Viral Infection in Marine Phytoplankton: Consequences for Carbon Cycling and the Biological Pump

Context and Objectives: The microbiome is fundamental to ocean functioning, driving most of biogeochemical transformations and ultimately regulating climate. At the ocean's surface, photosynthetic microbes (phytoplankton) mitigate rising CO_2 levels by converting it into organic carbon through photosynthesis. This newly generated organic carbon then fuels the microbial network and higher trophic levels, or reach the sediment mostly through sinking aggregates where it can be sequestered for millennia. The efficiency of this vertical transfer of carbon, also known as the **biological carbon pump (BCP)**, varies greatly depending on the type of photosynthetic organisms, their life strategies, and mortality processes[1,2].

Although long overlooked, **viruses** are now recognized as significant contributors to phytoplankton mortality, responsible for 50% of phytoplankton death globally through cell lysis[3,4,5,6]. As such, viruses are thought to play a key role in modulating biogeochemical processes mediated by phytoplankton. However, the fate of phytoplankton-derived carbon and the cascading effects of infection on biological carbon pump (BCP) efficiency remain debated, as carbon can be redirected through two opposing pathways: the viral 'shunt' or 'shuttle'[7].

The **'viral shunt' hypothesis** suggests that viral infection **slows** BCP. Through lysis, viruses divert phytoplankton-derived carbon away from higher trophic levels, transforming it into labile dissolved organic matter that is readily utilized by bacteria. This shift in organic matter would reduce production at higher trophic levels, generating fewer particles along the food chain and favoring the microbial network and carbon remineralization instead[8]. Additionally, two studies report that viruses, by hijacking the metabolism of their photosynthetic hosts, reduce their ability to fix CO_2 during infection[9,10]. This phenomenon could account for up to 10% of marine primary production for cyanobacteria alone.

Conversely, the **'viral shuttle' hypothesis** suggests that viral infection may **facilitate** carbon export by increasing the sedimentation of infected hosts[11], promoting spore formation[12,13], and enhancing aggregation during infection and lysis[14]. These studies are supported by observations of a significant correlation between carbon export efficiency and viral genes, including genes of phytoplankton viruses[15,16]. While these observations do not provide quantitative data, they collectively suggest that viral infection could accelerate BCP.

Virus research has fundamentally reshaped our understanding of marine food webs and biogeochemical cycles. However, the quantitative impact of viruses on the flux of carbon derived from microbial hosts remains unclear. **This PhD project aims to assess the magnitude, direction, and variability of biogeochemical fluxes linked to viral infection in ecologically relevant phytoplankton species using a multi-scale approach.**

Scientific Strategy: This project proposes to test the hypothesis that the viral impact on the BCP varies with the infected phytoplankton species and environmental conditions. It will focus on three dominant, cosmopolitan species—*Mediolabrus comicus* (diatom), *Micromonas commoda* (green picoalga), and *Synechococcus sp.* (cyanobacterium)—for which viruses have been isolated, characterized, and are maintained at the Roscoff Culture Collection. These virus–phytoplankton pairs will be used to assess how infection alters three key BCP processes—carbon fixation, remineralization, and export—across scales, from populations to ecosystems. The study is structured into three dedicated tasks:

- **Measuring the impact of viral infection on C fixation (Year 1)** - Parallel incubations with $NaHCO_3$ labeled with ^{13}C (99%) will assess C incorporation rates. After viral inoculation, labeled substrates will be added, and treatments incubated under host growth conditions. Samples will be collected throughout the infection period for virus and cell counts, as well as photosynthetic efficiency (PhytoPAM). Filters will be prepared for elemental analysis via isotope ratio mass spectrometry (EA-c-IRMS) to quantify C incorporation. **Protocols have been optimized through funding by the Institute of the Ocean (Master Fellowship 2024)**.

- **Assessing the impact of viral infection on carbon degradation vs. aggregation/sedimentation (Years 1 & 2)** - Laboratory experiments (2–4 weeks) will monitor how viral infection influences the degradation of organic and inorganic matter pools. Elemental composition (DOC, POC/PON, dissolved and biogenic silica) and particle abundance/size (TEP, CSP) will be tracked along with microbial diversity (using metabarcoding approaches). Roller tank experiments will assess viral effects on export by tracking aggregate formation and elemental composition of exported particles during infection of the three phytoplankton species[17]. Sedimentation rates of infected and control aggregates will be measured using non-invasive imaging and correlated with aggregate composition.

- **Extrapolating results to the ecosystem-scale (Years 2-3)**. This task leverages data from the APERO mission (R/V *Pourquoi Pas?*, June 2023), dedicated to the study of BCP in the Northeast Atlantic. Samples were collected throughout the water column at stations characterized by contrasting particle dynamics, C export efficiency, and microbiome diversity (eukaryote, prokaryote, and virus). Most analyses are already done or in progress. Viral infection in phytoplankton groups was assessed using classical methods and emerging single-cell approaches (currently being developed in host laboratory). The objective of this task are to (1) evaluate the distribution and magnitude of the studied viral infections, (2) establish a carbon budget related to infection based on in vitro results, (3) test statistical associations between carbon export efficiency vs remineralization and major viral groups through computational analysis.

Relevance to the Ocean Institute: Among all microbial life forms in the ocean, viruses are undoubtedly the most abundant entities[18], yet, they remain relatively understudied. The growing corpus of omics data has highlighted the enormous diversity of this virosphere[19,20]. The current challenge is not only to continue describing this diversity, but also to determine whether and how they influence the biogeochemical transformations mediated by their microbial hosts. Such novel knowledge is crucial for advancing ocean microbiome research and improving large-scale biogeochemical models. This Ph.D. project integrates **multiple disciplines including microbiology, ecology, biogeochemistry, and computational science** to investigate how viruses alter three key processes in planetary climate regulation: carbon fixation, remineralization and export from the cell to the ecosystem-scale. Thus, this project aligns fully with the Ocean Institute's priorities, particularly in the **"oceanic microbiome" theme**. It will bring together **two Sorbonne Université laboratories**, with complementary skills: (1) The UMR 7144, ECOMAP team, which studies biology, interactions and evolution of marine microbes. (2) The UMR 7093, COMPLEX team, which studies the microbiome and the oceanic biogeochemistry using computational methods and modelling. By integrating in vitro (lab experiments) and in situ (APERO campaign) approaches, this project follows modern systems biology principles, bridging traditionally disconnected sub-disciplines to provide a holistic understanding of oceanic processes.

The Supervising Team (gender parity 50/50) includes **Anne-Claire Baudoux** (UMR7144), a senior CNRS researcher (UMR7144) with extensive expertise in virus ecology and developing integrative approaches to explore their function in the ocean (49 publications) and **Lionel Guidi** (UMR 7093), a senior CNRS researcher (UMR7232) expert in C biogeochemistry and the Biological Carbon Pump using computational methods and modelling (85 publications). The Station Biologique de Roscoff provides all necessary infrastructure for molecular biology, cytometry, and mass spectrometry, along with a well-maintained virus and phytoplankton culture collection (collaboration with Charles Bachy). Degradation and aggregation experiments will be conducted at the 'aggregate laboratory' in collaboration with Brivaela Moriceau, with analyses performed on the PACHIDERM platform (LEMAR). This research is jointly funded by the ANR APERO and ANR BONUS projects. The selected candidate will benefit from strong intellectual and technical support from project partners, including Hiroyuki Ogata (Univ. Kyoto), Simon Ramondenc (SU, LOV), and Alexandra Worden (Univ. Chicago).

References (**bold** indicates implication of the supervising team)

[1] Tréguer, P. et al. (2018) Influence of diatom diversity on the ocean biological carbon pump. *Nature Geoscience 11, 27–37*.

[2] Letscher, R. T., et al. (2023) Biodiversity and stoichiometric plasticity increase pico-phytoplankton contributions to marine net primary productivity and the biological pump. *Global Biogeochemical Cycles*, *37*(8), e2023GB007756.

[3] Baudoux, A-C., et al (2006) Virally induced mortality of Phaeocystis globosa during two spring blooms in temperate coastal waters. *Aquatic microbial ecology*, *44*(3), 207-217.

[4] Baudoux, A-C., et al. (2007) Viruses as mortality agents of picophytoplankton in the deep chlorophyll maximum layer during IRONAGES III. *Limnol Oceanogr*, *52*(6), 2519-2529.

[5] Mojica, K. D., et al. (2016) Latitudinal variation in virus-induced mortality of phytoplankton across the North Atlantic Ocean. *The ISME journal*, *10*(2), 500-513.

[6] Vincent, F., et al. (2023) Viral infection switches the balance between bacterial and eukaryotic recyclers of organic matter during coccolithophore blooms. *Nature communications*, *14*(1), 510.

[7] Brussaard, C. P., et al. (2008) Global-scale processes with a nanoscale drive: the role of marine viruses. *The ISME journal*, *2*(6), 575-578.

[8] Fuhrman, J. A. (1999) Marine viruses and their biogeochemical and ecological effects. *Nature*, *399*(6736), 541-548.

[9] Puxty, R. J., et al (2016) Viruses inhibit CO2 fixation in the most abundant phototrophs on Earth. *Current biology*, *26*(12), 1585-1589.

[10] Jaouen, E. et al. (in prep) Infection by RNA virus alters the biogeochemical fate of the dominant nanodiatom *Mediolabrus comicus.*

[11] Lawrence, J. E. & Suttle, C. A. (2004) Effect of viral infection on sinking rates of Heterosigma akashiwo and its implications for bloom termination. *Aquatic Microbial Ecology 37, 1–7.*

[12] Yamada, Y., et al. (2018) Aggregate formation during the viral lysis of a marine diatom. *Frontiers in Marine Sciences 5, 1–7.*

[13] Pelusi, A. et al. (2021) Virus-induced spore formation as a defense mechanism in marine diatoms. *New Phytologist, 229, 2251–2259.*

[14] Walde, M., et al. (2023) Viral infection impacts the 3D subcellular structure of the abundant marine diatom *Guinardia delicatula*. *Frontiers in Marine Sciences,* 9: 1034235. doi:10.3389/fmars.2022.1034235

[15] Kaneko, H., et al. (2021) Eukaryotic virus composition can predict the efficiency of carbon export in the global ocean. *Iscience*, *24*(1).

[16] Guidi, L. et al. (2016) Plankton networks driving carbon export in the oligotrophic ocean. Nature, 532: 465–470. doi:10.1038/nature16942

[17] Long, M. et al. (2015) Interactions between microplastics and phytoplankton aggregates: Impact on their respective fates. *Marine Chemistry* 175, 39–46.

[18] Jacquet S., Baudoux A-C., et al. (2023) Les virus marins, simples parasites ou acteurs majeurs des écosystèmes aquatiques ? Editions QUAE, Versailles, France. 110 pp.

[19] Dominguez-Huerta, G. et al. (2022) Diversity and ecological footprint of Global Ocean RNA viruses. Science, 376: 1202–1208. doi:10.1126/science.abn6358

[20] Brum, J. R. et al. (2015) Patterns and ecological drivers of ocean viral communities. Science, 348: 1261498. doi:10.1126/science.1261498