

# Proposal for a SCOR Working Group to Investigate the Role of Viruses in Marine Ecosystems

## **Abstract**

Viruses are a crucial component affecting the trophodynamics and composition of marine food webs. While it is clear that viruses are extremely abundant and are responsible for substantial mortality of heterotrophic and autotrophic marine microbes, there is still very limited quantitative information on the mortality imposed by viruses on marine prokaryotic and eukaryotic microbial communities. Data are particularly sparse for historically undersampled environments such as the open and deep oceans (including sediments) as well as the Arctic. Gaining a qualitative and quantitative understanding of the role of viruses in oceanic carbon and nutrient cycling, food web processes and their effect on community diversity is pivotal for assessing the stability of marine food webs and understanding their effects on biogeochemical cycling.

The proposed working group would study the role of viruses in marine ecosystems over a period of four years, culminating in a final reports that (1) summarize past results on virus-mediated mortality of eukaryotic plankton and prokaryotes and its impact on oceanic carbon and nutrient cycling (2) coordinate data and international collaboration on the role of viruses in different water masses in particular in the open ocean and deep sea and (3) assess the current methodological limitations and develop recommendations for techniques to quantify virus-mediated mortality of microorganisms (eukaryotes and prokaryotes), their impact on carbon and nutrient cycling, and methods for assessing diversity in viral communities. An important aspect of the working group will be to stimulate research to investigate viruses and viral-mediated processes in different water masses, since this promises a better understanding of the effect of viruses on biogeochemical cycles. The working group will also establish and maintain a Web site as forum that can be used by the 'viral community' for exchanging data, ideas and future plans.

## **Rationale**

Understanding the role of viruses in oceanic carbon and nutrient cycling, food web processes and diversity is pivotal for assessing the stability of marine systems and their biogeochemical significance. This understanding is not only of scientific interest; it will also increase the predictability of the effects of global change on biogeochemical processes in the ocean. Moreover, quantitative data on the consequences of viral lysis are necessary to better understand the functioning of marine food webs. This will also facilitate the inclusion of viral effects into oceanic carbon models.

In addition to studying the role of viruses in surface open ocean and deep sea, we propose to assess the role of viruses in distinct water masses, i.e. , 'oceanic rivers', which show a variable degree of mixing. We argue that this approach will increase our understanding of biogeochemical process, since it takes into account a basic oceanographic reality, i.e. that the ocean consists of distinct water masses. Up to now, studies on microorganisms, which focus on distinct water masses, are sparse. A physical description of water masses (temperature, salinity, density) along with the assessment of viral parameters would be a first step to tackle this task.

The best mechanism to focus the scientific community on the role of viruses in marine ecosystems is a working group formed by SCOR. A non-governmental organization such as SCOR is the perfect forum to assemble the scientific expertise from different nations. Moreover, an international working group has the potential to implement this expertise in developing countries. SCOR is funding fundamental science and attracts top scientists to volunteer their time to participate in the group. This also increases the chance to attract further funding for the activity of the group. SCOR is the only organization ensuring that the activity is international and involves both established and young scientists as well as scientists from developing countries.

## Scientific Background

Marine prokaryotic and eukaryotic microorganisms, i.e. eukaryotic phytoplankton, cyanobacteria and heterotrophic prokaryotes (*Bacteria* and *Archaea*), are the main players in the marine carbon cycle. Dominance of autotrophic carbon fixation shifts from eukaryotic phytoplankton to unicellular cyanobacteria in offshore waters and thus the contribution of prokaryotes to primary production is higher in the open ocean than in coastal waters. Viral lysis of photosynthetic organisms results in a reduction of carbon fixation (Suttle et al. 1990). The world's ocean is inhabited by ca.  $1.2 \times 10^{29}$  prokaryotes producing ca.  $9.3 \times 10^{29}$  cells per year (Whitman et al. 1998), or in terms of carbon, about 10-20 Gt C  $y^{-1}$ . Thus global oceanic prokaryotic production amounts to about 50% of global oceanic primary production (20-30 Gt C  $y^{-1}$ ). From this comparison, it becomes clear that the fate of this prokaryotic production is of crucial importance for the oceanic carbon cycle.

About 15 years ago, it was shown that viruses are the most abundant biological entities ('life forms') in the ocean. It is now known that viral lysis are a major mechanism causing mortality of eukaryotic phytoplankton and prokaryotes (reviewed in Fuhrman 1999 and Wommack and Colwell 2000). Mortality of cells at all trophic levels due to viral lysis has considerable implications for the flow of energy and matter through the microbial food web. Lysis (disruption of cells) removes production and converts biomass into dissolved organic carbon (DOC) and small particles (Wilhelm & Suttle 1999), which are available to heterotrophic prokaryotes. This constitutes a short-circuit in the marine food web, the 'viral shunt' (Wilhelm & Suttle 1999), and increases the remineralization of DOC. A model suggests that between 5 and 26% of photosynthetically fixed carbon ends up in the DOC pool due to viral lysis. DOC is the largest pool of organic carbon in the ocean equaling approximately the carbon present in atmospheric carbon dioxide. Heterotrophic prokaryotes are the only group consuming significant amounts of DOC. Intensive research has been performed on the ecology of oceanic phytoplankton and prokaryotes during the past decades. Thus, it is surprising how little is known about the regulatory mechanisms and the fate of autotrophic and heterotrophic production. This information is urgently needed, since cell death has a major impact on carbon fixation and remineralization and on the composition and reactivity of oceanic DOC (Nagata & Kirchman 1997) and thus on carbon and nutrient cycling in the ocean. Quantitative studies on the fate of eukaryotic phytoplankton production have rarely considered the potential role of viral infection. There is increasing evidence that viral lysis stimulates the role of prokaryotes as oxidizers of DOC and remineralizers of  $CO_2$ , N, P and Fe. However, little is known how this affects autotrophic carbon fixation. In addition, the finding that *Archaea* can be as abundant as *Bacteria* in deep marine waters (Karner et al. 2001), has raised considerable interest in the activity and biogeochemical role of this group.

Almost nothing is known on viruses infecting pelagic *Archaea* and only a single experimental study suggests that their community composition is affected by viral infection (Winter et al. 2004).

Recent research using a metagenomics (community genomics) approach showed that viral diversity is extremely high (Breitbart et al. 2002) and accumulating evidence shows that viral infection is a driving force for microbial diversification and diversity (Weinbauer & Rassoulzadegan 2004). Since viral infection is typically species- or even strain-specific and depends on the abundance of host cells, viral lysis should prevent competitive dominants from taking over and thereby allowing the existence of highly diverse microbial communities. If this 'killing the winner' hypothesis (Thingstad 2000) holds true, viruses should have a major impact on the diversity of cellular organisms and on their biogeochemical role. In order to test this hypothesis, it is necessary to develop (and apply) molecular tools so that we can monitor population dynamics of both viral and host communities simultaneously in the natural marine ecosystem. Viral diversity and activity is tightly linked to host diversity and eukaryote- and prokaryote-mediated ecosystem functioning. However, there is a lack of 'hard' data on this influence in most parts of the ocean. While some data has been accumulated for coastal systems, the ocean and deep ocean (including sediments) are largely unexplored territory.

### **Statement of Work/Terms of Reference**

The proposed working group would

- (1) Summarize past results on virus-mediated mortality of algae and prokaryotes and the impact on oceanic carbon and nutrient cycling.
- (2) Coordinate data collection to assess the role of viruses in different water masses.
- (3) Assess the methodological limitations of the techniques available for quantifying the virus-mediated mortality of microorganisms (eukaryotes and prokaryotes) and their impact on carbon and nutrient cycling, and make recommendations for the best available approaches to study viruses and viral processes in the sea.
- (4) Establish and maintain a Web site as forum that can be used by the 'viral community' for exchange of data and ideas and future plans.
- (5) The SCOR effort will culminate with an International Symposium that could include a published proceeding such as a special issue of *Limnology and Oceanography* or *Deep-Sea Research*.

**Meetings.** We propose the first meeting of the Working group (**1<sup>st</sup> SCOR workshop**) to be held in Spain in 2005 in conjunction with the meeting of the American Society of Limnology and Oceanography (ASLO) in Santiago de Compostela, Spain. At this meeting the final identification of the membership, fine-tuning of the Terms of Reference, and creation of an agenda will take place. A second meeting will be held in association with the workshop (proposed below) in the year following the first meeting. An International Symposium on Viruses in the Ocean will take place approximately three years following the initial meeting in order to allow final discussion, input to the Working group's report, and culminate in a published proceedings.

**2<sup>nd</sup> SCOR Workshop in 2006.** An international workshop on oceanic viruses will be convened at the University of British Columbia in Vancouver (Canada) in order to facilitate input to the Working Group for fulfilling the above Terms of Reference. This workshop will

be held after the summer ASLO meeting, which is taking place at the relatively closely situated city of Victoria (Canada). This meeting will be held approximately one year after the first meeting, a period necessary to allow for preparing the workshop agenda, issue announcements and invitations, secure needed funds, and make other necessary preparations. This workshop will provide the opportunity to invite additional specialists that can be included in the working group in order to increase the expertise of the Working Group.

**Symposium in 2008.** The symposium will be held at the Laboratoire d'Océanographie de Villefranche-sur mer (France). We will try to get additional money from the French Science Organization (CNRS), from regional governments, from the Federation of European Microbiology Societies (FEMS) and the European Commission. The project would be completed by September 2008.

### **Working Group membership**

Working Group full membership is proposed to consist of ten specialists and will be international in scope. The members listed below have agreed to serve on the Working Group, pending approval and input of SCOR. The members consist of all scientists promoting the new field of marine viral ecology at the community level about 15 years ago, scientists from the 'second wave' in this field and junior scientists. This mixture has the greatest chance for innovation and developing new perspectives. The chairs will attempt to provide balance and will address coordination, Web site maintenance, dissemination of information and preparation of the final, published report. Two chairs were appointed to make sure these duties will be addressed in an appropriate way by sharing the work load.

#### Full members

Markus Weinbauer, Chair	France
Steven Wilhelm, Co-chair	USA
Gunnar Bratbak	Norway
Corina Brussaard	Netherlands
Eric Wommack	USA
Keizo Nagasaki	Japan
Mathias Middelboe	Denmark
Curtis Suttle	Canada

#### Associate members

Jed Fuhrman	USA
Gerhard Herndl	Netherlands
John Paul	USA
Telesphore Sime-Ngando	France
Feng Chen	USA
Grieg Steward	USA
Roberto Danovaro	Italy

Two additional full member and additional associate members may be appointed preferably from developing countries.

### **References**

- Breitbart M, Salamon P, Andresen B, Mahaffy JM, Segall AM, Mead D, Azam F, Rohwer F (2002) Genomic analysis of uncultured marine viral communities. Proc Natl Acad Sci U S A 99:14250-14255
- Fuhrman JA (1999) Marine viruses and their biogeochemical and ecological effects. Nature 399:541-548

- Karner MB, DeLong EF, Karl DM (2001) Archaeal dominance in the mesopelagic zone of the Pacific Ocean. *Nature* 409:507-510.
- Nagata T, Kirchman D (1997) Roles of submicron particles and colloids in microbial food webs and biogeochemical cycles within marine environments. *Adv. Microb. Ecol.* 15:81-103
- Paul JH, Sullivan MB, Segall AM, Rohwer F (2002) Marine phage genomics. *Comp Biochem Physiol B Biochem Mol Biol* 133:463-476
- Suttle CA, Chan AM, Cottrell MT (1990) Infection of phytoplankton by viruses and reduction of primary productivity. *Nature* 347:467-469
- Thingstad T (2000) Elements of a theory for the mechanisms controlling abundance, diversity, and biogeochemical role of lytic bacterial viruses in aquatic systems. *Limnol Oceanogr* 45:1320-1328
- Weinbauer MG, Rassoulzadegan F (2004) Are viruses driving microbial diversification and diversity? *Environ. Microbiol.* 6:1-11
- Whitman W, Coleman D, Wiebe W (1998) Prokaryotes: The unseen majority. *Proc. Natl. Acad. Sci. USA* 95:6578-6583
- Wilhelm SW, Suttle CA (1999) Viruses and nutrient cycles in the Sea. *Bioscience* 49:781-788
- Wilson WH, Mann NH (1997) Lysogenic and lytic viral production in marine microbial communities. *Aquat. Microb. Ecol.* 13:95-100
- Winter C, Smit A, Herndl G, Weinbauer M (2004) Impact of virioplankton on archaeal and bacterial community richness in seawater batch cultures. *Appl. Environ. Microbiol.* 70:804-813
- Wommack, K.E., Colwell, R.R. (2000). Virioplankton: Viruses in aquatic ecosystems. *Microbiol. Mol. Biol. Rev.* 64: 69-114