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Long-term trends in phytoplankton composition in the western and central Baltic Sea

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ABSTRACT

The phytoplankton biomass data of the period 1979–2005 of the Belt Sea area and the Baltic Proper, separated into spring, summer and autumn data, were checked for trends, together with the relevant abiotic factors (temperature, salinity, and nutrient concentrations). The Mann–Kendall test was used for detecting monotonic trends over the whole investigation period or, if trend breaks occurred, over the period before and after the trend breaks. The relationships between phytoplankton community composition and the environmental variables were assessed by a redundancy analysis (RDA), which could support some results of the trend analyses. Water temperature increased but salinity and inorganic nitrogen concentrations decreased in the southern Baltic Proper. Spring phytoplankton biomass and chlorophyll *a* concentrations increased in the Baltic Proper and decreased in Mecklenburg Bight. The biomass of Diatomophyceae decreased in spring at some stations but increased in autumn. If the Diatomophyceae spring blooms decreased, the total Dinophyceae biomass increased. Strong spring blooms of Diatomophyceae occurred in the 1980s and since 2000, but those of Dinophyceae in the 1990s. These two groups showed alternating oscillations. Trends in most phytoplankton components were different in the Baltic Proper and the Belt Sea area, confirming that Darss Sill is a biological border.

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1. Introduction

Man lives in a changing world, but his activities provoke environmental changes which are much stronger than naturally occurring evolution. To counteract the adverse effects of his activities is of vital importance for his future welfare. Actions to be undertaken involve the identification, analysis and mitigation of anthropologically caused changes. In this paper, we concentrate on the identification of changes in the marine environment, namely the phytoplankton of the Baltic Sea, irrespective of whether they are anthropogenic or natural.

The Baltic Sea is heavily impacted by eutrophication, caused by nutrient input from the densely populated and intensely cultivated catchment area and from the atmosphere, resulting in an increase in phytoplankton biomass, primary production and turbidity in the euphotic zone and oxygen deficit in deep water layers already in the early 1970s (Elmgren, 2001; Rönnerberg and Bonsdorff, 2004). The riparian countries recognised the increasing environmental problems and agreed to establish the Baltic Marine Environment Protection Commission (Helsinki Commission, HELCOM) in 1974. One of its aims

was to investigate long-term trends in trophic conditions by the Baltic Monitoring Programme (BMP, later the COMBINE programme), which has been conducted since 1979 according to a coordinated sampling schedule and binding methods.

The results of the HELCOM monitoring have been analysed in periodic assessments (e.g. HELCOM, 1996, 2002) or, recently, in thematic assessments (e.g. on eutrophication, see HELCOM, 2009) and Indicator Fact Sheets (e.g. Jaanus et al., 2007), published on the HELCOM web page. They show that not only eutrophication but also climate is a major trigger for changes in the Baltic ecosystem (BACC, 2008; HELCOM, 2007).

Hickel (1998) and Edwards et al. (2006) claimed that some phytoplankton bloom events, e.g. in the North Sea, may have been incorrectly attributed to eutrophication while the real modifier of change was of climatic or hydrodynamic origin. For several areas including the Baltic (Wasmund et al., 1998) and Mediterranean Sea (Goffart et al., 2002), a decrease in diatom and an increase in dinoflagellate abundance was detected in the late 1980s. In both cases this was related to the higher stability of the water column in the winter–spring period due to increasing winter temperatures. These higher winter temperatures were associated to a high positive North Atlantic Oscillation (NAO) index (Boyce et al., 2010; Reid et al., 2001). Significant changes in different trophic levels (phytoplankton, zooplankton, fish) and in larger areas (both in the central Baltic and

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the North Sea) in the late 1980s were termed a regime shift by Alheit et al. (2005). Likewise, a regime shift occurred in the North Pacific after a warming in 1988–1989 (Chiba et al., 2008; Hare and Mantua, 2000; Tian et al., 2008). Besides regime shifts in 1977/79 and 1988/89, indications of a further regime shift were identified in 1998 both in the North Pacific (Overland et al., 2008) and in the North Sea (Weijerman et al., 2005). At almost the same time, in 1999, an increasing trend in chlorophyll concentrations changed to a decreasing trend in the permanently stratified regions of the oceans (Behrenfeld et al., 2006).

The first step to identify complex alterations of an ecosystem is the identification of changes in biomass and composition of the key communities. Phytoplankton, as the basic primary producer in marine ecosystems, is directly dependent on abiotic variables and is very sensitive to environmental changes. The availability of consistent long-term data is the precondition for the detection of shifts in community composition. HELCOM provides such data which are stored in the ICES database.

The first statistically comprehensive analysis of the HELCOM long-term data for changes in phytoplankton composition of the Baltic Proper and the Kattegat/Belt Sea area was performed by Wasmund and Uhlig (2003). They analysed the data up to the year 1999 and found downwards trends for diatoms in spring and summer whereas dinoflagellates generally increased in the Baltic Proper, but decreased in the Kattegat. Möllmann et al. (2006) analysed phytoplankton, zooplankton, fisheries and abiotic data from the period 1974 to 2004 of the central Baltic Sea and the Gulf of Riga and confirmed the known regime shift between 1987 and 1989, but found another shift between 1993 and 1994. Suikkanen et al. (2007) performed trend analyses of the phytoplankton composition in combination with abiotic variables for the years 1979–2003. They restricted their analyses to the summer period and the northern Baltic Proper and the Gulf of Finland. Their main results concerning phytoplankton groups were: increase in biomass of chrysophytes and chlorophytes in both areas, increase in dinophytes and decrease in euglenophytes biomass in the northern Baltic Proper, increase in cyanobacteria and decrease in cryptophytes biomass in the Gulf of Finland.

Henriksen (2009) investigated six stations in the Kattegat and the western Baltic Sea for periods reaching from 1979–1997 up to 1979–2006. He detected a decrease in phytoplankton biomass, mainly diatoms, which correlated with reduced inputs of N to the Danish straits and with increases in water temperature. Moreover, he evaluated historical semi-quantitative data which showed that drastic changes in the dominant phytoplankton species occurred during the 20th century.

Wasmund et al. (2008) compared the earliest quantitative phytoplankton data of Kiel Bight from the beginning of the 20th century with recent data and found shifts in species composition and bloom characteristics. However, now as before the diatoms and dinoflagellates are the most important components of the phytoplankton although the total phytoplankton biomass has roughly doubled in the course of the last century.

As phytoplankton reacts directly to eutrophication, water acidification and climate change, the identification of trends in phytoplankton is of high scientific and political interest. Changes in phytoplankton, e.g. composition, amplitude and timing of the blooms, will have considerable consequences for the whole marine food web.

As the latest trend analyses covered only the northern and western parts of the Baltic Sea, the phytoplankton of the central Baltic Sea still requires re-evaluation because the earlier trend analysis stopped with the year 1999. Moreover, errors have been identified in older original data, which make a validation necessary. This paper provides a new trend analysis updating that of Wasmund and Uhlig (2003), based on newly validated and extended data. It not only considers taxonomic groups but also the key species and their correlations with abiotic variables.

2. 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 the freshwater input, mainly from the east, with the salt water input from the west causes a salinity gradient reaching from approximately 15 PSU in surface water of the Danish Belts to 2–3 PSU in the northern Bothnian Bay. The topographical structuring into relatively deep basins further increases variability. Accordingly, the Baltic is divided into regions, each with its own characteristic properties (Fig. 1). We restrict our analyses to the Baltic Proper (211 069 km²) and the Belt Sea (18 273 km²), which are separated by the Darss Sill. If further subdivided according to HELCOM (2009), our stations represent the Eastern and Western Gotland Sea, Bornholm Sea, Arkona Sea, Mecklenburg Bight and Kiel Bight. Our statements will only apply to these regions (Table 1).

3. Material and methods

3.1. Sampling and analyses

Sampling, microscopic examination, and analyses of nutrient and chlorophyll *a* concentrations were performed as described in the HELCOM guidelines (HELCOM, 1988), which have been only slightly modified during the three decades of the running monitoring programme. The phytoplankton biomass was calculated as described by Olenina et al. (2006).

3.2. Database

The data originate from the monitoring programme of HELCOM and from diverse research projects conducted by the Leibniz-Institute for Baltic Sea Research (IOW), provided that the HELCOM methods were applied. These data were already used by Wasmund and Uhlig (2003), but were revised for this publication. The data were updated by contributions of recent monitoring data by Sweden (Stat. J1, K2, and K4), Poland (Stat. K1 and K2), Lithuania (Stat. J1), Denmark (Stat. K2) and by own data (all stations).

After assembling the data they were checked for quality. We checked 68013 species level data records, and corrected errors if original information was sufficient for a recalculation. For example, biomass calculations based on abnormal volumes of the counting units, sometimes occurring for *Aphanothece* or *Gomphosphaeria* colonies, were corrected. If recalculation was not possible, the data of the complete sample was deleted. Mixed samples covering depth intervals deeper than 10 m were excluded. The species or higher taxa were assigned to classes and most of the “unidentified” taxa could also be allocated to a class. Heterotrophic (H) species were treated separately from autotrophic (A) and mixotrophic (M) species.

Stations in close proximity to each other and representing very similar environmental conditions were combined for statistical analyses. Stations K4, K5 and K7 were combined to a single station called K457, and stations M1 and M2 were combined to a station M12. These stations have a higher priority in our discussion than other stations with smaller amounts of data.

The monitoring programme covers all seasons but accentuates the growing season. The different bloom periods (spring, summer, and autumn) have to be analysed separately because they are characterised by completely different phytoplankton communities. The complete data set was split into four parts according to the seasons (Table 2), but winter was excluded from further analyses due to insufficient data. Note that the seasons differ in the Baltic regions because the spring bloom starts earlier in the Belt Sea than in the central Baltic Proper.

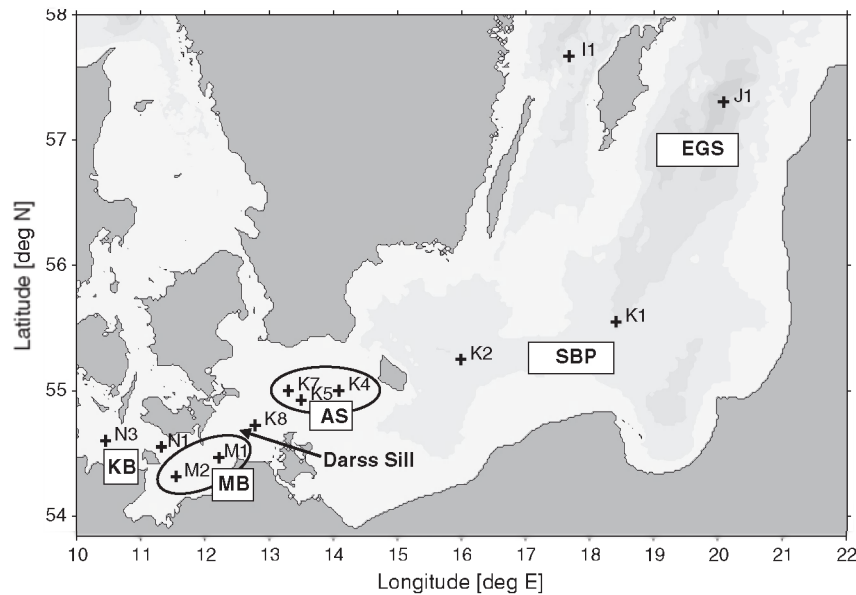


Fig. 1. The study area and sampling stations. The sea areas are abbreviated as follows: EGS—Eastern Gotland Sea, SBP—Southern Baltic Proper, AS—Arkona Sea, MB—Mecklenburg Bight, and KB—Kiel Bight.

3.3. Statistical analysis

3.3.1. Trend analysis

The Mann–Kendall trend test (McLeod, 2005) was used for detecting monotonic trends over time. Possible trend break points were detected by fitting a spline with one degree of freedom into the data (Sonderekker, 2008; Toms and Lesperance, 2003; Wood, 2000). A separate spline was fitted for every species and station combination, but for further analyses, the breakpoints were averaged at the station level. The presence of monotonic trends before and after the break point was then separately tested using the Mann–Kendall trend test. Only taxa that contained at least 10 observations per station and season were used for the statistical analyses. All trend analyses were performed in R 2.9.0 (R Development Core Team, 2009). Statistical tests were two-sided, and considered significant, if the *p*-value was less than or equal to 0.05.

3.3.2. Multivariate analysis

Redundancy analysis (RDA), (ter Braak, 1994), was used to assess relationships between the phytoplankton community composition and

five environmental variables. The analysis was run with the combined data from all stations, but separately for the three different seasons. Phytoplankton data was linked to temperature and salinity of the same sampling occasion, but to nutrient data from the previous sampling event (max. one month before). All biomass data were $\log(x+1)$ -transformed to stabilize variance and reduce the influence of dominant taxa on the ordination. RDA was performed using CANOCO for Windows 4.0 (ter Braak and Šmilauer, 1998) as described in Suikkanen et al. (2007). Due to the limitations of the program, samples containing missing environmental data had to be omitted.

4. Results and discussion

4.1. Changes in environmental drivers

The output of the trend analyses are summarized in Fig. 2 and showed very complex patterns across stations and seasons. Our analyses demonstrated a significant increase in the temperature of the surface waters especially in the Arkona and Bornholm Seas in summer and autumn. The warming of the upper water layers intensifies the

Table 1

Investigated stations and data frequency at the stations.

Station name	Sea area	Latitude (°N, in decimals)	Longitude (°E, in decimals)	Length of data series	Number of phytoplankton samplings (n) in spring/summer/autumn
<i>Baltic Proper</i>					
BMP I1	Western Gotland Sea	57.12	17.67	1979–1996	23/27/32
BMP J1	Eastern Gotland Sea	57.32	20.05	1979–2005	116/126/78
BMP K1	Southern Gotland Sea	55.56	18.40	1979–2005	73/63/50
BMP K2	Bornholm Sea	55.25	15.98	1979–2006	137/141/88
BMP K4	Eastern Arkona Sea	55.00	14.08	1979–2005	
BMP K5	Central Arkona Sea (GE)	54.93	13.50	1981–2005	224/191/152 ^a
BMP K7	Central Arkona Sea (DK)	55.00	13.30	1979–2002	
BMP K8	Darss Sill	54.72	12.78	1989–2005	52/34/26
<i>Belt Sea</i>					
BMP M1	Kadet Channel	54.47	12.22	1980–2005	
BMP M2	Mecklenburg Bight	54.32	11.55	1980–2005	138/154/106 ^b
BMP N1	Fehmarn Belt	54.57	11.33	1979–1997	46/85/72
BMP N3	Kiel Bight	54.60	10.45	1986–2000	24/37/25

^a Stations K4, K5 and K7 combined.

^b Stations M1 and M2 combined.

Table 2
Definition of seasons according to the HELCOM strategy (e.g. HELCOM, 1996).

Season	Belt Sea	Baltic Proper
Spring	February–April	March–May
Summer	May–August	June–September
Autumn	September–November	October–December

stratification and reduces the upward transport of deep water of higher salinity and nutrient contents. This may be one reason for the strongly decreased salinity in the surface water in the Baltic Proper (Fig. 2). The reduction in major inflows of marine water into the deep Baltic basins during recent decades is another reason for the reduced salinity (Matthäus et al., 2008).

A decrease in the concentrations of dissolved inorganic nitrogen (DIN) has been demonstrated for the southern Baltic Proper in all seasons. Phosphate concentrations changed only at two stations with a shorter time series and are therefore less relevant. Silicate concentration was slightly increasing in the Eastern Gotland Sea during spring and summer and in the Mecklenburg Bight in autumn (Fig. 2).

Nausch et al. (2008) stated that the main eutrophication pulse occurred until the 1980s. Afterwards, the nitrate plus nitrite concentrations decreased in the winter surface layer (0–10 m) of the Eastern Gotland Sea and the Bornholm Sea, whereas phosphate concentrations were strongly fluctuating at a high level. It is expected that also the silicate concentrations decrease because of reduced river loadings (as result of river damming) and eutrophication (Conley et al., 2008; Humborg et al., 2008). Papush and Danielsson (2006) found downwards silicate trends from 1970 to 2001 at most stations of the Baltic proper, but not if only the period from 1991 to 2001 was considered. Obviously, the termination of the eutrophication trend stopped the silicate decrease. The eutrophication ceased also in the northern Baltic Proper in the 1980s, and the DIN:silicate ratio of winter data declined since the 1990s (Fleming-Lehtinen et al., 2008). As stated above, our results revealed even increasing silicate trends in different seasons over the whole investigation period at stations J1 and M12.

4.2. Trends in phytoplankton biomass

The trends in different phytoplankton taxa, separated for stations and seasons, are summarized in Fig. 2. A selection of the most important data series is exemplified in Figs. 3–7 as a basis for discussion.

4.2.1. Total biomass

The plausibility of the trends of microscopically determined total A + M biomass, which represents the phytoplankton, can be checked by comparison with chlorophyll *a* data. We found interesting differences in chlorophyll trends (1979–2005) if different seasons were analysed separately (Fig. 2): The chlorophyll *a* concentrations increased in the Baltic Proper but decreased in Mecklenburg Bight in spring. Summer data revealed no trend and autumn data only increasing trends at stations J1 and K457. Similar results were described by Wasmund and Siegel (2008). In the northern Baltic Proper, even increasing trends in chlorophyll *a* concentrations were found in summer data (Fleming-Lehtinen et al., 2008; Suikkanen et al., 2007).

Our chlorophyll trends support our phytoplankton trends from spring (Fig. 3a, b) and from autumn but not those of summer (Fig. 3c). Therefore, and because the declining summer biomass trends are caused by only a few extreme values which occurred just at the beginning of the time series, we regard them with suspicion. The autumn data of phytoplankton biomass showed peak values at the end of the 1980s in the Baltic Proper (Fig. 3d, cf. HELCOM, 1996). Hence, stations with shorter time-series disclose increasing trends if covering mainly the 1980s (Station I1) and decreasing trends if covering mainly the 1990s (Station K8). In the Belt Sea, the autumn values tend to increase.

A recent decrease in chlorophyll concentration seems to be a world-wide phenomenon, caused mainly by increased water temperature, stronger water column stratification and reduced recycling of nutrients from deeper water layers (Behrenfeld et al., 2006; Boyce et al., 2010; see also Nixon et al., 2009). Eutrophication over-compensates this effect and may lead to a sustained increase in phytoplankton biomass, as found in the Baltic Proper. Especially the spring chlorophyll *a* concentrations may be a good indicator of eutrophication because they best reflect the nutrient concentrations accumulated during the winter.

4.2.2. Nostocophyceae (cyanobacteria)

The pronounced biomass decrease of Nostocophyceae in summer is of great interest because representatives of the Nostocales, mainly the potentially toxic genera *Aphanizomenon* and *Nodularia*, form large blooms in the Baltic Proper. There has been much debate about whether these blooms are increasing or not (Finni et al., 2001; Wasmund and Siegel, 2008). As the biomass of Nostocophyceae is related to high temperature (Fig. 8b), warming should enhance the cyanobacteria in summer. Trend analyses by Suikkanen et al. (2007) showed an increase in Nostocophyceae in the Gulf of Finland and isolated peaks in 1985, 1995, and 1996 in the northern Baltic Proper. In contrast, our data revealed strongly decreasing trends in the southern Baltic (K2, K457) for Nostocophyceae and its main representatives, *Aphanizomenon* sp. and *Nodularia spumigena* (Fig. 3e), following pronounced peaks in 1979/1980. Obviously, nitrogen-fixing cyanobacteria blooms are governed not only by temperature but also some other factors like N:P ratios (Pliński and Jozwiak, 1999).

Also Kononen and Niemi (1984) reported on very high biomass of *Nodularia* and *Aphanizomenon* in the summers 1979–1981 in comparison to the previous decade. Using satellite images, Kahru (1997) found large areas covered by cyanobacteria blooms in 1982–1984 and 1991–1994 and Kahru et al. (2007) observed the highest frequency of cyanobacterial accumulations in 1984, 1999 and 2005. HELCOM presents annual updates of satellite images on cyanobacteria blooms (Hansson and Öberg, 2009) and on composition of these blooms (Kaitala and Hällfors, 2008). Representative sampling of the buoyant and highly patchy surface blooms is difficult and would require many replicates (Rolff et al., 2007). As an extremely high biomass in Nostocophyceae was coincidentally recorded at the beginning of the time-series, a long-lasting decreasing trend is expected, which might represent an artefact resulting from methodological difficulties and has to be regarded with caution.

4.2.3. Dinophyceae (dinoflagellates)

Only the A + M Dinophyceae are considered in this section. They form late spring blooms in the Baltic Proper, sometimes after a diatom bloom, and are therefore associated with higher temperature and lower nutrient concentrations than the diatoms (Fig. 8a). Our data indicate increasing trends in the spring blooms of Dinophyceae at all stations of the Baltic Proper, except for the shorter time series at station K8 (Fig. 2). This is most impressive at station I1, whose data series ends in 1996 (Fig. 3f). Longer data series of stations K1 (Fig. 3g), K2 and K457, revealed trend breaks in the mid 1990s both for the total Dinophyceae and their main taxonomic components.

The dinoflagellate spring blooms of the mid 1990s were dominated by *Peridiniella catenata* (Fig. 3h, no general trend but break in 1994, compare with Fig. 3g). This contrasts with the previous decade, when in 1979–1983 HELCOM (1996) did not report *P. catenata* in the list of the 5 most important spring species in the Eastern Gotland Sea. It seems to move from the Northern Baltic Proper to the south; it was recorded in the Gulf of Gdansk only since the mid-1980s (Witek et al., 1997). It generally decreases since the middle of the 1990s which makes its total trends decreasing in contrast to that of the total A + M Dinophyceae. Contrary to the Gotland Sea, *P. catenata* has rarely been abundant in the Bornholm and Arkona Seas (Fig. 4a). The same holds true for the genus *Gymnodinium*. Dinophysiales with its main representatives *Dinophysis acuminata* and *D. norvegica* is never forming spring blooms in the upper water layer (Fig. 4b). Their

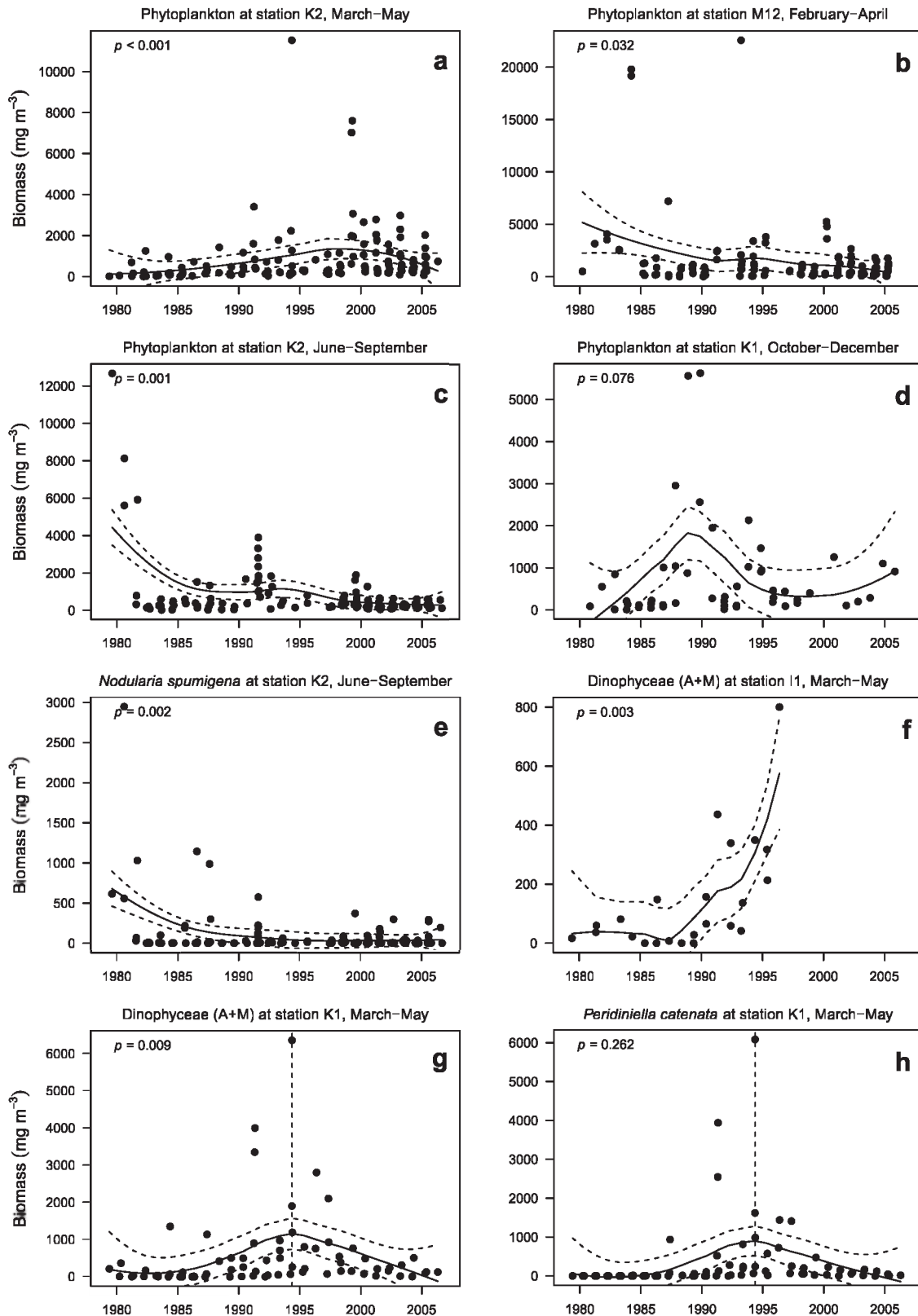


Fig. 3. Biomass of selected taxa over the investigation period at stations and in seasons specified in the headlines. A curve estimated with a locally weighted scatterplot smoother (LOWESS) is plotted with the solid line, and its 95% confidence interval with a dashed line. The p-value from the Mann-Kendall trend test is also indicated. The vertical dashed lines indicate break point locations for the taxa or ratios that had significant trends before and/or after the trends breaks.

highest spring biomass is found at the beginning of the 1990 s. The increase in total A+M Dinophyceae despite a decrease in single components may be explained by an increase in unidentified small

Dinophyceae in spring. One of these hardly identifiable groups is that of *Scrippsiella/Biecheleria/Gymnodinium* (Kremp et al., 2005; Moestrup et al., 2009; Sundström et al., 2009).

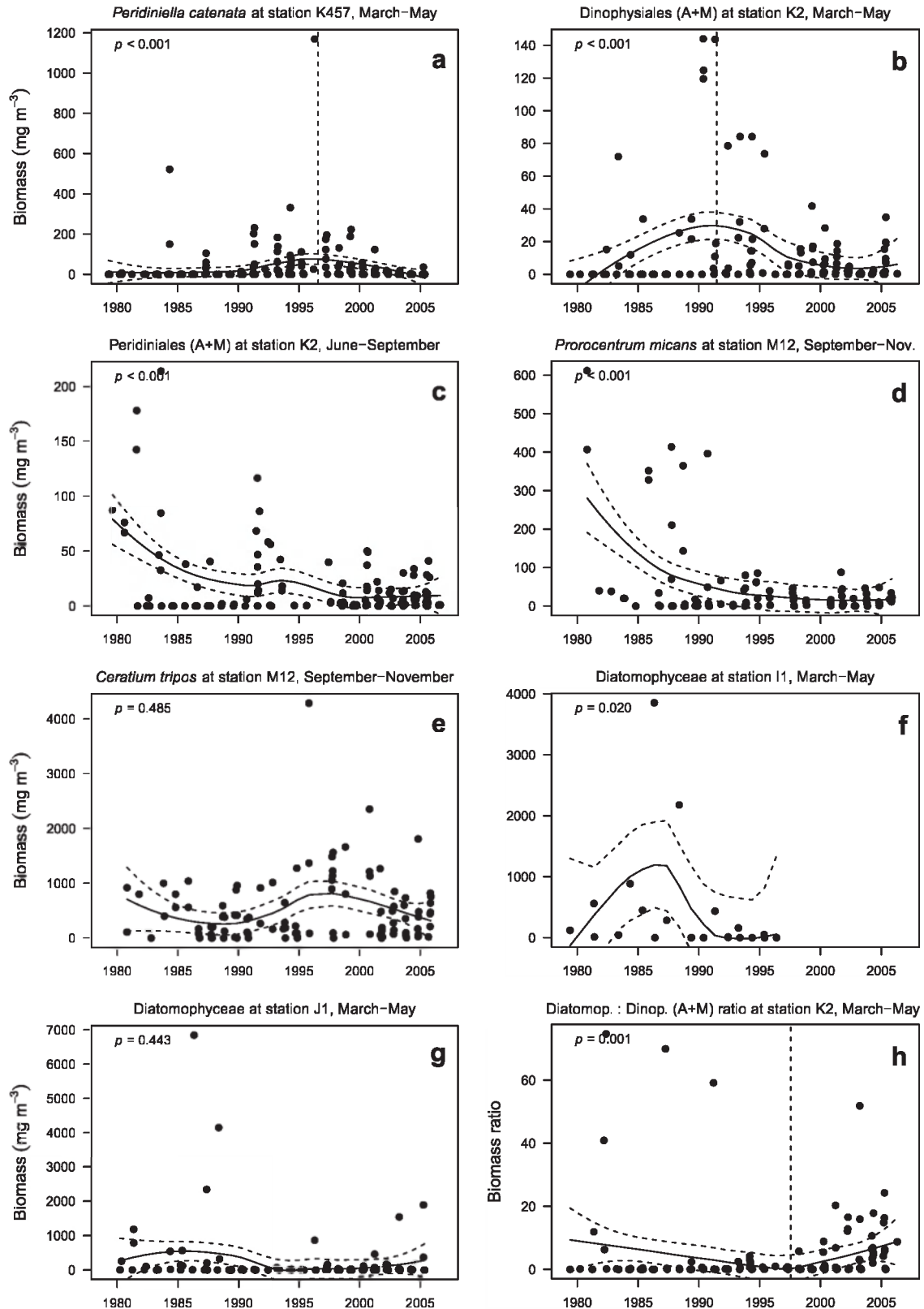


Fig. 4. Biomass of selected taxa over the investigation period at stations and in seasons specified in the headlines. A curve estimated with a locally weighted scatterplot smoother (LOWESS) is plotted with the solid line, and its 95% confidence interval with a dashed line. The p-value from the Mann-Kendall trend test is also indicated. The vertical dashed lines indicate break point locations for the taxa or ratios that had significant trends before and/or after the trends breaks.

Summer A+M Dinophyceae and their representatives show a decreasing trend. These were detectable in the Gymnodiniales (*Gymnodinium* spp.) and Peridinales (Fig. 4c) at stations K2, K457, M12, and N1.

They are less important as the biomass of these taxa did in general not exceed 500 mg m^{-3} apart from one peak in the Gymnodiniales (1400 mg m^{-3}) at station M12 in 1994. Peaks of *Prorocentrum micans*

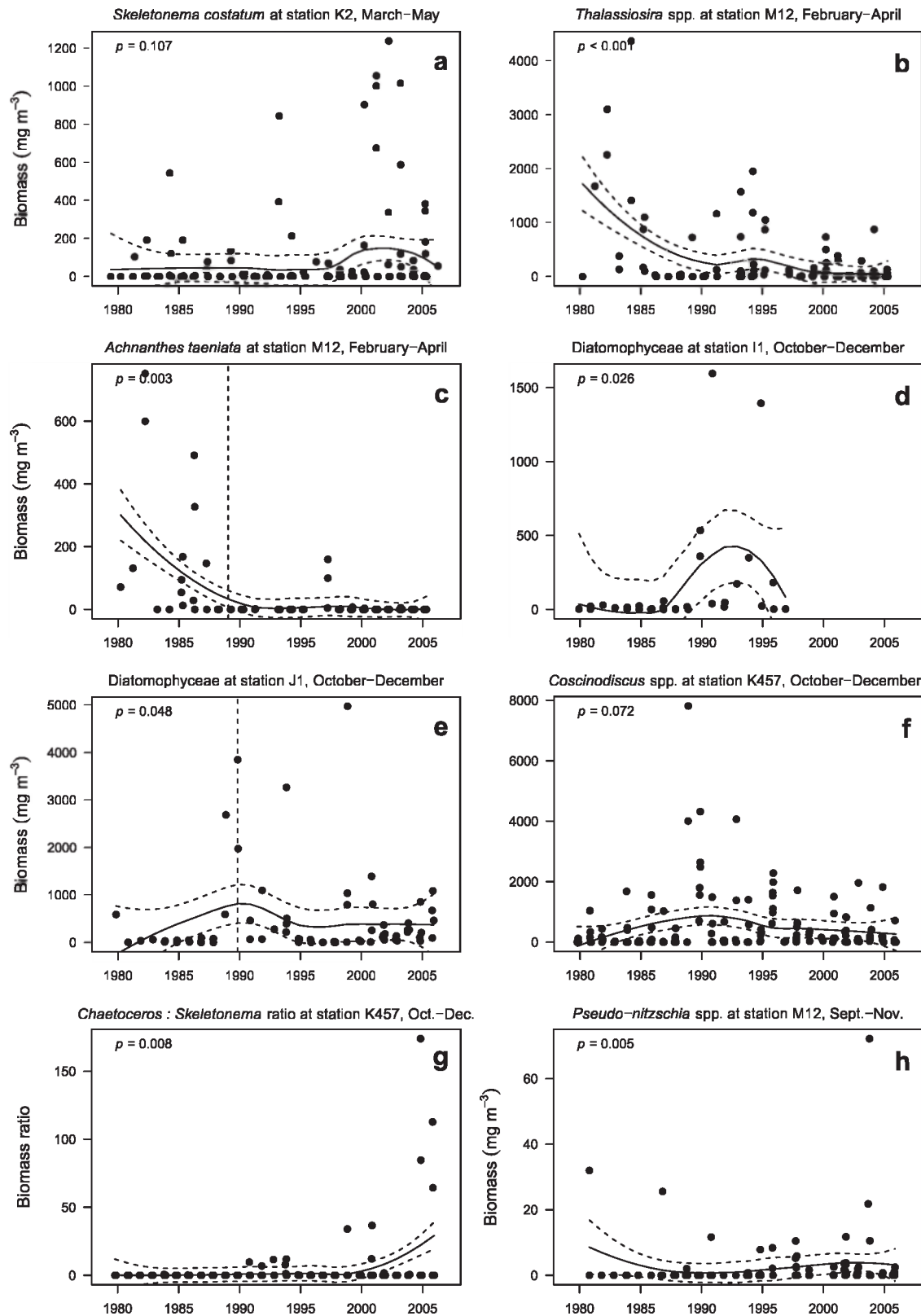


Fig. 5. Biomass of selected taxa over the investigation period at stations and in seasons specified in the headlines. A curve estimated with a locally weighted scatterplot smoother (LOWESS) is plotted with the solid line, and its 95% confidence interval with a dashed line. The p-value from the Mann-Kendall trend test is also indicated. The vertical dashed lines indicate break point locations for the taxa or ratios that had significant trends before and/or after the trends breaks.

(900 mg m⁻³) and *P. minimum* (1500 mg m⁻³) were found at stations M1 and K2, respectively, in August 1990 and in August 1992. Summer A + M Dinophyceae, including Gonyaulacales and Prorocentrales, were positively related to temperature, whereas Dinophysiales preferred

colder water (Fig. 8b). The latter sometimes concentrate at greater water depths (Carpenter et al., 1995; Gisselson et al., 2002).

Autumn biomass of A + M Dinophyceae was increasing at stations K1 and K2 (Fig. 2) but it did not exceed 260 mg m⁻³. The decreasing

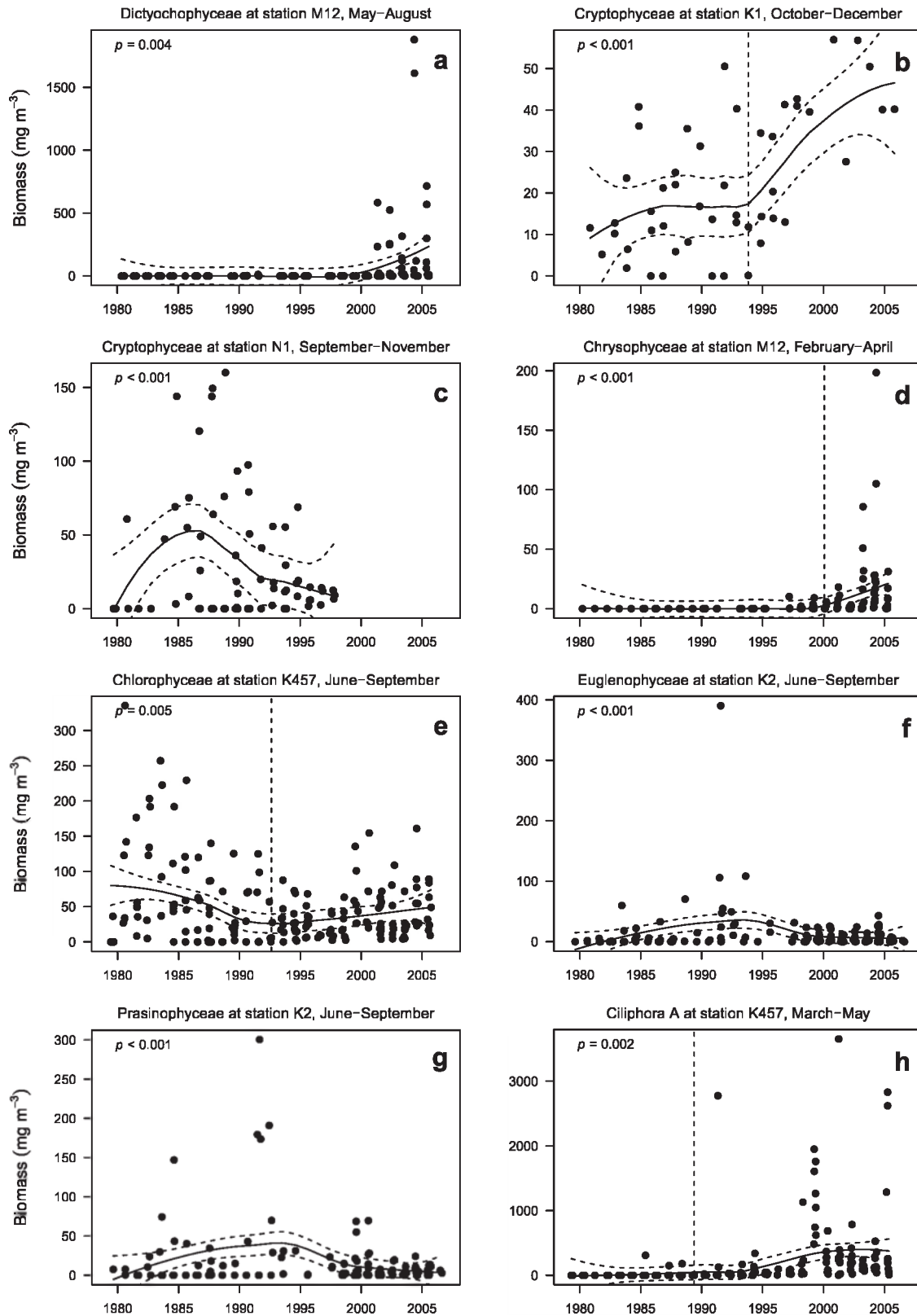


Fig. 6. Biomass of selected taxa over the investigation period at stations and in seasons specified in the headlines. A curve estimated with a locally weighted scatterplot smoother (LOWESS) is plotted with the solid line, and its 95% confidence interval with a dashed line. The p-value from the Mann-Kendall trend test is also indicated. The vertical dashed lines indicate break point locations for the taxa or ratios that had significant trends before and/or after the trends breaks.

trends of Prorocentrales and Gymnodiniales in the southern Baltic Proper were of lower importance because biomass stayed below 250 mg m⁻³ in autumn, except for the year 1997, when Gymnodiniales

exceptionally reached 3500 mg m⁻³. Prorocentrales were of some importance in Mecklenburg Bight, with biomass regularly up to 1000 mg m⁻³. *P. micans* was continuously decreasing (Fig. 4d) whereas

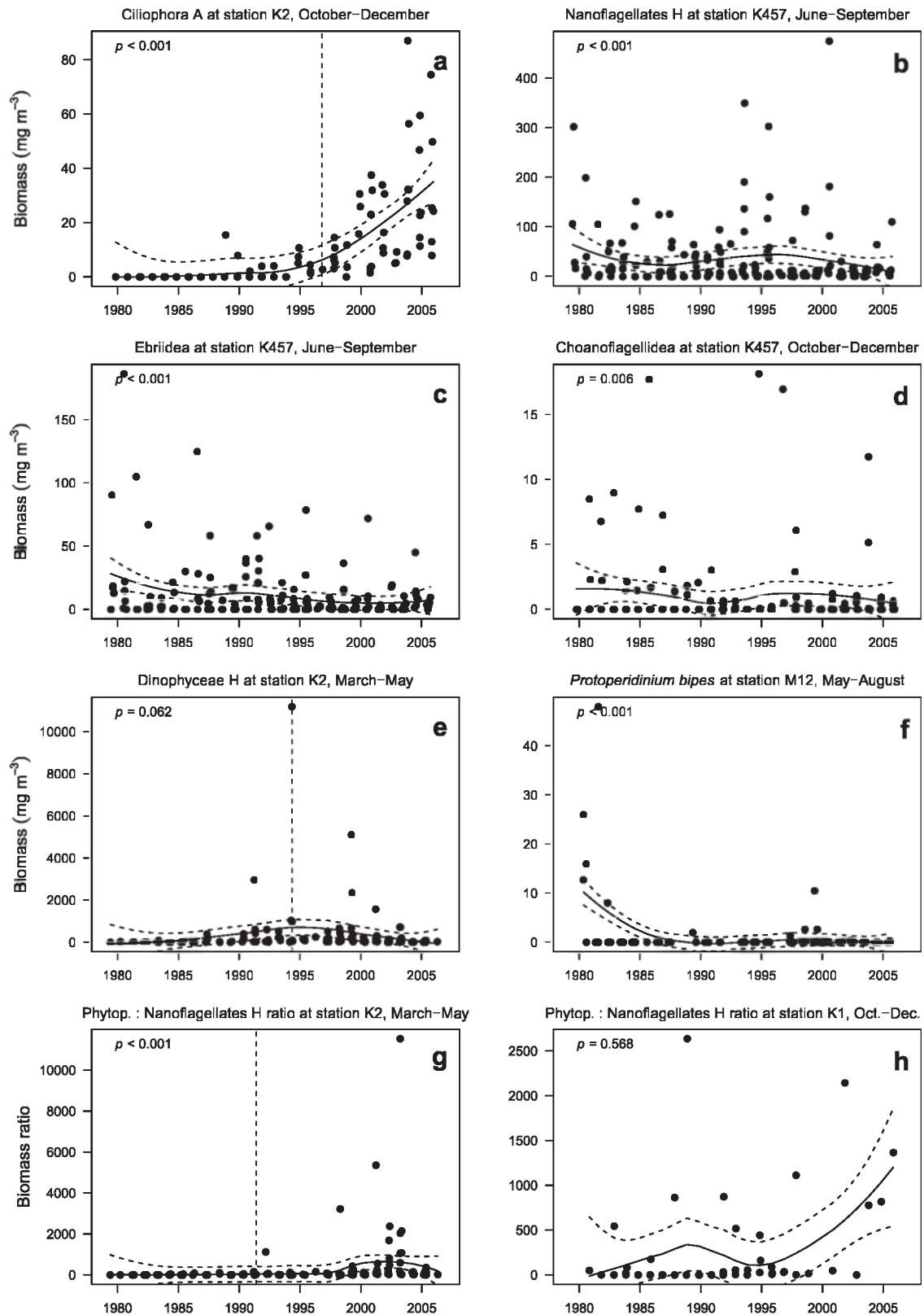


Fig. 7. Biomass of selected taxa over the investigation period at stations and in seasons specified in the headlines. A curve estimated with a locally weighted scatterplot smoother (LOWESS) is plotted with the solid line, and its 95% confidence interval with a dashed line. The p-value from the Mann-Kendall trend test is also indicated. The vertical dashed lines indicate break point locations for the taxa or ratios that had significant trends before and/or after the trends breaks.

P. minimum formed the maximum in 1997 in autumn. *P. minimum* invaded into the Baltic Sea, expanded until the mid of the 1990s and decreased afterwards (Olenina et al., 2010).

Dinophyceae were most important in autumn in the Belt Sea because of the blooms of *Ceratium* spp. These *Ceratium* blooms are the most stable feature in the succession during the last 100 years

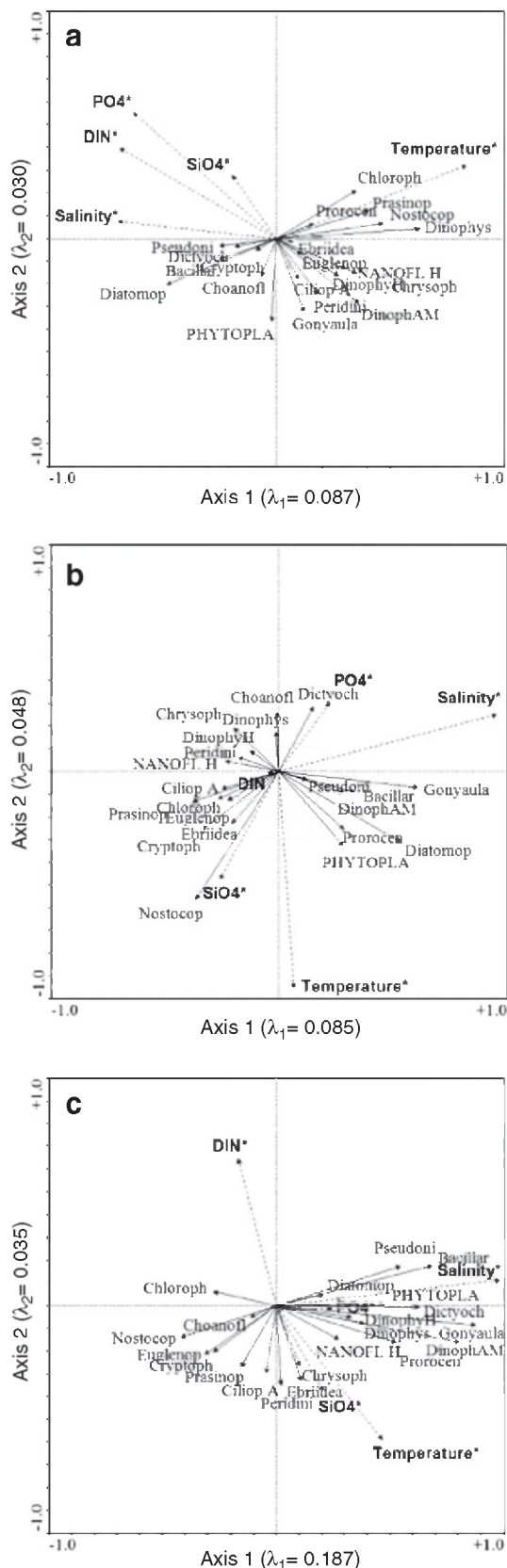


Fig. 8. Correlation plots of the redundancy analysis (RDA) for (a) spring, (b) summer and (c) autumn data, on the relationship between the biomass of phytoplankton taxa (solid vectors) and environmental variables (dashed vectors). The plots display 11.7, 13.3 and 22.2% of the variance in the phytoplankton biomass in spring, summer and autumn, respectively, and eigenvalues of the first two axes are indicated by λ_1 and λ_2 . Codes of the phytoplankton taxa are explained by bold letters in Table 3. Asterisks indicate statistical significance ($p < 0.05$) of environmental variables.

(Wasmund et al., 2008). Accordingly, no trends in biomass of *Ceratium tripos* were detected (Fig. 4e), except for station N3 with its shorter time-series. The A+M Dinophyceae of the autumn, including the Peridinales, Gonyaulacales, Dinophysiales and Proocentrales, prefer high temperature and salinity (Fig. 8c). The hydroclimatic changes that occurred since the late 1980s favour the growth and earlier succession of dinoflagellates, which are positively correlated with the NAO (Edwards et al., 2006).

4.2.4. Diatomophyceae (diatoms)

The Diatomophyceae appear early in the year and are related to low temperature and high nutrient concentrations, as shown in Fig. 8a. A very interesting feature is the sudden decrease in spring diatoms in the Baltic Proper at the end of the 1980s, caused by decreasing water temperature (Alheit et al., 2005; Wasmund et al., 1998; Wasmund and Uhlig, 2003). Suikkanen et al. (2007) reported a strong decrease in diatoms at the end of the 1980s even in the summer data of the northern Baltic Proper and Henriksen, 2009) in the annual biomass means of the Kattegat. Because of limited sampling frequency, the peak of the spring bloom could only be sampled on few occasions. However, (Wasmund et al., 1998) proved by calculation of the silicate consumption that the spring diatom communities grew very well in the 1980s but suddenly failed to grow in the 1990s. Shorter data series, as available from Station I1 until 1996, revealed a decreasing trend (Fig. 4f). However, the longer data series of stations J1 and K2 do not confirm a monotonous trend (Fig. 4g, h), showing high values in the 1980s, followed by a decrease at the end of the 1980s and a recovery since the year 2000.

The increase after 2000 was most pronounced at Station K2 with a strong increase in *Skeletonema costatum sensu lato* in 2000–2003 (Fig. 5a) and of *Chaetoceros* spp. in 2004–2005. Henriksen (2009) also reported these taxa especially in the 1980s and after the year 2000. These important representatives of the spring bloom were also the dominant Diatomophyceae at the beginning of the 20th century (Henriksen, 2009; Lohmann, 1908; Wasmund et al., 2008). *Achnanthes taeniata*, which is the main representative of the Bacillariales in the Baltic Proper, was dominant in spring blooms at the beginning of the 1980s (HELCOM, 1996; Kononen and Niemi, 1984) but decreased and did not recover. At station M12, the Diatomophyceae decreased more or less continuously, mainly caused by decreases of *Thalassiosira* (Fig. 5b), *A. taeniata* (Fig. 5c), *Chaetoceros* spp., *S. costatum* and *Leptocylindrus danicus*. Henriksen (2009) also described a strong decline of the cold water species *Detonula confervacea*.

The recovery of spring Diatomophyceae, namely only the Centrales, is most apparent when compared with the competing Dinophyceae. The ratio of these two dominating classes was used as an indicator of the ecosystem state by McQuatters-Gollop et al. (2009). They found increasing ratios of Diatomophyceae:Dinophyceae in the coastal North Sea, the northern Adriatic and in the north-western Black Sea, but did not try it for the Baltic Sea. We show this Diatomophyceae:Dinophyceae ratio for a representative station of the southern Baltic Proper in Fig. 4h. Diatomophyceae were strongly dominating over the Dinophyceae during the 1980s and since the year 2000. A decrease in the Diatomophyceae:Dinophyceae ratio in the North Sea was also described by Edwards et al. (2006) and related to changes in the NAO and resulting progressive warming and stronger stratification of the water.

The summer data of total Diatomophyceae showed no clear trend. At station K2, both the Bacillariales and the Eupodiscales were decreasing because of single high biomass data in 1980 and 1981. At station M12, *S. costatum* was decreasing but *Pseudo-nitzschia* spp. was increasing.

The autumn biomass of total Diatomophyceae was increasing in most areas (Figs. 2 and 5d, e). It is interesting that exceptionally high biomass occurred in 1988–1990, the years of the strongest decline of the spring diatoms (cf. Fig. 4f, g). The relatively low diatom biomass in spring of the years 1989–1999 is obviously compensated by high diatom biomass in autumn in the same period. The strong autumn bloom in

1988–1990 was found at stations I1, J1, K1, K457 and M12 and is already known from literature (HELCOM, 1996). The diatom autumn blooms are regularly formed by *Coscinodiscus granii* (cf. Fig. 5f). *Cerataulina pelagica* and *Actinocyclus* sp. show pronounced peaks in autumn 1993/1994 at station M12. Other species of Diatomophyceae decrease more or less continuously. However, *Chaetoceros* increased in comparison to *Skeletonema* in areas of higher salinity (Arkona Sea and Belt Sea; Fig. 5g). The potentially toxic *Pseudo-nitzschia* spp. occurred in summer and autumn mainly in the Mecklenburg Bight and is strongly related with salinity (Fig. 8c). Peaks were noted in summer 2002 and in autumn 2003 (Fig. 5h). An increase in this genus was also shown by Henriksen (2009).

4.2.5. Smaller phytoplankton groups

Dictyochophyceae are sometimes bloom-forming in Mecklenburg Bight in late spring or early summer and are associated with high salinity and high nutrient concentrations but low temperature (Fig. 8a, b). They are strongly increasing (Fig. 6a). In autumn, they occur in lower biomass (up to 250 mg m^{-3}) with a peak in the year 2000. The main representative is *Dictyocha speculum*, which occurs mostly in its naked form (Jochem and Babenerd, 1989). Therefore it is possible that it was not recognized in earlier years of investigation. Differentiation between this naked *D. speculum* and *Pseudochattonella verruculosa* is difficult but both belong to the same class.

Cryptophyceae are not bloom-forming. They increased in the southern Baltic Proper in spring and autumn (e.g. Fig. 6b) but decreased at station K457 in summer. At station N1, the trends were decreasing in summer and autumn (Fig. 6c), but because of the shorter data series we cannot exclude a strong increase after 1997, as it was found in the neighbouring Mecklenburg Bight and the Baltic Proper. The spring *Cryptophyceae* preferred low temperature and high salinity but the summer populations preferred high temperature and low salinity (Fig. 8a, b).

Chrysophyceae decreased at station K457 in spring. This decrease was mainly caused by a strong occurrence of *Dinobryon* sp. in 1987 (up to 450 mg m^{-3}). At station M12, however, *Chrysophyceae* increased strongly (Fig. 6d), together with *Dinobryon* sp. This species contributed 5–50% to the increase in *Chrysophyceae*. Suikkanen et al. (2007) identified increasing trends for *Chrysophyceae* in the northern Baltic Proper and the Gulf of Finland. *Chrysophyceae* preferred high temperature and low salinity in spring (Fig. 8a).

Chlorophyceae are generally less important in the open sea, especially in the more saline areas, because they are related to freshwater (cf. Fig. 8a–c). Our study showed biomass decreases in different sea areas and seasons. One example is displayed in Fig. 6e. However, Suikkanen et al. (2007) reported increasing trends in the northern Baltic Proper and the Gulf of Finland, in line with decreasing salinities, in summer 1979–2003.

Euglenophyceae revealed decreasing trends. In spring, a strong peak (up to 1100 mg m^{-3}) occurred in the southern Baltic Proper and Mecklenburg Bight in 1994 and 1995, respectively. Also the summer data have maxima (up to 800 mg m^{-3}) between 1991 and 1995 (Fig. 6f). A negative trend for *Euglenophyceae* was also found by Suikkanen et al. (2007) in the northern Baltic Proper. This class is associated with high temperature and low salinity (Fig. 8a, b).

Prasinophyceae are generally decreasing. The peaks are frequently found in 1990–1993 (Fig. 6g). The apparent slight increase at station I1 in autumn is again more likely to be due to the shorter time series in comparison with the other stations. This class is associated with high temperature and low salinity (Fig. 8a–c).

Ciliophora A is identical with the only auto- or mixotrophic species of *Ciliophora* in the Baltic Sea, *Mesodinium rubrum*. It is related to low salinity and partly to high temperature (Fig. 8a–c) and is increasing in all seasons and all regions in the Baltic proper (Fig. 6h), as expected from the trends in salinity and temperature. *M. rubrum* formed spring blooms mainly in the years 1999 and 2000. Its biomass was much

lower in autumn (Fig. 7a). It was strongly increasing during the 20th century (Henriksen, 2009; Wasmund et al., 2008).

4.2.6. Heterotrophs

In the microscopical analysis of phytoplankton, heterotrophic flagellates are also counted which are of the same size range as phytoplanktonic nano- and microalgae. This heterotrophic biomass, called Nanoflagellates H in Figs. 2, 7 and 8, is obviously decreasing in all sea areas and more or less in all seasons (mainly spring/summer; Fig. 7b). The slight increase at station N3 in autumn is of little explanatory power because it is based on only 10 records and the data series is short. At most stations, a peak occurred in 1993/1994.

Ebriidea (with *Ebria tripartita*) show a decreasing trend, as well (Fig. 7c). They prefer high temperature and low salinity (Fig. 8a, b).

Choanoflagellidea are a small group with biomass smaller than 35 mg m^{-3} , except for outliers in 1984 at station N1 (autumn), and in 1990 at stations M12 (summer) and K8 (spring). They may sometimes be overlooked and underestimated. They were strongly decreasing in the southern Baltic Proper (Fig. 7d) and slightly increasing in Mecklenburg Bight in different seasons. This class preferred high salinity and low temperature (Fig. 8a, b). Although usually considered a minor group, they are nevertheless significant predators of bacteria and as such can be an important component in the carbon cycle.

Many *Dinophyceae* (e.g. *Protoperidinium* spp.) are heterotrophic. Just like the A + M *Dinophyceae*, they show increasing trends in the spring and autumn data. At more or less all stations heterotrophic dinoflagellates peaked in the 1990s with a subsequent decrease (Fig. 7e), an exception being station K8 in autumn as this time series started only in 1989 and therefore only represents the late phase of biomass decrease. The only species of the heterotrophic *Dinophyceae* that showed trends was *Protoperidinium bipes*. In contrast to the total heterotrophic *Dinophyceae*, its biomass was decreasing at some stations (Fig. 7f). As its biomass was always very low, trends in *P. bipes* are of low relevance.

One interesting indicator for the state of the ecosystem, particularly of its food web, might be the total biomass of the phytoplankton (total A + M biomass) in comparison with the heterotrophic biomass of the same size range. Whereas the phytoplankton biomass is increasing in most cases (e.g. Fig. 3a), that of the heterotrophic flagellates is almost exclusively decreasing. Therefore, the ratio of total A + M biomass and total H biomass is strongly increasing (Fig. 7g, h). We have to admit that the counting of heterotrophic flagellates is a by-product of the phytoplankton analysis and may therefore be of lower precision. But if the decrease in heterotrophic flagellates will be confirmed with the continuation of the data series, it may indicate an increasing mismatch between phytoplankton growth and the consumers of the phytoplankton's exudates. The consequences for the food web and the ecosystem have to be investigated.

4.3. Relationships between environmental factors and phytoplankton groups

In all seasons, the RDA yielded four significant environmental variables explaining the variability in the phytoplankton biomass: salinity, temperature, PO_4 and SiO_4 concentration. The effect of DIN concentration was only significant in spring and autumn, but not in summer ($p > 0.05$). Together, all environmental variables considered (and all canonical axes) accounted for 14.6, 15.3 and 25.0% of the variation in the phytoplankton biomass data during spring, summer and autumn, respectively. In the RDA ordination (Fig. 8), the first two axes explained 11.7% (spring), 13.3% (summer) and 22.2% (autumn) of the total variance in the phytoplankton biomasses.

The phytoplankton taxa in the different seasons could be classified according to their association with these environmental variables. In spring, the phytoplankton formed two main groups (Fig. 8a). All Diatomophyceae including Bacillariales and *Pseudo-nitzschia* spp., as well as the *Dictyochophyceae* and *Cryptophyceae* were associated with high salinity and high inorganic nutrient concentrations, but

with low temperature. Most of the other taxa were associated with high temperature, low salinity and low nutrient concentrations. The opposed requirements of Diatomophyceae and Dinophyceae concerning temperature, salinity and nutrient concentrations can explain their interplay in the spring season.

In summer, the largest cluster comprised taxa that occurred mainly at high temperature and silicate concentrations, but low salinity and phosphate concentrations: Nostocophyceae, Cryptophyceae, Chlorophyceae, Euglenophyceae, Prasinophyceae, Ciliophora A and Ebridae (Fig. 8b). Another group was formed by the A + M Dinophyceae, Gonyaulacales and the Diatomophyceae, which were positively related to temperature, salinity and phosphate concentration, but negatively to silicate concentration. Some taxa, such as the Dinophysiales, Dictyochophyceae, and Choanoflagellida, were associated with low temperature and silicate concentration, but high salinity and phosphate concentration, whereas the total summer phytoplankton biomass and that of the Prorocentrales was associated with high temperature, salinity and silicate concentration, but low phosphate concentration.

During autumn, high temperature, salinity, phosphate and silicate concentrations, but low DIN concentrations, were related to the total A + M phytoplankton, all dinoflagellates except Peridinales, Dictyochophyceae, Chrysophyceae, Flagellates H and Ebridae (Fig. 8c). The diatoms were associated with high temperature, salinity and nutrient concentrations, and the Prasinophyceae and Ciliophora A with high temperature and silicate concentrations, but with low salinity, phosphate and DIN concentrations. The biomass of Nostocophyceae and Choanoflagellida was highest in low salinity, temperature and nutrient, especially PO_4 concentrations.

The taxa that were associated with a high temperature in all seasons included the Dinophyceae A + M, Prorocentrales, Prasinophyceae, Ciliophora A and Ebridae. Nostocophyceae, Chlorophyceae, Euglenophyceae, Prasinophyceae and Ciliophora A were mainly found at low

salinity and low PO_4 concentration, and the three diatom taxa and Dictyochophyceae at high salinity and PO_4 concentration. The total phytoplankton biomass, Nostocophyceae, Dinophyceae A + M, Gonyaulacales, Prorocentrales and Choanoflagellida were strongest at low DIN concentrations throughout the year, whereas Cryptophyceae were related to high and Choanoflagellida to low SiO_4 concentrations.

The relationships between nutrient concentrations and phytoplankton biomass are complex, as nutrient concentrations are a precondition but also the result of phytoplankton growth. If, for example, phosphorus concentrations are low during cyanobacteria blooms, this does not mean that cyanobacteria grow best without phosphorus but that they have already consumed it. We aimed at accounting for the growth conditions by introducing a time lag that relates the actual biomass with the nutrient concentration measured at the preceding sampling event. Nevertheless, the relationships between nutrient concentrations and biomass extracted from the RDA may not reflect the real causal connection. In some cases, the RDA could not support the relationships between abiotic and biotic trends because we have considered only a small part of the environmental variables that may affect individual phytoplankton species in nature and had to neglect other important factors like micronutrients, pH, interspecific competition, allelopathy, grazing, turbulence etc. The explained variability is therefore rather low in complex natural systems.

5. Summary and conclusions

The trends discussed above are summarized in Table 3. It is most interesting that the interactions among the main components of the phytoplankton themselves (and with relevant environmental drivers) actually appears to be oscillating rather than linear. Hickey (1998) analysed the phytoplankton data of Helgoland Roads (North Sea) and found diatom and dinoflagellate cycles which mostly alternated.

Table 3

Summary of the most relevant trends. In the column "Trend", "+" means increase and "-" means decrease. The bold and underlined letters in the taxa names explain the abbreviations in Fig. 8. The sea areas are abbreviated as follows: BP—Baltic Proper, SBP—Southern Baltic Proper, EGS—Eastern Gotland Sea, AS—Arkona Sea, BS—Belt Sea, MB—Mecklenburg Bight, and KB—Kiel Bight.

Abiotic factor or taxonomical group	Sea area	Season	Trend	Example
Temperature	SBP	Summer + autumn	+	
Salinity	BP	Spring–autumn	–	
DIN	SBP	Spring–autumn	–	
Silicate (SiO_4)	EGS	Spring–summer	+	
PHYTOPLANKTON and chlorophyll <i>a</i>	BP	Spring	+	Fig. 3a
PHYTOPLANKTON and chlorophyll <i>a</i>	MB	Spring	–	Fig. 3b
Nostocophyceae (with Nostocales and Chroococcales)	SBP	Summer	–	Fig. 3e
Dinophyceae (A + M)	BP + MB	Spring	+, trend break in mid 1990s	Fig. 3f, g
Gonyaulacales (with <i>Peridiniella catenata</i>)	BP	Spring	–, peak in mid 1990s	Figs. 3h and 4a
Dinophysiales (with <i>Dinophysis acuminata</i>)	BP	Spring	–, peak at beginning of 1990 s	Fig. 4b
Peridinales (A + M)	BP + BS	Summer	–	Fig. 4c
Prorocentrales (with <i>Prorocentrum micans</i>)	AS + MB	Autumn	–	Fig. 4d
Diatomophyceae ; ratio Diatomophyceae/Dinophyceae	BP	Spring	Tendency to decrease up to the 1990 s and to increase since 2000	Figs. 4f–h and 5a
Diatomophyceae (with <i>Chaetoceros</i> spp., <i>Thalassiosira</i> spp., etc.)	MB	Spring	–	Fig. 5b
Bacillariales (with <i>Achnanthes taeniata</i>)	BP + MB	Spring	–	Fig. 5c
Diatomophyceae (with <i>Coscinodiscus</i> spp.)	BP + BS	Autumn	+, peak around 1990	Fig. 5d–f
Ratio <i>Chaetoceros/Skeletonema</i>	AS - KB	Autumn	+	Fig. 5g
Pseudo-nitzschia spp.	MB	Summer + autumn	Peak in 2002/2003	Fig. 5h
Dictyochophyceae	MB	Spring + summer	+	Fig. 6a
Cryptophyceae	BP	Spring	+	Fig. 6b
Chrysophyceae (with <i>Dinobryon</i> spp.)	MB	Spring	+	Fig. 6d
Chlorophyceae	BP + BS	Spring–autumn	–	Fig. 6e
Euglenophyceae	BP + BS	Spring–autumn	–	Fig. 6f
Prasinophyceae	BP	Spring–autumn	–	Fig. 6g
Ciliophora A (with <i>Mesodinium rubrum</i>)	BP	Spring–autumn	+	Figs. 6h and 7a
NANOFLAGELLATES H	BP + BS	Spring–autumn	–	Fig. 7b
Ebridae	BP + BS	Spring + summer	–	Fig. 7c
Choanoflagellida	SBP	Summer + autumn	–	Fig. 7d
Dinophyceae H	BP + BS	Spring + autumn	+, trend break in mid 1990s	Fig. 7e
Ratio phytoplankton (A + M)/Flagellates H	BP + BS	Spring–autumn	+	Fig. 7g, h

Henriksen (2009) reported on unusually high dinoflagellate biomass in the Kattegat/Belt Sea area in 1987–1989, which was related to exceptionally low diatom biomass. If data of Kononen and Niemi (1984) from the entrance to the Gulf of Finland from the period before our data series are added, an interesting pattern of diatom versus dinoflagellate dominance in spring emerges in the Baltic Proper: dinoflagellate (*Peridiniella*) dominance in 1968–1975 and 1989–1999, diatom dominance in 1978–1988 and since 2000. The phase of these oscillations is approximately 10 years. This would agree with the succession of regime shifts described in literature, as shown above. Our data confirmed the known shift from 1988/89, which was characterised by a quick decline of spring Diatomophyceae (Fig. 4f, g) and an increase of spring Dinophyceae to a higher level, which lasted for almost 10 years (Figs. 3f–h and 4a, b). Our data series covered a period that was mainly characterised by an increase in Dinophyceae in spring, which took advantage of the decreasing salinity and nutrient concentrations, and probably of the generally increasing temperature. A possible regime shift in the years 1998/99, as reported by Weijerman et al. (2005), Behrenfeld et al. (2006) and Overland et al. (2008), might be indicated by a recovery of the spring Diatomophyceae (Figs. 4h and 5a) and a sudden but sustained increase in *M. rubrum* (Figs. 6h and 7a) at that time.

In years of low diatom growth in spring, their growth is strong in autumn (compare Figs. 4f with 5d and 4g with 5e).

Our data show that the length of the data series is decisive for the result. Short data series (e.g. station I1) show trends which must not be extrapolated because they may even invert with a continuation of the series, as shown by trend breaks in the middle of the 1990s at many stations. For our data series of 27 years, the analyses for monotonic trends with one break point were sufficient but a second trend break may have occurred in some cases. A continuation of the data series may reveal oscillations, whose identification will require other statistical methods (e.g. wavelet analysis).

Our results also re-emphasize that the investigated area of the Baltic Sea is not a uniform water body. Our study area alone can be divided in two areas, the Belt Sea area and the Baltic Proper which sometimes even show contrary trends, e.g. in spring phytoplankton biomass and chlorophyll *a*. The contrast in chlorophyll trends is supported by literature data, which show a decrease in the Kattegat/Belt Sea area (Henriksen, 2009) and an increase in the Baltic Proper (Fleming-Lehtinen et al., 2008; Nakonieczny et al., 1991). Darss Sill is obviously a strong biological border, as already suggested by Kell (1973) and Witkowski et al. (2005).

This paper shows that systematic monitoring programmes, conducted with comparable methods are valuable tools for the identification of long-term changes in biota if the sampling covers all seasonal stages of the biocoenosis and all relevant sub-regions of the water body in question. The retrospective causal analysis of ecosystem changes on the basis of few routinely taken abiotic parameters is, however, difficult and not always satisfying, especially if undersampling and high natural variability mask causal relationships. The large number of samples required for representing short-lived populations and large stretches of water can be managed by combining the efforts of different institutions in joint programmes. The integration of different datasets is a dedicated strategy to improve the data coverage, provided that various pre-conditions concerning the data quality are fulfilled (Kraberg et al., 2011; Vandepitte et al., 2010). The methodological frameworks and infrastructures put in place by HELCOM provide a unique opportunity for such large-scale analyses.

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