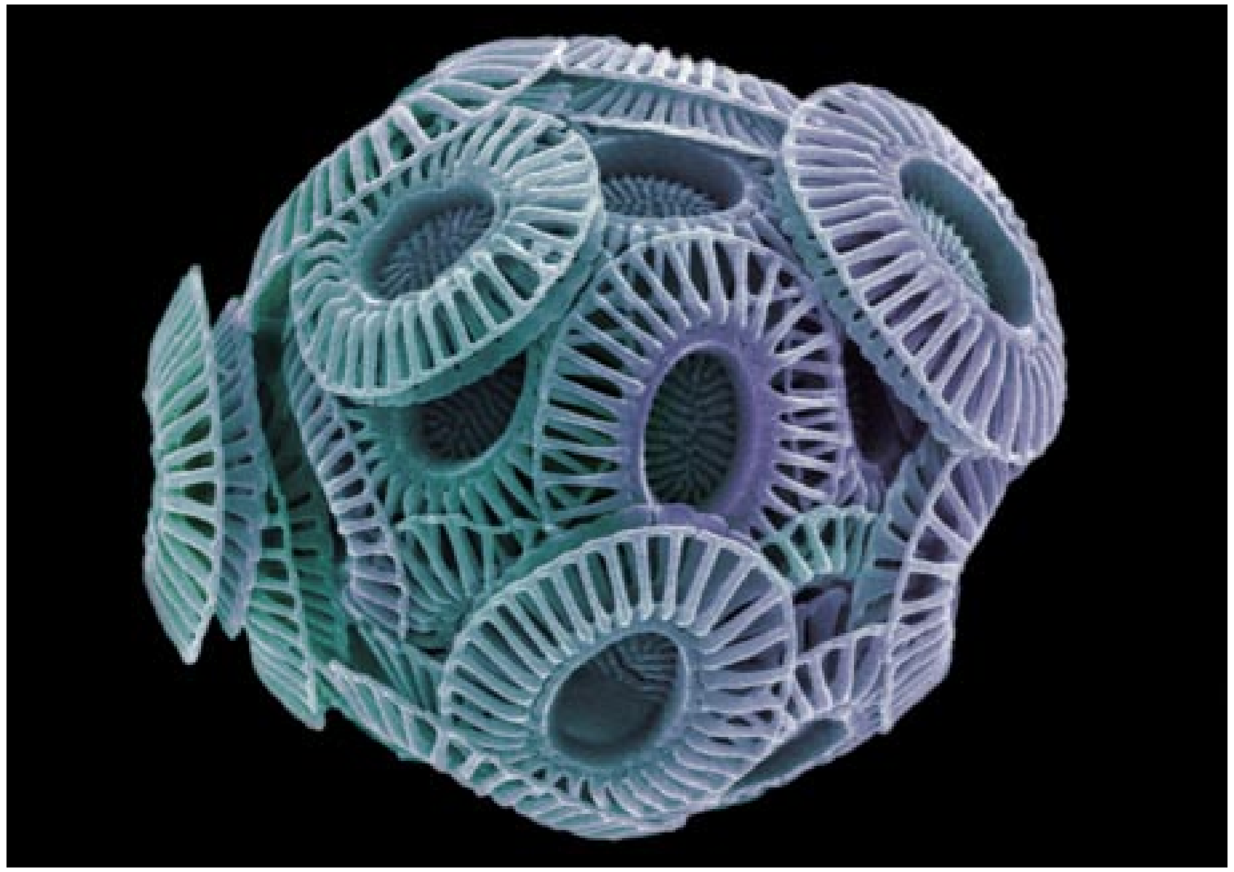
Microbes and oxygen

Where does all the oxygen on Earth come from? **Martha Clokie** explores the roles of cyanobacteria and microalgae in oxygen production and gives some surprising news about the input from viruses.



Two features that distinguish planet Earth from all other known planets are the presence of water on its surface and the oxygen in the atmosphere. The oxygen is a waste product of photosynthesis and all higher life on Earth is ultimately dependent on it. The microbial contribution to oxygen in our biosphere is often under-appreciated, but in this article I will discuss how microbes oxygenated and continue to oxygenate our planet. The microbes concerned are cyanobacteria and eukaryotic microalgae. The oceans, where oxygen-producing microbes predominate, can be thought of as forgotten tropical rain forests where at least 50 % of carbon fixation and consequent oxygen production is thought to occur. This article summarizes the evolutionary and natural history of these microbes and focuses on the surprising role of viruses in oxygen production.

Cyanobacteria oxygenated Earth's atmosphere

Cyanobacteria can be considered the largest wreakers of environmental havoc the Earth has ever experienced, probably causing in the past the demise of a large proportion of the bacteria and archaea that predominated before they came on the scene. Until around 2.6 billion years ago the Earth's atmosphere was largely composed of carbon dioxide, carbon monoxide, nitrogen and water. Plenty of non-oxygen-producing photosynthetic bacteria existed before cyanobacteria, generating chemical energy by using energy from light to remove an electron from available molecules and passing it through a chain of proteins to reduce molecules such as sulfur. Cyanobacteria adapted the photosynthetic machinery in many ways, including using water as their electron source and oxygen as their terminal electron acceptor. After their appearance, the atmosphere was gradually oxygenated to the current levels of around 21 % oxygen.

From cyanobacteria to photosynthetic phytoplankton

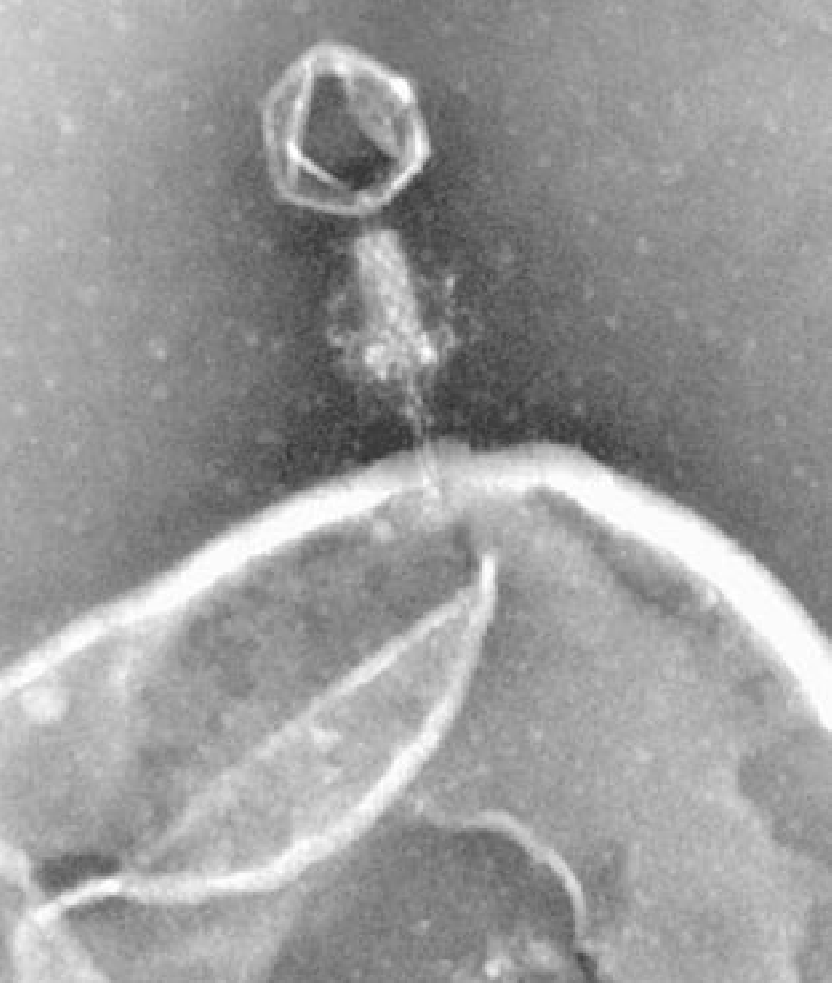
This oxygen-producing apparatus was only invented once, but it was then acquired by many lineages. The cyanobacteria were consumed by heterotrophic eukaryotes which retained their genome as a plastid. Further endosymbiotic and horizontal gene transfer events eventually gave rise to a plethora of lineages of primary producers that constitute the higher plants and the far more diverse algae, of which the photosynthetic phytoplankton are a subset.

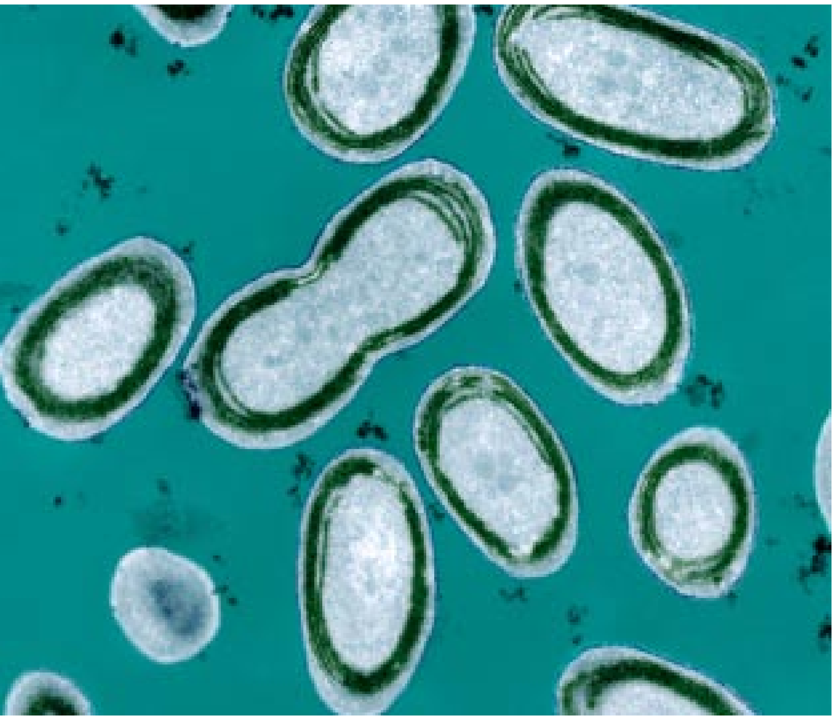
▲ Composite satellite image of Earth's western hemisphere, centred on the Atlantic Ocean. *NASA Earth Observatory / Science Photo Library*

◀ Coloured scanning electron micrograph of the haptophyte *Emiliana huxleyi*. *Steve Gschmeissner / Science Photo Library*

The key players in oxygen production

Despite all the acquisition and evolution of cyanobacterial genomes, cyanobacteria themselves remain important oxygen producers. Indeed marine cyanobacteria together with photosynthetic phytoplankton are thought to contribute equally to the global carbon fixation which amounts to half the total annual amount fixed, and therefore half the amount of oxygen produced. However, the identity and composition of the key players, particularly of the photosynthetic phytoplankton components, are poorly understood. These microbes are referred to as nanoplankton or picoplankton, depending on their size, and new classes are still frequently being discovered. Often this is based on molecular data





◀ Bacteriophage S-PM2 infecting a *Synechococcus* cell. *Stefan Hyman & Natalie Allcock, School of Biological Sciences, University of Leicester*

▼ Coloured transmission electron micrograph of a section through *Prochlorococcus* cells. *Claire Ting / Science Photo Library*

and they are difficult to isolate from the oceans and to culture. Important algal contributors to open ocean carbon fixation are the green algal flagellates, the heterokonts (a diverse group including the diatoms) and the haptophytes (including the calcite-precipitating *Emiliana huxleyi*); both these groups have red algal plastids.

Cyanobacterial distribution

As less is known about the distribution of photosynthetic phytoplankton, I will focus on the cyanobacteria which are found in most places where water exists, playing important environmental roles such as stabilizing desert sand for the colonization of other plants. They thrive in fresh water, salt lakes and hot springs, but are most numerous in the oceans where up to a million cells may be present per millilitre of sea water. By virtue of extremely efficient light-harvesting and nutrient-assembling machineries, surprisingly just two genera, *Synechococcus* and *Prochlorococcus* dominate the nutrient-poor oligotrophic areas of the open ocean where higher plants and even microalgae cannot survive. Their distribution changes according to ocean temperature, light availability and nutrient status. *Synechococcus* is the hardier of the two and it dominates in water with a latitude of more than 40°; *Prochlorococcus* is the softer cousin and is numerically superior in warmer waters.

Molecular studies based initially on ribosomal DNA and subsequently on whole-genome analysis have allowed us to further understand the relationships, distribution and physiology within *Synechococcus* and *Prochlorococcus*. Both genera can be divided into multiple clades or lineages. *Prochlorococcus* lineages are primarily correlated with light availability; the distribution of *Synechococcus* clades is less clear, but they are correlated to some extent with nutrient status and the temperature of the water column.

Oxygen-producing physiology

The proteins at the heart of the photosynthetic machinery where light energy is converted into chemical energy are called D1 and D2. They are encoded by the genes *psbA* and *psbD*. In a normally functioning cyanobacterium or plant there is a high turnover of these proteins, in particular D1. They are damaged by light, so new copies are constantly being generated and inserted into the photosystem to maintain active photosynthesis. Unlike higher plants, some cyanobacteria have multiple copies of the *psbA* gene. Different versions are used under specific environmental conditions with some versions being more efficient when the cyanobacteria are light-, temperature- or nutrient-stressed, and this allows them to survive where photosynthetic phytoplankton cannot.

Viruses and oxygen production

A twist on microbial oxygen production comes from our recent appreciation of the role of viruses in cyanobacterial ecology. Marine cyanobacteria are constantly under attack by viruses, and the turnover rates are thought to be as high as 50 % of all cyanobacteria lysed each day. The dynamics of viral infection are not uniform; many cyanobacterial viruses appear to be dependent on light to absorb to their hosts. Both cyanobacterial and algal viral infection are dependent on efficient photosynthesis for viral replication to occur.

Information from virus genome sequencing has revealed the presence of key genes involved in photosynthesis, including those which encode D1 and D2. This was a huge surprise as photosynthesis was not considered to be something that viruses could do. The viral versions of the gene are highly conserved at the amino acid level, but vary considerably at the nucleotide level. Phylogenetic analyses indicated that these genes originated in cyanobacteria and were subsequently acquired by viruses.

It appears that after the viruses infect the cyanobacteria, they shut down host photosynthesis machinery and provide their own alternative versions of the proteins necessary to maintain photosynthesis. This provides the viruses with enough energy to replicate.

Viruses: friends or foe?

It is not known how efficient the virus-encoded photosystem is compared to that encoded by the cyanobacteria. Modes of cyanobacterial viral infection are complex and they may infect and express their genes but not cause cell death in a process known as pseudolysogeny. During pseudolysogenic infection, cells expressing the viral version of *psbA* may be more efficient photosynthesizers than those with the cyanobacterial versions. Thus the viruses are acting as pseudosymbionts. Infected cyanobacteria will then reproduce more efficiently than uninfected cells, thus producing both more cyanobacteria and more viruses. A further unresolved question is. are viruses capable of 'donating' their versions of *psbA* back into the cyanobacterial community? Finally, are there parallels in the algal world? As I pointed out above, we are still unclear about many of the most important microalgal groups, let alone the composition and importance of their viral community. Viruses that have been studied have large complex genomes which suggests that they play multiple roles in host physiology.

Final thoughts

I have briefly described the who, when, where and the how when it comes to microbial oxygen production. I will leave you with the back of the envelope calculation that leads us to tentatively speculate that if half of the oxygen produced per year occurs in the oceans, and half of this is derived from cyanobacteria of whom half are infected by viruses at any one time, then up to one-eighth of the total oxygen we breath may have passed through the photosystem encoded by a virus.

Martha Clokie
Department of Infection, Immunity and Inflammation, Medical Sciences Building, University of Leicester,
PO Box 138, Leicester LE1 9HN,
UK (t 0116 2522959; e mrjc1@leicester.ac.uk)

Further reading

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