Deep-sea benthic ecosystems waste nothing and recycle everything, even viruses

Cinzia Corinaldesi

Department of Materials, Environmental Sciences and Urban Planning, Polytechnic University of Marche, Ancona, Italy

ABSTRACT

Viruses are the most abundant biological entities of the global ocean and have a pervasive role in marine ecosystems because, being a major cause of mortality, they module the functioning of food webs, and biogeochemical cycling. This role is due not only to their ability to infect and lyse marine organisms but also to the decomposition of their particles (viral decay). The organic matter of viral origin, indeed, can be recycled by benthic organisms thus representing an additional important food source for their metabolism, especially in deep-sea sediments, characterized by very low availability of trophic resources. This short note will present an overview of the available information on viral decay in deep-sea benthic ecosystems.

INTRODUCTION

Marine viruses are a relevant source of mortality for a wide range of organisms, and by killing their hosts they influence the functioning of the marine food webs and nutrient cycling in the oceans of the world (Wommack and Colwell, 2000; Weinbauer, 2004; Suttle, 2007; Danovaro *et al.,* 2016). Viral lysis, indeed, diverts cell biomass away from higher trophic levels, enhancing the supply of Dissolved (DOM) and Particulate Organic Matter (POM) pools (*i.e*., a concept also defined as viral shunt; Wommack and Colwell, 2000; Figure 1), thus modulating food webs and the functioning of the marine ecosystems (Suttle, 2007).

Due to their pervasive role, viruses have been proposed as integral components of global models of Carbon (C) cycling and nutrient regeneration (Suttle, 2007; Danovaro *et al.,* 2008b; Weitz *et al.*, 2015), and of current and future climate models (Danovaro *et al.,* 2011).

Deep-sea sediments (>200 m depth) represent over *ca*. 65% of the Earth's surface and have key roles in biomass production and biogeochemical cycles (Tyler, 2003; Danovaro *et al.*, 2014; Corinaldesi, 2015). In these systems, nearly all the prokaryotic C production is transformed into organic detritus by viral lysis, thus representing an additional important trophic resource for benthic metabolism (Danovaro *et al.,* 2008b).

The key role of viruses in benthic trophodynamics and biogeochemical cycles is not only modulated by the extent to which they infect and lyse their hosts (with the consequent release of the cell contents) but also by the extent to which they decay if they find no suitable hosts to infect or lose infectivity (Corinaldesi *et al.*, 2010; Dell'Anno *et al.,* 2015; Figure 1).

Viral decay is indeed the process concerning the decomposition of organic material of viral origin (*e.g*., largely proteins and nucleic acids), which being very labile and promptly usable, is recycled and re-channel in the food web by benthic prokaryotes (Dell'Anno *et al.*, 2015). Being deep-sea benthic systems characterized by very low inputs and availability of trophic resources (Corinaldesi *et al.,* 2010), it has been reported that viral decay can represent a relevant process in oligotrophic environments such as the deep-sea floor (Dell'Anno *et al.*, 2015).

The term 'viral decay' can be ambiguous since it might indicate either the loss of infectivity (due to damage of nucleic acids or viral receptors on the capsid) or the complete degradation of viral particles (Danovaro *et al.,* 2008a). So far the most reliable estimates of viral decay have been obtained by using a sediment dilution-based technique followed by viral nucleic-acid staining and epifluorescence microscopy (Dell'Anno *et al.*, 2009; Dell'Anno *et al.*, 2015). However, this approach does not allow us to discriminate between infective and non-infective viruses (without contextually calculating the virus-killed cells with additional procedures) because both remain equally visible under the microscope. Therefore, the term "viral decay" is generally used to indicate degraded or no longer detectable viruses under a microscope, whose decrease rate can be determined during time-course experiments (Corinaldesi *et al.*, 2010).

This note will present a brief overview of the available information on viral decay in deep-sea sediments, showing that while long-standing questions about the role of viruses in these ecosystems have been answered in recent decades, many more questions will arise as we get closer to understanding how, paradoxically, these biological entities help sustain life in our oceans.

Quantitative relevance of viral decay rates in deep-sea sediments

Pioneer studies in aquatic ecosystems have supposed that viral production is balanced by viral decay based on the assumption that viral dynamics are in a steady-state condition (Thingstad, 2000; Wommack and Colwell, 2000). However, further investigations in different benthic systems documented that viruses, decay at lower rates than they are produced (Glud and Middelboe, 2004; Corinaldesi *et al.*, 2007), possibly because viral production and viral decay are controlled by different factors (Parada *et al.*, 2007). Further investigations on deep-sea sediments on a global scale (spanning the Arctic Ocean, northeast Atlantic Ocean, and the Mediterranean Sea) and different habitats from the shelves to the abyssal planes (*i.e.*, continental slopes and margins, deep-sea anoxic basins, and seamounts) revealed that viral decay estimates range from *ca*. 7 to 163 x 10^{11} viruses m^{-2} d^{-1} (Corinaldesi *et al.*, 2007; Danovaro *et al.*, 2009; Corinaldesi *et al.,* 2010; Corinaldesi *et al.,* 2012; Corinaldesi et al. 2014; Dell'Anno *et al.,* 2015; Table 1). Such viral decay estimates account, on average, for *ca*. 30% of the gross viral production (*i.e.*, total viral production after lysis of infected cells; Corinaldesi *et al.*, 2010), thus viral decay is less than half of the net viral production (*i.e.*, viral production net of viral decay). This can explain the high infection rates, especially under 1000 m depth, where viruses are responsible for the abatement of a very large fraction of the prokaryotic heterotrophic production (Danovaro *et al.*, 2008b).

Factors influencing viral decay rates

While viral production depends on the abundance, metabolic activity, and burst size (*i.e.*, number of viruses released per infected cell) of prokaryotic hosts (Glud and Middelboe, 2004; Parada *et al.*, 2007), viral decay is influenced by a complex interaction of physical, chemical and biological variables (Danovaro *et al.*, 2008a). In particular, in aquatic systems, viral decay has been related to solar radiation, temperature, pH, organic matter, salts,

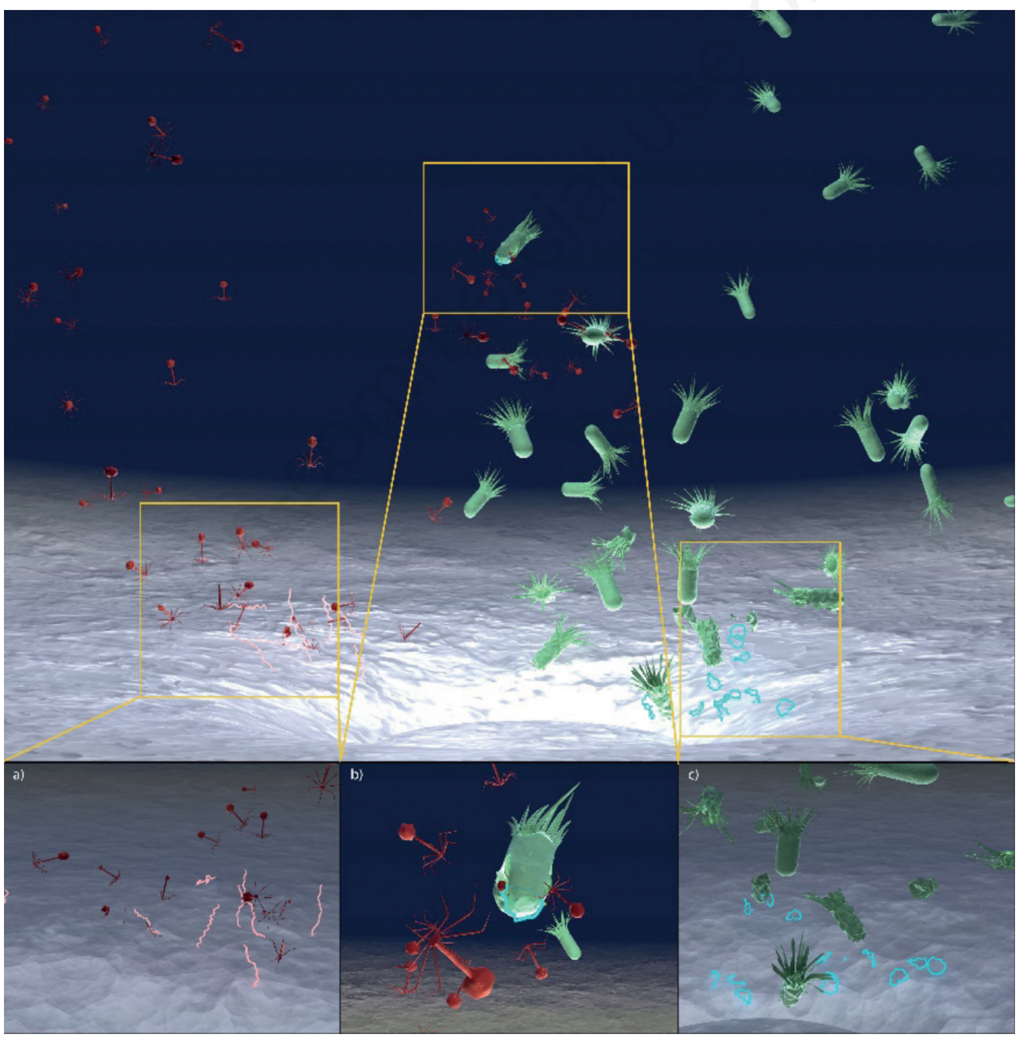

Figure 1. Infection and lysis of prokaryotic cells (in green) by viruses (in red) and viral decay in deep-sea benthic ecosystems. a) Viral decay: viruses decompose releasing genetic material and other components (*e.g.*, proteins), b) viral lysis and infection: prokaryotic cells are infected and lysed, with the replication of new viruses, and c) viral shunt: release of organic matter and nucleic acids by lysed cells. Image courtesy of Michael Tangherlini.

heavy metals, protozoan grazing, and enzymes (*e.g.*, Danovaro *et al.*, 2008a and references inside). Experimental investigations indicated a key role of the prokaryotic extracellular enzymes, such as DNases and proteases, in viral decomposition (Corinaldesi *et al.*, 2010) as the viral decay rates increased in the surface sediments after enzyme addition, even if this was not the case of the subsurface sediments. Further studies, in different oceanic regions, revealed that viral decay rates are controlled primarily by the extracellular enzymatic activities that hydrolyze the proteins of the viral capsids, confirming the key role of proteolytic activities in the viral decomposition (Dell'Anno *et al.*, 2015). Conversely, numerous studies have documented that the sedimentary matrix (especially clay minerals) can offer protection to viral particles by delaying the loss of infectivity of viruses and reducing their exposure to substances that cause their decay (*e.g.*, Gerba, 1984; Sakoda *et al.*, 1997, Danovaro *et al.,* 2008a and references inside). In this regard, some investigations proposed that viral decay rates in sub-superficial deep-sea sediments are lower than in the surface layers (Cai *et al*. 2019) and that they could persist in undisturbed sediments for hundreds of thousands of years (Middelboe *et al*. 2011). However, the implications of virus preservation in the subsurface have not yet been elucidated.

Contribution of viral decay to biogeochemical processes

Available estimations indicate that the decomposition of deep-sea benthic viruses releases□37–50 megatons of C per year, representing an important source of labile organic compounds. In particular, organic material deriving from decomposed deep-sea viruses accounts for 3±1%, 6±2%, and 12±3% to C, N, and P of the material photosynthetically produced, which is supplied to the bathyal/abyssal sediments through its sinking (Dell'Anno *et al.* 2015). Existing literature also indicates that benthic viral decay is significantly related to prokaryotic heterotrophic C production, which in turn is related to C released from viral decomposition. This suggests a tight interaction between virus decomposition and prokaryotic metabolism (Corinaldesi *et al*., 2010) as demonstrated by experimental assays, which confirmed that the addition of purified and inactivated virus concentrates significantly increases the growth rates of prokaryotes (Dell'Anno *et al*. 2015).

Since organic compounds released by the decomposition of virus particles (*i.e*. proteins and nucleic acids) in deep-sea surface sediments have much faster rates of degradation than most organic matter sinking to the ocean floor (Middelburg and Meysman, 2007), the use of labile C from decomposed viruses by benthic prokaryotes can contribute to rapid N and P cycling (Dell'Anno *et al.* 2015), thus supporting the functioning and biogeochemical processes of the largest biome of the biosphere.

Virus decomposition together with virus-induced cell lysis can also stimulate ammonia-dependent archaeal chemoautotrophic production, thus contributing to the major primary production processes occurring in deep-sea sediments (Danovaro *et al*. 2017).

CONCLUSIONS

There is no doubt that viruses play a key role in the life and death of all marine organisms, in controlling their biodiversity and biogeochemical cycles of the global ocean. Deep-sea viral ecology also shows how even the smallest particles, enemies of marine organisms, are recycled without waste. In the last decade, viral ecology has been driven by metagenomic analyses, which have expanded the catalog of viral genomes, most of which are still of unknown origin, and with functions that remain putative. This short note aims not only to provide some insights into the importance of viral decay in deep-sea sediments but also to underline the need to continue to explore their role in the global ocean to better elucidate how they influence ecosystem functioning, especially in light of current and future scenarios of global change.

Table 1. Estimates of Viral Decay rates (VD) and their contribution to Viral Production (VP) in surface sediments of different deep-sea benthic habitats (>200 m depth).

Basin	Habitat	Depth m	VD 10^{11} m^{-2} d^{-1}	VD/VP* %	Bibliographic sources
Eastern Mediterranean	Deep-sea anoxic basins	3575	42.2±27.5§	32	Corinaldesi *et al.* 2007
Western Mediterranean	Seamounts	3430-3581	36.7-75.5	35	Danovaro *et al.* 2009
Central and Western Mediterranean	Continental slopes and margins	300-990	11.5-63.4	37	Corinaldesi *et al.* 2010
Western Mediterranean	Continental slopes	217-222	7.1-26.3	29	Corinaldesi *et al.* 2012
Eastern Mediterranean	Deep-sea anoxic basins	2952-3352	134.0-163.0	16	Corinaldesi *et al.* 2014
Eastern Mediterranean	Continental slope	2793	34.9±27.3§	29	Corinaldesi *et al.* 2014
Arctic, Mediterranean, Atlantic	From continental shelves to abyssal plains	200-5600	8.0-128.0	25	Dell'Anno *et al.* 2015

*VP is the gross viral production; §Standard deviation.

Corresponding author: Cinzia Corinaldesi, Department of Materials, Environmental Sciences and Urban Planning, Polytechnic University of Marche, via Brecce Bianche 12, Ancona, Italy.
E-mail: c.corinaldesi@univpm.it

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