

# Algal viruses hitchhiking on zooplankton across phytoplankton blooms

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**V**iruses 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.

**Keywords:** coccolithophore, *Emiliana huxleyi*, marine viruses, phytoplankton blooms, transmission vectors, zooplankton

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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.<sup>5-8</sup> At the macroscale, EhV leads to the collapse of whole bloom-patches within about a week, with great ecological and biogeochemical implications.<sup>4,9,10</sup>

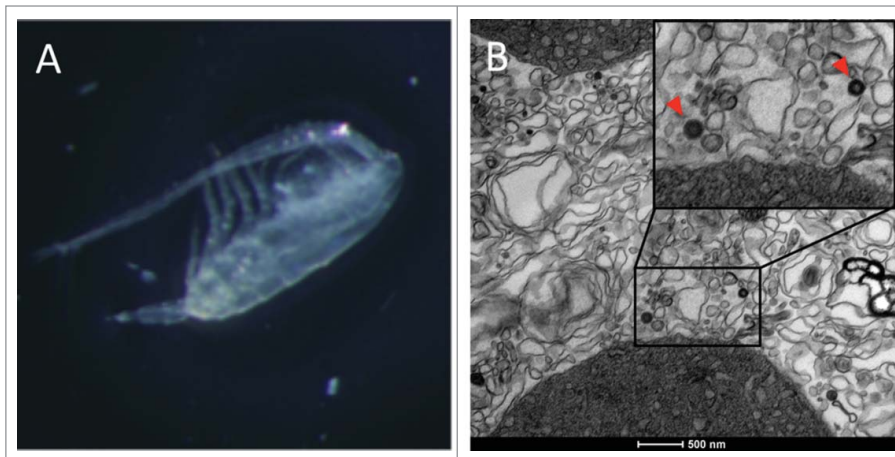
Although major progress has been achieved on the molecular basis for host-virus interactions, there is still limited understanding of this dynamic at the macroscale. In our study, we aimed to link scales and identify transmission mechanism that can link infection on the single cell level to large scale 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.<sup>11</sup> We estimated that EhV diffusion coefficient in seawater is about  $2 \mu\text{m}^2 \times \text{s}^{-1}$ .<sup>12</sup> Moreover, further advective processes often entail little internal mixing or create confined water bodies, thus constraining viral particle dispersal.<sup>13,14</sup> 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,<sup>15,16</sup> 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.<sup>12</sup> 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-

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 ocean-floor and composing the basis of marine food-webs.<sup>1</sup> A key bloom-forming species is the coccolithophore *Emiliana huxleyi*, a cosmopolitan calcifying microalgae whose large-scale blooms are detectable by satellite imagery.<sup>2-4</sup>

The interplay between *E. huxleyi* and a specific, lytic virus, *Emiliana huxleyi* virus (EhV), is known to regulate the termination



**Figure 1.** Zooplankton as vectors of marine phytoplankton viruses. (A) Light microscopy of a copepod collected in the North Atlantic Ocean during an *E. huxleyi* bloom. (B) Transmission electron microscopy image of a native copepod intestinal tract with viruses-like particles (red arrows).

ice 01) from a copepod microbiome, indicating that copepod-borne viruses maintained infectivity and thus were putatively transmissible to new algal populations. Copepods acted as a natural concentration system, retaining high viral titers in their microbiome (we detected up to  $2.5 \times 10^4$  EhV per copepod, relative to a few thousands suspended in the water column) by ingesting infected cells and viable viruses in their intestinal tracks. The isolation of marine viruses in the oceans often involves the concentration of large volumes of seawater. We therefore suggest this approach can be highly valuable for isolation of new aquatic viruses.

We also showed that copepods, as well as other zooplankton species, can also intake virions in the absence of host cells, possibly via feeding currents or bound non-specifically to other food particles or cells. Furthermore, virions can be adsorbed topically to the animals' exoskeleton. Subsequently EhV can be carried and be potentially dispersed by interaction with zooplankton both via viral-dense fecal pellets (Figure 1) or topical detachment. Transmitted by this proposed mechanism viruses can readily propagate to new host populations and considerably enhancing the rate of infection. Intriguingly, we demonstrated that the half-life of EhV residing within fecal pellets is prolonged by about 35% (35 hours) relative to EhV suspended in seawater (23 hours).

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 of 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 seascape topographies, possibly guided by the infochemical scent derived from prey hotspots.<sup>17-19</sup> Furthermore, zooplankton display daily migration patterns of tens to hundreds of meters along the water column.<sup>16,20</sup> 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.<sup>11,21</sup>

The notion of viral dispersal via animal vectors commonly observed in terrestrial ecosystems (e.g.<sup>22,23</sup>), 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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