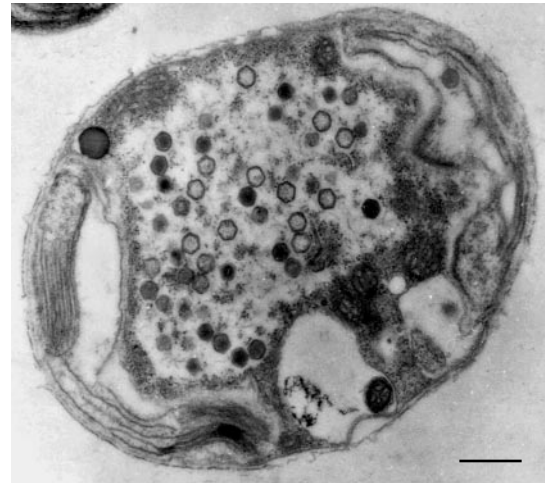
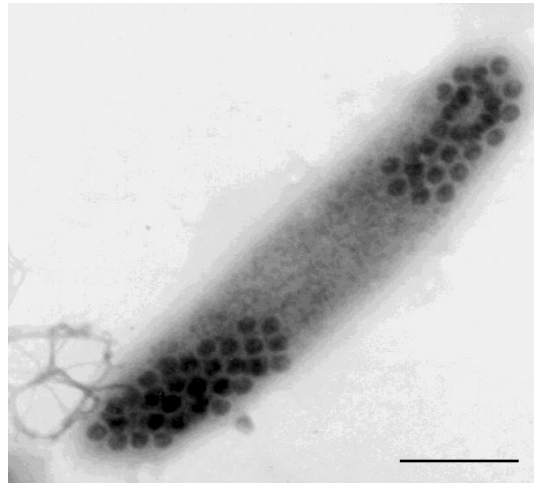


# Giant algal viruses: lubricating the great engines of planetary control

Willie Wilson

Many viruses have been isolated that infect marine eukaryotic phytoplankton. Some of these have the largest virus genomes known.



In a wonderful quote from *Light and Life in the Sea*, Paul Tett stated, 'the illuminated region is only a small part of the 3.7 km mean depth of the ocean yet it houses several of the great engines of planetary control'. It is well known that the absorption of heat energy by the ocean and light energy by tiny floating marine plants, known as phytoplankton, help to regulate many aspects of the global environment. Phytoplankton form the base of the marine food web and through their photosynthetic activity provide an important carbon sink which influences the global carbon cycle and even climate. If you find this difficult to believe then you only have to look at some of the compelling satellite images of massive phytoplankton blooms (<http://www.soes.soton.ac.uk/staff/tt/eh/satbloompics.html>), hundreds of square kilometres in area, that writhe spookily across the oceans. Of course, phytoplankton blooms don't last forever; they break down through a range of different processes such as simply running out of nutrients (known as 'bottom-up' control), being eaten by grazers ('top-down' control), or just sinking out as marine snow (see article by Carol Turley on pp. 177–179). Organic carbon produced in this breakdown process fuels heterotrophic bacterial production, which in turn drives nutrient flow and biogeochemical cycling through the marine microbial loop. Following the discovery of high concentrations of viruses in seawater reported in 1989 (up to  $10^8$  per ml), another breakdown process was added to the cogs of these great engines. Would this discovery throw a spanner in their works?

## ● Marine viruses

We now know that the majority of viruses in the ocean infect bacteria (Fig. 1), with numbers typically ranging from between 10-fold less and 10-fold more than bacterial concentrations, though usually dependent on trophic conditions. Over the last decade numerous reports have been made on the isolation

of different viruses that infect a range of marine eukaryotic phytoplankton. Most of these viruses belong to the family *Phycodnaviridae*, a group of viruses that infect eukaryotic algae, which have icosahedral symmetry and large dsDNA genomes ranging from 180 to 560 kb. Marine phytoplankton virus members of the *Phycodnaviridae* lie at the top end of this genome size range and represent the largest virus genomes known.

## ● History of algal viruses

Surprisingly, observations of phytoplankton viruses are not new. Numerous observations of 'virus-like' particles (VLPs) in eukaryotic algae were reported in the 1970s as well as many incidental reports of VLPs observed in thin-section ultrastructure studies of marine phytoplankton. For example, one ultrastructure report on natural phytoplankton, conducted in 1974 by Manton & Leadbeater, discussed that VLPs observed in *Chrysochromulina mantoniae* were apparently similar to VLPs commonly found in moribund or dead *Coccolithus huxleyi* (now referred to as *Emiliana huxleyi*) cells. Viruses were clearly openly discussed in these early papers; however, research into phytoplankton viruses never seemed to be followed up at the time. Just recently, I was shown some electron micrographs of thin sections of a marine *Pavlova* sp. that was full of hexagonal VLPs (Fig. 2). It was evident that this nutritious phytoplankton, often used as a food source for feeding zooplankton and shellfish in hatcheries, was in the latter stages of infection by a large virus. I was amazed to find that these exciting micrographs were actually prepared back in 1978! The VLP images had been 'filed' for long-term storage because there was no interest in phytoplankton viruses 25 years ago, perhaps surprising given the ecological implications of virus infection of the major oceanic primary producers.

TOP LEFT:

**Fig. 1.** Final stages of infection in a marine bacterium. The cell was harvested from a natural seawater sample directly onto a 400-mesh copper grid by ultra-centrifugation, then negative-stained with uranyl acetate. Bar, approx. 250 nm. COURTESY W. WILSON

TOP RIGHT:

**Fig. 2.** Final stages of infection in the marine phytoplankton *Pavlova vivescens*. Note the different stages of virus assembly in the cell cytoplasm. Samples prepared by thin-sectioning back in 1978! Bar, approx. 500 nm. COURTESY JOHN GREEN (NOW RETIRED, FORMERLY MBA, PLYMOUTH)

RIGHT:

**Fig. 3.** True colour satellite image of a high reflectance *E. huxleyi* bloom south of Plymouth, UK, on 30 July 1999. Water samples taken from this bloom contained up to 1 million *E. huxleyi*-specific viruses per ml. THE SEAWIFS IMAGE WAS PROCESSED BY THE PLYMOUTH MARINE LABORATORY REMOTE SENSING GROUP USING DATA FROM THE NERC DUNDEE SATELLITE RECEIVING STATION

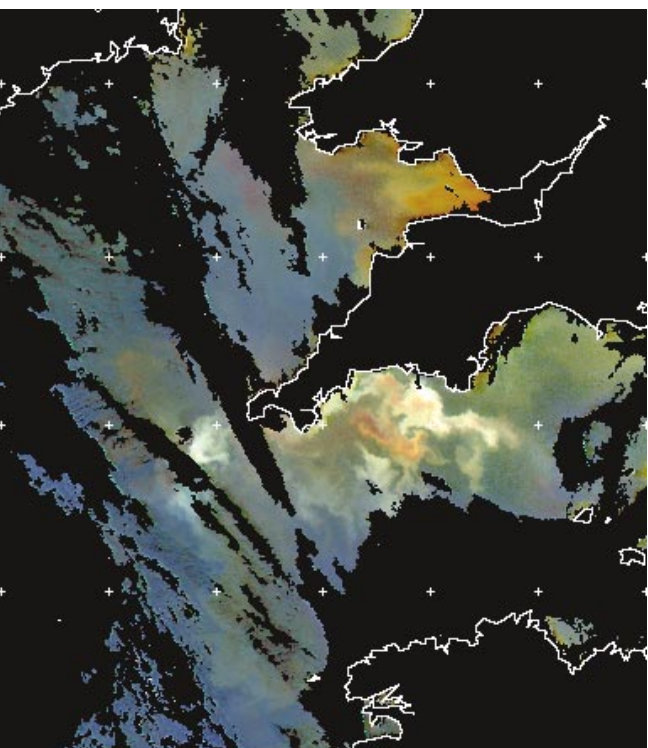


Despite a few reports of virus isolations between 1978 and 1982, it was not really until the early 1990s that research into phytoplankton viruses was taken seriously and started gaining momentum. Reports of high virus concentrations in seawater caused considerable excitement amongst biological oceanographers. It soon became clear that viral action on marine phytoplankton communities would go beyond the simple infect–replicate–kill cycle; their role would have far-reaching implications in determining microbial biodiversity, nutrient and energy flow, biogas production and global climatic control.

● ***E. huxleyi*-specific viruses**

Take for example, *E. huxleyi*, a marine coccolithophorid, which is well known for forming vast coastal and mid-oceanic blooms that can be easily seen from space. Following the sudden virus-induced death of *E. huxleyi* blooms we have measured high concentrations of dimethylsulfide (DMS). When pulses of DMS escape to the atmosphere it is oxidized into acidic compounds that form cloud condensation nuclei; this increases cloud formation and consequently affects global radiation.

Most years we see large blooms of *E. huxleyi* right on our doorstep in the English Channel, off Devon and Cornwall (Fig. 3). During these blooms we can easily isolate viruses that infect laboratory cultures of *E. huxleyi* (Fig. 4). This isolation data, taken together with biological data collected during the blooms,



suggest that viruses are responsible for the demise of these *E. huxleyi* blooms. Cycling of the carbon output through the microbial loop, following the bloom crash, ensures the succession from an *E. huxleyi*-dominated population to a more characteristic mixed summer phytoplankton community. Continuing with the ‘great engines’ analogy then these *E. huxleyi*-specific viruses could be seen as lubricants that ensure phytoplankton succession by killing one group to make room and provide nutrients for different groups.

During their characterization we discovered that the *E. huxleyi*-specific viruses belong to a new genus we have termed the *Coccolithovirus* (based principally on the phylogeny of their DNA polymerase gene), which is within the virus family *Phycodnaviridae*. With the addition of *Coccolithovirus* in the family, it questions the validity of some of the genera, even just something as simple as naming one of the genera ‘*Prymnesiovirus*’ is now wrong since *E. huxleyi* is a Prymnesiophyte, yet *E. huxleyi*-specific viruses do not fall into this genus. Clearly, the *Phycodnaviridae* will evolve into a large complex family or, more likely, split into several families as new algal viruses are isolated and characterized. Perhaps the reason for such complexity can be explained by a recent provocative paper that expanded this phylogenetic analysis and placed the *Phycodnaviridae* near the root of all eukaryotic DNA polymerases. It is believed that some of the first eukaryotic cells resembled unicellular green algae. If algal viruses appeared at around the same time and co-evolved with their hosts, then algal viruses could be dated back more than 1.2 billion years.

● **Ancient viruses?**

The genomes of two phycodnaviruses have been completely sequenced, a *Paramecium bursaria Chlorella*

ABOVE:  
**Fig. 4.** Virus attached to an *E. huxleyi* cell. Infected cells were dehydrated in an acetone series, oven dried and sputter coated with gold prior to viewing in a scanning electron microscope. The virus particle is approx. 190 nm in diameter.  
 COURTESY K. RYAN, MBA, PLYMOUTH

# Government funding of the scientific learned societies

## Further reading

*Emiliana huxleyi* home page:  
<http://www.soes.soton.ac.uk/staff/tt/>

Manton, I. & Leadbeater, B.S.C. (1974). Fine structural observations on six species of *Chrysochromulina* from wild Danish marine nanoplankton, including a description of *C. campanulifera* sp. nov. and a preliminary summary of the nanoplankton as a whole. *K Dan Vidensk Selsk Biol Skr* 20, 1–26.

Schroeder, D., Oke, J., Malin, G. & Wilson, W. H. (2002). *Coccolithovirus* (*Phycodnaviridae*): characterisation of a new large dsDNA algal virus that infects *Emiliana huxleyi*. *Arch Virol* 147, 1685–1698.

Van Etten, J.L., Graves, M.V., Müller, D.G., Boland, W. & Delaroque, N. (2002). *Phycodnaviridae* large DNA algal viruses. *Arch Virol* 147, 1479–1516.

Villarreal, L.P. & DeFilippis, V.R. (2000). A hypothesis for DNA viruses as the origin of eukaryotic replication proteins. *J Virol* 74, 7079–7084.

Wilson, W.H., Tarran, G.A., Schroeder, D., Cox, M., Oke, J. & Malin, G. (2002). Isolation of viruses responsible for the demise of an *Emiliana huxleyi* bloom in the English Channel. *J Mar Biol Assoc UK* 82, 369–377.

virus (PBCV-1) and an *Ectocarpus siliculosus* virus (EsV-1), and we are in the process of sequencing an *E. huxleyi* virus (EhV-86). Their genomes are 331 kb (PBCV-1), 336 kb (EsV-1) and 410 kb (EhV-86) with 376 (PBCV-1), 231 (EsV-1) and 493 (EhV-86) currently identified open reading frames (ORFs) that encode possible genes. In comparing the genomes of these three viruses, they only have nine genes in common, particularly surprising since they all come from the same virus family. This information alone indicates that algal viruses and their genes are ancient, which has allowed major differences in their sequence information to evolve. Consequently, studies on algal viruses should reveal interesting aspects about the evolution of genes and genomes.

## ● Future perspectives

As more researchers start investigating algal viruses it is inevitable that a much greater variety of viruses will be discovered. There are already reports of algal RNA viruses being isolated that have completely different characteristics and infection mechanisms to members of the *Phycodnaviridae*. We are clearly in the 'lag phase' of our understanding in algal virology and as new genomic technologies become more widely used in this field, I predict we will see an exponential rise in interest as the role of the many genes in these giant algal virus genomes become known.

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The Government provides substantial funding each year to the Royal Society (RS) (£29m) and the Royal Academy of Engineering (RAE) (£5m). The House of Commons Science and Technology Committee, chaired by Dr Ian Gibson MP, has recently published the report of its inquiry into whether good value for money is obtained. The inquiry – to which SGM submitted evidence – also ranged over a number of other aspects of the operations of scientific learned societies. As always with this Committee, the report is outspoken and provocative.

Most of the government funds provided to the RS and RAE are passed on to the scientific community in the form of research fellowships and awards. The inquiry concluded that these are highly regarded by the scientific community, and fund valuable work, but was unable to evaluate whether they were cost-effective in comparison with other schemes.

The Committee recognized that many of the 245 other scientific learned societies did excellent work, for example in providing scientific advice to government and in educational activities, while receiving no government funding. It recommended that government should make more extensive use of the expertise of these learned societies and provide adequate financial compensation for their efforts. Overall, the committee felt that government funding of the learned societies was haphazard rather than the product of strategic thinking in the Office of Science and Technology.

In a more controversial section of the report, the Committee expressed disappointment at the number of women among the fellows of the RS and RAE, their possible bias against newer scientific disciplines and universities other than London, Oxford and Cambridge, and a perceived lack of inclusiveness and transparency. The Committee was particularly critical of the way that Copus (formerly the Committee for the Public Understanding of Science) sits within the RS and the confusion and ill will that this has generated, and recommended that it be reformed as an entirely independent umbrella body for science communication efforts, receiving its funding direct from OST.

The full Report, written evidence and records of examination of witnesses are available at [www.parliament.uk/commons/selcom/s&thome.htm](http://www.parliament.uk/commons/selcom/s&thome.htm)

● **Ron Fraser, Executive Secretary**