic cycle. It appears that productive environments are dominated by lytic viruses, whereas low-production, oligotrophic (nutrient-poor) or anoxic (dissolved oxygen-deficient) environments are rather typical of lysogenic viruses. At least half of the so-called cultivable marine bacteria (i.e. those that can be isolated and cultured in the laboratory, probably less than 1% of the total actual bacterial diversity) have been shown to carry prophages that can be induced by chemical stresses; in other words, these bacteria are in a lysogenic state. In 2008, John Paul put forward the idea that these phages, if integrated into the cellular genome,

are true "time bombs" because they can become virulent and, when conditions are favourable, cause the death of a huge proportion of cells/populations.

It was long believed that reproductive modes or cycles are very independent, allowing viruses to be classified according to their mode of reproduction. Today, these cycles are seen more as a continuum: viruses can use different infection strategies depending on population density, host cell physiology and, more generally, their environment, which influences all biotic interactions. However, the precise mechanisms that trigger transitions between lysogenic, lytic or chronic cycles in marine viruses remain largely unknown.

Among the scenarios, it is often noted that lytic infections suppress high-growth bacterial hosts, leaving part of the ecological niche vacant for the development of prophage-carrying bacteria, or lysogens (bacteria harbouring dormant, integrated viruses known as prophages) to proliferate. These prophages provide their bacterial hosts with protection against lytic phages. As the population density of these lysogens increases, lysogenic phages may acquire mutations to overcome superinfection or homoimmunity (a mechanism by which a prophage protects its host from secondary infection by a closely related phage) and thereby regain control of the lysogenic population. The ongoing development of "omics" techniques, encompassing genomics, transcriptomics, proteomics and metabolomics, promises to reveal whether prophages are active or dormant and to provide detailed insights into the frequencies of lysis and lysogeny in the natural environment and on their dependency on environmental factors.

During pseudolysogeny, the phage enters neither the lytic nor the lysogenic phase but remains in the cell as an extra-chromosomal element that does not replicate and is not passed to both daughter cells after division. This mode of reproduction seems to be found in both DNA and RNA viruses. It can be observed when the host cell is in a resource-limiting environment. As soon as conditions become more favourable, the lytic cycle becomes the norm. It has been suggested that this viral strategy allows phages to protect themselves from environmental conditions such as the deleterious effect of ultraviolet (UV) radiation.

Among bacteria, 35–50% are susceptible to several phages. Thus, phages belonging to different taxonomic groups can infect a common host. Co-infections can also occur, complicating host-virus interactions, with different consequences for their ecology and evolution.

"OMICS" IN A NUTSHELL

Genomics is the science that studies the genome.
Transcriptomics is the science that studies how the overall expression of genes in an individual or set of organisms varies under varying environmental, experimental or pathological conditions.
Proteomics is the study of the proteome, the complete suite of proteins constituting a living organism.
Metabolomics is the comprehensive study of metabolites (small molecules, e.g. sugars, lipids, nucleic acids or vitamins, produced or modified during cellular metabolism within an organism or a tissue.

DIVERSITY AND STUDY METHODS

Initially, viruses were classified according to their morphological characteristics. While this classification is still used today to a limited extent, molecular approaches have greatly complemented it. Viruses with an elongated tail structure, used for host cell recognition (also known as tailed viruses), are still generally distinguished from those without a tail. In 2013, Brum *et al.* reported that tailless viruses dominated marine samples, comprising 50–90% of detected viruses. Among the tailed viruses, bacteriophages are the most prevalent, and these are still categorized depending on the size and flexibility of their tails. Specifically, siphoviruses have long, non-contractile tails; myoviruses have long, contractile tails; and podoviruses have short tails (Figure 2). However, this type of phenotypic classification captures only a small portion of the remarkable genetic diversity of marine viruses, which is now known to be exceptionally high and remains largely uncharacterized.

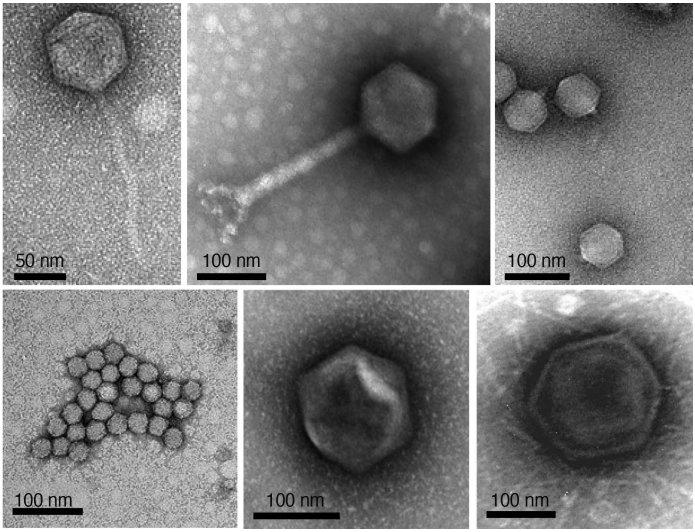

Figure 2. Major viral morphotypes.

The viruses presented here have a typical shape (with an icosahedral protein capsid) and may or may not possess a tail, which can be short or long, contractile or non-contractile. The upper part of the figures shows the three typical representatives of the tailed bacteriophage family (from left to right; Sipho-, Myo- and Podoviridae). The shapes in the bottom row are more characteristic of viruses that infect protists[4] (from left to right: Picornaviridae, Phycodnaviridae and an uncultivated giant virus). N.B.: there are other, often rarer, filamentous or pleomorphic morphologies (e.g. those of certain archaeal viruses, see Table 1). Source: © Baudoux A.-C./Photothèque, Station Biologique de Roscoff; © Schoehn G./Photothèque, Institut Biologie Structurale.

The analysis of nucleotide sequences (DNA or RNA) of marine viruses with metagenomic tools (see boxes: *Metagenomics* and *Studying marine viruses using environmental DNA*) provides new insights into ocean viral diversity. Data from the *Tara Oceans* mission (Figure 3) revealed an extraordinary diversity of viral

4. Protists are not a phylogenetically defined group. However, for reasons of clarity and legibility, we have decided to use this term without adding quotation marks. This editorial choice also applies to the terms prokaryotes, fish, algae, reptiles and invertebrates that are used in this book.

sequences in marine environments. When the *Tara* expedition began in 2009, viruses were known to be abundant (1-100 billion viruses per litre of seawater) and it was estimated that they killed about one-third of the microbial cells in seawater every day. However, these findings were largely derived from counting microscopic particles that resembled viruses and laboratory incubation experiments with environmental samples. Over the past decade, rapidly advancing sequencing technologies and molecular biology techniques have enabled systematic and quantitative studies of oceanic "viromes" (the total viral genomic content in a sample) on a global scale. These capabilities significantly expanded our understanding of oceanic viral genomes: from only 39 publicly available isolated genomes prior to the *Tara Oceans* mission to approximately 200,000 different populations of predominantly double-stranded DNA viruses (metagenome-derived sequences) in the global oceanic virome (GOV2).

Figure 3. The research schooner *Tara* photographed during one of its numerous research missions on viruses and other planktonic organisms.

Tara Oceans and the ship's subsequent expeditions have contributed a great deal to the discovery of marine plankton, its diversity and the interactions between microorganisms, including viruses. The schooner has travelled thousands of kilometres around the globe and collected several thousand samples of seawater and plankton from several hundred sites corresponding to a wide variety of ocean biogeographic provinces. For more information, visit the *Tara Oceans* Foundation website (https://fondationtaraocean.org/). Source: © Latreille F./Fondation Tara Océan.