Viruses infecting marine phytoplankton are key biogeochemical ‘engines’ of the oceans, regulating the dynamics of algal populations and the fate of their extensive blooms. In addition they are important ecological and evolutionary drivers of microbial diversification. Yet, little is known about mechanisms influencing viral dispersal in aquatic systems, enabling the rapid infection and demise of vast phytoplankton blooms. In a recent study we showed that migrating zooplankton as copepods that graze on marine phytoplankton can act as transmission vectors for algal viruses. We demonstrated that these grazers can concentrate virions through topical adsorption and by ingesting infected cells and then releasing back to the medium, via detachment or defecation, high viral titers that readily infect host populations. We proposed that this zooplankton-driven process can potentially boost viral dispersal over wide oceanic scales and enhance bloom termination. Here, we highlight key results and further discuss the ecological and evolutionary consequences of our findings.

Phytoplankton blooms are ephemeral events of exceptionally high primary productivity thriving seasonally in the sunlit layer of the oceans, while driving mass transfer of gases and elements between the water layer, the atmosphere and oceans-floor and composing the basis of marine food-webs. A key bloom-forming species is the coccolithophore *Emiliania huxleyi*, a cosmopolitan calcifying microalgae whose large-scale blooms are detectable by satellite imagery.4–6

The interplay between *E. huxleyi* and a specific, lytic virus, *Emiliania huxleyi* virus (EhV), is known to regulate the termination and fate of such vast blooms. At the cellular level EhV infection triggers a complete remodeling of the host metabolism, resulting in the production of hundreds of virions per cell that burst out to the environment.5–8 At the macroscale, EhV leads to the collapse of whole bloom-patches within about a week, with great ecological and biogeochemical implications.4,9,10

Although major progress has been achieved on the molecular basis for host-virus interactions, there is still limited understanding of this dynamic at the macroscale. In our study, we aimed to link scales and identify transmission mechanism that can link infection on the single cell level to large scale synchronized bloom demise. How are marine viruses able to rapidly spread killing such large scales bloom-features?

As submicron size particles, viruses are constrained by low Reynolds number viscous forces, thus diffusing slowly in seawater.11 We estimated that EhV diffusion coefficient in seawater is about 2 μm² s⁻¹.12 Moreover, further advective processes often entail little internal mixing or create confined water bodies, thus constraining viral particle dispersal.13,14 As blooms are also grazed by zooplankton such as copepods that are able to swim over large distances seeking phytoplankton patches to fulfill their nutritional requirements,15,16 we hypothesized that they can act as transmission vectors enhancing viral dispersal within and across water masses at sea.

Our field observations supported this concept.17 Over 80% of copepods collected at 2 locations in the North Atlantic, where *E. huxleyi* were abundant, contained EhV DNA. This clearly confirmed the association between zooplankton and phytoplankton viruses. We further isolated a new infective EhV strain (EhV-
This suggests that zooplankton activity can significantly enhance EhV resilience and effective transmission. Taken together our results indicated that zooplankton can concentrate, carry and promote the dispersal and dynamic infection of phytoplankton populations. We propose that while foraging zooplankton can rapidly connect phytoplankton micropatches within a same water mass along typically heterogeneous centimeter scale seascapes topographies, possibly guided by the infochemical scent derived from prey hotspots. Furthermore, zooplankton display daily migration patterns of tens to hundreds of meters along the water column. Such pervasive behavior can enable the translocation of virions across water bodies separated by density gradients otherwise impassable for small particles as algal cells and viral particles. The notion of viral dispersal via animal vectors commonly observed in terrestrial ecosystems (e.g.,), can be therefore extrapolated to aquatic systems, and likely to be extended to other marine groups of both vectors and viruses (or other types of parasites). The interplay between the 2 main competing “top-down” regulators of algal blooms in viruses-vector association as demonstrated in our current study adds a new perspective to the complexity of trophic interactions and on mechanisms of pathogen transmission in the oceans.

**Disclosure of Potential Conflicts of Interest**

No potential conflicts of interest were disclosed.

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**References**

1. Field CB, Behrenfeld MJ, Randerson JT, Falkowski P. Primary Production of the Biosphere. Integrating Terrestrial and Oceanic Components. Science 1998; 281:237–40; PMID:9657713; http://dx.doi.org/10.1126/science.281.5374.237
2. Holligan PM, Voiller M, Harbour DS, Camus P, Champagne-Philippe M. Satellite and ship studies of coccolithophore production along a continental shelf edge. Nature 1983; 304:339–42; http://dx.doi.org/10.1038/304339a0
3. Tyrrell T, Menza A. Emiliania huxleyi: bloom observations and the conditions that induce them. In: Thierstein HR, Young, J.R., ed. Coccolithophores: From the molecular processes to global impact. New York: Springer Verlag, 2004.
4. Leihun Y, Koron I, Schatz D, Frada M, U. S, Ross E, Efriani S, Rudich Y, Tzamis M, Sharoni S, Lamer C, et al. Decoupling physical and biological processes to assess the impact of viruses on a mesoscale algal bloom. Curr Biol 2013; in press; PMID:25155511
5. Schroeder DC, Oke J, Malin G, Wilson WH. Coccolithovirus (Phycodnaviridae): characterisation of a new large dsDNA algal virus that infects Emiliania huxleyi. Arch Virol 2002; 147:1685–98; PMID:12209309; http://dx.doi.org/10.1007/s00705-002-8841-3
6. Vardi A, Van Mooy BAS, Fredrickse HF, Poppendorf Kj, Ososkinik JE, Haryamary L, Bidle KD. Viral glycosphingolipids induce lytic infection and cell death in marine phytoplankton. Science 2009; 326:861–5; PMID:19892986; http://dx.doi.org/10.1126/science.1177322
7. Rosenwasser S, Mauze MA, Schatz D, Sheyn U, Malitsky S, Aharoni A, Weinstock E, Tzafidia O, Ben-Dor S, Felder E, et al. Rewiring host lipid metabolism by large viruses determines the fate of Emiliania huxleyi, a bloom-forming alga in the ocean. The Plant Cell 2014; 26:2689–707; PMID:24928329; http://dx.doi.org/10.1105/tpc.114.125641
8. Schatz D, Shemi A, Rosenwasser S, Sahary N, Wolf SG, Ben-Dor S, Vardi A. Hijacking of an autophagy-like process is critical for the life cycle of a DNA virus infecting oceanic algal blooms. New Phytopathol 2014; 204:854–63; PMID:25195618; http://dx.doi.org/10.1111/nph.13008
9. Wilson WH, Taran GA, Schroeder D, Cox M, Oke J, Malin G. Isolation of viruses responsible for the demise of an Emiliania huxleyi bloom in the English Channel. J Mar Biol Assoc UK 2002; 82:369–77; http://dx.doi.org/10.1017/s002531540200656x
10. Vardi A, Haramany L, Van Mooy BAS, Fredrickse HF, Kimmance SA, Larsen A, Bidle KD. Host-virus dynamics and subcellular controls of cell fate in a natural coccolithophore population. Proc Natl Acad Sci USA 2012; 109:19127–32; PMID:23114731; http://dx.doi.org/10.1073/pnas.1208895109
11. Murray AG, Jackson GA. Viral dynamics: a model of the effects of size, shape, motion and abundance of single-celled planktonic organisms and other particles.
12. Frada MJ, Schatz D, Farstey V, Ossolinski JE, Sabanay H, Ben-Dor S, Koren I, Vardi A. Zooplankton may serve as transmission vectors for viruses infecting algal blooms in the ocean. Curr Biol 2014; 24:2592-7; PMID:25438947; http://dx.doi.org/10.1016/j.cub.2014.09.031
13. Hernandez-Garcia E, Bettencourt JH, Garcon V, Hernandez-Carrasco I, Lopez C, Rosi V, J. S, Tew Kai E. Biological impact of ocean transport: A finite-size lyapunov characterization. 3rd Conference on Nonlinear Science and Complexity. Ankara: Springer, 2010.
14. d’Ovidio F, De Monte S, Alvain S, Dandonneau Y, Levy M. Fluid dynamical niches of phytoplankton types. Proc Natl Acad Sci USA 2010; 107:18366-70; PMID:20974927; http://dx.doi.org/10.1073/pnas.1004620107
15. Harris RP. Zooplankton grazing on the coccolithophore *Emiliania huxleyi* and its role in inorganic carbon flux. Mar Biol 1994; 119:431-9; http://dx.doi.org/10.1007/BF00347540
16. Kimbro T. A Mechanistic Approach to Plankton Ecology. Princeton: Princeton University Press, 2008.
17. Mitchell JG, Yamazaki H, Seuront L, Wolk F, Li H. Phytoplankton patch patterns: Seascape anatomy in a turbulent ocean. J Mar Syst 2008; 69:247-53; http://dx.doi.org/10.1016/j.jmarsys.2006.01.019
18. Seymour JR, Seuront L, Doubell M, Waters RI, Mitchell JG. Microscale patchiness of virioplankton. J Mar Biol Ass UK 2006; 86:551-61; http://dx.doi.org/10.1017/S0025315406013464
19. Lombard F, Koski M, Kimbro T. Copepods use chemical trails to find sinking marine snow aggregates. Limnol Oceanogr 2013; 58:185-92; http://dx.doi.org/10.4319/lo.2013.58.1.0185
20. Farstey V, Lazar B, Genin A. Expansion and homogeneity of the vertical distribution of zooplankton in a very deep mixed layer. Mar Ecol Prog Ser 2002; 238:91-100; http://dx.doi.org/10.3354/meps0238091
21. McManus MA, Woodson CB. Plankton distribution and ocean dispersal. J Exp Biol 2012; 215:1008-16; PMID:22357594; http://dx.doi.org/10.1242/jeb.059014
22. Wewald PW. Host-parasite relations, vectors, and the evolution of disease severity. Ann Rev Ecol Syst 1983; 14:465-85; http://dx.doi.org/10.1146/annurev.es.14.110183.002341
23. Lofgren E, Fefferman NH, Naumov YN, Gorski J, Naumova EN. Influenza seasonality: underlying causes and modeling theories. J Virol 2007; 81:5429-36; PMID:17182688; http://dx.doi.org/10.1128/JVI.01680-06