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High-resolution dynamics of the spring bloom in the Gulf of Finland of the Baltic Sea

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A B S T R A C T

During the period from March to the end of May in 2009 and 2010, intensive measurements and sampling were undertaken in the Gulf of Finland. The compiled results indicate a high variability of the phytoplankton distribution both temporally and spatially. The spring bloom dynamics and heterogeneity was influenced by physical forcing, such as prevailing circulation in the surface layer and the development of stratification, including the upward and downward movement of the seasonal thermocline. The estimated ratio of nitrogen to phosphorus consumption during the growth phase of the spring bloom was close to the Redfield ratio during both springs. The maximum phytoplankton carbon biomass was observed after the depletion of inorganic nitrogen from the surface layer, which coincides with the transition in the community dominance from diatoms to dinoflagellates. Diatoms exhibited a short, well-defined period of high biomass, and we argue that measurements with low temporal resolution can overlook this period of diatom dominance in the Gulf of Finland. The observed dominance of dinoflagellates (*Peridiniella catenata* and the *Scrippsiella/Biecheleria* complex) and the ciliate *Myrionecta rubra* might have a substantial biogeochemical impact because these species increase the retention time of newly produced material in the nutrient-limited surface layer in late spring.

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1. Introduction

According to the European Water Framework Directive (WFD, 2000/60/EC) and the Marine Strategy Framework Directive (MSFD, 2008/56/EC), the phytoplankton community composition, abundance and biomass are one of the biological quality elements that are used in the assessment of the ecological/environmental status of coastal and marine waters. During the last decade, climate change and global warming have received much attention in the context of changes to the marine ecosystem. Thus, the spring bloom, which is a typical feature in temperate aquatic ecosystems, has also received extensive attention in the assessment of the impact of anthropogenic pressure and climate change. The wintertime accumulation of inorganic nutrients in the whole water body and the physical conditions in the surface layer determine the spring bloom in the Baltic Sea (Kahru and Nõmmann, 1990; Stipa, 2004; Sverdrup, 1953). Nitrogen is considered the limiting nutrient in the Baltic Sea, and nitrate is the main form of inorganic nitrogen present at the commencement of the spring bloom. In the Gulf of Finland, nitrate depletion during the bloom is obviously a major cause of the rapid decline in the phytoplankton biomass, especially under the recently observed nutrient conditions, which usually include detectable residual amounts of

phosphates and silicates in the surface layer after the spring bloom (e.g., Hällfors et al., 1981; Tamelander and Heiskanen, 2004).

In the Baltic Sea, a major part of the spring bloom phytoplankton biomass is lost by sedimentation due to the slow development of mesozooplankton. Johansson et al. (2004) showed that 85% of the spring heterotrophic biomass (micro- and mesozooplankton) in the Baltic Sea is composed of ciliates. The mesozooplankton species are mostly in the nauplii stage during the vernal bloom. Because nauplii feed on smaller particles, these organisms cannot control the spring bloom biomass, which mostly consists of large chain-forming diatoms and dinoflagellates (Lignell et al., 1993). Ciliates are known to reach their peak biomass shortly after the spring bloom, and, according to carbon consumption estimates (Johansson et al., 2004), up to 15% and 4% of the spring net primary production are potentially consumed by ciliates and mesozooplankton, respectively. The marine photosynthetic ciliate *Myrionecta rubra* (Lohmann, 1908) Jankowski 1976 is an important protist in the stratified Baltic Sea, where it can exploit the available resources through diurnal vertical migration (Crawford and Lindholm, 1997; Lindholm and Mörk, 1990; Thamm et al., 2004). This ciliate can attain high biomasses during spring bloom (e.g., Wasmund et al., 2013) and inhabits different depths in the summer (e.g., Rychert, 2004).

Studies in the 1970s demonstrated the dominance of cold-water diatoms in the Baltic Sea during the spring bloom (Hällfors et al., 1981 and references therein). Several recent analyses have shown long-term changes in the phytoplankton community composition,

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abundance, and annual succession. The observed changes in phytoplankton include a higher overall spring bloom biomass throughout the Baltic Sea (Alheit et al., 2005), an increased dinoflagellate contribution to the spring bloom biomass (Wasmund and Uhlig, 2003), and an earlier onset of the spring bloom (Fleming and Kaitala, 2006). In the latest reports of the periodic assessment of the state of the marine environment in the Baltic Sea published by the Helsinki Commission (HELCOM), the spring bloom was not thoroughly described due to a clear focus shift toward summer cyanobacterial blooms. However, five dominant vernal bloom species in the Baltic Sea basins during three periods (1979–83, 1984–88, and 1989–93) were reported in the third periodic assessment (HELCOM, 1996) and allow us to determine whether there have been clear changes in the species dominance in the Gulf of Finland during the spring bloom since that time.

There are few data available on the phytoplankton community composition due to the costs associated with traditional marine environment monitoring using research vessels and manpower for the quantitative counting of samples. This lack of data results in a reduction in the spatial coverage and temporal resolution that is required to study phytoplankton dynamics and the correlations between phytoplankton and physical, chemical, and other biological parameters. This is especially true during the spring bloom period due to the high variability in the phytoplankton community, i.e., if the aim is to follow the seasonal dynamics in detail or to study the long-term trends in the composition of the spring bloom community. To fill the gaps and increase the knowledge and understanding of the dynamics in a marine environment, the use of different autonomous platforms in marine research and monitoring in the Baltic Sea area is increasing (Fleming and Kaitala, 2006; Jaanus et al., 2009; Lips and Lips, 2008; Lips et al., 2011; Rantajärvi et al., 1998; Schneider et al., 2006; Vepsäläinen et al., 2005). In addition, autonomous platforms have been used to improve the prognostic capabilities of circulation, especially in areas with complex hydrography (e.g., Grayek et al., 2011), and biogeochemical models (Roiha et al., 2010).

Several recent studies have analysed conventional phytoplankton monitoring data with the aim of showing the trends or shifts in the Baltic Sea ecosystem, including the characteristics of the spring bloom (e.g., Klais et al., 2011; Wasmund et al., 2011). A more detailed temporal evolution of the spring bloom can be obtained using the ships-of-opportunity/Ferrybox technique, but most of these studies have focused on chlorophyll a (Chl a) or fluorescence data (Fleming and Kaitala, 2006). High-resolution data (in both space and time) on the phytoplankton species composition and biomass that cover the full spring bloom period have not been available until now.

Attempts have been made to model the long-term and seasonal dynamics of nutrients and the Chl a content or phytoplankton/cyanobacteria biomass in the Baltic Sea and its sub-basins (e.g., Eilola et al., 2009; Maar et al., 2011; Müller-Karulis and Aigars, 2011). Mostly constant values have been used for the conversion factors that link carbon (C) to the nitrogen (N) and phosphorus (P) contents in accordance with the Redfield ratio (molar ratio 106:16:1) and the nutrient contents to the Chl a content, e.g., carbon to chlorophyll as 50 µg C to 1 µg Chl a (Eilola et al., 2009) and nitrogen to chlorophyll as 0.63 µM N to 1 µg Chl a l^{-1} (Eilola et al., 2009) or 0.5 µM N to 1 µg Chl a l^{-1} (Maar et al., 2011). Based on the analysis of Ferrybox nutrient data from the period of 1993 to 2009, it was suggested that spring bloom phytoplankton have the ability to excessively uptake phosphorus in relation to nitrogen (Raateoja et al., 2011). To match the model outputs with observations, it was suggested that the classical Redfield ratio should be replaced with a constant but lower ratio for the N:P uptake, e.g., 10:1 (Wan et al., 2011). In addition, the use of constant conversion factors under changing nutrient and light conditions in natural systems has been questioned (Mateus et al., 2012), and high-resolution data appear to be essential to understand the links between the phytoplankton dynamics and the environmental conditions and to suggest relevant approaches that should be used in ecological models.

The main aim of the present paper was to describe the dynamics of the spring bloom in the Gulf of Finland based on high-resolution measurements and sampling in 2009 and 2010 and to correlate the observed features and the temporal and spatial variability of the bloom to physical and chemical patterns. Employing new technologies and high-resolution sampling, we linked the dynamics of the spring bloom, e.g., the dominance and peaking of different species and the related nutrient dynamics, to the environmental conditions and physical processes. Based on the observational results, we also discuss several key concepts and recent suggestions, such as a shift toward the dominance of dinoflagellates and the use of a non-Redfield ratio for the uptake rates of nitrogen and phosphorus.

2. Materials and methods

The study was conducted in the Gulf of Finland of the Baltic Sea. The sampling transect was located in the central part of the gulf between Tallinn and Helsinki (Fig. 1). The width of the gulf in the study area is less than 80 km, and the measurements were collected in a 72-km wide area along the ferry route (excluding an area of approximately 4 km close to each harbour).

The Ferrybox system, which was installed aboard the passenger ferry "Baltic Princess" (AS Tallink Grupp) that travels between Tallinn and Helsinki, was used for the measurements and sampling in the surface layer in 2009 and 2010. Water was pumped through the measuring system as the ferry travelled. The water intake was located at a depth of approximately 4 m. The temperature (T; PT-100 sensor), salinity (S; FSI Excell thermosalinograph), and Chl a fluorescence (SCUFA Turner Design) were recorded twice a day along the ferry route (Fig. 1) with a time resolution of 20 s, which corresponds approximately to a spatial resolution of 150 m between each collected data point. The water sampling from up to 17 locations along the ferry route was conducted using an automatic refrigerating (4 °C) sampler (Sigma 900 MAX) on the dates shown in Tables 1–3. The collected water samples were analysed to determine the concentrations of PO_4^{3-}, $NO_2^- + NO_3^-$, and Chl a, the phytoplankton species composition, wet weight, and carbon (C) biomass. The success of sampling during early spring is dependent on the ice conditions because the system may automatically switch off if even small pieces of ice are detected in the debubbling chamber. Because there were relatively heavy ice conditions in the Gulf of Finland, the sampling was less successful in March 2010.

CTD measurements using an Ocean Seven 320plus CTD probe (Idronaut S.r.l.) equipped with a Seapoint Chl a fluorometer and water sampling aboard the research vessel were performed at Station AP5 on 8, 14, 21, and 26 April and 5, 11, and 21 May in 2010 (Fig. 1). The vertical resolution of the water sampling was in the range of 5 to 10 m. The water samples were analysed to determine the inorganic nutrient (PO_4^{3-} and $NO_2^- + NO_3^-$) concentrations and the Chl a content. Samples were also collected on 9, 17, and 30 June to describe the nutrient and phytoplankton dynamics during the summer. These results are not shown in the present paper but are partly used in the discussion to support a suggestion.

The samples collected for nutrient analysis were deep-frozen at −20 °C after collection and analysed at the shore-based laboratory using the automatic nutrient analysers µMac 1000 (Systea S.r.l.) and Lachat QuikChem 8500 Series 2 (Lachat Instruments, Hach Company). The nutrient analyses were performed according to the guidelines of the American Public Health Association (APHA, 1992; methods 4500-NO3 F and 4500-P F for µMac 1000) and recommendations made by USEPA, ISO, and DIN standards (methods 31-107-04-1-D NO3 (Lachat Instruments, 2000) and 31-115-01-1-I PO4 (Lachat Instruments, 2001) for the Lachat instrument). The lower detection range for PO_4^{3-} and $NO_2^- + NO_3^-$ using the µMac 1000 was 1 ppb (parts per billion; 0.03 and 0.07 µM, respectively; with a measurement uncertainty of