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## Ecological role of planktonic bacteriophages in the North Sea and the tropical Atlantic Ocean

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## Summary

The viral impact on bacterioplankton in the North Sea estimated via the frequency of infected prokaryotic cells (FIC) and viral production by a virus-dilution approach is significantly higher in June–July (FIC: 34%, viral production:  $34 \times 10^4 \text{ mL}^{-1} \text{ h}^{-1}$ ) than in the period from September–December (FIC: 13%, viral production:  $15 \times 10^4 \text{ mL}^{-1} \text{ h}^{-1}$ ). Additionally, viral abundance is related to prokaryotic activity indicating that an active bacterioplankton community maintains high viral abundance in the North Sea. FIC varies on a diel scale with high values during the night and low values during the day in the surface layers of the North Sea. Viral lysis of bacterioplankton appears to occur around noon to afternoon and infection during the night. Computational models based on artificial neural networks support these findings. Moreover, lysis and viral production seem to take place at high bacterial activity, which might be interpreted as a strategy to increase the efficiency to produce new viruses.

Viral lysis converts particulate organic carbon into dissolved organic carbon and stimulates bacterioplankton activity by reducing the amount of organic carbon available to higher trophic levels such as heterotrophic nanoflagellates. In systems such as the North Sea with high viral and bacterial abundance and a strong viral impact on bacterioplankton, a diel cycle in viral infection and lysis should strengthen this coupling between dissolved organic carbon production and bacterial consumption.

Batch-culture experiments performed with water from the North Sea and the tropical Atlantic Ocean showed that the effects of virus amendment on bacterial and archaeal communities are rather small compared to the strong influence of confinement. However, individual members of the bacterial and archaeal communities responded differently to virus amendment. The disappearance of some members of the bacterioplankton communities as a result of the addition of intact viruses presents strong evidence that viral lysis does affect *Bacteria* and *Archaea* during confinement. The results led to the

conclusion that marine *Archaea* respond to confinement and to virus amendment. This further substantiates the emerging notion that marine pelagic *Archaea* are metabolically active in the ocean and that viral lysis potentially influences the community composition of pelagic *Archaea*. However, *in situ* observations made in the tropical Atlantic Ocean on the relation between the ratio of bacterial to archaeal community richness and viral abundance and infection suggest that lytic viruses might act primarily on the bacterial community in the mixed surface layer.

In the North Sea, bacterial richness in unfiltered seawater is negatively correlated with viral abundance and in  $0.8 \mu\text{m}$  filtered seawater with bacterioplankton activity and viral abundance. Computational models of bacterial richness based on artificial neural networks differ between the whole community (unfiltered seawater) and the free-living community ( $0.8 \mu\text{m}$  filtered seawater). This might be explained by differences in the bacterial communities colonizing different kinds of particles. It is concluded that a small number of highly active members of the bacterial community maintains high viral abundance in the North Sea. In addition, the observations support the hypothesis that predicts the existence of a reciprocal feedback loop between viruses and bacterial richness.