Abundance and distribution of vernal bloom dinoflagellate cysts in the Gulf of Finland and Gulf of Riga (the Baltic Sea)

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A B S T R A C T

In the northern Baltic Sea, brackish water dinoflagellates Peridiniella catenata, Wołoszyńska spp. and Scrippsiella hangoei form a major part of the spring bloom biomass, comparable to, or even exceeding the biomass of diatoms. The life cycle of these dinoflagellates involves a relatively short period of vegetative growth in early spring (2–3 months), followed by encystment during the first part of May, and a resting period in the form of benthic cysts. The bloom intensity of the Wołoszyńska/Scrippsiella complex in the Baltic Sea is spatially variable, with peak abundances in the central and eastern Gulf of Finland, while the species are rare in the Gulf of Riga. During a field survey in late May 2004, we investigated the abundance and distribution of benthic cysts of P. catenata and Wołoszyńska spp. in surface (5 cm) sediments around the Estonian coast. The broad distribution patterns of benthic cysts reflected the overall knowledge of basin-wide planktonic phase distribution of the species. On a finer scale, sediment properties (percent of clay, organic matter content) demarked the accumulation regions of the cysts. Wołoszyńska cyst abundances in the surface 5 cm sediment were up to 3.2 × 10⁶ cysts cm⁻² and Peridiniella cyst abundances were approximately an order of magnitude less, up to 0.3 × 10⁶ cysts cm⁻².

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1. Introduction

Diatoms usually dominate the phytoplankton spring bloom in temperate waters. The Baltic Sea is an exceptional coastal brackish water body, where large dinoflagellates (20–30 μm) constitute a major, often dominant fraction of the phytoplankton spring bloom (Heiskanen and Kononen, 1994; Olli and Heiskanen, 1999; Jaanus et al., 2006; Spilling, 2007b). In recent decades dinoflagellates have generally increased in the Baltic Proper, which has been interpreted as a shift in the ecosystem (Wasmund and Uhlig, 2003). The reasons for this are not clear. The inter-annual variation in the diatom-to-dinoflagellate ratio during the spring bloom has been linked to winter severity and winter ice conditions (Kononen and Niemi, 1986; Wasmund et al., 1998). Variable ice conditions may alter the seeding success of the winter and spring phytoplankton species in the Baltic Sea (Kremp, 2000b).

There are two major spring bloom dinoflagellate groups in the Baltic Sea. The chain-forming Peridiniella catenata (Levander) Balech – a common cold-water species in Arctic and Boreal seas (Okolodkov, 1999) that was recently shown to produce benthic resting cysts (Kremp, 2000a). This species forms a large fraction of the Baltic Sea spring bloom biomass (Heiskanen and Kononen, 1994; Spilling et al., 2006), and particularly in the central Baltic Sea contributes an increasing fraction of the spring new production (Wasmund et al., 1998). P. catenata blooms in the northern Baltic Sea occur in April and May (order of 10⁶ cells L⁻¹) and terminate with nitrogen depletion (Heiskanen and Kononen, 1994; Spilling, 2007b). During the decline phase of the bloom, the abundance of P. catenata single-cell form increases, which is presumably a stage preceding encystment (Spilling et al., 2006). Prior to encystment vertically migrating cells (Olli et al., 1998; Olli, 1999) descend to below the euphotic layer (at 30–40 m depth) where cyst formation takes place, followed by deposition to the sediment surface (~10⁶ cysts m⁻² d⁻¹; Spilling et al., 2006).

The second major spring bloom group, reported mainly in the northern Baltic Sea and the Gulf of Finland, is composed of single-celled medium-sized (15–30 μm) cold-water dinoflagellates with delicate thecal plates, which can contribute in some years, 60–90% of the total spring bloom biomass (Heiskanen, 1993; Larsen et al., 1995). In the northern Baltic Sea, these blooms commonly start by forming a very dense (up to 3.6 × 10⁷ cells l⁻¹, > 300 μg Chl-a l⁻¹, Spilling, 2007a) thin layer in the strongly stratified waters under the melting ice in March, which disperse into the upper water column after ice break up (peak biomass ca. 5 × 10⁶ cells L⁻¹ in upper 10 m layer). Blooms terminate with massive cyst formation and sedimentation (order of 10⁸ cysts m⁻² d⁻¹) in mid-May.
(Heiskanen, 1993; Kremp and Heiskanen, 1999; Kremp et al., 2005). During strong bloom years the vertical flux of cysts can account for 230 mg C m\(^{-2}\) d\(^{-1}\), equivalent to ca. 45% of the spring bloom POC (total particulate organic carbon) sedimentation (Heiskanen, 1993).

Before the re-description of the peridinoid dinoflagellate Scrippsiella hangoei (Larsen et al., 1995) a variety of taxonomic names were used for this species in the literature – Peridinium sp., P. hangoei, Gymnodinium sp., Glenodinium sp. (e.g. Niemi, 1973). Recently another species, re-assigned to Woloszyńska halophila (Biecheler) Elbrächter et Kremp and co-occurring with S. hangoei was discovered in the northern Baltic Sea (Kremp et al., 2005). In fact historical SEM images (Heiskanen, 1993; Kremp et al., 2005) confirm that the species causing the massive flux of resting cysts into the benthos in the Gulf of Finland belonged to Woloszyńska, suggesting that quantitatively W. halophila is more abundant in the northern Baltic Sea. The two species cannot be separated with confidence using light microscopy in routine monitoring samples and thus the proportion of either species in the spring bloom, and their basin-wide spatial distribution and temporal dynamics remains yet to be investigated by more modern techniques.

The present study was motivated by the lack of quantitative information about the abundance and broad distribution patterns of the benthic cyst populations in the northern Baltic Sea. The objective was to map cyst abundance in surface sediments and to define the locations of major cyst beds. The field study was undertaken after the termination of the spring bloom in order to elucidate pelagic-benthic coupling within the spring dinoflagellate community and quantify the effect of the blooms on the location and density of cyst beds. For logistical reasons the study was restricted to the coastal waters surrounding Estonia.

2. Methods

2.1. Sampling areas

In 24–29 May 2004, samples were collected from 23 stations in the northern Baltic Sea (Table 1). The time of the collection was just after the known spring bloom dinoflagellate cyst deposition in the region (Heiskanen, 1993; Kremp et al., 2005) and we expected to sample all the freshly settled cysts. Sediment samples were obtained with Ekman-Birge bottom sampler (Hydro-Bios Apparatebau GmbH, Germany). Three replicate sub-samples were taken from the top 5 cm undisturbed sediment surface using a 1.5-cm-diameter syringe with its top cut off. The exact sediment accumulation rate in the sampling stations is not known, but the top 5-cm layer corresponds to approximately 15 years based on \(^{210}\)Pb dating of a reference core (Olli et al., 2008). The three replicates were pooled and placed into containers that were tightly sealed to prevent germination. All samples were kept dark at 4 °C until processing.

2.2. Sediment sample processing

Sub-samples (1–8 g) were diluted with GFF-filtered Baltic Sea seawater (6 psu) and sonicated using a Branson S250-D sonifier with a 3.2-mm microtip operated for 30 s at 60% amplitude. The sonified sediments were fractionated through Nitex screens to obtain a 10–45 µm size component. The <10 and > 45 µm fractions were checked to confirm the absence of cysts. The processed sediment aliquots were diluted (depending on the cyst concentration) and examined in 2-ml volume plankton plate chambers (Utermöhl-chamber) at a total magnification of 500× (Leica DM IL inverted microscope, phase contrast 40× lens). Examination with higher magnification (Leica DM RB, 100× oil immersion lens) revealed that most of the Scrippsiella/Woloszyńska-type cysts had clearly visible spines on the cyst wall and belonged to the genus Woloszyńska. In many cysts the spines were barely detectable using light microscopy, but we believe that all of them belonged to Woloszyńska. With routine quantification under 40× objective it was not possible to unambiguously differentiate between the two genera. We present the data as cysts of Woloszyńska, but cannot exclude the possibility that the counts include a few Scrippsiella cysts.

Aliquots of the samples were oven-dried at 105 °C for 6 h to determine sediment dry weight. Organic matter content was determined by the weight loss after combustion of dried samples for 2 h at 550 °C.

Microscopic counts were converted to cyst abundance (cysts cm\(^{-2}\) in the upper 5 cm surface sediment) by taking into account the area of the sampling syringe and the dilution factors during sample processing. The dry weight of the sediments was used to calculate cysts g\(^{-1}\) dry weight.

Granulometric analysis of sediment samples were done as follows: samples were dispersed in distilled water with a few ml of 4% sodium hexametaphosphate. Stirring and a short ultrasonic treatment (70 W, 2 min) with a probe were used to facilitate the dispersion. Dispersed samples were separated by a combination of standard wet-sieving and gravity sedimentation procedures (Griffiths, 1967) into 10 size fractions ranging from clay (< 0.002 mm) to silt (3 fractions from 0.002 to 0.063 mm) to sand (5 fractions from 0.063 to 2 mm) and gravel (> 2 mm).

2.3. Planktonic stage

The spatial distribution of planktonic stages were obtained from phytoplankton-monitoring datasets originating from the Estonian Marine Institute (Tartu University), the Institute of Aquatic Ecology (University of Latvia) and the Finnish Environment Institute. From these datasets we extracted March–May (the expected interval of bloom occurrence) surface samples from 1995 to 2005. All the historic data were counted from Lugol fixed

<table>
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<tr>
<th>Basin</th>
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<th>Depth (m)</th>
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Basis codes: e-GOF=eastern and central Gulf of Finland; w-GOF=western Gulf of Finland; GOR=Gulf of Riga. ND=no data.

Table 1 Details of sampling stations, sediment organic matter content (OM) and percent of clay fraction in the 5 cm surface sediment.
samples with inverted microscope after settling for 24 h as suggested by Edler (1979). Species-specific cell volumes were used to calculate the wet weight biomass (Edler, 1979). The data presented here are calculated as average wet weight biomass in the 0–10 m surface layer. The geographic span of samples was restricted to between 56.7 and 61 N. The datasets contained 801 quantitative phytoplankton samples. We made no assumptions that W. halophila and S. hangoei were distinguished in routine monitoring sample counts and so the results for the two species are pooled together and presented here as Woloszynskia/Scrippsiella. Due to the taxonomic confusion of the past, we used taxa are pooled together and presented here as Woloszynskia/Scrippsiella complex was present with non-zero biomass in 486 samples and P. catenata in 700 samples. The low proportion of non-zero biomass in 700 samples was caused by the rarity of this species complex in the Gulf of Riga samples. The vegetative stage biomass values were used to model the average predicted spring bloom density of the P. catenata and the Woloszynskia/Scrippsiella complex in order to compare with the observed cyst distribution in the sediments. Spatial interpolation was done using a geostatistical kriging method including all the extracted samples and the geoR software (Ribeiro Jr and Diggle, 2001). In brief, wet weight biomass values were log transformed and an empirical exponential variogram model was fitted to the data to explore the spatial structure of autocorrelation. The spatial prediction over the grid of the Baltic Sea between 56.7 and 61 N was calculated using ordinary kriging algorithm with covariance parameters estimated from the variogram model. All samples were given equal weight and the best linear unbiased estimate at each grid location was calculated. The uneven distribution of stations and variability in sampling frequency contributes to uncertainty in the predictions in areas with low sampling density, but the broad basin-wide distribution features are robust, as indicated by convergent results obtained by varying the kriging options and variogram models.

3. Results

3.1. Resting cyst distribution

The 5 cm surface sediment samples contained abundant populations of Woloszynskia (up to \(3.3 \times 10^6\) cells cm\(^{-2}\)) and P. catenata (up to \(0.3 \times 10^6\) cells cm\(^{-2}\)) resting cysts. Cyst morphology was in accordance with the descriptions in Kremp et al. (2005) and Kremp (2000a). In addition, a negligible number of unidentified dinoflagellate cysts of different morphology, large numbers of valves of planktonic centric diatoms, and pollen grains of higher plants were the most commonly observed biological structures. Cysts of Woloszynskia and P. catenata looked fresh and healthy under the microscope and probably originated from the spring bloom of the sampled year. However, many Woloszynskia cysts from the Gulf of Riga looked old, having granular cell content indicative of moribund cells (Anderson, 1980).

The distribution of cysts is presented in Table 2 and Fig. 1. Woloszynskia cysts showed a distinct basin-wide pattern, revealing high abundance (average \(1.4 \times 10^6\) cysts cm\(^{-2}\); \(404 \times 10^3\) cysts g\(^{-1}\)) in the central and eastern Gulf of Finland east of ca 24°30'E, moderate abundance in the western Gulf of Finland (average 295 \(\times 10^3\) cysts cm\(^{-2}\); \(175 \times 10^3\) cysts g\(^{-1}\)) and low abundance in the Gulf of Riga (36 \(\times 10^3\) cysts cm\(^{-2}\); \(10^3\) cysts g\(^{-1}\); Fig. 1). The distribution of P. catenata cysts was variable, but with less clear distinction between the basins. On average P. catenata cyst

![Fig. 1. Distribution of Woloszynskia and Peridiniella cysts in the 5 cm surface sediments around the Estonian coast. The area of the symbols is proportional to the cyst abundance. Note the scale difference of one order of magnitude between the panes. GOF – Gulf of Finland; GOR – Gulf of Riga.](image-url)
abundance tended to be higher in the Gulf of Riga (average $83 \times 10^3$ cysts cm$^{-2}$; $21 \times 10^3$ cysts g$^{-1}$), compared to the western ($24 \times 10^3$ cysts ml$^{-1}$; $14 \times 10^3$ cysts g$^{-1}$) and eastern Gulf of Finland ($34 \times 10^3$ cysts cm$^{-2}$; $9 \times 10^3$ cysts g$^{-1}$). Overall, Woloszynskia cysts were more abundant by a factor of 33 compared to P. catenata cysts, with the exception of the Gulf of Riga, where Woloszynskia cysts were less abundant by a factor of 0.55.

### 3.2. Planktonic population distributions

The large-scale predicted distribution of planktonic populations of Woloszynskia/Scrippsiella and P. catenata show distinct and different patterns (Fig. 2). The spatial prediction (decadal scale) of the Woloszynskia/Scrippsiella spring bloom revealed regions of highest bloom density in the central and eastern Gulf of Finland, moderate density in the western Gulf of Finland, and low density in the Gulf of Riga. Similarly, high bloom densities of P. catenata were predicted in the central and eastern Gulf of Finland and lower densities in the western Gulf of Finland. In contrast, P. catenata had very strong predicted spring blooms in the Gulf of Riga (Fig. 2).

Overall Woloszynskia/Scrippsiella was predicted to dominate the dinoflagellate spring bloom in large parts of the central and eastern Gulf of Finland, while P. catenata was predicted to be more abundant in extensive areas of the northern Baltic Proper and spectacularly in the Gulf of Riga (Fig. 3).

### 3.3. Sediment properties and bloom distribution as predictors of the benthic cyst densities

There was a highly significant ($p < 0.001$) correlation ($r=0.87$) between the clay fraction and the organic matter content of the sediments. However, the relation between benthic cyst abundance
and sediment properties was more complex. We found no statistically significant relationship between the cyst abundance of \textit{P. catenata} and sediment properties. The relationship was also non-significant to \textit{Woloszynskia} cyst abundance, when all the data were pooled. However, the disjunct basin-wide pattern of \textit{Woloszynskia}/\textit{Scrippsiella} blooms (Fig. 2) suggests that an overall relationship between benthic cyst densities and sediment properties is unlikely, and a meaningful association could only be analyzed in the more homogeneous sub-basins. Fig. 4 shows a relationship between \textit{Woloszynskia} cyst density with sediment organic matter content and the percent of clay fraction. Both plots imply a close relationship between sediment properties and cyst abundance in the eastern and western Gulf of Finland (with one outlying station), but no relationship in other basins. A linear regression model with \textit{Woloszynskia} cyst density in dry weight sediment as dependent variable, and organic matter and clay percent as independent variables has highly significant slope terms (organic matter, slope $0.19 \pm 0.01$ SE, $n=11$, $p<0.001$; clay fraction, slope $3.9 \pm 0.4$ SE, $n=12$, $p<0.001$), and non-significant intercept terms (Fig. 4).

Fig. 5 shows the point estimates from the predicted decadal-scale bloom densities (Fig. 2) at the sediment sampling locations. Log–log transformation gave the best fit between the observed \textit{Woloszynskia} cyst concentrations in surface sediments and the corresponding predicted bloom intensity (slope $0.53 \pm 0.06$ SE and intercept $11.4 \pm 0.3$ SE significant at <0.001 level), with the exception of one outlier station (Fig. 6). The log–log relationship between \textit{Peridiniella}-predicted vegetative population size and observed cyst abundance was also positive (slope $0.69 \pm 0.5$ SE, $n=23$), but not statistically significant (data not shown).

4. Discussion

The sediments of the northern Baltic Sea receive a large amount of dinoflagellate cysts after the termination of the spring
The second predictor of benthic cyst distribution is the magnitude and location of vegetative blooms in the upper water column. We do not have sufficient data for 2004, and can only rely on the decadal-scale bloom patterns as depicted in Fig. 2. Moreover, due to the dynamic nature and high variability in space and time of the Baltic Sea spring blooms (Kahru et al., 1990), it would be logistically difficult to obtain a representative time-averaged bloom pattern on a basin-wide scale. In this study we compare a single synoptic benthic cyst distribution with the predicted vegetative bloom intensity. This would inevitably introduce extra noise due to the inter-annual variability based on decadal-scale sampling effort. There is no a priori reason to assume that the relative spatial pattern of the 2004 spring bloom would represent a long-term ‘average’. However, this is a reasonable approach if we assume that sediments accumulate cysts over a number of years.

Nevertheless, comparing the expected bloom intensity of Woloszynskia/Scrippsiella in the locations of the sampling stations (Fig. 5) shows an immediate similarity with the observed benthic cyst distribution (Fig. 1). The regression plot in Fig. 6 reveals two outlier stations. Outlier stations are to be expected in such an analysis, because of the inter-annual variability. It is unlikely that the spatial pattern of the bloom in 2004, and thus cyst deposition, is a perfect reflection of the average bloom pattern over a decadal scale. It has been suggested that despite inter-annual differences, the relationship between production and sedimentation remains relatively constant during the diatom spring bloom (Bienfang and Zimmermann, 1992). A similar proportionality can be envisaged for cyst-forming spring bloom dinoflagellates in the northern Baltic Sea (Heiskanen, 1998), implying that species-specific encystment efficiency remains relatively constant.

The positive relationship in Woloszynskia/Scrippsiella is favored by the high dynamic range of the data, and major differences between the basins. Within the basin the relationship loses significance and sediment properties becomes a better predictor of cyst abundance. The lack of a significant relationship between Peridiniella-predicted vegetative population size and observed cyst abundance was due to the high variability in the data (a function of counting statistics) and more homogeneous distribution of cysts between sub-basins. The number of Peridiniella cysts counted was lower due to the overall lower cyst production efficiency of this species. For a significant relationship more samples would be needed or more counting effort spent to reduce the standard error of the data. The variability in Peridiniella cyst data led to low power of the regression analysis (0.3), and to achieve a statistically significant regression slope would have required a sample size of 129 (instead of the 23 collected in this study).

An interesting issue is how many cysts does a particular bloom produce, or what is the ratio of deposited cysts to the vegetative population size. As the same quantity of cysts can be produced by a long-lasting low-intensity bloom, or a short high-intensity bloom, we cannot rigorously assess the encystment rate with the present data (Olli et al., 2004). However, basin-wide and between species comparisons reveal interesting features. Fig. 7 shows the cyst abundance of Woloszynskia relative to predicted bloom intensity rescaled to 0–1. The high values in the Gulf of Riga give a strong indication that most of the recovered cysts from the sediments were not produced in situ, but rather imported from adjacent areas. The single low value in the Gulf of Riga is Stn. 34A, is actually outside the Irbe Strait and thus in a different hydrographic and ecological regime, while all the within-basin stations have abnormally high values. This accords with the observed differences in appearance of the cysts with a more granular inner structure, which also suggests that they were old and possibly of allochthonous origin. The disjunct distribution of
Wołoszynskia/Scrippsiella in the northern Baltic Sea remains poorly understood (Jaanus et al., 2006). Particularly, in the Gulf of Riga, the species complex has not yet established a viable local population, although there is no apparent spreading barrier to cysts from neighboring basins with similar temperature and salinity regimes.

The cyst abundances of *P. catenata* relative to bloom intensity were less variable between basins, but consistently lower compared to *Wołoszynskia*. We can compare the observed cyst abundance in the sediments with the predicted vegetative standing stock in the upper 10 m layer to get a relative cyst production efficiency for the two species. Excluding the Gulf of Riga, where *Wołoszynskia* cysts were obviously over-represented, the relative values in the eastern and western Gulf of Finland were, respectively 33 and 180 cysts veg cell\(^{-1}\) for *Wołoszynskia*, and 3 and 22 cysts veg cell\(^{-1}\) for *P. catenata*. These figures should individually not be interpreted as encystment efficiency, as they compare an instantaneous predicted bloom intensity with cysts accumulated over longer period, but it indicates that in relative terms *Wołoszynskia* is an order of magnitude more efficient cyst producer than *P. catenata*.

Differences in the cyst production efficiency of high biomass spring bloom dinoflagellates have consequences on pelagic–benthic coupling in sub-basins with different species compositions. Applying the approximate conversion factor between *Wołoszynskia* cysts and organic carbon content from Heiskanen (1993), we can calculate that cyst beds in the high deposition areas of the central and eastern Gulf of Finland are equivalent to a pelagic input of 10–16 g POC m\(^{-2}\). This is a substantial fraction of the post spring bloom (30–50 g POC m\(^{-2}\)) or annual (70–115 g POC m\(^{-2}\)) organic carbon flux to the benthos in the Gulf of Finland (Heiskanen, 1998). If the spring bloom is dominated by the less-efficient cyst producer *P. catenata*, the fate of the high biomass is largely microbial decomposition in the water column (Olli and Heiskanen, 1999; Tuomi et al., 1999).

There are very few published studies, which can be used to compare the relatively high *Wołoszynskia* cyst abundance (up to \(>3 \times 10^6\) cysts cm\(^{-2}\)) in our study. In studies from the western Gulf of Finland, the vertical flux of *Wołoszynskia* cysts after the spring bloom have been estimated directly with sediment traps moored below the productive layer at 20 m depth. Kremp and Heiskanen (1999) present data revealing a cumulative sinking flux of *Wołoszynskia* cysts southeast off the Hanko peninsula near the entrance to the Gulf of Finland as high as 0.30, 0.27 and \(0.07 \times 10^6\) cysts cm\(^{-2}\) for the spring bloom periods of 1993, 1995 and 1996, respectively. They acknowledge the inter-annual variation and the relatively high dominance of *P. catenata* in 1996, leading to low *Wołoszynskia* cyst deposition. According to our study, the sea area in the western Gulf of Finland, off the Hanko peninsula, does not belong to the high cyst deposition and bloom regions compared to the central and eastern parts of the Gulf. However, these reported cumulative depositions, measured directly with sediment traps, compare well with our estimates from the closest stations H1 and 25, 0.4 and \(0.23 \times 10^6\) cysts cm\(^{-2}\), respectively. In 1983, the phytoplankton spring bloom in the western Gulf of Finland was exceptionally strong (Heiskanen, 1993), being approximately four times higher compared to the long-term average in the region (Kononen and Niemi, 1984), and dominated by *Wołoszynskia* sp. The massive encystment and cyst flux to the benthos accounted for a cumulative deposition of \(1.16 \times 10^6\) cysts cm\(^{-2}\) after the spring bloom termination. This exceeds our cyst counts from the nearby stations H1 and 25 by a factor of 3–5. However, it is still less than half the figure we found in the high cyst deposition areas in the central and eastern Gulf of Finland (stations 14, 18, N12, F1). Thus our results compare well with the results of earlier studies, obtained with completely different methods. Also, according to this comparison, the *Wołoszynskia* spring bloom in 2004 was probably normal in intensity.

A distinction in the benthic *Wołoszynskia* cyst abundance in the Gulf of Finland, at approximately at 24.3°E suggests major separation in the water column bloom density. This separation line coincides with the quasy-stationary frontal system in the western Gulf of Finland (Kahru et al., 1995), and has also been associated with large-scale patterns of summer cyanobacteria bloom distributions in the region (Kahru et al., 2000). Further, Fig. 2 reveals that the vegetative populations of *Wołoszynskia/ Scrippsiella*, and also *P. catenata* have a strong density gradient across this front. Our *Wołoszynskia/Scrippsiella* bloom distribution map (Fig. 2) is in remarkable agreement with the map published by Jaanus et al. (2006), even though the source of the data and interpolation methods were completely different. Jaanus et al. (2006) used maximum bloom densities of *Wołoszynskia/Scrippsiella* recorded in any sampling station, and transformed these into arbitrary ranks before interpolation. Nevertheless, the main distribution features of the blooms in the northern Baltic Sea, including the strong density gradient over the 24.3°E frontal system, appear to be robust and feature in both studies. The true impact of this frontal system to the plankton community structure and dynamics has yet to be investigated.

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