



Spring bloom dinoflagellate cyst dynamics in three eastern sub-basins of the Baltic Sea



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ABSTRACT

Dinoflagellate cyst abundance and species composition were investigated before, during and after the spring bloom in the Gulf of Finland, north-eastern Baltic Proper and Gulf of Riga in order to detect spatial and temporal dynamics. Transport of newly formed cysts by currents was modelled to explore the possible distance travelled by cysts before sedimentation. The cyst community of the spring bloom dinoflagellates was dominated by the cysts of *Biecheleria baltica* in all basins, despite its marginal value in the planktonic spring bloom community in the Gulf of Riga. Dinoflagellate cyst abundance in the surface sediments displayed temporal dynamics in all basins, however, this appeared to be also influenced by physical processes. The model simulation showed that newly formed cysts are transported around 10–30 km from the point of origin before deposited. The latter suggests that transport of resting stages in the water column significantly affects spatial cyst distribution in the sediments and thus needs to be considered in the interpretation of temporal biological productivity patterns of a water body from cyst proxies.

1. Introduction

Dinoflagellates are a diverse group of unicellular organisms that form an important part of planktonic biomass in aquatic habitats (Dale and Dale, 2002). Dinoflagellates can be autotrophic, heterotrophic or mixotrophic (Graham et al., 2008), whereas photosynthetic species are globally important primary producers (Delwiche, 2007). The majority of dinoflagellate species are found in marine habitats, including brackish water and estuaries (Gómez, 2012), and around 10% of dinoflagellates are known to produce resting cysts to survive unfavourable conditions (Head, 1996). Cyst formation results from asexual and sexual processes (Bravo and Figueroa, 2014) and can be triggered by environmental signals or stress, e.g. changes in temperature or nutrient limitation (Ellegaard et al., 1998; Figueroa et al., 2005; Kremp et al., 2009). Once formed, resting cysts sink through the water column and accumulate into sediments (Dale, 1983), thus building up a seed bank that maintains biodiversity during unfavourable environmental conditions and allows seeding of new pelagic populations (Boero et al., 1996; Kremp, 2001; Nehring, 1996). Depending on the species, cysts may remain viable in the sediments from months up to a century (Lewis et al., 1999; Lundholm et al., 2011; McQuoid et al., 2002).

Extensive cyst formation, dense cyst beds and efficient recruitment

of cysts from sediments are among factors supporting the dominance of dinoflagellates over diatoms in some basins of the northern Baltic Sea (Klais et al., 2011). As the input of newly produced organic matter in temperate marine environments is the highest during spring (Blomqvist and Heiskanen, 2001; Heiskanen and Tallberg, 1999), the dominance of dinoflagellates has implications for the availability of food for benthos (Tamelander and Heiskanen, 2004). Most of the dinoflagellate vegetative cells disintegrate in the water column, thereby providing food to the microbial food web in the upper layer. At the same time, the resting cysts, which are resistant to degradation (e.g. Dale, 1983), and for some species also to grazing (e.g. Kremp and Shull, 2003; Montresor et al., 2003), settle to the seabed (Blomqvist and Heiskanen, 2001; Heiskanen, 1993; Heiskanen and Kononen, 1994).

In the northern Baltic Sea, the dinoflagellates *Biecheleria baltica* Moestrup et al., 2009, *Scrippsiella hangoei* (Schiller) Larsen 1995, *Gymnodinium corollarium* Sundström, Kremp & Daugbjerg 2009 and *Peridiniella catenata* (Levander) Balech 1977 form an important part of the spring bloom (Heiskanen and Kononen, 1994; Hällfors et al., 2013; Klais et al., 2013; Lips et al., 2014). These cold-water species also produce resting cysts to survive unfavourable water temperatures and to seed new blooms (Heiskanen, 1993; Kremp, 2000a; Kremp et al., 2005; Moestrup et al., 2009; Sundström et al., 2009). Particularly *B.*

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baltica is known for massive cyst production, with about 44% of the vegetative population producing cysts (Heiskanen, 1993; Kremp and Heiskanen, 1999). For *P. catenata* the exact magnitude of encystment is not known, as it forms cysts in the deep water layers (Spilling et al., 2006). However, its cumulative sedimentation is reported to be several magnitudes lower compared to *B. baltica* (Tamelander and Heiskanen, 2004). Cysts of *G. corollarium* have approximately equal sedimentation rates than cysts of *B. baltica* (Sundström et al., 2009). There is no information available regarding the proportion of cysts produced by *S. hangoei* relative to its vegetative population. However, the species is assumed to be present in low abundances in the spring bloom (Sundström et al., 2009). Dinoflagellate cyst species composition, relative and total abundances of cysts in the sediment surface layer can be influenced by the seasonal dynamics of different parameters, e.g. temperature, stratification, or availability of nutrients (Harland et al., 2004; Marret and Scourse, 2003; Warns et al., 2013). In the Gulf of Finland cysts of *B. baltica* and *P. catenata* display seasonal dynamics most probably related to germination and input of newly produced cysts (Kremp, 2000a, 2000b) (*B. baltica* cysts then considered to be cysts of *S. hangoei*). Distribution, abundance and species composition of cysts in the sediments provide valuable information regarding previous and future blooms (Anderson et al., 2014; Dale, 2001).

Cyst abundance in the surface sediments and the locations of the main cyst beds consisting of cysts produced by *B. baltica* (there as *Woloszynskia* spp.) and *P. catenata* have been mapped after the spring bloom in the Gulf of Finland, north-eastern Baltic Proper and in the Gulf of Riga previously by Olli and Trunov (2010). Dense cyst beds were detected in the central and eastern Gulf of Finland (Olli and Trunov, 2010), which have been suggested to promote dinoflagellate dominance (Klais et al., 2011). However, to what extent the cysts from different deep and shallow accumulation areas contribute to the seeding of the respective blooms has remained unknown. Furthermore, Olli and Trunov (2010) found inconsistencies between cyst distribution patterns and spatial abundances of motile cells in the overlying water column indicating that the areas of cyst production may not be the same as the areas of cyst deposition.

The Baltic Sea is a shelf sea in the northeast of Europe (Fig. 1) connected to the Atlantic Ocean via the Danish Straits, Kattegat and Skagerrak. It is one of the largest brackish water bodies in the world. The inflow of saline water from the North Sea is limited by the shallow Danish straits (Lass and Matthäus, 2008; Leppäranta and Myrberg, 2009). Northern and eastern basins receive larger freshwater input than basins in the south and west (Bergström and Carlsson, 1994).

Thus, the surface water in the northern basins is less saline (e.g. around 3 in the Bay of Bothnia) than in the southern basins (e.g. around 8 in the Arkona basin) (Leppäranta and Myrberg, 2009). The outflow of low salinity water in the surface layer and sporadic major inflows of saline North Sea water through the Danish Straits (Lass and Matthäus, 2008) maintain the salt balance and strong salinity stratification in the Baltic Sea (e.g. Leppäranta and Myrberg, 2009). The halocline (located at a depth of 60–80 m) separates upper low salinity (6–8) layer and deep more saline (10–14) layer in the central Baltic Sea (Leppäranta and Myrberg, 2009). Changing wind forcing modulate the large scale circulation. In the Gulf of Finland estuarine circulation can be reversed, i.e. outflow in the bottom layer and inflow in the surface layer, when south-westerly winds prevail (Elken et al., 2003; Liblik et al., 2013). Strong and long enough pulses of south-westerly winds in winter may cause estuarine circulation reversals, resulting in the vanishing of stratification and mixing of the entire water column (Elken et al., 2014; Liblik et al., 2013; Lips et al., 2016). Water temperature in the Baltic Sea has a characteristic annual cycle. In winter, the northern Baltic is usually ice-covered, while the average surface temperature is 2–3 °C in the south (Leppäranta and Myrberg, 2009). During spring, thermal stratification starts to develop as the surface layer is heated by solar radiation (Leppäranta and Myrberg, 2009). When the upper mixed layer becomes shallower than the euphotic zone the spring bloom starts to develop (Wasmund et al., 1998). Increasing solar radiation strengthens the seasonal thermocline, which allows temperature to rise quickly in the upper mixed layer and prevents input of nutrients from below (Hagström et al., 2001). The spring bloom ends when mineral nutrients become exhausted above the seasonal thermocline (Hagström et al., 2001). During summer, the seasonal thermocline is located at a depth of 15–30 m and the average sea surface temperature is 13–18 °C (Leppäranta and Myrberg, 2009).

In this study, the resting cysts of the three most abundant spring dinoflagellate species were investigated in surface sediments of the eastern Baltic Sea to detect spatial and temporal dynamics in cyst abundance and species composition. Ratios of empty versus live cysts of *B. baltica* were analysed to detect the potential influence of the spring bloom related life cycle events to the cyst community. To explore the geographical extent of the spread of the newly formed cysts in the water column when settling and to assess the interannual variability of such processes, transport by currents was modelled for two spring situations with different atmospheric forcing using a three-dimensional hydrodynamical model.

2. Method

2.1. Sampling

Surface sediment (0–5 cm) samples from 13 stations in the Gulf of Finland (GoF), north-eastern Baltic Proper (NEBP) and the Gulf of Riga (GoR) were collected during three national open sea monitoring cruises in 2013 (Fig. 1., Table 1) by using a Niemistö gravity corer. The sampled sediments consisted of mud and sand. More details regarding the sediment properties from most of the stations are available in Olli and Trunov (2010). Sediment from 0 to 5 cm was collected to ensure comparability with a previous study by Olli and Trunov (2010). Although the cysts in this layer represent an integration from several years depending on the sedimentation rates at each specific location, seasonal changes in cyst abundances were expected to be visible in the differences between total cyst abundances in each sampling month. Data from sediment samples taken before (January), during (April) and after the spring bloom (May) was compared to account for temporal cyst dynamics affected by benthic-pelagic coupling during the bloom season. Samples were stored in the dark at 4 °C until processing.

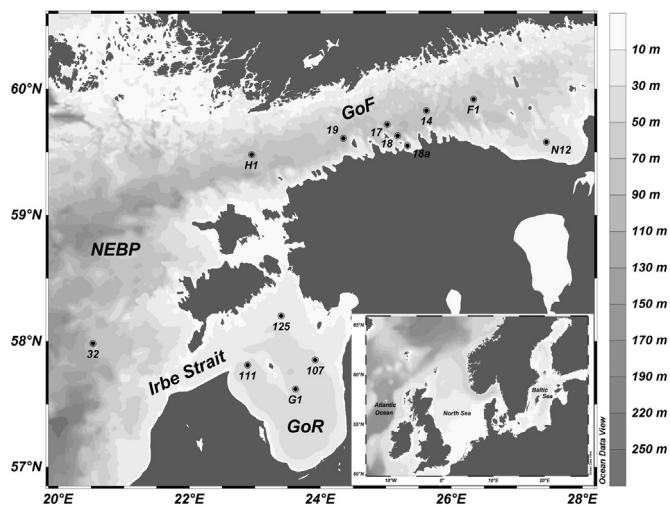


Fig. 1. Sediment sampling stations in the Gulf of Finland (GoF), north-eastern Baltic Proper (NEBP) and the Gulf of Riga (GoR). Scale bar indicates bottom depth. Inset shows the wider spatial context of the area.

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