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REVIEW

Phaeocystis and its interaction with viruses

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Abstract Over the years, viruses have been shown to be mortality agents for a wide range of phytoplankton species, including species within the genus *Phaeocystis* (Prymnesiophyceae). With its polymorphic life cycle, its worldwide distribution, and the capacity of several of the *Phaeocystis* species to form dense blooms, this genus is a key player for our understanding of biogeochemical cycling of elements. This paper provides an overview of what is know to date about the ecological role of viruses in regulating *Phaeocystis* population dynamics. It explores which variables affect the algal host–virus interactions, and examines the impact of virally induced cell lysis of *Phaeocystis* on the function and structure of the pelagic food web as well as on the flow of organic carbon and nutrients.

Keywords Characteristics · Mortality · *Phaeocystis* · Phycodnaviridae · PgV · Viruses

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Abbreviations

PgV	Phaeocystis globosa virus
PpV	Phaeocysis pouchetii virus
TEP	Transparent exopolymeric particles
MPN	Most probable number
TEM	Transmission electron microscopy
DsDNA	Double-stranded DNA
HAB	Harmful algal bloom species
PFGE	Pulsed-field gel electrophoresis
DMS	Dimethyl sulfide
DMSP	Dimethylsulfoniopropionate
DOC	Dissolved organic carbon
DOM	Dissolved organic matter

Introduction

The presence of viruses in marine environments has been acknowledged for many years, and it is now well established that viruses are dynamic and important members of the microbial food web (Bergh et al. 1989; Proctor and Fuhrman 1990; Gobler et al. 1997; Fuhrman 1999; Wommack and Colwell 2000; Weinbauer 2004). Viruses infect not only the numerically dominant bacteria but also prokaryotic and eukaryotic primary producers. Unicellular photosynthetic organisms are a major group of organisms in natural aquatic communities and viruses have been recognized as mortality agents for phytoplankton (Van Etten et al. 1991; Reisser 1993; Brussaard 2004). Viruses or virus-like particles have

been reported in many different taxa of eukaryotic algae, including harmful algal bloom (HAB) species (see review by Brussaard 2004; Nagasaki et al. 2004; Tomaru et al. 2004; Baudoux and Brussaard 2005).

The fate of phytoplankton biomass, whether through sinking, grazing or cell lysis, has major implications for carbon and energy cycles in marine ecosystems. Lysis-mediated release of the cellular content can greatly enhance bacterial activity and subsequently force the food web towards a more-regenerative system. Energy and nutrients released by cell lysis and excretion is transferred to higher trophic levels via the microbial loop (Azam et al. 1983). Lytic viral infection of phytoplankton causes rapid cell lysis, which may affect not only the energy and nutrient flow, but also the phytoplankton community composition and succession. Recognizing viral lysis of phytoplankton as a major process has emphasized the importance of the microbial loop including a viral shunt.

Theoretical models suggest that a 2–10% loss of phytoplankton due to viral infection increases the flow of organic carbon, bacterial production and respiration by more than 25% (Fuhrman 1999; Wilhelm and Suttle 1999). Especially during algal blooms, when high algal cell abundances enhance the virus-host encounter rates, virally mediated lysis can have a profound effect on population dynamics, community diversity and transfer of energy and matter within the pelagic food web.

The *Phaeocystis* genus, with its cosmopolitan distribution, includes several high-biomass-forming species (Cadée and Hegeman 2002; Verity and Medlin 2003; Schoemann et al. 2005). *Phaeocystis* has a life cycle dominated by single cells (with and without flagellae) and embedded colonial non-flagellated cells. Several species of *Phaeocystis*, e.g., *P. pouchetii* and *P. globosa*, regularly dominate the phytoplankton community and sequester huge amounts of nutrient resources, predominantly in the form of colonies. These blooms occur mostly in colder and temperate waters, such as the coastal zone of the North Atlantic and the North Sea. Because of the importance of these blooms for the pelagic ecosystem and the socioeconomic interest in these HAB species, substantial research has been conducted on factors controlling the wax and wane of these blooms. With light and nutrients as important factors initiating *Phaeocystis* blooms, grazing and viruses are considered the relevant loss factors. Field studies indicate that these viruses are a dynamic component, notably involved in the decline of the blooms. Laboratory and seminatural studies provided insight into host–virus interactions and revealed how environmental factors may influence viral infection. The scope of the present paper is to provide a summary and synthesis of available information and some unpublished data related to *Phaeocystis* and the viruses infecting it.

Isolation and characterization of viruses infecting *Phaeocystis*

Viruses that infect species of *Phaeocystis* have been isolated during and directly after natural blooms (Jacobsen et al. 1996; Brussaard et al. 2004; Baudoux and Brussaard 2005). *Phaeocystis pouchetii* viruses (PpV) were successfully isolated after 100-fold concentration by continuous centrifugation and exposure to ultraviolet (UV) for 15 and 30 s (Jacobsen et al. 1996). Exposure to UV light was intended to cause induction of virus production in algal cells containing lysogenic viruses, but as the virus isolated was lytic this treatment was most likely not necessary. So far, all viruses infecting eukaryotic microalgae are lytic and none have been reported to enter a lysogenic relationship with the host. *Phaeocystis globosa* viruses (PgV) were isolated from filtered (GF/F Whatman glass fiber filters) natural water that was added to exponentially growing *P. globosa* host cultures (Baudoux and Brussaard 2005). Incubation of the natural seawater with the addition of nutrients for a week at in situ temperature and irradiance (excluding UV) before adding a subsample to cultures of *P. globosa* occasionally advanced successful isolation of PgV. At the decline of the bloom, when most free viruses can be expected to occur, nutrients regularly become depleted. By adding nutrients more algal biomass was generated and the encounter rate between algal host and virus enhanced.

The *Phaeocystis* viruses isolated so far are species specific, i.e., they only infect one of the *Phaeocystis* species (Jacobsen et al. 1996; Bau-