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The role of the virus-phytoplankton system in marine biogeochemical cycling: possible impacts of climate change

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Introduction

Phytoplankton is the main driver of ocean net primary production (Falkowski *et al.*, 1998) and a dominant force behind biogeochemical cycling in the ocean. It is a component of one of the oldest and best described virus-host relationships (e.g. Suttle *et al.*, 1990).

Viruses have typically been viewed as pathogens of marine organisms but it has become clear that they also play a critical role in biogeochemical processes in marine systems, themselves falling into the category of dissolved organic matter (DOM) (Wilhelm & Suttle, 1999). Viruses play a large part in carbon (Middelboe & Lyck, 2002), sulphur (Hill *et al.*, 1998) and iron cycling (Poore *et al.*, 2004) in the world's oceans.

Earth's climate has warmed by approximately 0.6°C during the last 100 years. The rate of warming has doubled in the second half of the century (Houghton, 2001). This rapid change has been attributed to the impact of anthropogenic activities on the atmosphere. Climate change is already affecting marine ecosystems and more extreme changes are predicted for the future (Walther *et al.*, 2002).

Whilst a number of studies have examined the effects of climate variables on phytoplankton, it is unclear how marine viruses are affected by these changes. This is important because of the close relationship between viruses and their phytoplankton host. This review will outline the nature of phytoplankton and marine viruses, with a virocentric bias. Relevant biogeochemical cycles and the impact of climate change are described and the possible effects of the altered environment on the phytoplankton-virus system are considered.

Phytoplankton & Virus Overview

Phytoplankton

Phytoplankton comprises single-celled, photoautotrophic organisms in 12 taxonomic divisions and spanning three Kingdoms. Phytoplankton is an ancient group; cells similar to extant cyanobacteria have appeared in the fossil record 3.45 x 10⁹ years ago. Its diversity and highly conserved metabolic pathways has allowed phytoplankton to adapt to environmental change on geological timescales and continue to be successful. In steady state, phytoplankton production is balanced by mortality due to grazing, viral attack, autocatalysed cell death and sinking below the euphotic zone (Falkowski *et al.*, 1998). However, some species form large blooms where numbers reach unsustainable levels and collapse (“boom-bust” cycles) causing the massive release of organic and inorganic matter into the water column. It is this that drives many biogeochemical cycles (see Box 1 for definitions). Thingstad (2000) proposed a model where phytoplankton diversity is maintained by ‘killing the winner’; the most abundant or successful organism is a target for regulatory mechanisms such as viruses and grazers. The causes behind the collapse of phytoplankton blooms are unclear, although it is now widely accepted that bloom termination is most likely caused by large scale viral infection, the effects of grazing should not be overlooked. In naturally occurring phytoplankton populations Kimmance *et al.* (2007) found that the rate of viral lysis was low (<0.1 d⁻¹) and microzooplankton grazing was the main source of mortality during a study of natural blooms. However, the most likely theories involve the combined effects of grazing and viral lysis in bloom collapse.

Some species of cyanobacteria and bacterioplankton form blooms in oligotrophic waters with relatively low densities due to nutrient limitation, slow growth rates and grazing pressure (Jackson, 1980). This review will only address large-scale phytoplankton blooms in coastal or eutrophic waters, where nutrient levels are high enough to support their large biomass. Viral infection has a major impact in these systems, as discussed below.

Marine viruses

Viruses are the most abundant members of the marine ecosystem (Suttle, 2005). Current estimates range from 3 x 10⁶ ml⁻¹ in the deep sea to 10⁸ ml⁻¹ in coastal waters, making them the second largest component of biomass after prokaryotes (Suttle, 2005). There is also high viral abundance in surface marine sediment, with a mean concentration of 0.96 x 10⁹ g⁻¹ (Danovaro *et al.*, 2008). Viruses are small (~100 nm), obligate, transmittable parasites that direct viral replication by the synthesis of virion components within an appropriate host cell (Brussaard, 2004). Viruses are genetically and biologically diverse, with a multitude of different morphotypes and no universally conserved viral gene (Suttle, 2005).

Viruses have a variety of reproductive strategies, including lytic and lysogenic infection. In lytic infection strategies, the virus injects its nucleic acid into the host cell, directing it to produce numerous progeny viruses which are released by fatal bursting of the cell. In lysogenic infections, the nucleic acid of the viral genome becomes part of the host cell and reproduces in the host

cell line. An induction event, such as stress to the host, can trigger a switch to lytic infection (Fuhrman, 1999).

Viral lysis is a very different process to grazer-mediated cell death, releasing the total cell contents into the water column. Some of these products require the action of enzymes or UV radiation to make them biologically labile. Grazing causes the release of inorganic nutrients which differ in nature to viral lysates (Wilhelm & Suttle, 2000). Thus, whether cells are grazed or lysed has significant biogeochemical implications due to changes in the flow of matter through the microbial loop (Evans *et al.*, 2003). There are also ecological differences: grazers may exhibit a preference for certain prey (e.g. Epstein & Shiaris, 1992) but this is insignificant when compared to the high specificity of viral infections. The processes that are driven by phytoplankton-virus interactions will now be addressed.

Box 1 Glossary of terms

Analytical Flow Cytometry (AFC)- a technique for counting, examining, and sorting microscopic particles suspended in a stream of fluid.

Aphotic- layer of the water column where there is little or no sunlight.

Biogeochemical cycle- pathway by which a chemical element or molecule moves through both biotic and abiotic compartments of Earth.

Carbonate pump- processes associated with the production and dissolution of marine calcifying organisms.

CDOM- coloured dissolved matter; the optically measurable component of dissolved organic matter, mainly entering the ocean via terrestrial runoff in coastal areas, strongly absorbs short wavelength light.

CLAW hypothesis- suggests that a homeostatic feedback mechanism exists between oceanic phytoplankton and climate through the production of DMS.

Degenerate primers- mixtures of similar primers (nucleic acid serving as the starting point for DNA replication) often used if the same gene is to be amplified from different organisms.

DOM- defined as the material passing through a 0.2 or 0.4 μm pore-size filter.

DMS- $(\text{CH}_3)_2\text{S}$; an organosulfur compound derived from the enzymatic cleavage of DMSP (See CLAW hypothesis).

DMSP- $(\text{CH}_3)_2\text{S}^+\text{CH}_2\text{CH}_2\text{COO}^-$; produced in high concentrations in marine phytoplankton.

Emiliania huxleyi- single celled, photosynthetic, member of the coccolithophorids, a biogeochemically important phytoplankton group.

Euphotic- layer of the water column which is exposed to sufficient light for photosynthesis to occur.

Mesocosm experiment- an experimental system that simulates real-life conditions as closely as possible, whilst allowing the manipulation of environmental factors.

Microbial Loop- a trophic pathway in aquatic environments where DOC is reintroduced to the food web through incorporation into bacteria.

Ozone layer- a layer in Earth's atmosphere containing high concentrations of ozone (O_3) which absorbs 93-99% of the sun's UV radiation.

Partial pressure- the pressure which a gas would be if it alone occupied the volume occupied by a mixture of gasses.

pH- measure of the acidity or basicity of a solution, measured on a log scale.

POM- defined as the material retained by a 0.2 or 0.4 μm pore-size filter.

Redfield Ratio- C:N:P=106:16:1. The global elemental composition of marine organic matter is fairly constant in all areas and between coastal to open ocean regions.

Siderophores- mainly non-ribosomal peptides which form soluble Fe^{3+} complexes that can be taken up by organisms active transport mechanisms.

Solubility pump- physicochemical process that transports carbon, as DIC, from the ocean's surface to its interior.

Biogeochemical Cycles

The carbon cycle

All organisms store energy in the form of chemical bonds within carbon-based complexes. It is estimated that the atmosphere and surface ocean contain 780 Gt C and 1,000 Gt C respectively (Robinson *et al.*, 2007). Phytoplankton is responsible for the vast majority of photosynthesis and carbon production in the sea. Viruses themselves contain around 0.2 fg of carbon, which translates into 200 Mt C in marine viruses alone (Suttle, 2005).

Organic carbon in marine systems can be broadly separated into dissolved organic carbon (DOC) and particulate organic carbon (POC). These two pools of carbon behave differently. Most DOC is recycled in the microbial loop and subsequently not transferred to higher trophic levels, whereas most POC is directly transferred to higher trophic levels by grazing. Viral lysis diverts carbon from the POC to the DOC pool, effectively 'short-circuiting' the microbial loop away from the grazers. This DOC is composed of a variety of cellular materials, including nucleic acids and proteins (Proctor & Fuhrman, 1991). Some structural materials may be more refractory to biological assimilation and cycle in a manner more similar to POC; hence viruses can control the speciation of carbon in the water column. Viral lysis and the subsequent regeneration of DOC can increase bacterial abundance 10-fold (Gobler *et al.*, 1997), leading to an increase in bacterial production but a decrease in the transfer of carbon to higher trophic levels (Fuhrman, 1992). Many estimates of viral fluxes may be inaccurate as it cannot be assumed that all marine viruses are active or infective. The molar ratio of C:N:P 106:16:1 is known as the Redfield ratio (Redfield, 1934) and tends to be roughly constant in phytoplankton tissue. Viral lysis may alter the ratio of these elements, particularly carbon, in water, with implications for primary productivity and biogeochemical cycles (e.g. Gobler *et al.*, 1997).

The sulphur cycle

The ocean contributes over 30% of the atmospheric sulphur budget (Nguyen *et al.*, 1978). Phytoplankton is a key synthesiser of the volatile, biogenic, organosulphur compound dimethyl sulphonium propionate (DMSP), the precursor to dimethyl sulphide (DMS). DMS is a gas that influences cloud nucleation and thus the radiative balance of the earth (Chin *et al.*, 1996). DMS accounts for over half of all non-anthropogenic gaseous sulphur inputs to the atmosphere and is the most abundant volatile sulphur compound in seawater (Hill *et al.*, 1998).

The release of DMSP from intact algal cells is quantitatively insignificant (Bratbak *et al.*, 1995). Zooplankton grazing and viral lysis are reported to be involved in DMS production through the release of algal DMSP to the dissolved pool where it is rapidly converted to DMS by bacteria possessing DMSP lyase (Niki *et al.*, 2000). Viral lysis can lead to the rapid, total, release of DMSP to the dissolved pool (Hill *et al.*, 1998). However, Bratbak *et al.* (1995) concluded that in order to overcome dissolved DMSP (DMSP_d) bacterial degradation rates, the rapid collapse of large blooms must occur and only in these conditions would viral lysis represent an efficient mechanism of net DMSP and DMSP_d production in seawater.

The iron cycle

Iron appears to limit primary productivity in large areas of the ocean, known as high-nutrient, low-chlorophyll regions (Hutchins, 1995). Due to its stability in multiple valencies, iron is an integral component of many enzymes involved in photosynthesis, electron transport and nutrient acquisition (Wilhelm & Suttle, 1999). However, iron is not always bioavailable. When in contact with seawater, iron rapidly forms iron hydroxide Fe(III), which has an extremely low solubility. The solubility and bioavailability of Fe(III) can be controlled by organic complexation. Rue and Bruland (1997) found that iron can be kept solubilised, and thus potentially available as low-molecular weight, soluble Fe(III)-chelates, rather than precipitating in colloidal form and aggregating. Siderophores are ferric ion specific chelating agents elaborated by some phytoplankton. Their role is to scavenge iron from the environment and to make it available to the microbial cell (Neilands, 1995). Photoreactions of complexed iron also enhance its biological availability, a process that may stimulate productivity in parts of the sea that are iron limited (Zepp *et al.*, 2003). Iron availability may therefore increase with higher solar UV due to climate change and ozone depletion.

Viral lysis releases intracellular iron into the dissolved phase at a greater rate than it is released from cells in the absence of phages. This iron can be rapidly assimilated by other plankton (Poorvin *et al.*, 2004). Mioni *et al.* (2005) found that organic Fe complexes released during viral lysis are ca. 1000 times more bioavailable and efficiently assimilated by bacterial cells than Fe(III). Viral lysis is therefore important in the regeneration of bioavailable iron species and may provide an important fraction of total bioavailable iron.

Phytoplankton Exudation & Cell Lysis Products

Healthy phytoplankton cells exude dissolved organic matter (DOM), the function of which is unclear. It has been suggested that phytoplankton exudation could be a tactic to increase the biomass of bacteria or small flagellates and thus decrease the population of marine viruses (Murray, 1995).

Viral lysis contributes to the physical 'gel' characteristics of sea water through the release of polymers which can facilitate aggregation and sinking of material from the euphotic zone (Peduzzi & Weinbauer, 1993). These particles may be "hot spots" for viral infection (Mari *et al.*, 2007), converting some sinking particulate organic matter (POM) into non-sinking DOM at the depth lysis occurs (Proctor & Fuhrman, 1991). This could lead to a more uniform distribution of cell lysis products within the water column.

Impacts of Climate Change

The primary climate change factors that will be addressed in this review are: increased UV radiation, increased CO₂ and changes to mixing processes. Temperature has been shown to affect the distribution and abundance of phytoplankton (Hays *et al.*, 2005), however, there is currently no evidence that it is likely to affect marine viruses in the same way and will therefore be omitted from this review. Figure 1 shows a basic conceptual diagram of the phytoplankton-virus system discussed and some possible impacts of the aforementioned variables.

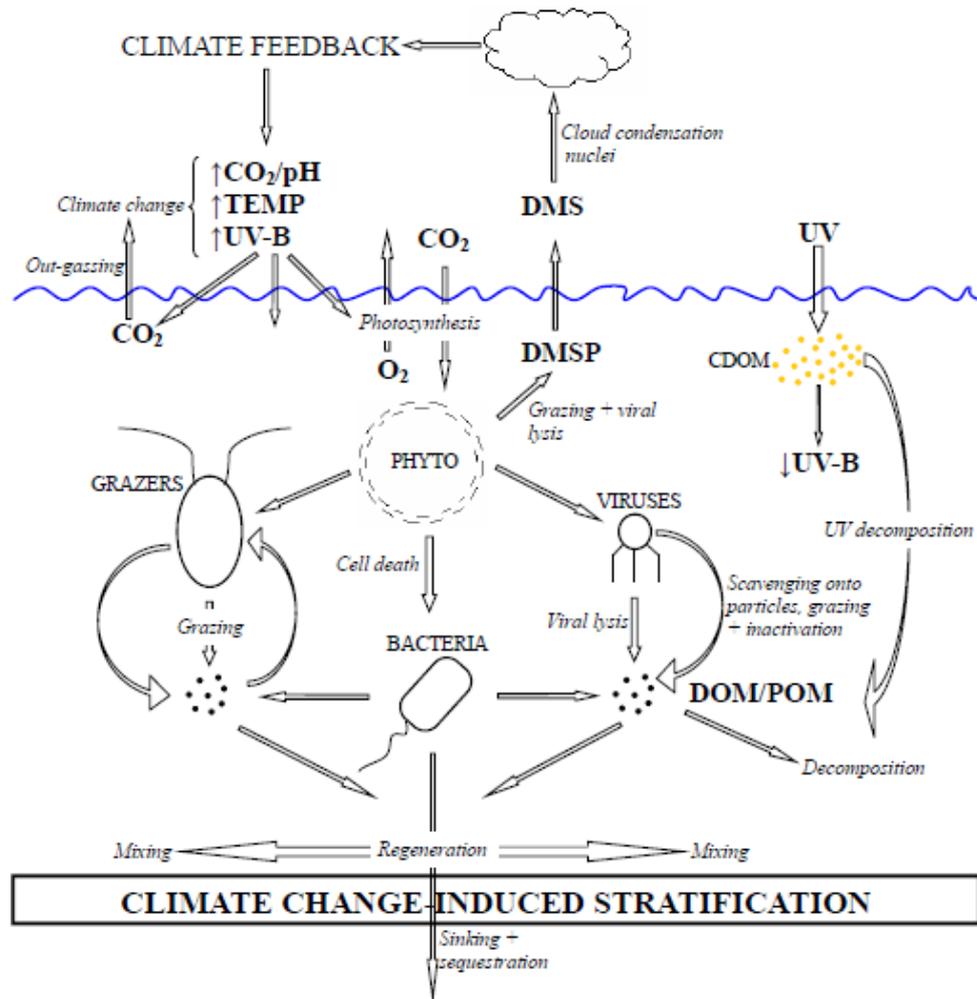


Figure 1. – A basic conceptual diagram showing some ways in which the phytoplankton-virus system affects biogeochemical cycles and possible impacts of climate change.

Impacts of increased UV radiation

Ozone depletion is caused by the release of gases that catalytically destroy ozone; a separate factor to climate change but it is clear that climate change interacts with ozone depletion (Kelfkens *et al.*, 2002). The effects of climate change on UV radiation are due to its influence on total ozone. Climate change also affects UV radiation through influences on other variables such as clouds and snow cover (McKenzie *et al.*, 2007).

The consequences of increased solar UV radiation due to stratospheric ozone reduction are not well understood (Caldwell & Flint, 1994). Solar UV-B radiation (280–320 nm) has been shown to have deleterious effects on photo-autotrophs, including inhibition of photosynthesis, growth and mutagenesis. These effects occur in spite of efficient means of algal defense such as avoidance, screening and repair (Jacquet & Bratbak, 2003). UV-A (320-400 nm) may have some positive effects; as an energy source for photosynthesis or in DNA repair mechanisms (Häder *et al.*, 2007).

Viral activity and distribution in the euphotic zone is known to be sensitive to UV-B exposure (Wilhelm *et al.*, 1998). Viruses do not have effective sunscreens or photo-repair capabilities and, as a consequence, are prone to solar UV damage. The peak deactivation wavelength of nucleic acids is around 300 nm (UV-B) (Murray & Jackson, 1993) but the presence of viruses may provide some protection, through an unknown mechanism, to their phytoplankton hosts (Häder *et al.*, 2007). Contrary to previous assumptions, it appears that most pelagic viruses are infective in surface waters because of efficient repair and mixing processes that reduce DNA damage accumulation (Jacquet & Bratbak, 2003). Wilhelm *et al.* (2003) found that UV-induced damage was a result of prolonged exposure and subsequent DNA damage accumulation. It seems probable that different phytoplankton hosts and viruses have different degrees of sensitivity to UV-B radiation (e.g. Jacquet & Bratbak, 2003). This has implications for phytoplankton-virus community dynamics, and thus biogeochemical cycles, due to their varying abilities to cope with increased solar UV-B radiation as a result of climate change. Significantly, Weinbauer *et al.* (1999) found laboratory isolates to be poor proxies for UV impacts on natural viral communities, so caution must be exercised when relating these results to large-scale systems.

UV-B accelerates the decomposition of coloured, dissolved, organic matter (CDOM) in the ocean, influencing oceanic carbon cycle dynamics. CDOM plays an important role in the attenuation of solar UV radiation (Siegel *et al.*, 2002). It effectively protects aquatic ecosystems from harmful UV-B radiation whilst permitting UV-A and photosynthetically active radiation to be efficiently transmitted into the water (Zepp *et al.*, 2003).

Impacts of increased CO₂

Atmospheric CO₂ levels are currently around 387 ppm, up almost 40% since the industrial revolution, the highest for 650,000 years (Williams, 2008). A feedback mechanism exists where atmospheric CO₂ causes warming, which decreases the solubility of CO₂ in water and thus exacerbates the warming trend by weakening the ability of the oceans to buffer the carbon-climate system ('solubility pump'). The decrease in CO₂ solubility in the ocean, and its subsequent release, known as out-gassing, may cause world CO₂ to increase by 30% per 0.5 °C (Robinson *et al.*, 2007).

Phytoplankton photosynthesis lowers the partial pressure of CO₂ (pCO₂) in surface waters, promoting the drawdown of atmospheric CO₂. Some species form CaCO₃ shells, which sink and are dissolved at depth, leading to a sub-surface maximum of dissolved inorganic carbon, a process known as the 'carbonate pump' (Falkowski *et al.*, 2000).

The response of marine viral populations to elevated pCO₂ has been overlooked in the past. Larsen *et al.* (2008) found some viral populations were present or absent at different pCO₂ levels. Viral abundance decreased significantly with increasing pCO₂, despite their hosts showing the opposite response and increasing in abundance, suggesting that reduced viral concentration is an effect of altered host-virus interaction or changes in viral replication. The study data are not significant enough to prove such a strong conclusion and the lack of supporting research makes this hypothesis tentative. The suitability of enriched gas experiments as a model has been questioned and experimental methods are a topic of debate (e.g. Iglesias-Rodriguez *et al.*, 2008).

Emiliana huxleyi has layers of protective calcite plates, known as coccoliths, which have been speculated to afford some protection against viral attack (e.g. Young, 1994). Increased pCO₂ may cause coccolith malformation and reduced calcification in *E. huxleyi* and other marine phytoplankton (Riebesell *et al.*, 2000). It is therefore possible that virus attachment and production could be interfered with due to changes in coccolith structure. *E. huxleyi* calcification varies on the individual level; and coccolith formation can also be related to reproductive stage (Frada *et al.*, 2008). Consequently it is extremely difficult to draw solid conclusions when relating coccolith structure to other variables. This is demonstrated by the discrepancies in recent literature with some research finding increased calcification with increased pCO₂ (Iglesias-Rodriguez *et al.*, 2008) and others; reduced calcite production (e.g. Zondervan *et al.*, 2001). Bias may be introduced when examining coccolith malformation with microscopy as it is possible to find deformed individuals under all conditions.

Viruses are known to have varying tolerances to pH. However, the adsorption of marine phages is only affected by pH values deviating from that of seawater (Weinbauer, 2004). CO₂ may therefore result in less effective phytoplankton viruses. The uptake of anthropogenic CO₂ by the ocean is predicted to drive seawater pH to the lowest levels in the past 20 million years by the end of this century (Royal Society, 2005), reducing pH by about 0.35 (Bernard *et al.*, 2008).

It is possible that extreme ocean acidification in the future could affect the microbial food web at the viral level. The use of degenerate primers and analytical flow cytometry limited the specificity of the conclusions in the Larsen *et al.* (2008) study; nevertheless it suggests the existence of a relationship that warrants further study. Mesocosm experiments may diverge when starting conditions are identical, strongly dominating observed variations (Martinez-Martinez *et al.*, 2006). Therefore precautions must be taken to ensure the realism of these experiments before relating them to large-scale processes.

Impacts of physical processes

Physical factors are important in determining the dynamics of biogeochemical cycles, as well as the residence time of viruses in surface waters. The euphotic zone is the region where most biological activity occurs and where physical processes most actively move water vertically. Vertical movement of a virus alters its exposure to solar UV radiation, due to the attenuation of light with depth (Murray & Jackson, 1993). Anthropogenic global warming could lead to increased stratification of the water column (Sarmiento *et al.*, 1998). This may reduce vertical carbon transport, reducing the sequestration of carbon in the deep ocean (Falkowski *et al.*, 2000). Virus survival increases with mixed layer depth, depending largely on virus UV sensitivity (Murray & Jackson, 1993). The frequency and severity of extreme weather events will be altered by climate change and, in turn, affect the intensity of ocean mixing (Hays *et al.*, 2005). The interaction between UV and physical processes is likely to be immaterial in deep sea or aphotic benthic virus communities due to the lack of light penetration. However, changes in ocean circulation may occur as a consequence of climate change, potentially affecting benthic and deep pelagic viruses. Physical factors alone are unlikely to have a significant impact on marine viruses but, when coupled with climate change-related changes in solar UV radiation and CO₂, the effects may be more significant.

Induction of the Lytic Cycle

Induction of the lytic cycle commonly occurs following stimulation of a lysogenic cell by an environmental factor (Jiang & Paul, 1996). These inducing factors may increase in magnitude and prevalence with climate change. In surface seawater, UV light is a significant factor in inducing the lytic cycle (Noble & Fuhrman, 1997). It seems unlikely that climate change-related temperature increase alone would have a significant effect on the termination of lysogeny in the marine environment (Wilson & Mann, 1997). Jiang and Paul (1998) found that lysogenic viral production contributes less than 0.02% of total viral production but could contribute significantly to viral production during natural induction events. Large scale induction events could contribute a larger amount to total virus production and upset virus-induced mortality in marine systems.

Conclusion

Climate change has the potential to affect marine ecosystems in several ways including changes in solar UV radiation, atmospheric CO₂ and physical processes. The complex nature of ocean-climate interactions makes accurate experimental simulations of the effects of anthropogenic climate change on marine ecosystems very difficult. Marine viruses are diverse in their response to climate change variables. Although their responses may differ on an individual level, it can be concluded that a rapid, extreme, change in climate will have an effect on marine viruses, either directly or through effects on their hosts. Any significant effect on the virus-host system is likely to have an influence on biogeochemical cycling in the ocean, possibly mediated by climate-induced changes to variables such as ocean circulation. The possible susceptibility of biogeochemically important phytoplankton groups to climate

change-mediated processes may have a significant effect on ocean chemistry. In the short term, changes due to climate change are likely to be small and only affect the most sensitive organisms, others that are not on the edge of their physical limits may adapt. The main effects of climate change may influence the biogeochemical cycles directly due to the extreme sensitivity of chemical speciation to changes in variables such as temperature and pH. Whether climate change will affect the virus-host system favourably or adversely is uncertain. The relationship between many complex, interdependent factors makes predictions highly speculative given the current level of knowledge.

Further Research

Future work should employ a multi-disciplinary approach, tackling each variable specifically, before examining their interactions. Modelling studies are vital, in addition to experimental data, to pinpoint research efforts. Sea-ice brines have recently been recognized as areas of high viral abundance (e.g. Wells & Deming, 2006) and are extremely sensitive to climate change. More research is required to assess possible impacts on this system.

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