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Basin-scale spatio-temporal variability and control of phytoplankton photosynthesis in the Baltic Sea: The first multiwavelength fast repetition rate fluorescence study operated on a ship-of-opportunity

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ABSTRACT

This study presents the results of the first field application of a flow-through multi-wavelength Fast Repetition Rate fluorometer (FRRF) equipped with two excitation channels (458 and 593 nm). This device aims to improve the measurement of mixed cyanobacteria and algae community's photosynthetic parameters and was designed to be easily incorporated into existing ferrybox systems. We present a spatiotemporal analysis of the maximum photochemical efficiency (F_v/F_m) and functional absorption cross section (σ_{PSII}) recorded from April to August 2014 on a ship-of-opportunity commuting twice per week between Helsinki (Finland) and Travemünde (Germany). Temporal variations of F_v/F_m and σ_{PSII} differed between areas of the Baltic Sea. However, even though the Baltic Sea is characterized by several physico-chemical gradients, no gradient was observed in F_v/F_m and σ_{PSII} spatial distribution suggesting complex interactions between biotic and abiotic controls. σ_{PSII} was sensitive to phytoplankton seasonal succession and thus differed according to the wavelength used to excite photosystems II (*PSII*) pigments. This was particularly true in summer when high $\sigma_{PSII}(593)$ values were observed later and longer than high $\sigma_{PSII}(458)$ values, reflecting the role of cyanobacteria in photosynthetic light uptake measured at community scale. In contrast, F_v/F_m variations were similar after excitation at 458 nm or 593 nm suggesting that the adjustment of F_v/F_m in response to environmental factors was similar for the different groups (algae vs. cyanobacteria) present within the phytoplankton community.

1. Introduction

Phytoplankton primary production, the process by which microalgae and cyanobacteria produce organic matter using sunlight and atmospheric CO_2, forms the basis of the marine food web (Cloern, 1996; Falkowski and Raven, 2007) and defines the carrying capacity of aquatic ecosystems (Kromkamp et al., 2008). It is thus challenging to understand the functioning of a marine ecosystem and to sustainably manage its resources and health without a reliable estimate of phytoplankton primary production. The quality of this estimate in turn depends on our knowledge of the dynamics and processes controlling phytoplankton photosynthetic performances (Geider et al., 2001; Kromkamp et al., 2008).

Measurements of phytoplankton photosynthetic activity are not widely included in monitoring programs. Consequently, our estimates of phytoplankton primary production at the global scale and our knowledge of factors controlling phytoplankton photosynthesis are still crude (Falkowski and Raven, 2007; Lawrenz et al., 2013). Even in coastal areas with long running monitoring programs, such as the Baltic Sea, our understanding of the dynamics and controls of phytoplankton photosynthesis are limited to studies conducted occasionally or in spatially small areas (e.g. Müller and Wasmund, 2003; Raateoja et al., 2004a; Raateoja, 2004; Renk and Ochocki, 1998; Rydberg et al., 2006).

This scarcity of data can be explained by the prohibitive cost of operating studies from research vessels and from the methodological constraints associated with phytoplankton photosynthesis measurements. Phytoplankton photosynthesis has traditionally been measured as oxygen production (Gaarder and Gran, 1927; Montford, 1969) and carbon isotope uptake (Hama et al., 1983; Steemann Nielsen, 1952). These methods are sensitive but laborious (they require incubation) and are not easily automated (Marra, 2002). Carbon isotope uptake methods have also become increasingly difficult to apply due to stringent health, safety and environmental regulations (Robinson et al., 2014).

In the last decades, inducible fluorescence-based methods have been developed to measure phytoplankton photosynthetic parameters free from the constraints associated with the traditional methods (Suggett et al., 2010). Their use to conduct studies at large spatio-temporal scale and their incorporation into monitoring operations are, however, still limited. This slow adoption has been because commercially

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available instruments were not easily automated and incorporated into operational monitoring platforms. Additionally, the wavelength of light used to excite fluorescence could be non-optimal for phytoplankton communities with an important cyanobacterial component (Kromkamp and Forster, 2003; Raateoja et al., 2004b; Simis et al., 2012). Fast Repetition Rate fluorometers (FRRF) were initially equipped with a blue excitation light to approximate the spectral light quality in clear oceanic waters. Blue light, however, preferentially excites the photosystem II (*PSII*) antenna of algae containing chlorophylls *a*/*b*/*c* and photosynthetic carotenoids but greatly under-samples species with a low *PSII* cross section in the 400–500 nm region, relying instead on phycobilisomes rich in phycocyanin or long-wavelength variants of phycoerythrin, such as cyanobacteria and rhodophytes (Kromkamp and Forster, 2003; Raateoja et al., 2004b; Simis et al., 2012; Suggett et al., 2009). This makes the blue excitation light inappropriate in systems where cyanobacteria form an important component of the phytoplankton community such as in the Baltic Sea and eutrophic freshwater environments (Raateoja et al., 2004b). Moreover, some photosynthetic parameters, such as the functional absorption cross-section of photosystems II (σ_{PSII}), are strongly species and wavelength-dependent. Consequently, relative changes in these parameters, measured in situ on naturally mixed communities using just one excitation wavelength, can be properly interpreted as temporal or spatial variations only if changes in the relative concentration of different pigment types can be ruled out (Schreiber et al., 2012; Suggett et al., 2009).

There thus exists a need for variable fluorometers equipped with multiple light excitation wavelengths to optimize the measurement of algae and cyanobacteria contributions in the fluorescence signal measured at community scale (Simis et al., 2012). In recent years, commercial FRRF have been brought to the market with two or three excitation wavebands to meet this need. One of these instruments, the FFL-40 (Photon System Instruments, Czech Republic) was specifically designed to excite the pigment groups present in mixed cyanobacteria and algae communities encountered in freshwater and coastal seas and to be easily maintained while incorporated into ferrybox systems.

In this paper, we present the results of the first study testing this device in the acquisition of phytoplankton photosynthetic parameters at basin scale with high spatial and temporal resolution from a ship-of-opportunity in a marine system (the Baltic Sea) where mixed cyanobacteria and algae communities occur naturally (Bianchi et al., 2000). This study is intended to provide a first proof-of-concept of the FFL-40 in an autonomous flow-through setting operated during phytoplankton blooms and the intermediate periods with low phytoplankton biomass. The primary objective of this work was to characterize the spatio-temporal dynamics, along the dominant physicochemical and optical gradients in the Baltic Sea, of two phytoplankton photosynthetic parameters describing the physiological state of photosystems II (*PSII*): the maximum photochemical efficiency (F_v/F_m) and the functional absorption cross section (σ_{PSII}). The second objective was to compare the photosynthetic parameters measured at community scale using the two different excitation wavelengths of the FFL-40. Finally, this works aimed to relate, to the extent possible, observed variability in photosynthetic parameters measured at both wavelengths to environmental conditions observed from the ferrybox platform. Because the 458 nm (blue) excitation light of the FFL-40 should be more efficient to excite the antenna pigments of algae while the 593 nm (amber) light excitation corresponds better to the absorption peaks of antenna pigments of cyanobacteria, different dynamics in F_v/F_m and σ_{PSII} measured at community scale using these both wavelengths were expected. Further, because the Baltic Sea is characterized by several physicochemical (temperature, salinity) and optical gradients, spatio-temporal variability in F_v/F_m and σ_{PSII} were expected along these gradients. Finally, different spatio-temporal dynamics of F_v/F_m and σ_{PSII} between the Helsinki-Travemünde (southward) and Travemünde-Helsinki (northward) transects were expected due to sampling at different times during the day while F_v/F_m and σ_{PSII} are expected to exhibit a diel cycle.

F_v/F_m and σ_{PSII} are considered here because they are essential parameters to study phytoplankton photosynthesis in nature (Suggett et al., 2009). F_v/F_m corresponds to the number of electrons produced as the result of the absorption of a photon by a single separation event in photosystems II (*PSII*) (Kromkamp and Forster, 2003). σ_{PSII}, also called *PSII* effective absorption, is a measure of the photochemical target area size of *PSII* and corresponds to the product of absorption by the suite of *PSII* antenna pigments (i.e. optical absorption cross section) and the probability that an exciton within the antenna will cause a photochemical reaction (Mauzerall and Greenbaum, 1989; Moore et al., 2006; Suggett et al., 2009). Under actinic light, F_v/F_m and σ_{PSII} both reflect how the absorbed light energy is used by *PSII* and both parameters are strongly influenced by environmental conditions and phytoplankton community structure (Suggett et al., 2009). Studying the response of these parameters to environmental conditions and phytoplankton dynamics is thus fundamental to understand phytoplankton photosynthesis. Additionally, they are needed to calculate electron transport rates (Silsbe et al., 2015; Suggett et al., 2004) and subsequently feed into models of primary production.

2. Materials and methods

2.1. Study area

The Baltic Sea is a semi-enclosed non-tidal shelf sea surrounded by nine countries. It is the largest body of brackish water in the world and is characterized by relatively stable gradients of salinity, coloured dissolved organic matter (CDOM) and nutrient availability (Olli et al., 2011; Tamminen and Andersen, 2007). Narrow shallow straits in the western part offer the only limited water exchange with the North Sea. The residence time of water in the Baltic Sea is estimated at 30 years (HELCOM, 2003). This limited exchange rate combined with a high river discharge from a wide catchment area (approximately 1.7 million km^2) results in high concentrations of nutrients, organic matter and pollutants in Baltic Sea waters. Consequently, the Baltic Sea is severely affected by eutrophication and is considered as one of the most polluted seas in the world (Lehtonen and Schiedek, 2006). Phytoplankton blooms in the Baltic Sea include a high biomass spring bloom (between March and May) consisting mainly of diatoms and dinoflagellates and a summer bloom (between June and August) dominated by filamentous cyanobacteria. A late autumn bloom of varying composition is also occasionally observed. In the Baltic Sea, cyanobacteria populations are composed of small-sized picocyanobacteria (mainly *Synechococcus* sp.) and larger colony-forming filamentous N_2-fixing cyanobacteria dominated by *Nodularia spumigena*, *Aphanizomenon flos-aquae* and *Dolichospermum* sp. (Hällfors et al., 2013; Stal et al., 2003).

2.2. Sampling methodology

Field measurements were carried out between April and August 2014 at high spatio-temporal resolution from a ship-of-opportunity: "MS Finnmaid" commuting twice a week between Helsinki (Finland) and Travemünde (Germany). The ship route nominally took 28 h and covered the Western Gulf of Finland, Northern Baltic Proper, Gotland Sea, Bornholm Basin, Arkona Sea and Mecklenburg Bight i.e. 1132 km crossing several ecological areas of the Baltic Sea (Fig. 1). Water was pumped continuously from 4 m-depth through the ferrybox measuring system and at specific locations, water samples were collected for laboratory analyses (see further below). While the location of sampling stations was somewhat variable between the different devices used, the ship route can be divided into 17 sampling zones as depicted in Fig. 1. The pumping system was switched to a washing cycle with diluted TRITON-X at each harbour.