

# **Chapter 8**

## **General Discussion**

Over the last few decades, mathematical models have played an essential role in elucidating and evaluating the consequences of increasing concentrations of atmospheric CO<sub>2</sub> on global climate (Meehl et al. 2007, Gruber and Doney 2009). Due to this success, models are increasingly used for making quantitative predictions with direct consequences for climate policy. Modeling the effect of global climate change on marine biogeochemistry and ecology is demanding due to the complexity of interactions among biological, physical, and chemical variables. Additionally, marine biogeochemical/ecological modeling is currently restricted by the scarcity of data required to formulate and parameterize key processes and/or to evaluate the model predictions (Gruber and Doney 2009).

Biogeochemical and ecological processes in the surface ocean are ultimately regulated by the rate at which carbon is fixed photosynthetically into organic matter by phytoplankton, which is distributed heterogeneously in the ocean by variations in the availability of light and nutrients. Vertical stratification of the water column suppresses turbulence and reduces mixing depth, affecting the availability of light and nutrients to phytoplankton in the surface water (Mahadevan et al. 2012). Ocean-climate models agree that warming of the surface oceans will strengthen surface stratification and decrease winter mixing, leading to an earlier onset and increasing the duration of seasonal stratification (Sarmiento 2004, Saenko et al. 2011, Collins et al. 2013). These changes will eventually impact the growth, spatial distribution and species composition of phytoplankton communities (Follows and Dutkiewicz 2001, Jöhnk et al. 2008, Dutkiewicz et al. 2013). The incorporation of the vertical turbulence structure of the water column, with parameters such as Brunt-Väisälä frequency ( $N^2$ ) and mixing depth, is likely to improve existing models by refining differentiation between different phytoplankton functional types (Chapter 3; Huisman et al. 2004, Jäger et al. 2008, Ryabov et al. 2010). The combination of pigment analysis (HPLC-Chemtax) and flow cytometry permits phytoplankton community structure to be examined from both size and taxonomic perspectives (Chapter 3; Veldhuis and Kraay 2004, Suzuki et al. 2005, Cassar et al. 2015). However, it is recommended here to further complement this by size-fractionated HPLC analysis in order to better discriminate affects on size class distribution within specific taxonomic groups (Chapter 3). Moreover, models focusing exclusively on bottom-up (i.e. resource availability) control may fail to capture a substantial proportion of the variability in the structure and distribution of phytoplankton communities (Chapter 3). This is due to the considerable top-down (i.e., grazing and viral lysis) control of phytoplankton communities, which

can also be distributed heterogeneously across ocean basins and may be regulated by processes related to the vertical stratification of the water column (Chapter 4; Behrenfeld and Boss 2014).

Biogeochemical and ecological models have traditionally credited grazers as the main loss factor for net primary production in the euphotic zone (i.e. sunlit surface layers), with a small fraction lost to sinking (Gruber and Doney 2009, Ducklow et al. 2010). However, studies indicated that viruses can be a significant factor regulating primary production (Suttle et al. 1990) and phytoplankton bloom dynamics (Castberg et al. 2001, Brussaard et al. 2005, Ruardij et al. 2005, Baudoux et al. 2006). To my knowledge, Chapter 4 represents the largest data set of viral lysis rates of different marine phytoplankton groups and in addition provides simultaneous measurements of microzooplankton grazing. The data reveal that for all phytoplankton groups, (determined by flow cytometry) the losses from viral lysis rival microzooplankton grazing (Chapter 4; Baudoux et al. 2006, Tsai et al. 2012). Moreover, rates of viral-induced mortality can vary significantly over latitudinal scales and across different phytoplankton groups (Chapter 4). In the oligotrophic Northeast Atlantic Ocean, viral lysis was found to be the dominate loss factor for phytoplankton during summer, while microzooplankton grazing dominated at higher latitudes (Chapter 4). The switch in mortality type was related to water column stability through the vertical mixing coefficient ( $K_T$ ). However, it most likely represents an interplay between physical and biological processes that in turn regulate the formation of transparent exopolymer particles (TEP) and subsequently led to the (temporarily) inactivation of viral infectivity at higher latitudes (Chapters 2 and 4).

Bacterial turnover of dissolved organic matter (DOM) and the associated remineralization of nutrients close the major biogeochemical cycles of these elements in the ocean (Falkowski et al. 2008). The DOM-bacteria pathway of the microbial loop represents a major mechanism by which primary production is respired to  $\text{CO}_2$  (Kirchman et al. 2013). Availability of dissolved organic carbon (DOC) is thought to be the primary factor regulating the abundance and activity of heterotrophic prokaryotes in much of the world's oceans (Carlson and Ducklow 1996, Church et al. 2000). However, in oligotrophic regions of the North Atlantic, inorganic nutrient limitation of heterotrophic prokaryotic populations may also be a significant factor regulating bacterial production (Chapter 6; Cotner et al. 1997, Rivkin and Anderson 1997, Mills et al. 2008). Due to the reliance of viruses on their hosts to provide the energy required for replication, inorganic nutrient limitation

may then also effect viral infection dynamics. Viral lysis was shown to be the dominate mortality factor for prokaryotes in the Northeast Atlantic during summer stratification (Chapter 6), wherein lytic infection was the favored life strategy in the surface mixed layer (ML). Data show that lytic viral production rates in the ML were tied to inorganic nutrients most likely through nutrient limited host physiology. In contrast, inducible prophages were detected within the deep chlorophyll maximum (DCM) layer of every oligotrophic station. Lysogeny is thought to represent a survival strategy to persevere conditions of low host productivity and abundance (Williamson et al. 2002, Weinbauer et al. 2003, Payet and Suttle 2013). However, no direct correlation was found between lysogeny, inorganic nutrient concentrations, and heterotrophic prokaryotic production or abundance (Chapter 6). It could be that the host groups (species) that underwent induction of prophage are not dominant, which would obscure the correlations made to total heterotrophic abundance and production such as those presented here. Quantitative analysis of the heterotrophic prokaryotic community composition may shed more light on alterations occurring during viral infections and may also clarify members involved in prophage induction. The induction of prophages within the DCM was negatively correlated to chlorophyll *a*. Pico-sized *Prochlorococcus* spp. were dominant in the DCM (93%), with abundances decreasing with latitude (Mojica et al. 2015). These autotrophic prokaryotic counterparts could have effectively competed with heterotrophic prokaryotes and pushed nutrient limitation to a point at which lytic viral production could no longer be effectively sustained and consequently triggered a switch to lysogenic infection. This hypothesis is supported by evidence that inorganic nutrients may at times be an important factor modulating lysogeny in natural heterotrophic populations (Williamson et al. 2002, Motegi and Nagata 2007). Overall, these results support prokaryotic host physiology and growth as important factors regulating virus abundance in aquatic environments (Chapters 2 and 6; Proctor et al. 1993, Moebus 1996, Middelboe 2000).

The incorporation of virus-induced mortality rates of the different microbial populations at rates which rival or exceed those of zooplankton grazing has important implications for biogeochemical and ecological models (Chapter 7). First, the flux of photosynthetically fixed carbon (PFC) through the viral shunt is much higher (up to 80%) than previously thought (up to 26%) for steady state ecosystems such as those found under oligotrophic conditions (Chapter 7; Wilhelm and Suttle 1999). Consequently, less PFC is available to be transferred to higher trophic levels via the classical grazer food chain, decreasing the overall efficiency

and carrying capacity of the ecosystem (Fuhrman 1999, Wilhelm and Suttle 1999). Secondly, the different sources of dissolved and particulate dead matter, whether through passive diffusion across phytoplankton cell membranes, actively excreted, released from sloppy feeding, diffused from fecal pellets or released from viral lysis, vary in their chemical composition and bioavailability (Middelboe and Jorgensen 2006, Kirchman et al. 2013, Lønborg et al. 2013). The dominance of viral lysis as a loss factor for both autotrophic and heterotrophic prokaryotic production in the oligotrophic region suggests that bacterial C-demand is not restricted to excretion and DOC released from grazing activity. Furthermore, recent evidence has demonstrated that bacteria within subtrophic regions possess a diverse array of enzymatic weaponry to hydrolyze high molecular weight organic substrates (Arnold et al. 2011). Together these results may explain consistent reports of net heterotrophy (i.e., bacterial carbon demand exceeds phytoplankton carbon fixation) in subtropical regions of the Northeast Atlantic Ocean (Agusti et al. 2001, Duarte et al. 2001, Serret et al. 2001, Gonzalez et al. 2002, Hoppe et al. 2002, Moran et al. 2004).

The data presented in this thesis indicate that climate change-induced alterations in the timing and strength of seasonal stratification will reinforce or shift the ecosystem towards a more viral-lysis dominated system. Increased carbon recycling at the expense of trophic transfer will have cascading effects on the overall structure and functioning of pelagic microbial food webs, reducing productivity and biological carbon export into the ocean's interior (Weinbauer et al. 2011). As the North Atlantic is one of the key areas of global carbon sequestration, such alterations could have global implications for the potential for the ocean to function as a long-term sink for anthropogenic carbon dioxide.

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