Summary

Marine microorganisms represent the largest reservoir of living organic carbon in the ocean and collectively manage the pools and fluxes of nutrients and energy. Climate-induced increases in sea surface temperature and associated modifications to vertical stratification are affecting the structure and production of autotrophic and heterotrophic microorganisms in ocean surface waters. However, little is known about how future alterations will affect the mortality of marine microbes. The various modes of mortality influence the cycling of biogeochemical elements very differently. This in turn affects the production to respiration ratio of the ocean and thus the efficiency with which photosynthetic organic carbon is transferred to higher trophic levels or exported to the deep ocean (via the biological pump). The Atlantic Ocean provides a meridional gradient in stratification, is essential to global circulation and acts as a major sink for anthropogenic carbon dioxide. The Northeast Atlantic thus provides an ideal model system for the current study which aims to investigate the influence that vertical stratification has on the source of mortality (i.e., viral lysis versus grazing).

After a general introduction, this thesis begins by providing a comprehensive overview of what is currently known about how environmental factors in the marine environment affect virus-host interactions. Abiotic and biotic variables can influence the infectivity and survival of marine viruses, and regulate the physiology, production and distribution of the host. Ultimately, these aspects govern the efficiency with which viruses can replicate and thus propagate through the marine environment (Chapter 2). The review illustrates that at this moment in time, our ability to identify general ecologically functional patterns important in governing virus dynamics over broad oceanic scales is restricted by the availability of information regarding both the effect of individual environmental factors and by the scarcity of reported rates.

In order to better understand the importance of vertical mixing and physicochemical features in structuring phytoplankton (unicellular algae) host populations, a high-resolution mesoscale description of the phytoplankton community along a meridional gradient in the Northeast Atlantic Ocean was conducted during the spring and summer (Chapter 3). Vertical stratification was identified as a key factor governing the distribution and separation of different phytoplankton taxa and size classes, indicating that incorporation of vertical turbulence structure of the water column will improve biogeochemical and ecological modeling studies. The data support predictions that climate-change induced increases in ocean surface temperature and expansion of oligotrophic (nutrient-limited) areas will increase the contribution of pico-sized (< 2 μm) eukaryotic phytoplankton (while decreasing the abundance of cryptophytes and diatoms), and expand the geographic range of *Prochlorococcus* spp. northward (leading to alterations in phylogeography within unicellular cyanobacterial populations). This will likely result in large-scale biogeographical changes in virus distributions, including an expansion of the V3 viruses associated with picocyanobacterial hosts (Chapter 4).

More importantly, simultaneous measurements of viral lysis and microzooplankton grazing rates conducted along the latitudinal transect during summer (Chapter 4) show that (i) viral lysis was responsible for half of the total mortality occurring in all phytoplankton groups, (ii) average virus-mediated lysis rates were higher for eukaryotic phytoplankton than for the prokaryotic cyanobacteria *Prochlorococcus* spp. and *Synechococcus* spp., (iii) overall the total phytoplankton mortality rate (viral lysis plus microzooplankton grazing) was comparable to phytoplankton gross growth rate, signifying high turnover rates of marine phytoplankton populations, and finally (iv) viral lysis rates were reduced in the north (> 58°N), resulting in grazing-dominated phytoplankton mortality.

A method optimization for the enumeration of samples with low viral abundance (pH modification of the TE-buffer used for the dilutions) substantially improved total virus counts in North Atlantic samples compared to those obtained using the standard method (Chapter 5). This method was applied to enumerate field samples which utilized a virus reduction approach to investigate the viral life strategy and magnitude of infection in heterotrophic prokaryotic populations (Chapter 6). Compared to grazing, viruses were the dominant mortality factor regulating prokaryotic losses in the surface waters of the Northeast Atlantic Ocean during summer. Lytic infection (virus replication and host lysis proceeds immediately after infection) was the favored life strategy in the surface mixed layer, while lysogeny (virus incorporated into host genome where it remains until triggered into lytic cycle upon stimulation by an environmental factor) was only relevant within the deep chlorophyll maximum layer of oligotrophic southern stations. The data revealed a close to steady state situation and rapid turnover in the south and net heterotrophic production in the north, suggesting that alterations in stratification will also affect heterotrophic prokaryote production.

Implementing measured production and loss rates of autotrophic (Chapter 4) and heterotrophic (Chapter 6) organisms into a steady state carbon-flux model demonstrates that 80% of the photosynthetically fixed carbon flowed through the viral shunt in the oligotrophic south, which is more than 2-fold higher than the northern region. These results illustrate that viruses play a more prominent role in stratified (steady state) marine ecosystems than thought previously.

Overall, this thesis reveals that viral lysis is an important factor regulating the biomass and productivity of marine microbial populations during summer stratification in the Northeast Atlantic Ocean. Moreover, the data support the hypothesis laid out in this thesis that alterations in microbial communities due to global warming-induced changes in vertical stratification will affect mortality processes and the distribution of predators (e.g. mortality agents). The partitioning of photosynthetic carbon through the separate mortality pathways has important implications for ecosystem functioning as each pathway affects the structure and activity of the pelagic food web in different ways. Grazing transfers biomass to higher trophic levels, thus increases the overall efficiency and carrying capacity of the ecosystem. On the other hand, viral activity stimulates recycling via heterotrophic prokaryotes by shunting biomass to the dissolved organic matter pool, and therefore enhances the availability of inorganic nutrients in the oligotrophic surface waters of the ocean. In conclusion, the data presented in this thesis indicate that climate change-induced alterations in the timing and strength of seasonal stratification at the higher latitudes will shift the ecosystem towards a more viral-lysis dominated system. A more prominent future role of viral lysis in the northern region of the North Atlantic Ocean would thus markedly reduce biological carbon export into the ocean's interior in one of the key areas of global carbon sequestration, reducing the potential for the ocean to serve as a long-term sink for anthropogenic carbon dioxide.