LETTER

Phaeoviruses found in recovering *Nereocystis luetkeana* kelp forest community

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Phaeoviruses found in recovering *Nereocystis luetkeana* kelp forest community

Kelp forests are ecologically and economically valuable marine ecosystems located worldwide. In the northeast Pacific, kelp forests dominated by *Nereocystis luetkeana* are home to many vertebrates and invertebrates, including commercially important species. However, throughout much of its range, *Nereocystis* populations are experiencing prolonged and intense ocean warming events and subsequent ecosystem imbalance. In Northern California, *Nereocystis* forests have become the target of restoration efforts. Here, we aimed to determine whether *Nereocystis* carries latent phaeoviral infections, previously reported in other kelps, to better understand the potential role of viruses in population stability and recovery. Using a novel combination of PCR and ONT sequencing, we detected at least two phaeovirus variants infecting *Nereocystis*. We observed that ~70% of sampled *Nereocystis* tested positive for phaeovirus, with subgroup C kelp phaeoviruses being the most prevalent. More research is required to untangle the role complex biotic and abiotic pressures, now including viral infection, have on the ecological success of kelp.

Kelp forest ecosystems are among the most productive on earth (Mann, 2000), yet kelp populations and the ecosystems they support are declining worldwide (Eger, Layton, et al., 2022; Eger, Marzinelli, et al., 2022; Krumhansl et al., 2016). Along its range in Eastern Pacific, *Nereocystis luetkeana* populations are increasingly under pressure from multiple stressors. Depending on geographic location, these stressors can include some combination of ocean warming events (e.g., El Niño, marine heat waves; Rogers-Bennett & Catton, 2019), associated poor nutrient availability (García-Reyes et al., 2022), and loss of apex predators resulting in ecosystem imbalances, such as high kelp-grazer densities (notably, high densities of the Pacific purple sea urchin *Strongylocentrotus purpuratus*; McHugh et al., 2018, Smith & Tinker, 2022; also see figures 6, 10, and 15 from McHugh et al., 2018 as cited in Hohman et al., 2019). In Northern California, *Nereocystis* populations have been in decline since 2014. Many of these populations have not fully recovered to historical levels even though environmental conditions have been favorable, suggesting biotic mechanisms are at play, most likely extreme herbivory by *S. purpuratus* (García-Reyes et al., 2022).

Algal viruses are not commonly studied; yet, can pose a major threat to aquaculture industries and potentially wild populations (Benites & Alves-Lima, 2022), including to many kelp species (Beattie et al., 2018; McKeown et al., 2017). Indeed, we lack information on the role viruses might have in shaping kelp ecology and evolution, including on short timescales during kelp population loss and recovery. Phaeoviruses were first described infecting species in the order Ectocarpales (McKeown et al., 2017; Oliveira & Bisalputra, 1978). Currently, members of the genus Phaeovirus are known to infect seven species from four families of the order Ectocarpales and putatively infect eight kelp species from three families of the order Laminariales (McKeown et al., 2017). All these viruses can be identified by the Phaeovirus major capsid protein (mcp/MCP) using PCR (McKeown et al., 2017; Stevens et al., 2014).

Phaeoviruses are the only described phycodnaviruses that employ latent infection strategies. The genome of the virus can integrate within the host's genome, persisting as a provirus and being transmitted through mitosis to all cells of the developing alga. This stable evolutionary coexistence between virus and host makes phaeoviruses unique compared to other algal–virus systems. Infected algae carrying the provirus can appear normal, presenting no survival or growth impairment, yet produce viable spores or gametes that contain the proviral genome. The Laminaria digitata virus (LdV) is the only kelp phaeovirus that leaves microscopic evidence of infection. Nonetheless, reduced fertility can also occur when the reproductive organs become deformed and produce virions (reports have shown a range of 10^5 to 10^6 viruses per deformed reproductive organ) instead of gametes or spores (Dunigan et al., 2006). Infection in kelps appears to be common in vegetative cells of the haploid gametophytic generation, and it might only be expressed in the gametophytes (McKeown et al., 2017). Moreover, phaeoviral symptoms in *Ectocarpus* are temperature sensitive (i.e., temperature can influence virus induction rates; Müller

Abbreviations: MCP, major capsid protein; ONT, Oxford Nanopore Technologies; NGS, Next Generation Sequencing; OPC, Ocean Protection Council; PCR, polymerase chain reaction.

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