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Silicate consumption: an indicator for long-term trends in spring diatom development in the Baltic Sea

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Long-term data sets from 1979 to 2011 were analysed for trends in spring diatom development. As irregular phytoplankton sampling cannot record phytoplankton blooms completely, diatom growth during spring was estimated by silicate consumption. The spring diatom biomass decreased sharply at the end of the 1980s in the Baltic Proper but not in the neighbouring western Baltic area. The diatoms, mainly *Thalassiosira* spp. and *Chaetoceros* spp., reappeared after a series of cold winters. A strong negative correlation between the minimum water temperature and the magnitude of the diatom growth in the southern Baltic Proper confirms that diatom growth has decreased after mild winters, when motile phytoplankton, such as dinoflagellates and *Mesodinium rubrum*, may form blooms instead of diatoms. Silicate limitation did not occur in the Baltic Proper. Decreased convective mixing after mild winters may hamper diatom growth (stratification hypothesis), but this effect could not be proved. Our study supports the hypothesis that increased selective grazing pressure after mild winters may control diatom spring blooms (feeding hypothesis).

KEYWORDS: diatoms; silicate; temperature; trend; Baltic Sea

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INTRODUCTION

Diatoms are one of the most important phytoplankton components in marine waters. They dominate export production (biological carbon pump) and are an important food for zooplankton and, consequently, the whole marine food web (Smetacek, 1999; Sarthou *et al.*, 2005). Disturbances in the availability of this food may have far-reaching consequences for the whole ecosystem since the carbon transfer efficiency from phytoplankton to zooplankton is highly dependent on the size structure, quality and potential toxicity of the food (Dahlgren *et al.*, 2010). Diatom spring blooms have been a recurring feature in the western Baltic Sea for at least a century (Wasmund *et al.*, 2008). In the southern Baltic Proper, however, diatom spring blooms have almost disappeared in the late 1980s (Wasmund *et al.*, 1998). At the same time, key copepod species that are essential in fish diets experienced pronounced changes leading to changes in the biomass of key fish species such as cod and sprat (Alheit *et al.*, 2005). Such regime shifts have been observed simultaneously in different areas of the world's oceans (Kraberg *et al.*, 2011). Changes in the state of the environment, caused by variations in climate or anthropogenic influences, must be considered based on specific indicators. One of these indicators can be the floristic composition of the phytoplankton, e.g. the diatom to flagellate ratio (McQuatters-Gollop *et al.*, 2009; Ferreira *et al.*, 2011). However, a problem with this indicator is that the occurrence of diatoms in large blooms, which last only a few weeks, may be overlooked in low-frequency monitoring programmes. Even if a diatom bloom is detected, its peak is rarely observed and it is impossible to estimate the real magnitude of the bloom. This weak data base makes the use of this ratio as an indicator and for trend analyses generally problematic. Wasmund *et al.* (Wasmund *et al.*, 1998) faced this problem and applied data of silicate consumption during spring instead of phytoplankton biomass data in order to estimate the magnitude of the diatom spring bloom. Using this approach, they identified the above mentioned sudden decrease in diatom spring bloom intensity in the southern Baltic Proper in 1989, which persisted until the end of their analysis in 1996. This decrease was related to a series of mild winters, which may directly or indirectly impede diatom spring blooms but also stimulate dinoflagellate growth. Recent trend analyses on the basis of phytoplankton data until 2005 show that diatoms have slowly recovered since 2000 (Wasmund *et al.*, 2011). However, the analysis suffered from low data density, which could not properly reflect diatom blooms.

The aim of this study was to investigate the long-term development of diatom spring blooms in the southern Baltic Sea on the basis of the successful silicate approach of Wasmund *et al.* (Wasmund *et al.*, 1998), but with an extended and updated database. The analysis of Wasmund *et al.* (Wasmund *et al.*, 1998) was based on one to three fixed sampling stations per region and ended in 1996. In the present analysis, we used all data available from larger areas in the respective regions and extended the data series up to the year 2011. Moreover, the Kiel Bight and the Eastern Gotland Sea were also included. We checked if the diatom development is dependent on temperature and the silicate pool and if differences between sea areas occurred. Possible reasons for the diatom trends are discussed.

STUDY AREA

The Baltic Sea is a shallow intra-continental shelf sea which has only a small connection to the fully marine North Sea. The mixture of freshwater input, mainly from the east, with the salt water input from the west causes a salinity gradient at the surface reaching from ~18 g/kg in the Danish Straits to 3 g/kg in the northern Bothnian Bay. Dense salt water flows into the Baltic Sea via the Great Belt near the bottom, whereas the brackish Baltic water flows out at the surface. Between these two water masses, a halocline establishes. According to the topographical structuring into separate basins, which become deeper to the centre of the Baltic Sea, the halocline is situated at different depths: between 15 and 25 m in Kiel Bight and Mecklenburg Bight, between 30 and 40 m in the Arkona Sea, between 50 and 60 m in the Bornholm Sea and between 60 and 80 m in the Eastern Gotland Sea (cf. Fig. 1).

We restricted our analyses to Kiel Bight and the Mecklenburg Bight, which are parts of the western Baltic, and to the Arkona Sea, Bornholm Sea and Eastern Gotland Sea belonging to the Baltic Proper. The southern part of the Eastern Gotland Sea has to be considered separately due to the specific characteristics that resemble those of the Bornholm Sea. We call this area the "Southern Gotland Sea". The Arkona Sea, Bornholm Sea and Southern Gotland Sea may be pooled as the "southern Baltic Proper". The Western Baltic and Baltic Proper are separated by the Darss Sill, an important biological border. The areas investigated together with characteristic salinity values are shown in Table I.

The spring phytoplankton community is different in these areas, as outlined by Wasmund and Siegel (Wasmund and Siegel, 2008). In general, the bloom occurs in the shallow Kiel and Mecklenburg Bight in March, sometimes even in February, but in the

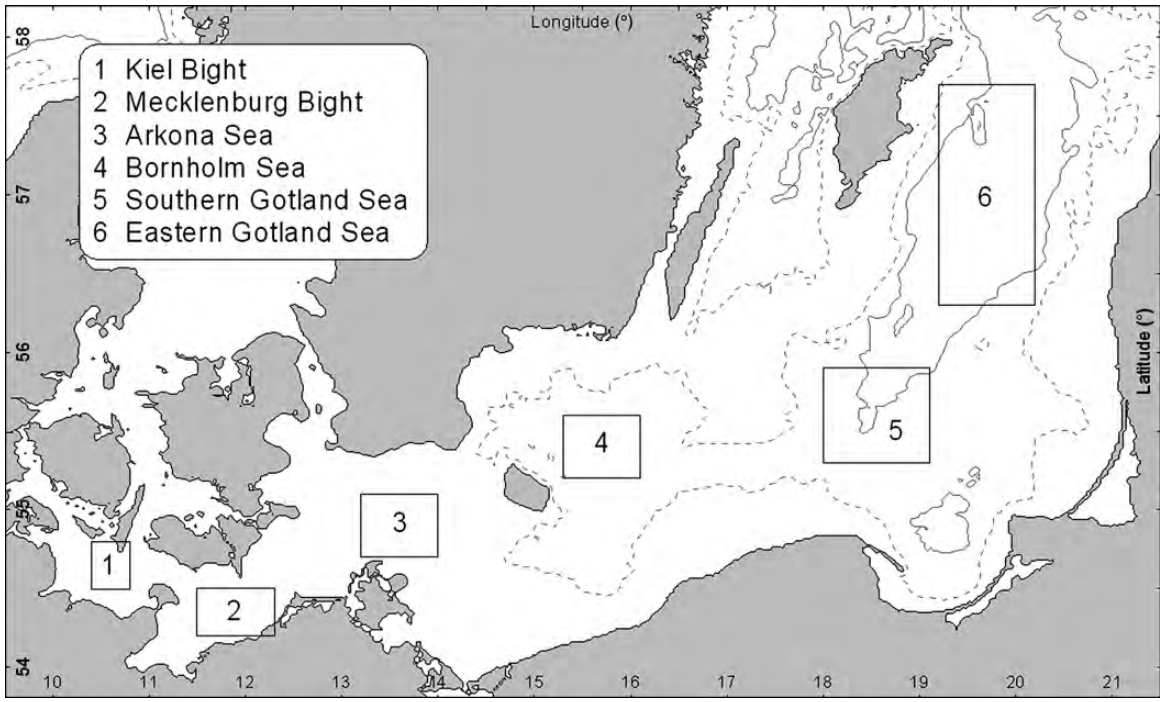

Fig. 1. Map of the western Baltic and the Baltic Proper with indication of the areas considered for the analysis. Depth contour of 50-m depth as broken line and of 100-m depth as solid line.

Table I: Investigated areas and the mean (1979–2011) salinity with standard deviation at the time of minimum temperature and the corresponding temperature of the density maximum

Sea area	Borders of investigated areas		Salinity (g/kg) at time of temperature minimum	Temperature (°C) of maximum density at the given salinity
	Longitude (°E)	Latitude (°N)		
Kiel Bight	10.4–10.8	54.5–54.8	15.57 ± 2.73	0.6
Mecklenburg Bight	11.5–12.3	54.2–54.5	12.44 ± 2.44	1.3
Arkona Sea	13.2–14.1	54.7–55.1	8.18 ± 0.44	2.3
Bornholm Sea	15.3–16.1	55.2–55.6	7.50 ± 0.30	2.4
Southern Gotland Sea	18.0–19.1	55.3–55.9	7.42 ± 0.29	2.4
Eastern Gotland Sea	19.2–20.2	56.3–57.7	7.32 ± 0.26	2.4

Bornholm Sea and Eastern Gotland Sea in April or even May. The early spring bloom in the Mecklenburg Bight consists almost exclusively of diatoms, in some years followed by Dictyochophyceae. A succession from diatoms to dinoflagellates occurs in the spring bloom of the Arkona Sea, accompanied by the mixotrophic ciliate *Mesodinium rubrum*. In the Bornholm Sea and Eastern Gotland Sea, spring blooms are frequently dominated by dinoflagellates and *Mesodinium rubrum*.

METHOD

For this study, we used common data taken in the frame of the international monitoring programme of the Helsinki Commission (HELCOM), which are stored in the ICES data bank. Additional data of the Swedish Meteorological and Hydrological Institute (SMHI) and the Polish Institute of Meteorology and Water Management (IMGW), provided to the "Baltic Atlas of Long-term Inventory an Climatology" of the Leibniz Institute for Baltic Sea Research Warnemünde (IOW), were also included (Feistel *et al.*, 2008b). As the sampling frequency influences the quality of the results, the numbers of data for each year (period January to May) and in each area are compiled in Table II. At least one pre-bloom and one post-bloom measurement was necessary ($n = 2$), otherwise insufficient data are indicated by "n.d." in Table II. The problem of data frequency is discussed below.

Table II: Number of silicate data available from the period from January to May in the areas and years indicated

Year	Kiel Bight	Mecklenburg Bight	Arkona Sea	Bornholm Sea	Southern Gotland Sea	Eastern Gotland Sea
1979	n.d.	2	5	4	n.d.	n.d.
1980	5	4	6	3	3	n.d.
1981	5	2	3	8	4	9
1982	4	3	6	7	4	7
1983	2	3	7	5	4	4
1984	4	3	7	6	7	16
1985	4	n.d.	8	7	7	5
1986	n.d.	n.d.	4	6	6	6
1987	5	5	6	7	6	7
1988	6	5	7	7	4	8
1989	10	7	13	12	6	11
1990	10	9	20	10	10	12
1991	2	n.d.	6	10	10	14
1992	3	7	13	20	8	21
1993	11	10	23	21	18	25
1994	8	14	24	30	22	49
1995	6	13	30	26	21	32
1996	4	15	25	24	17	29
1997	6	18	25	29	18	24
1998	5	21	29	33	18	34
1999	2	19	13	29	20	22
2000	5	22	31	37	18	44
2001	12	12	23	24	18	36
2002	12	14	26	30	20	33
2003	10	15	25	23	20	35
2004	9	14	24	28	17	26
2005	10	14	28	29	18	27
2006	4	12	19	21	15	24
2007	7	14	13	23	14	26
2008	10	14	18	23	11	27
2009	6	16	13	22	11	28
2010	6	17	24	15	10	14
2011	6	17	29	10	9	12

n.d., no sufficient data.

During CTD casts, water samples were taken on standard stations using rosette samplers from standard water depths according to the stipulated HELCOM methodology (HELCOM, 2008b).

The determination of dissolved silicate is based on the formation of a yellow silicomolybdic acid when the sample is treated with molybdate solution. The low intensity colours of this complex are reduced to an intensely blue complex with ascorbic acid as reductant (Koroleff, 1983). The coloured complex is measured either manually or with autoanalyzer systems.

For this study, only values from the water layer that is significant for phytoplankton growth were considered. As the water is mostly well mixed in the euphotic zone during the season of interest, the upper 10 m is used as being representative. The mean silicate value of the upper 10 m is in most cases based on original values from the surface, 5 and 10-m depth. Temperature data were taken from the corresponding depths. The highest and lowest silicate concentrations in the period from January to May of each year and in each sea area were identified as well as the lowest temperature. Examples of the calculation of silicate consumption are given in Fig. 2 for a non-bloom and for a bloom situation. It was of interest to determine whether the measured minimum temperature fell below the temperature at which the brackish water had its highest density (sigma-t). The temperature at which sigma-t was highest at a given salinity (salinity measured at the date of minimum temperature) was taken from the tables of Keala (Keala, 1965).

For phytoplankton analyses, water from five depths (0, 2.5, 5, 7.5 and 10 m) was mixed to a representative surface sample, which was quantitatively analysed using an inverted microscope according to the HELCOM manual (HELCOM, 2008a).

We restricted the study to the six sea areas which are regularly investigated by the IOW. All stations located in the rectangular central parts, with borders defined by longitude and latitude, were considered for the analysis (Table I and Fig. 1).

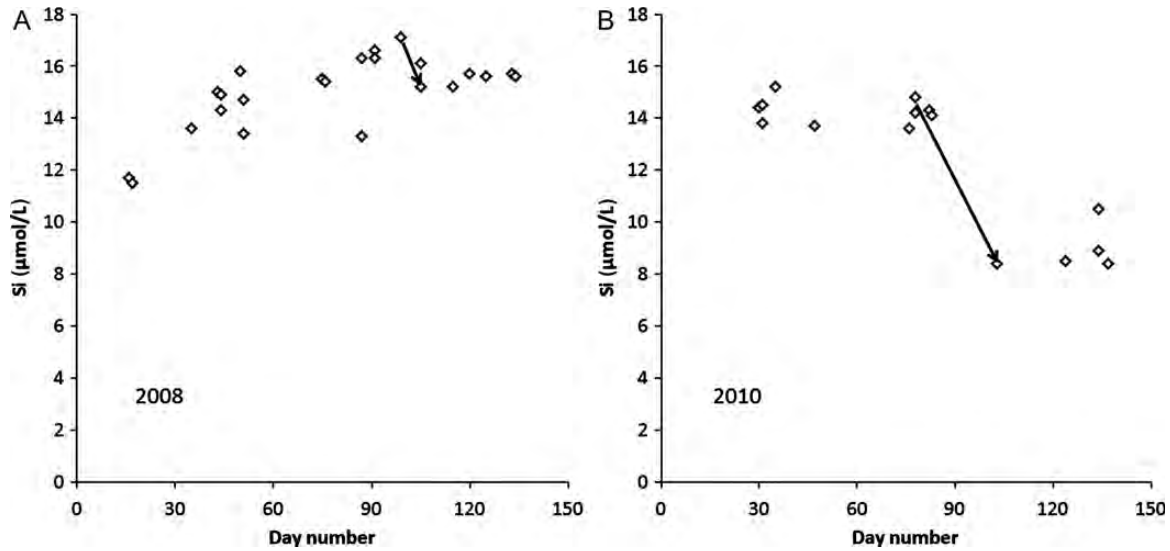

Fig. 2. Annual silicate cycle in the surface layer (0–10 m) of the Bornholm Sea in 2008 and 2010.

RESULTS

The results are shown in Fig. 3 in the format used already by Wasmund *et al.* (Wasmund *et al.*, 1998) in order to make them easily comparable. The maximum silicate concentration of winter/spring is shown as the upper line bordering a grey area. The difference between maximum and minimum silicate concentration, reflecting the consumption, is shown as columns (data see Table III). It is assumed that silicate consumption is strongly related to diatom growth as no other process and no other plankton component consumes silicate. The Dictyochophyceae forming blooms in some years in the western Baltic appear as naked cells without silicon skeleton (cf. Jochem and Babenerd, 1989). The development of the annual minimum temperature in winter/spring is added as a line.

In the Kiel and Mecklenburg Bight, strong diatom spring blooms occur every year. They exhaust the silicate reserves almost completely and may become limited by silicate. Further to the east, the diatom spring bloom intensity declines. For example, the silicate reserves were never (except for 1981) used up in the Bornholm Sea (cf. also Fig. 2).

It is clear that the annual minimum water temperature increased significantly from 1987 to 1990 in all areas considered. The diatoms response differed in the different regions. In Kiel Bight, there was no reaction. In Mecklenburg Bight and the Arkona Sea, diatoms did not respond immediately but were delayed in 1989 with a decrease in spring bloom intensity which was stronger in the Arkona Sea than in Mecklenburg Bight. The period of low diatom spring blooms lasted until 1992 in these areas. In the Bornholm Sea and Southern Gotland Sea, the decrease in diatom spring bloom intensity was most striking. The low-bloom period lasted until 1999 in the Bornholm Sea and until 2002 in the Southern Gotland Sea. This pattern was not clear in the Eastern Gotland Sea.

The relationship between annual minimum water temperature and silicate consumption in spring is shown in Fig. 4. A strong negative correlation ($P < 0.01$) between these parameters was observed in the Southern Gotland Sea, the Bornholm Sea and the Arkona Sea. In the other sea areas, no significant linear relationship ($P = 0.05$) between these parameters could be found. Despite not being significant, a dashed regression line is drawn and the coefficient of determination (R^2) is given in the corresponding figures.

As temperature is obviously of importance, the preceding winters were grouped into "cold" and "mild" winters. The surface water temperature falls below the temperature of the density maximum in cold winters, causing convective mixing. The temperature of maximum density is between 2.4°C at 7.3 g/kg and 0.6°C at 15.5 g/kg salinity as shown in Table I (Feistel *et al.*, 2008a). In mild winters, this stratification instability does not occur, and the water stays stratified if wind-induced mixing does not disturb this weak stratification.

The results for silicate consumption are compiled in Table III. The values of silicate consumption are shown in bold in years with cold preceding winters and in italics after mild winters. They confirm that the highest diatom blooms have occurred after cold winters and the lowest after mild winters in the Baltic Proper. In some

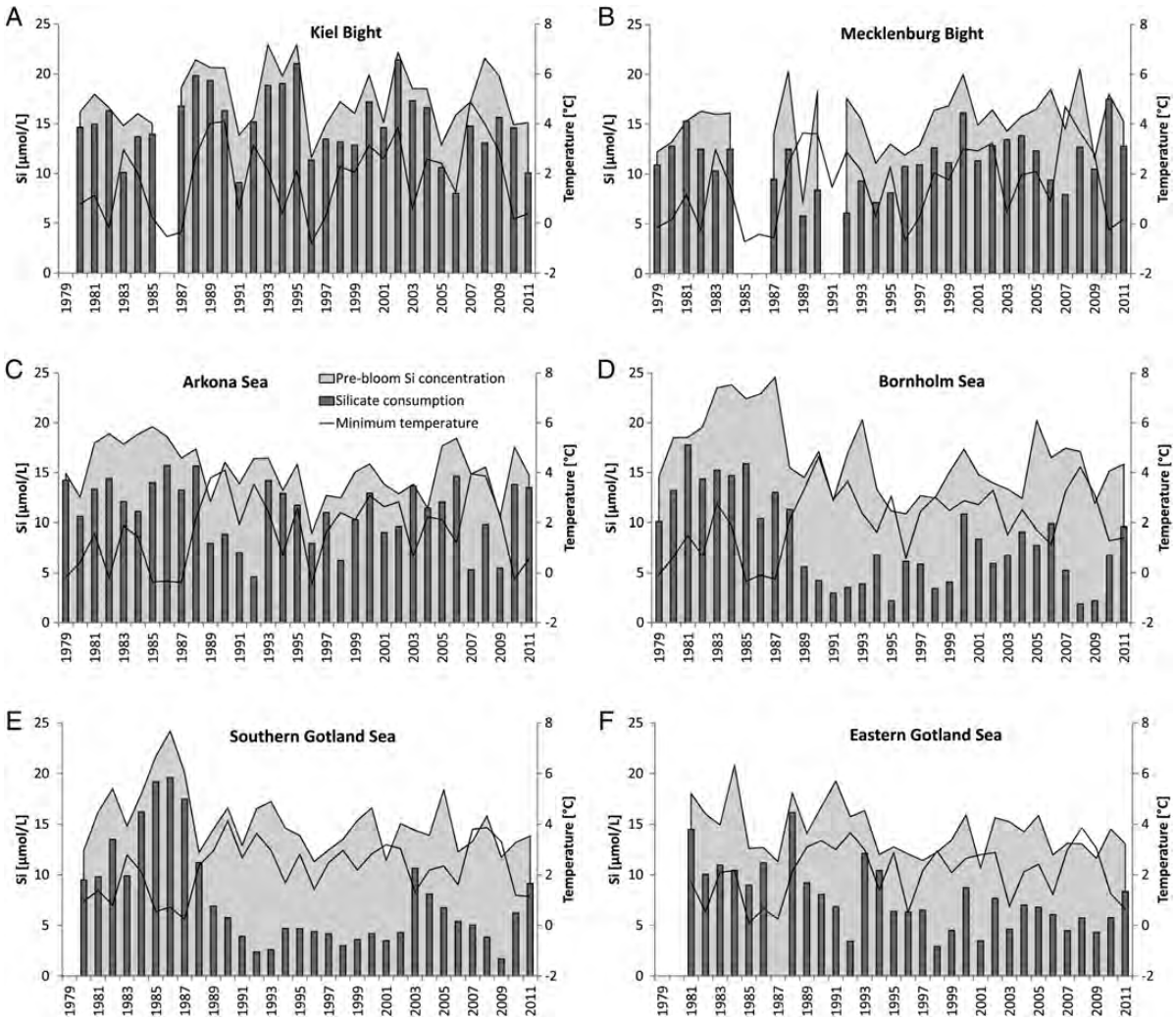

Fig. 3. Development of pre-bloom silicate concentrations, consumption of silicate during the spring bloom and minimum temperature in the different sea areas.

years, the winter characteristics are different in the sea areas. As an indicator of the general winter conditions in the Baltic Sea area, the maximum area of ice cover is shown in Table III (Schmelzer *et al.*, 2008; Schmelzer and Holfort, 2011). If the critical value is set at an area of 140 000 km^2, there is a good agreement between the water density approach and the Baltic ice cover concerning the severity of the winter.

The diatom biomass production can be estimated from the silicate consumption by using conversion factors. These factors are variable (Brzezinski, 1985), but for rough estimates a constant ratio of N:Si = 1.25 mol/mol is applicable (Sarthou *et al.*, 2005). The nitrogen units can be converted into carbon units by the Redfield ratio of C:N = 6.625 (Redfield *et al.*, 1963). As biomass production is usually given in mass units instead of molar units, a further multiplication with 12 is recommended. The total factor for conversion of silicate consumption (in µmol/L) to carbon production (in µg C/L) is roughly 100. This makes it very easy to convert the data given in Table III into carbon units.

We use this conversion in order to check the reliability of our approach. The peak biomass value of spring diatoms in the Baltic Proper, presented by Wasmund *et al.* (Wasmund *et al.*, 2011), was found on 4 May 1986 in the Eastern Gotland Sea with a wet weight of 6848 µg/L. For comparison, we calculate the potential biomass production based on the silicate consumption as follows: The silicate consumption of 11.2 µmol/L (cf. Table III) corresponds to a carbon production of

Table III: Values of silicate consumption during spring (μmol/L) in each of the sea areas

Year	Kiel Bight	Mecklenburg Bight	Arkona Sea	Bornholm Sea	Southern Gotland Sea	Eastern Gotland Sea	Area of ice cover (*1000 km^2)
1979	n.d.	10.9	14.2	10.1	n.d.	n.d.	325
1980	**14.6**	**12.8**	**10.6**	**13.2**	**9.5**	n.d.	**260**
1981	**15.0**	**15.3**	**13.4**	**17.8**	**9.8**	**14.5**	**175**
1982	**16.3**	**12.5**	**14.4**	**14.4**	**13.5**	**10.1**	**255**
1983	*10.1*	*10.3*	**12.1**	*15.3*	*9.9*	**11.0**	*117*
1984	*13.7*	*12.5*	**11.1**	**14.7**	**16.2**	**10.5**	**187**
1985	**14.0**	n.d.	**14.0**	**15.9**	**19.2**	**9.0**	**355**
1986	n.d.	n.d.	**15.7**	**10.4**	**19.6**	**11.2**	**337**
1987	**16.8**	**9.5**	**13.3**	**13.0**	**17.5**	n.d.	**405**
1988	*19.8*	*12.5*	**15.7**	**11.3**	**11.2**	**16.1**	**149**
1989	*19.3*	*5.8*	*7.9*	*5.6*	*6.9*	*9.2*	*52*
1990	*16.3*	*8.4*	*8.9*	*4.2*	*5.8*	*8.1*	*67*
1991	**9.1**	n.d.	**7.0**	*3.0*	*3.9*	*6.9*	*122*
1992	*15.2*	*6.1*	*4.6*	*3.5*	*2.4*	*3.4*	*66*
1993	*18.8*	*9.3*	*14.2*	*3.9*	*2.6*	*12.1*	*70*
1994	**19.0**	**7.1**	**12.9**	**6.8**	**4.7**	**10.4**	**206**
1995	*21.0*	*8.1*	*11.7*	*2.2*	*4.7*	*6.4*	*68*
1996	**11.4**	**10.8**	**7.9**	**6.2**	**4.4**	**6.3**	**278**
1997	**13.4**	**10.9**	**11.0**	*5.9*	**4.2**	**6.5**	*128*
1998	*13.2*	*12.6*	*6.2*	*3.4*	*3.0*	*2.9*	*129*
1999	*12.8*	*11.1*	**10.3**	*4.1*	**3.6**	**4.5**	**157**
2000	*17.2*	*16.1*	*12.9*	*10.9*	*4.2*	*8.7*	*95*
2001	*14.6*	*11.3*	*9.0*	*8.4*	*3.5*	*3.5*	*128*
2002	*21.4*	*12.8*	*9.6*	*6.0*	*4.3*	*7.7*	*102*
2003	*17.3*	**13.5**	**13.6**	**6.8**	**10.6**	**4.6**	**232**
2004	16.6	13.9	**11.5**	9.1	**8.1**	**7.0**	**152**
2005	*10.6*	*12.3*	**12.1**	**7.7**	**6.7**	**6.8**	**177**
2006	*8.0*	**9.4**	**14.7**	**9.9**	**5.4**	**6.1**	**210**
2007	*14.8*	*7.9*	*5.3*	*5.3*	*5.0*	*4.5*	*139*
2008	*13.1*	*12.7*	*9.8*	*1.9*	*3.9*	*5.7*	*49*
2009	*15.6*	*10.5*	*5.5*	*2.2*	*1.7*	*4.3*	*112*
2010	**14.6**	**17.5**	**13.8**	**6.8**	**6.3**	**5.8**	**240**
2011	**10.1**	**12.8**	**13.5**	**9.6**	**9.1**	**8.4**	**309**

The last column shows the area of maximum ice cover in the Baltic. The bold figures indicate cold winters, the italics indicate mild winters. n.d., no sufficient data. For calculating the diatom biomass production in carbon units (μg C/L), the values in the table have simply to be multiplied by 100.

1120 μg/L. If we assume that all the carbon fixed goes into biomass during non-limited bloom growth, we can take the carbon value of 1120 μg/L as the potential peak value of the bloom. A rough conversion from carbon to plasma biomass can be made by the factor $1/0.11 = 9$ suggested by Edler (Edler, 1979). The resulting diatom plasma biomass at the peak would be ~10 mg/L, which corresponds to wet weight if small cells are considered. Large diatom cells contain large vacuoles, which increase their biomass (wet weight) further. We did not make a detailed biomass calculation because we only wanted to show by this example that the biomass measured and the calculated biomass lay in the same range of magnitude. As loss processes occur, the calculated value cannot be attained in reality, but it indicates that calculations on the basis of silicate consumption may give a realistic estimate of the diatom growth potential.

We checked some typical abundant spring taxa for their occurrence after cold and mild winters, respectively. In years of low diatom occurrence in spring, dinoflagellates and the mixotrophic ciliate *Mesodinium rubrum* become the dominant components of the spring phytoplankton and have to be considered, too. The calculation of a realistic average biomass over the spring period is problematic because the real bloom development is not reflected in the low-frequency data. When considering a constant spring period, many zero-values before and after the blooms depress the average value artificially. We decided to use the peak value of each taxon during the spring period, being aware that this can only give rough information on the magnitude of the few selected taxa, as the peak is usually not met. The averages of all spring peak values of the cold and mild years in each sea area are compiled in Fig. 5. It becomes obvious that the western part (Kiel Bight, Mecklenburg Bight and Arkona Sea) is clearly different from the eastern part (Bornholm Sea and the two subregions of the Gotland Sea). It was reasonable to separate the Southern Gotland Sea from the Eastern Gotland Sea because the former is rather similar to the Bornholm Sea, at least after cold winters. As expected,

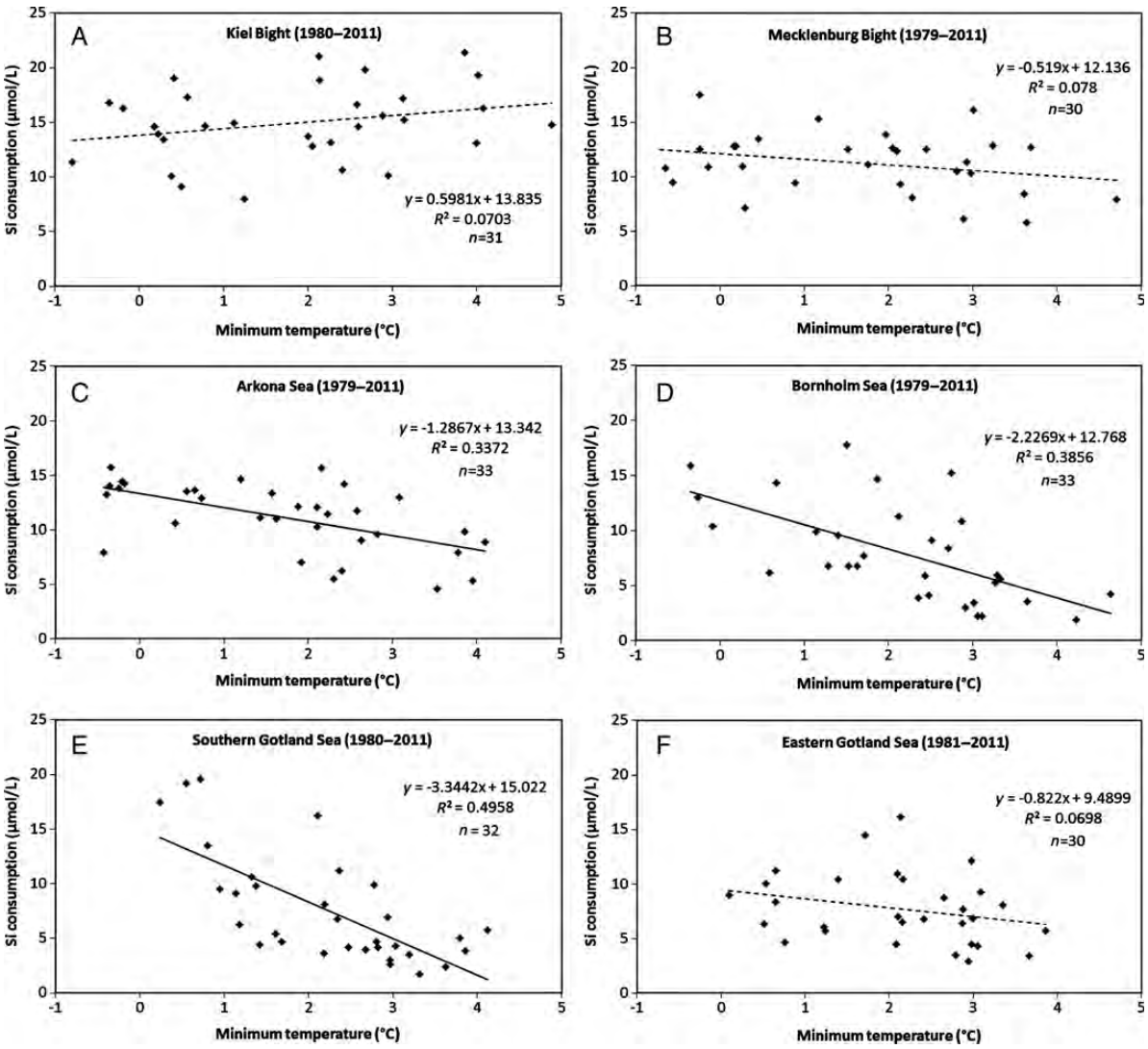

Fig. 4. Relationship between annual minimum water temperature and silicate consumption in spring in the different sea areas. Mean values of the upper 10 m were used. The regression line is inserted as full line if the correlation was significant (*t*-test; $P < 0.01$) and as a dotted line if not significant.

the sum of the dominant diatom taxa (*Thalassiosira* spp., *Chaetoceros* spp., *Skeletonema* sp.) is clearly higher in the western part than in the eastern part of the investigation area. The relatively low spring diatom biomass in the eastern part is more or less compensated by a higher proportion of dinoflagellates (*Peridiniella catenata*) and *Mesodinium rubrum*, which appear later than the usual diatom peak. The differences after cold and mild winters are most striking in the Eastern Gotland Sea, where the selected diatom species were almost absent after mild winters.

As shown in Fig. 5, *Thalassiosira* species (*T. levanderi*, *T. baltica*) seem to prefer lower temperatures. In the eastern part of the investigation area, *Thalassiosira* species even do not occur after mild winters. *Chaetoceros* species are different in the western and central parts. In Kiel Bight and Mecklenburg Bight, they grow mainly after mild winters (e.g. *Ch. borealis*, *Ch. curvisetus*, *Ch. decipiens*, *Ch. debilis*, *Ch. teres*), whereas *Ch. ceratosporus*, *Ch. holsaticus*, *Ch. similis*, *Ch. subtilis* and *Ch. wighamii* appear in the Baltic Proper rather early after cold winters. *Skeletonema* sp. (nowadays identified as *S. marinoi*) appears rather late in spring and does not show a strict temperature preference. The most interesting species is the pennate diatom *Achnanthes taeniata*. This occurs only after cold winters. It belongs to the dominant spring species in the 1980s and seemed to disappear completely (Wasmund *et al.*, 2011), but it reappeared more recently

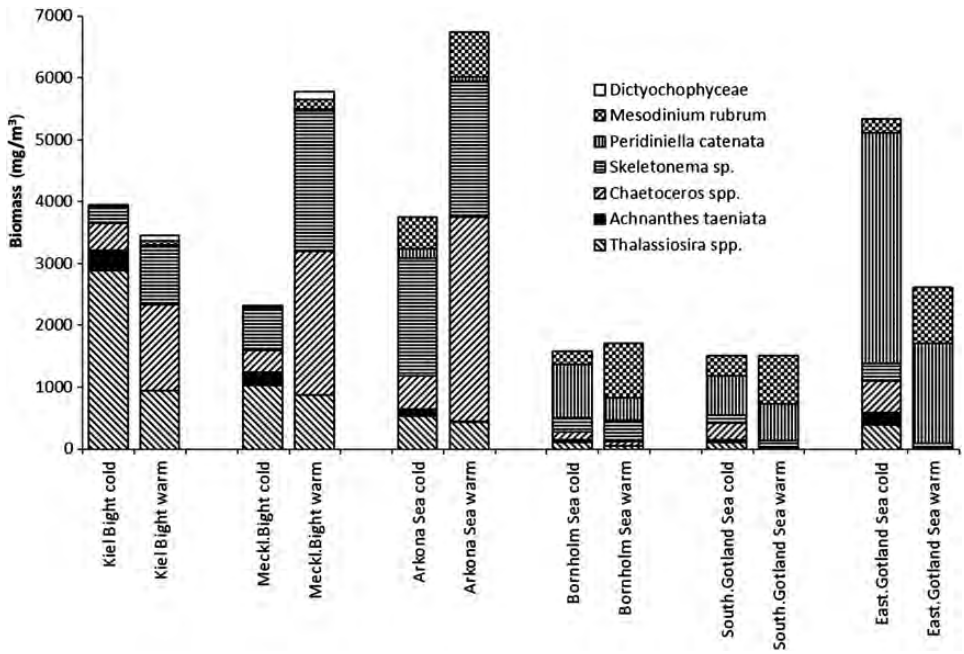

Fig. 5. Biomass peak of selected taxa in spring, averaged for all mild and cold years in the different sea areas.

after cold winters (Wasmund *et al.*, 2012). On the other hand, Dictyochophyceae (mainly *Dictyocha speculum*, but without a silicon skeleton) reach high biomass only after mild winters (e.g. 2007 and 2008) and occur only in the western Baltic.

DISCUSSION

The phenomenon of decreasing diatom spring bloom intensity in the southern Baltic Proper, identified by decreased silicate consumption, was originally described by Wasmund *et al.* (Wasmund *et al.*, 1998). They found a strong decline in diatom spring blooms especially after an increase in the winter minimum water temperature. The new period of low blooms after mild winters in 2007–2009 and the reappearance of diatom blooms after the cold winters in 2010 and 2011 confirms the influence of the temperature.

Wasmund *et al.* (Wasmund *et al.*, 1998) explained the relationship between long-term diatom decline and temperature increase as follows: Brackish water has its density maximum between 0 and 4°C, depending on its salinity. For example, the temperature of the density maximum is 2.4°C in the surface water of the Baltic Proper at an average salinity of ~7.4 g/kg (cf. Table I). If the water cools down to this temperature, the water column is mixed completely down to the permanent halocline (or in shallower areas to the bottom) and is stabilized again with further cooling at the surface. When the warming starts in spring, this convective mixing occurs again. This type of winter is called a "cold winter". In "mild winters", the water does not cool down to the temperature of the density maximum and deep convective mixing does not occur. The preserved stratification is, however, weak and may be disturbed by wind-induced mixing. In particular when the temperature of the maximum density of seawater is approached, the water column above the halocline becomes unstable and even weak wind events may penetrate to great depths (Feistel *et al.*, 2008a; IOC *et al.*, 2010).

We tried to verify the stratification hypothesis on the basis of depth profiles of temperature and salinity from winter and spring of the years investigated (not shown). This revealed that the uniform temperature surface layer extends down to the halocline even after mild winters. This was also shown by Reissmann *et al.* (Reissmann *et al.*, 2009) by a simulation of the potential temperature and salinity for the years 1989 and 1990. Consequently, the effect of wind-induced turbulence seems to exceed the effect of convective mixing. Specific investigations of the validity of the stratification hypothesis are necessary in the future.

Deep mixing supplies the initial populations to the euphotic zone (Backhaus *et al.*, 1999). The introduction of benthic resting stages to surface waters influences bloom development and composition (McQuoid and

Godhe, 2004). In general, diatoms need turbulence to stay in suspension in contrast to motile organisms, which prefer stratified water columns (Reynolds *et al.*, 1984; Spilling and Markager, 2008).

Our stratification hypothesis would also explain the differences between the sea areas because the non-motile diatoms would need convective mixing for seeding in the deep areas (Bornholm and Gotland Sea), which was assumed to be effective only after cold winters. In the shallow areas of the Baltic Sea like Kiel Bight and Mecklenburg Bight, wind-induced mixing would regularly reach down to the bottom independently of the severity of the winter, leading to diatom blooms in every year.

Although we could not show a stepwise decrease in silicate consumption with temperature increase in Fig. 4, we kept the differentiation between cold and mild winters on the basis of minimum winter temperature as long as the stratification hypothesis is not fully rejected. Fennel (Fennel, 1999) applied the same strategy in explaining differences in the timing of the spring blooms in the Baltic basins. She also realised that wind-induced mixing modifies the effect of thermal convection, but she was able to simulate spring bloom characteristics in a coupled three-dimensional model solely on the basis of the thermal convection regime without considering wind effects. At least in the Bornholm Sea, it seems that diatom spring blooms always occur after cold winters, if a diatom bloom is defined at a silicate consumption of >6 μmol/L (Fig. 4d). This threshold is reached in the example shown in Fig. 2b. After mild winters, a diatom bloom may occur or not, probably depending on wind-induced deep mixing.

The importance of the onset of stratification for the start of the spring bloom is generally accepted (Sverdrup, 1953; Smetacek and Passow, 1990; Chiswell, 2011). We have to note that not only thermal, but also shallow haline stratification can initiate a spring bloom as shown by Kahru and Nõmmann (Kahru and Nõmmann, 1990). This may be the dominant mode in the northern Baltic, which is heavily influenced by ice melt. Perhaps the southern Baltic behaves in a different way from the northern Baltic in this respect (Stipa, 2004). We exclude the northern Baltic from our considerations, but even the Eastern Gotland Sea may have been influenced by melt water, which may make the relationship between minimum temperature and silicate consumption insignificant in this area (Fig. 4f).

As an alternative hypothesis to explain the decreasing diatom biomass, increasing silicate limitation can be considered. Papush and Danielsson (Papush and Danielsson, 2006) as well as Conley *et al.* (Conley *et al.*, 2008) described a decrease in silicate concentrations in the Baltic Sea over the last 40 or even 100 years. This is caused by the combined effects of eutrophication and river damming (Conley *et al.*, 1993; Humborg *et al.*, 2008). The decrease in silicate concentration in the surface water was steepest from the 1950s to the 1960s and levelled out during the last three decades (Nausch *et al.*, 2008). Our results (Fig. 3) show that the winter silicate concentration fluctuated between 10 and 20 μmol/L with some exceptional peaks up to 25 μmol/L. These concentrations give rise to regular diatom blooms in the Kiel Bight and Mecklenburg Bight, which may exhaust the silicate resources completely. In the other sea areas, the silicate resources were still available but not used up in many years, primarily after the year 1988. Consequently, silicate limitation cannot be the reason for the decline in the diatom spring blooms. Egge and Aksnes (Egge and Aksnes, 1992) have shown in mesocosm experiments that diatom dominance occurred if silicate concentration exceeded a threshold of ~2 μmol/L. This condition is fulfilled in the Baltic Proper. Not silicate but nitrogen limitation causes the termination of the diatom blooms (Höglander *et al.*, 2004; Nausch *et al.*, 2008).

Also a top-down regulation may be considered. Sommer and Lewandowska (Sommer and Lewandowska, 2011) concluded from mesocosm experiments with spring plankton from the western Baltic Sea that spring blooms cannot be understood without considering grazing by overwintering zooplankton. In contrast to cold conditions (2.4–3.6°C), warmer conditions (8.4–9.2°C) led to higher numbers of zooplankton, decreased phytoplankton concentration and decreased phytoplankton cell size. Mesocosm experiments conducted in the northern Baltic Sea in spring showed a much higher stimulation of heterotrophic biomass in comparison with the autotrophic biomass when temperature was raised from 5 to 10°C (Müren *et al.*, 2005). Another mesocosm experiment with 5 and 10°C treatments showed that higher temperature stimulated metazooplankton production much more than primary production (Dahlgren *et al.*, 2011). In general, grazing pressure increases with temperature (Gaedke *et al.*, 2010).

Especially in early spring, the zooplankton is dominated by copepods, which may feed selectively on large-celled diatoms (Sommer and Sommer, 2006). Selective grazing by calanoid copepods has also been described by Leising *et al.* (Leising *et al.*, 2005). In a Baltic lagoon, crustacean grazing pressure restricted the development of diatoms (Gasiūnaitė and Olenina, 1998). Behrends (Behrends, 1996) noticed very high peaks in the occurrence of the dominant copepod *Oithona similis* especially after the mild winter of 1989. Also the abundant copepod genera *Acartia* and *Temora* increased strongly after the mild winters since 1988 (Alheit *et al.*, 2005).

Põllumäe (Põllumäe, 2011) found high copepod abundances after warmer winters and copepod trends related to temperature in Tallinn Bay. We conclude that zooplankton, dominated by copepods in early spring, may primarily control the diatom biomass, but not the small flagellates. This is possible only after mild winters, when zooplankton grow early enough to control the phytoplankton. Under cold conditions (1.4–2.0°C), the zooplankton (*Acartia bifilosa*) biomass and growth rate were too low to influence the diatom bloom, as shown in a mesocosm experiment by Kuuppo *et al.* (Kuuppo *et al.*, 1998).

The differences in diatom bloom patterns in the sea areas can be explained if the match or mismatch between phytoplankton and zooplankton growth is considered. Normally, a major part of the spring bloom is lost through sedimentation and not by grazing because of the slow development of the zooplankton (Heiskanen, 1998). The mesozooplankton is mostly in the nauplius stage during the spring bloom. As nauplii are feeding on a smaller size range of particles they cannot control the diatom biomass (Lignell *et al.*, 1993). It is known that the spring bloom occurs in the shallow western Baltic within the period from late February to early April (Wasmund and Siegel, 2008) when the zooplankton biomass is still low and not able to control the diatom bloom (Albjerg *et al.*, 1996).

In the Baltic Proper, the spring bloom occurs in April or May. After cold winters the situation is similar to that in the western Baltic: The zooplankton reaches its peak in May (Wasmund *et al.*, 2003), which is still too late to affect the diatom bloom significantly. Owing to this mismatch, diatoms may develop without significant grazing pressure. However, the higher temperatures after mild winters support the hatching and growth of the zooplankton, which becomes quickly abundant and is able to control the diatom bloom. The temperature control of egg hatching of *Acartia* spp. from the sediment was verified in laboratory experiments by Dutz *et al.* (Dutz *et al.*, 2004). Their field samples from the Bornholm Sea after the mild winter in 2002 showed growth of copepodites and adults of *Acartia* spp. already in April which matched with the diatom occurrence. Therefore, the earlier zooplankton growth may explain the lower diatom biomass after mild winters. A similar situation was described in the North Sea where zooplankton populations remained higher during a mild winter, feeding on the early spring bloom stages and causing a delay of the bloom's peak (Wiltshire and Manly, 2004). According to Schlüter *et al.* (Schlüter *et al.*, 2012), the start of the growth period is determined by a complex relation between Secchi disc depth, *Acartia* biomass, initial phytoplankton biomass and sea surface temperature.

Our findings and interpretations agree with those of Gaedke *et al.* (Gaedke *et al.*, 2010). They showed that edible phytoplankton (mainly diatoms) is indirectly strongly temperature-sensitive via grazing, which resulted in lower and later algal peaks at higher temperatures. They concluded that trophic interactions may overrule direct climatic effects. We will not go into details with the feeding hypothesis but refer to the latest review of Thackeray (Thackeray, 2012). We are in favour of the top-down control of the diatom blooms by copepods, but the opposite causality cannot be excluded: mild winters suppress diatoms and the copepods are bottom-up controlled by the lack of food (Alheit *et al.*, 2005). A detailed analysis of the zooplankton data from our investigation area was not possible because of sparse data background from the monitoring cruises.

The declining trend in spring diatoms in the open Baltic Proper was accompanied by an increase in dinoflagellate biomass, which lasted at least until the mid of the 1990s. Dinoflagellates decreased after 1995 in the Baltic Proper (Klais *et al.*, 2011) while the competing *Mesodinium rubrum* increased (Wasmund *et al.*, 2011). Spilling and Markager (Spilling and Markager, 2008) found much better photosynthetic and growth characteristics in diatoms than in the competing dinoflagellates. Therefore, we conclude that dinoflagellates may form blooms only in years of low diatom biomass. On occasions when diatoms failed or were grazed, new or regenerated nutrients would be left for dinoflagellate growth.

The diatom biomass production was estimated from the silicate consumption by using a conversion factor of N:Si = 1.25 mol/mol (Sarthou *et al.*, 2005). However, this value may be too low according to Spilling *et al.* (Spilling *et al.*, 2010), who found N:Si uptake ratios of 2–3 in dominant, slightly silicified diatoms of the Baltic Sea. For our rough estimate, we applied the factor mentioned above, which is in the general range given by Brzezinski (Brzezinski, 1985). As growing blooms are not limited by nutrients, a further conversion into carbon units could be made by the use of the Redfield ratio of C:N = 6.625.

We conclude that the use of nutrient consumption data is a promising method for an approximate estimate of phytoplankton growth during a specific period. As it is an integrating method, it overcomes problems with low-frequency sampling that may overlook short-term blooms. The nutrient levels before and after the blooms are rather stable and not subject to high fluctuations (cf. Fig. 2). Therefore even in low-frequency monitoring, the maxima and minima are nearly represented. The effect of advective transport is reduced by considering larger areas instead of single stations. Only the small

and shallow Kiel and Mecklenburg Bight areas are sometimes subject to stronger short-term fluctuations that may complicate the identification of the silicate maxima and minima. In some years, only one pre-bloom and one post-bloom measurement were available, but even they allowed reasonable results. Low amounts of data were available in the years 1979–1988, which were just the years with high diatom blooms. A higher data frequency could lead to a further increase of the calculated silicate consumption if new maximum and minimum values were found. The lower silicate consumption after 1988 is not caused by undersampling because data frequency is high just in that period.

The nutrient approach has drawbacks if the results are influenced by interfering processes such as bacterial nutrient uptake, or the complex of grazing, exudation and remineralization. These disturbing processes are, however, minimal in the case of silicate because it is not as strongly involved in different biological processes as phosphorus and nitrogen. The use of silicate in this approach enables the specific consideration of a very important phytoplankton group, the diatoms. As the consumption of silicate is related to diatom growth, it allows the calculation of the potential diatom biomass peak in the spring bloom. The results of this calculation are close to the measured peak data of diatom spring blooms in the Baltic Sea and confirm that our approach leads to realistic diatom bloom data.

If diatom spring blooms are considered as an indicator for environmental change, e.g. in the Marine Strategy Framework Directive (European Commission, 2008), the silicate consumption approach is the most promising strategy to estimate the magnitude of these blooms.

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