Spring phytoplankton communities shaped by interannual weather variability and dispersal limitation: Mechanisms of climate change effects on key coastal primary producers

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Abstract

Spring bloom composition in the Baltic Sea, a partially ice-covered brackish coastal waterbody, is shaped by winter–spring weather conditions affecting the relative dominance of diatoms and a heterogeneous assemblage of cold-water dinoflagellates, dominated by the chain-forming *Peridiniella catenata* and a complex of at least three medium-sized, single-celled species: *Biecheleria baltica, Gymnodinium corollarium,* and *Scrippsiella hangoei.* During the last decades, the bloom community has dramatically changed in several basins. We analyze here a 30 yr time series of quantitative phytoplankton data, as predicted by hindcast modeled ice thickness and storminess for three distinct Baltic Sea localities, to verify climate-driven mechanisms affecting the spring bloom composition. Thick (> 30 cm) and long-lasting ice cover favored diatom-dominated spring blooms, and mild winters, with storms and thin ice cover (10 to 20 cm), supported blooms of the *B. baltica* complex. Dispersal limitation plays an important role in the spatial extent of blooms of the *B. baltica* complex, caused by intricate interplay of local hydrodynamics and the dinoflagellate life cycle. Proportion peaks of key phytoplankton groups have shifted about 10 d earlier in the northwestern Baltic Sea (*P. catenata* and diatoms) and in the Gulf of Riga (*P. catenata*). The significant weather effects imply future shifts in spring bloom composition and consequent biogeochemical cycles, driven by the predicted changes in winter storminess and decrease in ice cover extent and duration in climate change models.

The Baltic Sea is a semi-enclosed nontidal brackish estuary, with a narrow connection to the North Sea in the southwest and strong freshwater discharges from the catchment, creating a surface salinity gradient from 2 to 20. A major part of the annual new production takes place during the spring bloom in April–May. The initial stratification, necessary for the spring bloom commencement, is due to spreading of freshwater from the coastal zone in the Baltic Sea, instead of the temperature-driven stratification characteristic of lakes and full-saline marine regions.

The algal spring bloom in the Baltic Sea represents an anomaly from the winter–spring bloom patterns worldwide in terms of frequent and recurring dominance of dinoflagellates over diatoms (Klais et al. 2011 and references therein). In a recent study (Klais et al. 2011), we showed a dramatic shift in the regional proportions and dominance patterns of diatoms and dinoflagellates in the Baltic Sea spring bloom over four decades (1966 to 2008), implying substantial effects on the biogeochemistry of the Baltic Sea.

Both phytoplankton groups have comparable nutrient requirements (excluding the need for silica), and provide similar ecosystem services with respect to annual new production and nutrient uptake (Kremp et al. 2008). At the spring bloom peak, the phytoplankton community shows a depletion potential over 24 h equivalent to the total wintertime accumulation of inorganic nitrogen, highlighting the importance of the event for basin-wide seasonal nutrient cycles (Tamminen 1995). However, the fate of the spring bloom production is highly group- and even species-specific, affecting the pelagic nutrient cycling and benthic oxygen demand, and by and large the biogeochemical cycling between pelagic and benthic realms (Heiskanen and Kononen 1994).

There are at least four cold-water dinoflagellate species known to build up high biomasses during the spring blooms in the Baltic Sea. The recently redescribed dinoflagellate *Biecheleria baltica* Moestrup, Lindberg & Daugbjerg is so far considered endemic to the Baltic Sea (Moestrup et al. 2009) and is one of the dominant spring bloom species in the Gulf of Finland. With optimal salinity (6 to 20) and temperature (0°C to 6°C) ranges (Kremp et al. 2005) and massive resting cyst production (Kremp and Heiskanen 1999; Olli and Trunov 2010), it is well adapted to the Baltic Sea spring bloom conditions. The recently described *Gymnodinium corollarium* Sundström, Kremp & Daugbjerg (Sundström et al. 2009) dominates the spring bloom in the open Baltic Proper, but also inhabits coastal waters in the northern Baltic Proper (Suikkanen et al. 2011). *Scrippsiella hangoei* (Schiller) Larsen is a minor component of the spring bloom.

These three dinoflagellates cannot be unambiguously separated under conventional light microscopy. Therefore, when analyzed jointly, we call the *B. baltica, G. corollarium,*

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and *S. hangoei* phytoplankton group for brevity as "*B. baltica* complex" hereafter, but keep the name *B. baltica* when discussing experimental results, or field data focusing on the particular species. The fourth dinoflagellate species, the chain-forming and modestly cyst-producing *Peridiniella catenata* (Levander) Balech, is widespread in the Arctic and sub-Arctic seas (Okolodkov 1999). As a trade-off between simplicity and realism, the spring bloom diatoms, many of which produce benthic resting spores (McQuoid and Godhe 2004), are treated as a homogeneous guild in this study.

A multiyear series of indoor mesocosm experiments with natural communities indicated that mineral nutrient availability does not determine the spring bloom dominants, but it is rather the seeding success and early head start that can lead to the dominance of the relatively slow-growing dinoflagellates, particularly of *B. baltica* (Kremp et al. 2008). Several field studies have also linked the spring bloom composition, with respect to relative proportion of diatoms and dinoflagellates, to weather conditions in the winter–spring period. Kononen and Niemi (1984) reported that in the Gulf of Finland, diatom-dominated spring blooms tended to follow cold winters with long-lasting ice cover, and dinoflagellates dominate after warm winters, when ice is missing or breaking up already in March. Similar relationships may be at work in the vast Arctic shelves, where cold-water, ice-associated dinoflagellates compete successfully with spring diatom blooms (Okolodkov 1999).

Recently, exceptional under-ice densities (up to 300 μg L^{-1} chlorophyll *a* [Chl *a*]) of the *B. baltica* complex were reported in the Gulf of Finland in March (Spilling 2007), which could serve as the critical head start at the onset of the spring bloom. Klais et al. (2011) outlined a hypothesis describing weather conditions favorable for the *B. baltica* complex, including wintertime resuspension of cysts from seed banks and ice cover prior to the bloom period. With successful seeding and a sufficient head start, the *B. baltica* complex has the potential to affect dinoflagellate-to-diatom dynamics during the rest of the spring bloom.

Wind speed can have multiple effects on different algal groups before and during the spring bloom. Winter (December, January) storms resuspend the cells from the sediments in shallow areas (Kremp 2001). Although both dinoflagellates (Kremp 2001) and diatoms (McQuoid and Godhe 2004) often rely on benthic resting stages in their life-cycle strategies, there are differences in the amount and type of the resting cysts produced, as well as in the length of the obligatory dormancy time (Kremp 2001). The significance of early resuspension on the success at later phases of the spring bloom thus differs among the species. Of the major spring dinoflagellates, the *B. baltica* complex in particular is ready to germinate already in January, and field surveys have shown that it is also more effectively resuspended than *P. catenata* (Kremp 2001).

Successful germination of the *B. baltica* complex depends also crucially on prevailing irradiance. Wind-induced mixing and resuspension of the cysts into the euphotic zone considerably increases germination success and seeding of the *B. baltica* complex (Kremp 2001). In contrast, *P. catenata* germinates equally successfully in the light and at darkness (Kremp 2001), and we expect the success of *P. catenata* to be less dependent on wintertime resuspension. If winter storms are followed by development of the ice cover through February and March, subsequent stabilization of the water column causes the resuspended diatoms to sediment out of the water column, in contrast to the germinated, motile dinoflagellates.

Diatoms and dinoflagellates have contrasting preferences as groups for ambient water turbulence: diatoms are generally found in high-turbulence habitats, whereas dinoflagellates are sensitive to turbulence (Margalef 1978). In addition to the ice conditions and wintertime resuspension events prior to the spring bloom, we expected the ambient turbulence during the bloom, therefore, to favor the diatoms and disfavor dinoflagellates.

The climatically modulated rivalry between diatoms and dinoflagellates is neither unique to the Baltic Sea nor to the spring blooms. Shifts in the relative abundance of the two groups have been observed in the North Atlantic Ocean and North Sea, linked to the changing sea surface temperature and windiness (Hinder et al. 2012).

The aim of the present study is to test how climatically driven ecosystem properties will affect the spring bloom composition under projected climate change in the northern hemisphere. We therefore utilize wind speed and ice thickness data from meteorological and sea-ice models, in order to test the role of winter harshness (ice-cover thickness in March), winter storminess, and ambient turbulence, for the long-term patterns in the assembly of spring bloom algal communities in the northern Baltic Sea.

Although the phytoplankton community is also shaped by several other mechanisms, such as zooplankton grazing, differential sedimentation, and nutrient availability, they have a minor effect on the selection of spring bloom dominants. Mesozooplankton does not overwinter as adults in the northern Baltic Sea, and due to the mismatch between phytoplankton production and ontogenetic development of copepods, only < 10% of the spring bloom primary production is grazed (Lignell et al. 1993). Phytoplankton sedimentation occurs as a pulsed event during the termination phase of the spring bloom (Heiskanen and Kononen 1994). As inorganic nutrients are abundant during the bloom buildup phase, the peak-phase composition mostly reflects the recruitment success of the respective species (Kremp et al. 2008). Thus, our analysis is tailored to match variables that can be hypothesized to influence recruitment success and that represent a direct coupling to changing climate.

The data were extracted and analyzed for three hydrographically contrasting localities in the northern Baltic Sea (in terms of depth, average ice cover, and proximity to major freshwater runoff), to outline the importance of interannual weather variability for the different algal groups. In addition to differences in hydrography, the selected regions differ in their overall bloom intensity (biomass) and the relative importance of *P. catenata,* the *B. baltica* complex, and diatoms (Klais et al. 2011). Utilizing meteorological reanalysis data (hindcast modeled ice thickness and wind speed) to explain spring bloom patterns allows us to draw conclusions on the mechanisms of the
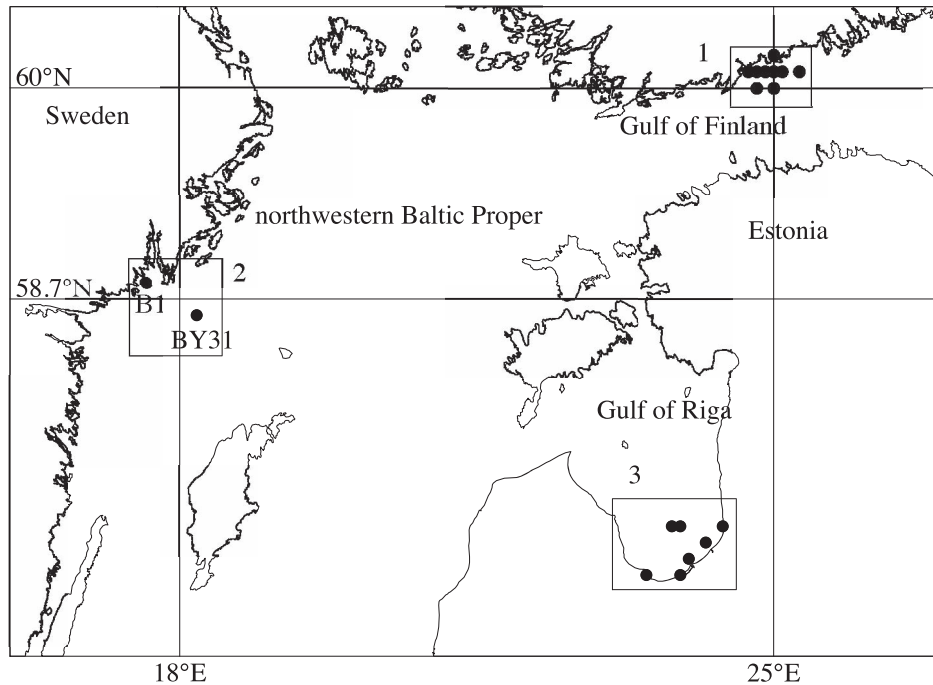
Fig. 1.   Geographical localities of the data. 1—Helsinki archipelago (640 samples), 2—Swedish locality (300 samples, divided between the coastal Askö [B1] and offshore Landsort Deep [BY31] stations), 3—Gulf of Riga (220 samples).

predicted climate change effects on bloom composition, and consequently on Baltic Sea biogeochemical cycles. Finally, we analyze the long-term trends unexplained by the environmental predictors, as an evidence of decadal-scale shifts in community composition.

Methods

Data and the study area—The quantitative phytoplankton data originate from national monitoring agencies around the Baltic Sea (Olli et al. 2013). In short, the phytoplankton data were counted from Lugol-fixed samples under an inverted microscope after settling for 24 h as suggested by Edler (1979). No semiquantitative or plankton net samples were included in our data set. Phytoplankton sampling involved pooling discrete surface samples from predefined depths, or taking an integrated sample with a sampling hose. Species-specific cell volumes were used to calculate the biovolume of each species (wet weight, μg L^{-1}) (Edler 1979) from the surface samples. We use phytoplankton spring bloom data (days of the year: 60–180) from three coastal localities in the northern Baltic Sea: Helsinki archipelago (640 samples from 1975 to 2008), Swedish east coast south of the city of Stockholm (300 samples from 1983 to 2004), and the Gulf of Riga (220 samples from 1976 to 2004) (Fig. 1). The taxonomy of the *B. baltica* complex has changed several times during the study period and is still under revision (Sundström et al. 2009). For the *B. baltica* complex, we pooled medium-sized (cell volume 1200–12,000 μm³) dinoflagellates assigned in the historical records to *Scrippsiella hangoei*, *Scrippsiella malmogiense*, *Peridinium hangoei*, or *Glenodinium* sp. Also, we checked

for other records of similarly sized spring dinoflagellates in the data, except for *Peridiniella catetana*, which is easily recognized under the light microscope.

Helsinki archipelago is a relatively shallow coastal area (mean depth ~ 20 m) in the central Gulf of Finland. Ice cover usually forms in February and breaks up by the end of March, with significant interannual variability in the duration and thickness of ice (Granskog et al. 2006). The spring bloom in the central Gulf of Finland has in general relatively equal contributions of diatoms, *B. baltica* complex, and *P. catenata*. During the last decades, the *B. baltica* complex often dominates over the other groups (Klais et al. 2011).

The Swedish data set comprises records from a coastal Sta. B1 near Askö (40 m deep; Fig. 1) and from the open-sea Sta. BY31 at Landsort Deep (459 m deep; Fig. 1). In average winters, both stations are ice covered (Granskog et al. 2006). In the area, the spring blooms start with diatoms, followed by the dominance of *P. catenata* towards the end of the bloom, with moderate abundance of species from the *B. baltica* complex (Höglander et al. 2004).

The Gulf of Riga data set consists of the phytoplankton records from the southern part of the Gulf of Riga (average depth 28 m), a semi-enclosed basin in the eastern Baltic Sea. In the Gulf of Riga, winter ice cover forms annually (Kotta et al. 2009). As a notable difference from the other two sites, viable *B. baltica* complex populations are absent in the Gulf of Riga, and the spring blooms are to a great extent diatom dominated (Jurgensone et al. 2011).

Ice-thickness time series was calculated with the Baltix model at the Finnish Meterological Institute, based on a nonlinear free surface Nucleus for European Modelling of

the Ocean, Océan Parallélisé (NEMO-OPA) model, coupled to a comprehensive Louvain-la-Neuve Sea Ice Model (LIM3) (Vancoppenolle et al. 2009). Baltix has a horizontal resolution of 3.7 km. Hindcast simulation was performed using the forcing data from the downscaled European Centre for Medium-Range Weather Forecasts reanalysis (ERA40) for the time period of 1961–2007.

Wind speed data were based on the geostrophic winds from a gridded database developed at the Swedish Meteorological Institute, reduced to 10 m level, with one estimate of wind speed per day and basin (Omstedt and Axell 2003).

Statistical analysis—Analyses were performed with statistical models combining linear and nonlinear (generalized additive model [GAM]) effects ("gam" function from "mgcv" package in R; Wood 2006), in the R statistical environment (R Development Core Team 2012). We modeled the biomass of diatoms, the *B. baltica* complex, and *P. catenata* as functions of a minimum set of significant climate-related environmental variables: average locality-specific wind speed in January, bloom period wind speed before the phytoplankton sampling as a proxy to ambient turbulence, and average ice thickness in March. January wind speed serves as a proxy for the intensity of cyst resuspension from the sediments. March ice thickness was used for two reasons. Ice thickness in March correlates with the duration of ice cover and overall winter harshness (Kononen and Niemi 1984). Also, specific ice conditions in March are pivotal for successful recruitment of species and selecting the spring bloom dominant (Spilling 2007).

The spring bloom biomass has a regular seasonal pattern: the early buildup phase, the peak of the spring bloom, and a decline phase. For the statistical modeling purposes, we calculated the biomass anomaly for each group from the expected multiyear average seasonal pattern. A seasonal GAM was fitted to the multiyear log-transformed biomass data of each group, and model residuals were used as a dependent variable in subsequent statistical analysis. In the Swedish data set, the GAMs were fitted separately for both stations, to account for the different patterns of bloom development and length of the time series in the coastal and open-sea stations. In other basins, a common smoother was used for all stations.

Similarly to phytoplankton biomass, the daily wind speed data had a regular seasonal pattern (data not shown), which was removed with a seasonal GAM smoother before calculating the bloom period wind. Bloom period wind, a proxy for ambient turbulence during the spring bloom, was approximated as a mean of daily wind speed anomalies over the period of 8–21 d before a phytoplankton sample was taken.

Statistical modeling of the effect of weather variables was done with data from all stations pooled. Initially, each model, with diatoms, *P. catenata,* or the *B. baltica* complex as dependent variables, included January and bloom time wind as a linear, and ice thickness as a nonlinear predictor. If the nonlinear effect of ice thickness was not significant, it was relegated to a linear relationship, and the model was reassessed. Nonsignificant effects were excluded by backward elimination, i.e., removing the least significant effect one at a time, until all remaining effects were significant.

Single variables seldom explain a high fraction of variability in long-term community data. The observed statistical significances, however, clearly verify directions of the underlying processes and support the plausible mechanistic connections between weather conditions and success of competing algal groups. The variance in the phytoplankton data that remained unexplained by the ice and wind variables was subsequently regressed against time using GAM, to reveal long-term multi-decadal temporal dynamics of the phytoplankton groups. If the unexplained variance had a significant time pattern, we interpreted the direction and magnitude of the trend as a long-term temporal expansion or decline of the respective phytoplankton group.

Seasonal succession of diatoms, the *B. baltica* complex, and *P. catenata* during the spring bloom was visualized by GAM curves of the biomass proportion of respective phytoplankton groups for each studied locality. Furthermore, the analysis was done separately for years before and after 1990, which represents roughly the long-term midpoint of the data, and also separates time periods with lower and higher frequency of warm winters, respectively (The BACC Author Team 2008). By splitting the data into two periods, we aimed at detecting the most prominent decadal shifts in succession sequence over the whole observation period.

Results

Ice and wind effects—The average ice thickness in March varied from completely ice-free years to ∼ 50 cm, 30 cm, and 20 cm in the Helsinki archipelago, Gulf of Riga, and the Swedish locality, respectively (Fig. 2). A significant nonlinear association between the *B. baltica* complex and ice thickness showed preference of thin ice (10–20 cm) (Fig. 3). *P. catenata* was not affected by ice, diatoms had a slight positive linear relationship with ice thickness (Table 1; Fig. 4D).

Storminess in January was favorable only for the *B. baltica* complex, but not for other phytoplankton groups (Table 1; Fig. 4B), whereas ambient turbulence was unfavorable for all dinoflagellates (Table 1; Fig. 4A,C). Unexpectedly, we did not find any positive effect of turbulence on diatom biomass.

Long-term trends in phytoplankton groups—After accounting for the environmental predictors, the variance in most of the phytoplankton groups still had a significant long-term temporal trend in the Helsinki archipelago and the coastal Sta. B1 in the Swedish locality (Fig. 5), but not in the Landsort Deep, where the data start only from 1990, and in the Gulf of Riga (data not shown). In the Helsinki archipelago and Sta. B1 in Sweden, the *B. baltica* complex showed a temporal increase. Concomitantly, diatoms had a decreasing long-term trend in both localities, and *P. catenata* had a negative trend in the Helsinki archipelago, but not in the Swedish locality (Fig. 5).
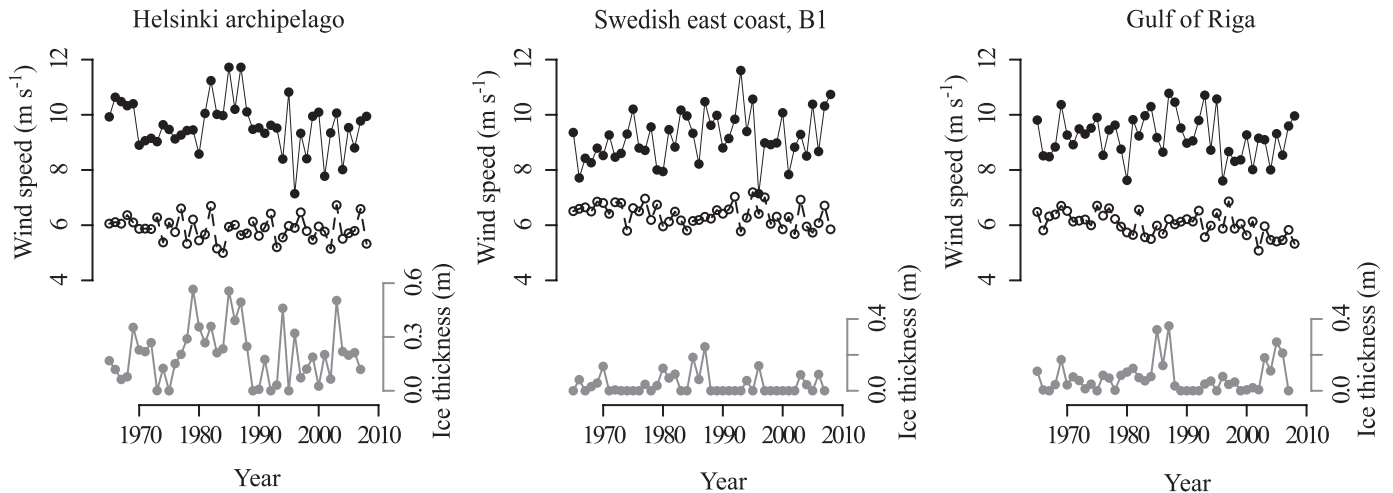
Fig. 2. Predictor variable time series by localities. Mean January wind speed (m s^{-1}) (black filled circles), mean spring wind speed (m s^{-1}) (empty circles), and mean March ice thickness (m) (gray circles).

Shifts in the seasonal sequence of phytoplankton groups—
The common spring bloom succession in the Baltic Sea follows a distinct sequence from diatoms to dinoflagellates (Fig. 6). In the Gulf of Riga, the biomass proportion peak of *P. catenata* shifted ~ 10 d earlier during the investigated period. A comparable 10 d shift of both *P. catenata* and diatom proportion peaks occurred in the Swedish locality. In the Helsinki archipelago, the main long-term change was a dramatic increase in the proportion of the *B. baltica* complex, which overrode signs of any seasonal shift. A slight long-term increase in the proportion of the *B. baltica* complex was also evident in the coastal Sta. B1 of the Swedish locality (Fig. 6).

Discussion

*Mechanisms of weather effects on phytoplankton competition—*Almost three decades ago, Kononen and Niemi

Fig. 3. The effect of the ice thickness on the success of *Biecheleria baltica* complex. The y-axis shows departure from the multiyear average biomass.

(1984) for the first time suggested that mild ice-free winters, or early ice breakup in spring, favor the dominance of dinoflagellates in the spring bloom in the northern Baltic Sea, while cold winters with late ice breakup favor diatom-dominated blooms. Since then, numerous studies (Klais et al. 2011 and references therein) have empirically supported the link between winter harshness and the dominance of diatoms vs. dinoflagellates in the spring bloom, also in other parts of the Baltic Sea. However, the evidence remained largely circumstantial and the causal mechanisms therefore unverified. Here we have synthesized over three decades of observational evidence, augmented with experimental studies (Spilling 2007; Kremp et al. 2008) and hindcast weather data, to test the mechanistic links between the winter–spring environmental conditions and spring bloom composition.

The unimodal relationship between ice thickness and *B. baltica* complex reinforces our earlier hypothesis (Klais et al. 2011) that thin ice in March favors the proliferation of dense (up to hundreds of milligrams of Chl *a* per liter) under-ice patches of the *B. baltica* complex, and is instrumental for its dominance by the commencement of the bloom (Spilling 2007). Thin ice in March serves multiple purposes. Ice reduces turbulence in the surface water by protecting from wind action. Reduced mixing in the surface layer permits extensive river water dispersal under the ice and creates a thin layer of highly stratified surface water, which is further strengthened by ice melt.

The stratified under-ice lens of less saline water strongly selects for the motile *B. baltica* complex against the nonmotile diatoms, which are prone to sink into the deeper aphotic layer. When ice breaks up, the dense under-ice patches provide the necessary head start for the *B. baltica* complex to dominate the spring bloom biomass (Kremp et al. 2008). Also, higher January wind speed, a proxy for winter storminess, favors the success of the *B. baltica* complex, but not *P. catenata*, which can be explained by the different recruitment strategies. First, the germination and seeding success of the *B. baltica* complex depends on the availability of light, whereas *P. catenata* germinates
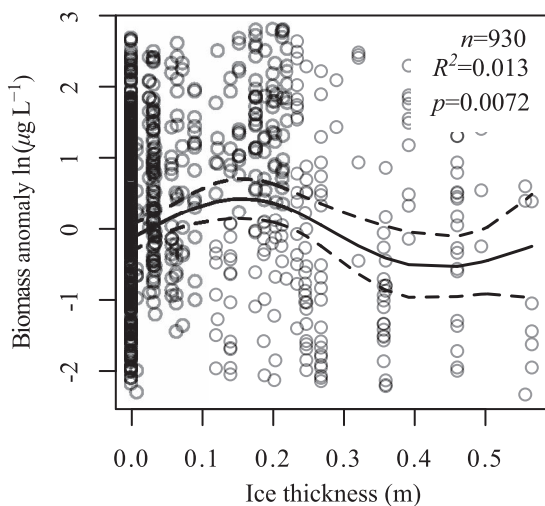
Table 1. Effects of weather variables on the biomass of *B. baltica* complex, *P. catenata*, and diatoms. Three separate phytoplankton-specific models were analyzed with all localities included in each. Variables were added as linear (lm) or nonparametric smooth (GAM) components. Variability in the phytoplankton biomass explained by the models is given as deviance explained (when a nonlinear effect was included) or as R^2 (when only linear effects were included). na—response is nonlinear and parameter estimate is not applicable.

Studied group or species	Studied effect	Parameter estimate	Significance (p)
B. baltica complex	Ice_{March} (GAM)	na	0.0009
	$Wind_{Jan}$ (lm)	0.35	6.2×10^{-5}
	$Wind_{instant}$ (lm)	−0.40	4.8×10^{-7}
	Deviance explained: 5.5%		
P. catenata	$Wind_{instant}$ (lm)	−0.29	9.3×10^{-11}
	R^2: 0.036		
Diatoms	Ice_{March} (lm)	1.2	3.9×10^{-6}
	R^2: 0.018		

equally successfully in light and complete darkness (Kremp 2001). Second, winter storms do not significantly increase the number of *P. catenata* cysts in the water column compared to calm winters, whereas in contrast, *B. baltica* complex cysts are readily resuspended from the sediments (Kremp 2001). The difference in resuspension potential

may further be evolutionarily linked to the light requirement during germination.

In contrast to diatoms, dinoflagellates in general prefer high water column stability and are negatively affected by turbulence and mixing (Margalef 1978; Hinder et al. 2012). We thus expected strong winds prior to sampling to disrupt
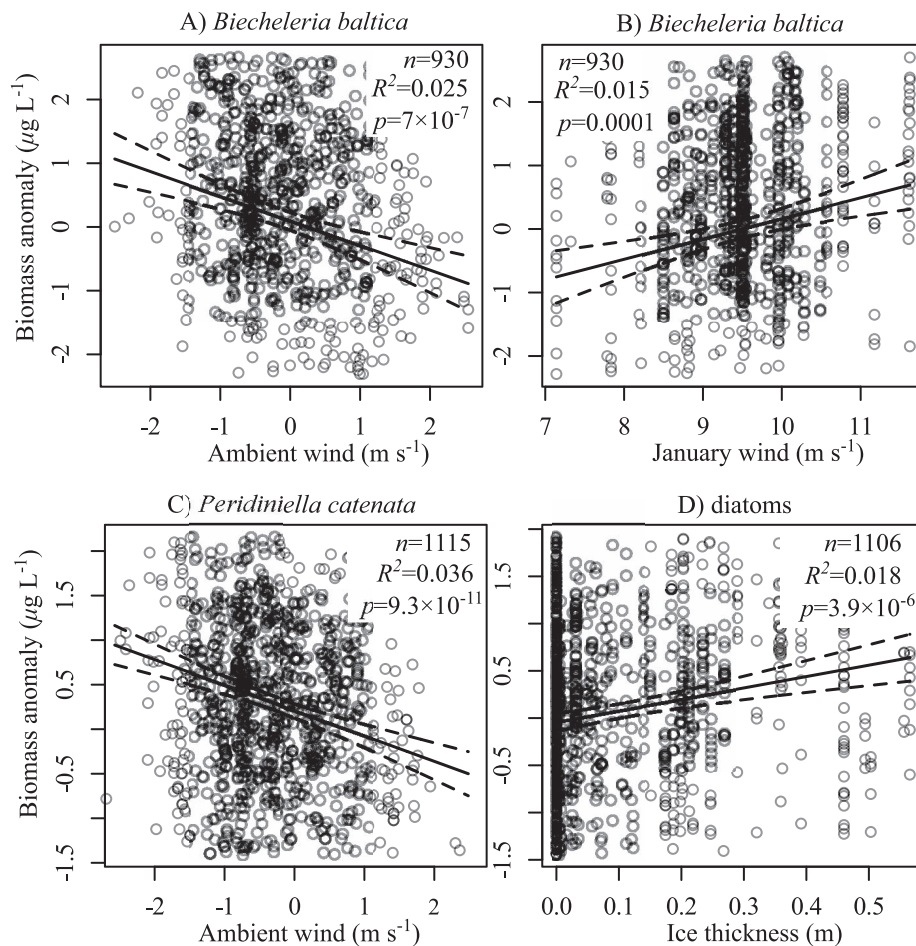

Fig. 4. Significant linear effects. On the y-axis are the anomalies from the multiyear average log-transformed biomass. (A) and (B) show the partial effects of ambient wind speed and winter storminess on the success of *Biecheleria baltica* complex, the only component of the spring blooms where there was more than one significant effect in the final model, by using the residuals from the models with ice thickness and either January wind speed or ambient wind speed, respectively.

Helsinki archipelago

$B.\ baltica$: 9.8%, $p= 6.85 \times 10^{-14}$
$P.\ catenata$: 8.2%, $p= 6.3 \times 10^{-13}$
diatoms: 24.7%, $p= {<}2 \times 10^{-16}$

Swedish east coast, B1

$B.\ baltica$: 5%, $p=0.002$
$P.\ catenata$: 4.9%, $p=0.11$
diatoms: 7.5%, $p=0.003$
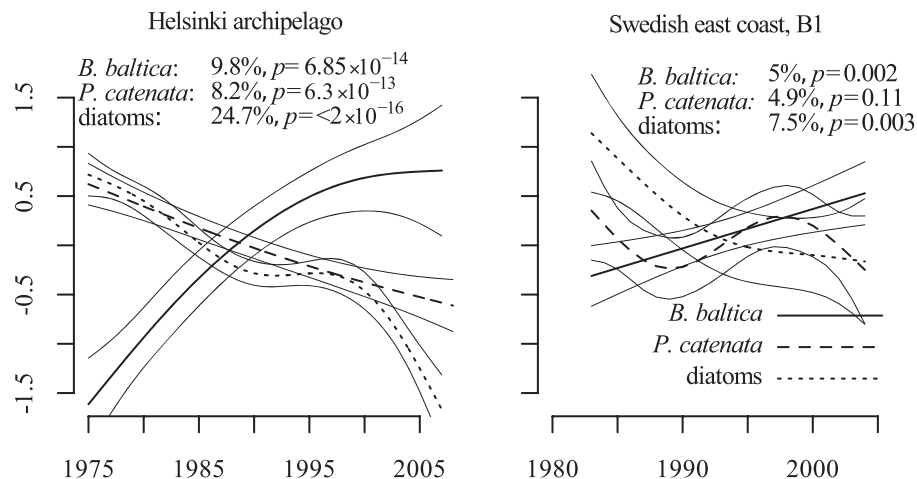
$B.\ baltica$ ⎯⎯⎯
$P.\ catenata$ ⎯ ⎯ ⎯
diatoms ⋯⋯⋯

Fig. 5. Long-term trends of phytoplankton groups in the Helsinki archipelago (1975–2008) and Swedish east coast (1983–2004). The long-term trend curves are estimates with GAM models after accounting for all significant weather variables. Thin solid lines denote double standard errors. *Biecheleria baltica* on the figure refers to the *B. baltica* complex.

Helsinki archipelago   Swedish east coast, B1   Gulf of Riga

Before 1990

After 1990

$B.baltica$ ⎯⎯⎯
$P.catenata$ ⎯ ⎯ ⎯
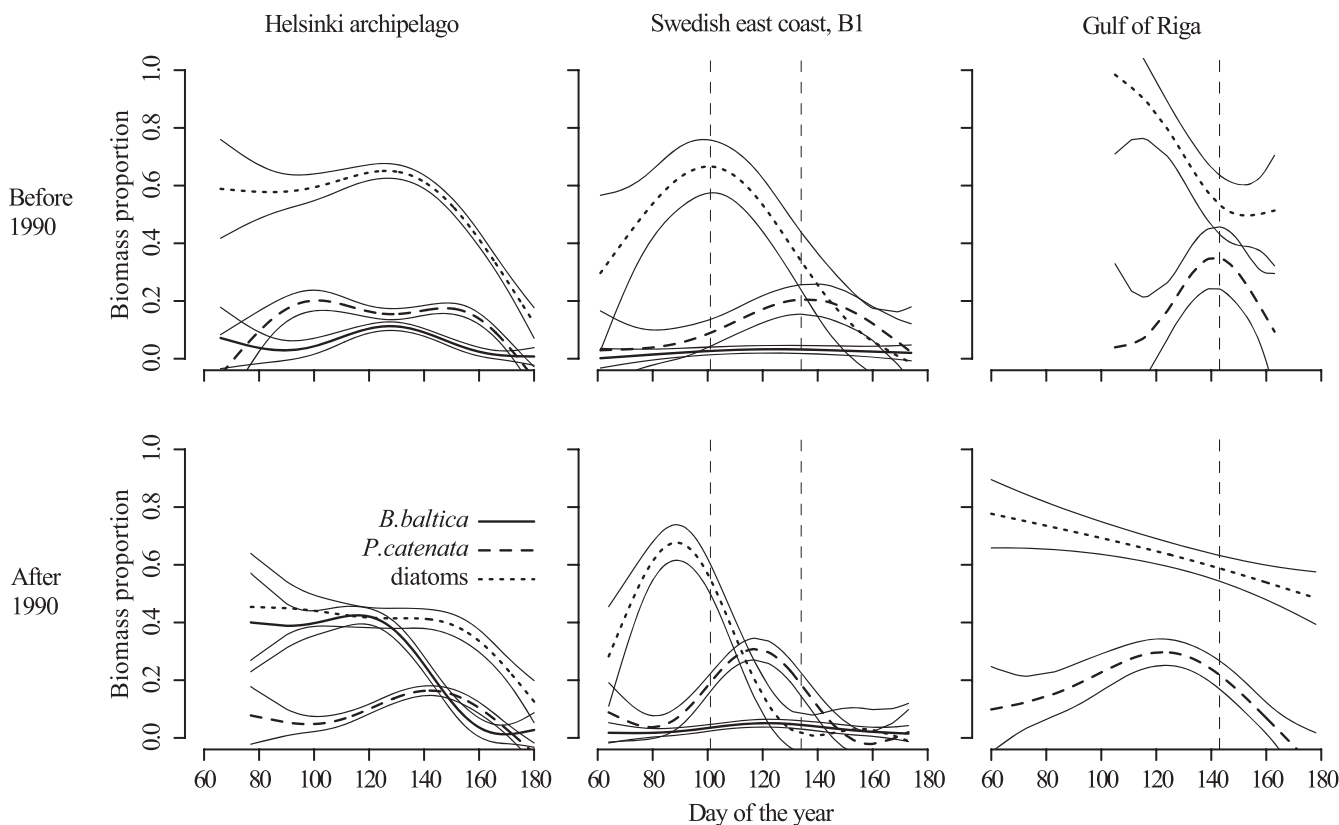diatoms ⋯⋯⋯

Biomass proportion

Day of the year

Fig. 6. Temporal shifts in the spring bloom succession in the three localities (columns). Different timing and sequence of spring bloom dominants before and after 1990 (rows) is shown with the seasonal GAMs. The y-axis is the proportion of each phytoplankton group from the total spring bloom biomass, the x-axis is the day of the year. Vertical dashed lines denote the timing of the bloom peaks of diatoms and *Peridiniella catenata* in the coastal Sta. B1, east coast of Sweden, and *P. catenata* in the Gulf of Riga before 1990. Thin solid lines along GAM curves denote double standard errors. The GAM curves are statistically significant, except for the *Biecheleria baltica* complex in the Swedish locality before 1990.

cell proliferation and associate with low dinoflagellate biomass. This was indeed verified, as both dinoflagellate groups were negatively affected by the bloom period wind speed.

However, we found no effect of ambient wind mixing on diatoms, which is opposite to the common perception that diatoms are favored by high-turbulence conditions. This evidence suggests that the spring bloom diatoms tolerate turbulence, but do not directly benefit from it. Their apparent success in turbulent conditions may thus mainly reflect weakened competition from more turbulence-sensitive dinoflagellates.

The positive linear relationship between ice thickness and diatom biomass recapitulates the empirical observation of diatom preference for cold winters. It has been suggested that earlier thermal stratification in warm years may disfavor diatoms compared to the motile dinoflagellates (Wasmund et al. 1998), but this correlation appears to be spurious, as the bloom dominance is mainly caused by initial conditions well before the establishment of thermal stratification (Kremp et al. 2008). Here the specific niche requirements of cold-water dinoflagellates contest the generalist diatoms, reflecting competition between planktonic *r*- and *K*-strategists (Klais et al. 2011). The widespread success of diatoms seems to be due to a combination of their robust environmental requirements for seeding, and superior growth rates, which compensate for low initial population sizes in the absence of dinoflagellate competitors with sufficient head-start populations.

Long-term trends and dispersal limitation—The variation in phytoplankton biomass beyond what could be explained by ice and weather conditions had a significant long-term temporal trend, indicating decadal-scale shifts in species abundances and dominance. Apart from the Gulf of Riga and Landsort Deep stations in Sweden, the long-term trend always explained more of the variation in the phytoplankton groups than environmental predictors.

We propose that the long-term shifts in community composition are driven by a gradual expansion of the *B. baltica* complex. The most dramatic changes took place in the central Gulf of Finland, where the proportion of the *B. baltica* complex increased from $\sim 10\%$ to $> 80\%$ over the investigated period, markedly modifying the overall succession pattern of the spring bloom groups. Since the total phytoplankton spring bloom biomass has not changed in time (Klais et al. 2011), the long-term increase of the *B. baltica* complex has been accompanied by decreasing biomass of diatoms, and to a lesser extent that of *P. catenata*. This supports the notion that the groups are directly competing within the basic niche framed by the wintertime nutrient accumulation, and thus functionally surrogates in terms of seasonal nutrient depletion potential (Kremp et al. 2008). As an early bloom former, the temporal expansion of the *B. baltica* complex harnesses an ascending proportion of the limiting resources, thus leaving less for other phytoplankton groups.

The overall evidence also points to the temporal and spatial expansion of the *B. baltica* complex in the northern Baltic Sea. The extraordinarily dense blooms (10^6–10^7 cells L^{-1}) and benthic cyst beds ($> 3 \times 10^{11}$ cysts m^{-2}) pinpoint the central Gulf of Finland as the center of expansion (Spilling 2007; Olli and Trunov 2010). Only ~ 300 km apart from this center of expansion, the conspicuous absence of viable *B. baltica* complex populations in the Gulf of Riga exemplifies a disjunct geographic distribution.

The contemporary distribution of the *B. baltica* complex reflects dispersal limitation, superimposed by the prevalent surface current system and the specific life-history strategies. The *B. baltica* complex in the offshore Landsort Deep station in the northwest Baltic Sea is likely consisting of the expatriates from the Gulf of Finland populations. The overall counterclockwise circulation pattern of the surface currents in the Baltic Sea (The BACC Author Team 2008) transports the vegetative populations from the central and western Gulf of Finland to the west, towards the Swedish coast in the northwest Baltic Sea. The biomass of the *B. baltica* complex in the Swedish locality was higher in the open-sea Landsort Deep site (data not shown), compared to the coastal Askö station. The offshore waters are more influenced by the major currents from the north and east than by the coastal local seedbeds, containing only low concentrations of cysts (A. Kremp unpubl.). Also, the *B. baltica* complex appears later during the bloom in the Swedish locality, not together with or before diatoms, as in the Helsinki archipelago. This further suggests that a major proportion of the *B. baltica* complex population in the deep northwestern Baltic Proper is not recruited from the local cyst beds, but mainly transported by currents from the Gulf of Finland. Molecular studies are needed to confirm if the same species or populations inhabit the Gulf of Finland and the Swedish east coast. At least in the coastal Swedish site, *G. corollarium* can form a high proportion of the *B. baltica* complex (A. Sundström pers. comm.).

When progressing southwards, the vegetative *B. baltica* complex populations originating from the Gulf of Finland are exposed to incrementally warmer surface water invoking rapid encystment at $\sim 6°C$ (Kremp et al. 2009) before reaching the entrance to the Gulf of Riga. We consider the present absence of the *B. baltica* complex in the Gulf of Riga, which hosts favorable environmental conditions for the species but remains outside the dispersal conveyor currents, therefore an example of dispersal limitation, imposed by a combination of dominant current patterns and the life cycle of the species.

Climate change effects on key primary producers—Projections of climate change suggest that water temperature and wind speed will increase and ice cover will decrease in the future Baltic Sea (Meier et al. 2012). The positive relationship between the ice-cover thickness and diatom success suggests the decreasing diatom abundance with the future climate in the Baltic Sea area. Apart from the conspicuous expansion of the *B. baltica* complex that cannot be attributed to changing climate alone, the climate warming effect was visible in our data as shifts in the seasonal peaks of dominant spring bloom phytoplankton groups in the Swedish locality and the Gulf of Riga (Fig. 6). The biomass peaks of diatoms and *P. catenata* have shifted ~ 10 d earlier during the three decades of observation,

which is in line with the increasing frequency of warmer winters, and similarly to advancement of spring events in terrestrial ecosystems in the northern hemisphere (Menzel and Fabian 1999).

Climate-driven community changes potentially constrain essential ecosystem functions, particularly in aquatic environments, where the success of higher trophic levels depends on synchronization with the seasonally highly pulsed planktonic production. However, the trajectory of change may depend on the functional group of organisms. For example in the North Sea, increasing sea surface temperature and stratification have advanced the bloom peak of dinoflagellates, but not that of diatoms, which may be more tightly linked to the day length (Edwards and Richardson 2004). Experiments in the southern Baltic Sea indicate that temperature advances the development of herbivores, but not the commencement of the light-limited phytoplankton spring bloom (Sommer and Lengfellner 2008). The partially ice-covered northern Baltic Sea shows a different pattern, where climate change may advance the spring bloom through earlier availability of light and water column stability.

The narrow ice thickness range favoring the *B. baltica* complex in the Gulf of Finland indicates that with evolving changes in ice cover, the geographical distribution could shift, but a necessary precondition for major changes appears to be gradual overcoming of the current dispersal limitation to adjacent basins. The role of accumulating seeding potential from sediments is critical for this. The present dominance of the species complex in the Gulf of Finland developed over several decades, well within the projected climate change pace.

Shifts from diatom- to dinoflagellate-dominated spring bloom have major consequences on important basin-wide biogeochemical cycles, like the vertical transport of organic matter and benthic oxygen consumption. Bloom termination and sedimentation of the biomass, within an ~ 2 week time window, accounts for $\sim 50\%$ of the annual organic matter input to the benthos in the northern Baltic Sea, and depending on the dominant species, it can account for 30–65% of the bloom period primary production (Heiskanen and Kononen 1994).

Diatoms mostly sink rapidly as intact cell aggregates, whereas the bulk of dinoflagellate biomass disintegrates in the water column and sinks slowly as refractory phytodetritus (*P. catenata*) or massively in the form of resistant resting cysts (the *B. baltica* complex) (Heiskanen and Kononen 1994). The quality of the settling material as a food source for the benthic food web, as well as the subsequent benthic oxygen demand, increases rapidly on a gradient of the *B. baltica* complex → *P. catenata* → diatom-dominated blooms (Spilling and Lindström 2008), with consequences on the spreading of anoxic deep water in the Baltic Sea.

Our analyses highlight the necessity of sufficiently detailed description of the competition between the key species, to capture the dynamics and consequences of the changing spring bloom. In order to predict the overall climate change effects on the Baltic Sea ecosystem, as well as on high-latitude coastal ecosystems in general, mechanistic description and modeling of the complex interplay between weather forcing of the spring bloom composition, species-specific ecophysiological responses and life cycles, and spatial dispersal dynamics, is therefore required.

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