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Seasonality of coastal phytoplankton in the Baltic Sea: Influence of salinity and eutrophication

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Abstract

In this study long-term (1984–2001) phytoplankton and physico-chemical monitoring data representing different salinity regimes of the Baltic Sea were compiled from HELCOM, national and regional databases. The aim was to define seasonal succession patterns of phytoplankton in seven different areas of the Baltic sea, characterised by different salinity, climate, and trophic conditions and to delineate a set of phytoplankton community indicators that are independent of season and salinity, but indicative of trophic status of different coastal areas. The cluster analysis of the combined data set resulted in eight phytoplankton community types, common for all locations, and characterised by different taxonomic composition representing different stages of seasonal succession. A hierarchy of explanatory variables that best predicted the communities, dominated by either diatoms, cyanophytes, cryptophytes or dinoflagellates, was revealed through a redundancy analysis (RDA). Nutrients were not found to be significant factors shaping the common phytoplankton community types for all locations. RDA analysis at the location level, covering all seasonal succession stages, confirmed phytoplankton community composition to be sensitive to nutrient concentrations. Even with the limitations of utilizing databases from different sources we identified community types that were indicative of climatic conditions (particularly temperature), salinity and eutrophication. The dominance of cyanobacteria as such, would not be an appropriate indicator of trophic conditions in the Baltic Sea, in the areas where cyanobacteria blooms occur naturally. The structure of both diatom- and cyanophyte-dominated communities is governed by salinity, and thus the abundances of these groups cannot be directly used as an indicator across the whole Baltic Sea.

Keywords: nutrients; geographic gradient; indicators

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1. Introduction

Eutrophication is a problem in many lakes (Vollenweider and Kerekes, 1982) and marine coastal areas (Vollenweider, 1992; Nixon, 1995; Cloern, 2001), leading to hypoxia and anoxia in bottom waters, nuisance algal blooms and changes in the species composition of phytoplankton. Phytoplankton biomass, species composition and community structure are commonly monitored in surface waters (e.g. HELCOM, 2002), however, these parameters, except for biomass, have seldom been applied as classification elements in assessing different eutrophication levels.

Tools and methods for classification of the ecological quality of coastal waters are required for assessing the status of coastal waters as well as setting the environmental objectives for management purposes. The Water Framework Directive (2000/60/EC; WFD), a recent EU legislation, requires that, in addition to other biological elements, phytoplankton taxonomic composition, abundance, and biomass as well as the frequency of phytoplankton blooms be used in the classification of the ecological status of lakes, rivers, and coastal and transitional waters. The overall objective of the WFD is to maintain and improve the ecological quality of surface waters, and ultimately to achieve good ecological status of all surface waters. Furthermore, the results of the ecological quality classification systems should be comparable between countries sharing similar types of surface waters within the same "ecoregion" (Heiskanen et al., 2004). Assessment based measurable alterations in the structure and functioning of ecosystem from high status to good and moderate sets new demands for the developing of classification tools for the coastal and transitional waters, such as the Baltic Sea.

In developing a classification system for phytoplankton, it is important to define regimes of environmental variables that affect species composition and community structure in different parts of an ecoregion. Salinity is one of the abiotic factors which may be highly variable in coastal and estuarine ecosystems (Remane, 1955, 1958; Gasiūnaitė, 2000). In typical estuaries, changes in salinity within short time periods are usually considerable due to tidal actions. In contrast, the tidal influence is minor in the microtidal or non-tidal Baltic Sea (Stigebrandt, 2001), while the freshwater influence results in oligohaline (below 3) to euhaline (20–30) salinity variations. Thus, an important prerequisite for the analysis of phytoplankton in relation to eutrophication is the clustering of salinity regions.

Phytoplankton dynamics are also dependent on physico-chemical and biological factors which have been shown to exhibit pronounced seasonal variations due to climatic factors (Rantajärvi et al., 1998; Schiewer, 1998). The short-lived phytoplankton reacts drastically to the annual climatic cycle. In the Baltic Sea, seasonality in phytoplankton growth differs between the east–west and north–south gradient. Therefore in the assessment of eutrophication level, it is important to identify appropriate time periods in which the eutrophication indicators are the most sensitive and significant.

Characterization of phytoplankton communities is multidimensional; interferences between nutrient and salinity dependencies lead to combined changes in phytoplankton composition and abundance, requiring different classification schemes for each. Moreover, development of a classification system is often hampered by the limited number of data sets in which there are similar climatic and salinity conditions but different eutrophication levels. As far as we know, there are no ecoregion-wide efforts to study seasonality of phytoplankton assemblages in different salinity regimes, as a first step towards the use of phytoplankton taxonomic indicators as quality elements for classification and ecological quality status assessments of coastal waters.

In this study long-term data set on both phytoplankton and physico-chemical variables from coastal areas of the Baltic Sea was compiled. The aim was to define phytoplankton seasonal succession patterns along the salinity gradient and to delineate a season and salinity independent set of phytoplankton community structural indicators in relation to eutrophication in the Baltic Sea.

2. Material and methods

2.1. Sampling locations

A data set was compiled from the monitoring programmes of the Baltic Sea (HELCOM) and from the national and regional monitoring programmes of Finland, Latvia, Lithuania, Germany and Denmark. The data included phytoplankton biomasses for large number of nano- and microplanktonic species and the main physico-chemical variables from eight locations, each representing different salinity regimes, for the period of 1984–2001 (Fig. 1, Table 1). The locations were selected for analysis according to data availability and average salinity. The variation of salinity at each of the locations was within ±0.3–0.8 (standard deviation). Additionally, these locations represented the north–south (approx. 1200 km) and west–east (approx. 2000 km) gradients in the Baltic Sea.

Phytoplankton analysis was carried out on biomass determined from enumeration and measurements using inverted microscope according to Utermöhl (1958) and HELCOM COMBINE recommendations (HELCOM, 2001). Taxonomic identification was carried out mostly to species level. Counts were converted to biomass ($mg\ m^{-3}$) and presented as wet weight by calculating the algal plasma volumes following the guidelines in Edler (1979) and HELCOM (2001), where stereometric shapes

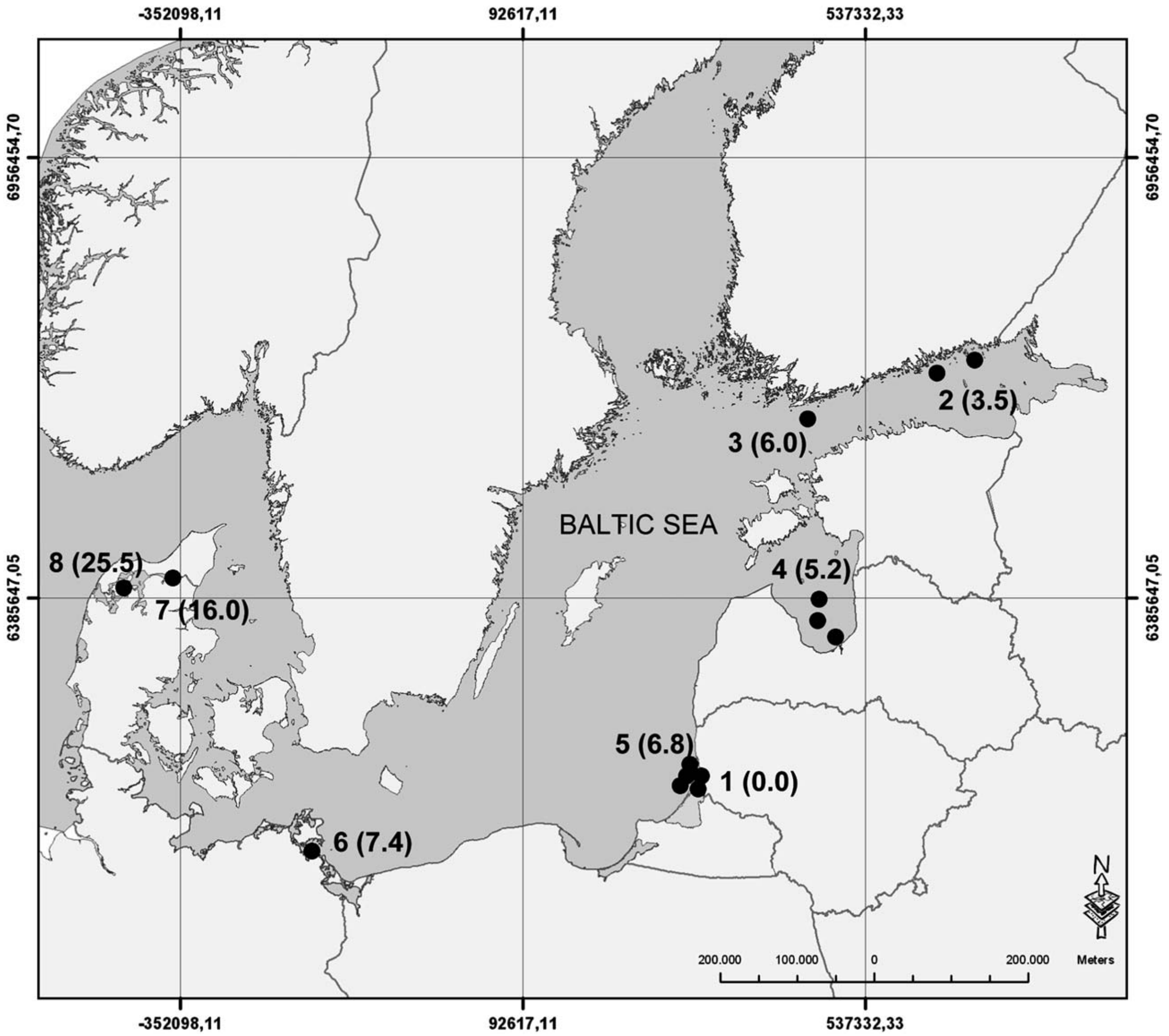

Fig. 1. Sampling locations and mean salinity (numbers in brackets). Location numbers correspond to those in the Table 1.

and formulas for common phytoplankton and protozooplankton in the Baltic are presented, and assuming density of 1 g cm^{-3} for algal cells. HELCOM phytoplankton courses and campaigns, arranged for taxonomists responsible for the identification of phytoplankton species, ensured the comparativeness of the data.

Phosphate phosphorus, nitrate-, nitrite- and ammonium nitrogen (DIN), and silica were analysed from unfiltered samples according to Koroleff (1969, 1983a,b). Salinity was measured using the Practical Salinity Scale.

Monitoring data from the semi-enclosed Curonian lagoon (location 1; Table 1, Fig. 1) was selected to represent freshwater conditions (salinity 0). The lagoon is highly eutrophic, shallow (average depth 3.5 m) and strongly influenced by riverine inflows (Gasiūnaitė and Razinkovas, 2004). The main freshwater source, the Nemunas River, is a lowland river typical of the southern Baltic, and has high nutrient loads originating from agriculture and livestock production in the catchment area (Žaromskis, 1996). The Curonian lagoon is favourable for the present analysis because unlike most other semi-enclosed estuaries along the southern Baltic coast, it does not have any significant additional point sources for nutrients.

Data from two stations in the eastern Gulf of Finland (Huovari and Ängsön, location 2; Table 1, Fig. 1) were combined to represent the average salinity of 3.5. Huovari (48 m deep), located in the outer archipelago is directly influenced by the River Neva (Pitkänen et al., 1993; Kauppila et al., 1995). The whole eastern archipelago area is eutrophied by heavy nutrient loading from the eastern part of the Gulf (Pitkänen, 1991). Ängsön (27.5 m deep), located in the inner archipelago,

Table 1
Description of the major physical and chemical characteristics of the locations and sampling stations selected for this study. The location number (No.), average annual salinity ± 1SD, number or name of sampling stations according to Baltic Sea monitoring programmes, coordinates of each sampling station (WGS 84 system), the depth of the sampling station, duration of monitoring included in the present study, total number of samples (*n*) used in the analysis from each sampling station, phytoplankton sampling strategy (SP = surface pooled; DI = discrete surface samples), average winter phosphate-phosphorus (PO_4-P; mmol m^{-3}), and dissolved inorganic nitrogen (DIN; mmol m^{-3}) concentrations (mean ± 1SD), geographic index (GI; see text for explanation)

No.	Location name	Salinity	Sampling station	Coordinates: latitude; longitude	Depth (m)	Duration (years)	*n*	Sampling strategy	Winter PO_4	Winter DIN	GI
1	Curonian lagoon (LT)	0.0	2	55°41.7′; 21°07.9′	12	1987–2000	55	DI	1.7 ± 0.6	61.1 ± 29.4	1010
			5	55°31.9′; 21°07.6′	3.4		52	DI			
			12	55°20.0′; 21°10.2′	3.2		95	DI			
2	Eastern Gulf of Finland (FIN)	3.5 ± 0.3	Huovari	65°08.0′; 24°35.8′	48	1987–2001	80	SP	0.3 ± 0.3	16.0 ± 1.1	1830
			Ängsön	60°25.2′; 27°38.9′	27.8		46	SP			
3	Gulf of Riga (LV)	5.2 ± 0.4	101A	57°10.0′; 23°98.3′	15	1996–2001	25	SP	0.6 ± 0.3	12.6 ± 5.3	1383
			119	57°30.0′; 23°85.0′	40		81	SP			
			121	57°61.7′; 23°61.7′	53		45	SP			
4	Western Gulf of Finland (FIN)	6.0 ± 0.4	Längden	59°46.4′; 23°15.6′	60	1994–2001	119	SP	0.4 ± 0.2	7.67 ± 2.8	1531
5	Lithuanian coastal waters (LT)	6.8 ± 0.4	1B	56°01.7′; 20°50.0′	27	1984–2000	36	SP	0.5 ± 0.4	12.8 ± 9.2	1005
			2	55°55.5′; 20°58.5′	18		27	SP			
			3	55°49.0′; 21°01.0′	18		15	SP			
			4	55°44.1′; 21°03.0′	16		16	SP			
			5	55°43.1′; 21°03.7′	15		21	SP			
			6	55°33.5′; 21°04.7′	13		26	SP			
			7	55°18.7′; 20°57.4′	14		29	SP			
6	German coastal waters (G)	7.4 ± 0.7	GB19	54°12.4′; 13°34.0′	9	1988–1999	132	DI	1.1 ± 0.6	21.3 ± 14.0	347
7	Mariager Fjord (DK)	16.0 ± 0.6	5503	56°39.8′; 9°58.4′	29	1990–2001	165	SP	2.6 ± 0.6	112.3 ± 14.0	357
8	Skive Fjord (DK)	25.5 ± 0.8	3727-1	56°37.3′; 9°04.6′	5	1989–2001	155	SP	0.8 ± 0.5	56.6 ± 16.1	322

is strongly affected by the Kymijoki River. The eutrophication level is similar to that in the outer archipelago.

In the Gulf of Riga, data from the stations 101A, 119 and 121 were combined for analysis at the salinity of 5.2 (location 3; Table 1, Fig. 1). The gulf is a semi-enclosed basin in the northeastern part of the Baltic Sea, with an area of 18,500 km^2 and an almost constant depth of 30–40 m (Olesen et al., 1999). The southern part of the gulf receives a large input of freshwater from the main rivers Daugava, Lielupe and Gauja. During the summer, strong temperature stratification is recorded, especially in its eastern part (Wasmund et al., 2000). Station 101A is located directly at the mouth of river and receives the largest part of these nutrients from the river. Station 119 is situated at the outer part of the river plume, while station 121 is rarely reached by river waters. The majority of nutrients come from agricultural lands in the catchment area and from Riga City municipal wastewaters (e.g. Andrushaitis et al., 1995).

The data from the station Längden in the western Gulf of Finland (location 4; Table 1, Fig. 1) were used in the analysis to represent the salinity regime of 6.0. Längden is located in the outer archipelago, nearly 10 km from the coast. The site (60 m deep) is influenced by the surface water flow of the Gulf of Finland and deep water originating from the layer near the permanent halocline (Heiskanen, 1998). Surface water flow originating from the River Karjaanjoki episodically reaches the station during early spring (e.g. Niemi, 1975; Laakkonen et al., 1981; Heiskanen, 1998). The hydrography and plankton dynamics are described in detail by Niemi (1973).

Data from stations 1, 1B, 2, 3, 4, 5, 6, and 7 in the Lithuanian coast were pooled to represent the salinity of 6.8 (location 5; Table 1, Fig. 1). These stations represent generally mesotrophic coastal Lithuanian waters influenced by outflow of eutrophic freshwater from the Curonian lagoon (Wasmund et al., 2000). Station depth varies from 13 to 27 m.

For the southern Baltic Sea (Pomeranian Bay; average salinity 7.4) data from the German station GB19 were used (location 6; Table 1, Fig. 1). This station is located in the central part of a semi-enclosed coastal lagoon, the Greifswalder Bodden. With an area of 510 km^2 and a volume of approx. 3 km^3, it is the largest German coastal lagoon. The system is classified as mesotrophic and has large macrophyte coverage irrespective of its average depth of 6 m. A detailed description is given by Hübel et al. (1995).

Data from the Danish stations 5503 (Mariager Fjord, location 7; Table 1, Fig. 1) and 3727-1 (Skive Fjord, location 8) represented average salinities of 16.0 and 25.5, respectively. Mariager Fjord is located on the eastern coast of Jutland, Denmark. The fjord consists of an outer shallow part and an inner deeper part, where the sampling station 5503 is located. The outer part of the fjord acts as a sill for the inner part. The area and volume of the inner part of Mariager Fjord are 19.4 km^2 and 0.2 km^3, respectively. This part of the fjord has permanent salinity stratification. Skive Fjord (St. 3727-1) is located in Northern Jutland, Denmark, as a part of the Limfjorden. The area, volume and average depth of Skive Fjord are 119 km^2, 0.49 km^3 and 4.2 m, respectively. The catchment area of both fjords is mainly agricultural land.

2.2. Data analysis

The data consisted of 1220 phytoplankton samples with contemporaneous physico-chemical measurements. In total, approximately 120–200 pooled samples for each location were analysed (see Table 1 for details of the number of samples, time interval, frequency, and sampling strategy at each station).

A cluster analysis (Bray–Curtis similarity coefficient, group average linking) was used to derive different types of phytoplankton communities. Samples were classified according to the relative biomass (percentage of total biomass in the sample) of the main taxonomic groups of phytoplankton: cyanophyceae, diatomophyceae, dinophyceae, cryptophyceae, chlorophyceae, ciliophora (consisting mostly of *Myrionecta rubra* (= *Mesodinium rubrum*)) and one cumulative group containing the rest of the phytoplankton species. These groups were intended to reflect seasonal successional stages (e.g. Sommer et al., 1986) as well as potentially indicate eutrophication level. This type of grouping was also used to minimise effects caused by possible differences in taxonomic analysis.

A "geographic index" (GI) was constructed to relate different succession patterns to the geographic location of sampling stations. This GI was based on the assumption that the sampling stations were distributed along west–east and north–south gradients. To combine both gradients, the index for each location was calculated as a sum of distance in kilometres from the location to the westernmost longitude and southernmost latitude.

Winter nutrient concentrations are known to be related to phytoplankton development, particularly during the spring (Peinert et al., 1982) as well as throughout whole vegetation period (Vollenweider, 1992), however, the relationship between these two parameters could be modified by other factors (e.g. nutrient retention rate). Moreover, phytoplankton blooms in the Baltic Sea features several biomass peaks during the growth period. Thus it was decided to find the biomass parameter, best reflecting the winter phosphate and DIN concentrations. The indicator of trophic status for each location was detected through analysis of the correlation (Pearson *r*) between average spring biomass, maximum spring biomass, average summer biomass and maximum summer biomass for each location and each year and winter nutrient concentrations.

Multivariate redundancy analysis (RDA) was applied as a tool to evaluate the relationships between environmental and biological variables. This method is normally used in ecology for ordination by direct gradient analysis, where a matrix of species variables is analysed with regard to a corresponding matrix of environmental variables (see Legendre and Anderson, 1999). For establishing the main cluster types, the relationships between nutrient concentrations, temperature, salinity, GI and maximum summer biomass (MSB) (designated as explanatory variables), and biomass values of main phytoplankton groups (designated as response variables) were evaluated. The relationships between nutrient values and temperature as explanatory variables and biomass values of main phytoplankton groups as response variables were estimated for each location. Non-normality of the data was treated by using a log $(x + 1)$ transformation (Clarke and Warwick, 1997). An automatic forward selection procedure was applied in order to rank the explanatory variables according to their importance. For means of interpretation, the first two axes were portrayed as biplots and the eigenvalues of significant explanatory variables were tabulated.

PRIMER 5 (PRIMER-E Ltd.) and BRODGAR 2.2.8 (Highland Statistics Ltd.) statistical packages were used for data analysis.

3. Results

3.1. Phytoplankton community types

For each location 3–4 clusters of samples were derived at 50–60% similarity level. The mean relative biomasses of the main taxonomic groups of phytoplankton, as percentage of total phytoplankton biomass for each of the clusters, are presented in Table 2. In each of these clusters, one, or at the maximum two, of the taxonomic groups listed exceeded a relative contribution of 30% per individual group. According to the prevailing taxonomic group, eight types of clusters were derived, dominated, respectively, by diatoms (I), cyanophytes (II), dinophytes (III), cryptophytes (IV), ciliophors (V), both diatoms and cyanophytes (VI), both

Table 2
Mean relative biomass values (as percentage of total phytoplankton biomass ± 1SD; bold values for dominant taxa) of main phytoplankton taxa for each group of samples, derived by cluster analysis; No. – location number (as in Table 1), *n* – number of samples in each cluster, Diat – Diatomophyceae, Cyan – Cyanophyta, Din – Dinophyta, Crypt – Cryptophyta, Cil – Ciliophora, Chlor – Chlorophyta

No.	Cluster type	*n*	Diat	Cyan	Din	Crypt	Cil	Chlor	Others
1	I	107	**80.9 ± 10.4**	6.4 ± 6.1				8.2 ± 6.4	4.5 ± 3.2
	II	40	21.4 ± 11.5	**69.6 ± 16.0**				6.8 ± 7.1	2.1 ± 3.1
	VI	55	**53.8 ± 15.2**	**31.1 ± 14.4**				9.2 ± 6.6	5.7 ± 7.9
2	I	26	**74.1 ± 16.4**	6.0 ± 11.1	9.6 ± 9.4	3.3 ± 5.1			6.9 ± 7.0
	II	42	4.5 ± 5.7	**48.1 ± 16.5**	3.3 ± 4.5	19.1 ± 10.7			25.0 ± 11.6
	VII	40	**30.2 ± 17.8**	0.5 ± 1.2	**62.8 ± 19.1**	0.9 ± 0.9			5.4 ± 6.0
	IV	18	22.4 ± 10.9	9.8 ± 10.1	8.7 ± 8.9	**36.1 ± 19.3**			22.9 ± 18.9
3	I	85	**70.0 ± 18.0**	6.3 ± 7.4	15.0 ± 15.0	3.2 ± 3.7			6.2 ± 5.7
	II	50	12.6 ± 12.3	**42.3 ± 19.3**	14.8 ± 11.9	10.9 ± 11.5			19.3 ± 11.3
	III	16	12.7 ± 9.1	3.6 ± 4.2	**73.6 ± 10.7**	0.8 ± 0.6			9.5 ± 9.8
4	I	27	**52.9 ± 18.8**	2.9 ± 5.9	21.2 ± 13.7	3.9 ± 3.9	10.4 ± 9.9		8.6 ± 9.7
	II	19	2.2 ± 4.8	**35.8 ± 22.3**	18.2 ± 11.4	17.3 ± 15.0	5.8 ± 5.3		20.3 ± 10.0
	III	31	8.4 ± 8.9	2.4 ± 5.0	**77.5 ± 10.8**	1.2 ± 2.9	6.6 ± 6.3		3.8 ± 4.1
	V	42	4.2 ± 6.1	8.1 ± 7.7	27.0 ± 14.8	9.2 ± 11.0	**33.3 ± 14.1**		18.2 ± 12.3
5	I	54	**80.3 ± 14.7**	6.5 ± 9.2	4.8 ± 6.3			5.6 ± 7.0	2.7 ± 3.8
	II	43	11.2 ± 10.3	**49.7 ± 15.7**	22.7 ± 15.7			9.1 ± 7.9	7.3 ± 5.7
	III	73	20.2 ± 18.5	4.14.8	**67.5 ± 22.3**			3.5 ± 7.4	4.6 ± 5.3
6	I	18	**69.9 ± 19.8**	4.9 ± 7.2	4.5 ± 13.0	14.6 ± 14.2		0.8 ± 1.1	5.1 ± 12.4
	II	28	12.1 ± 15.6	**71.3 ± 22.1**	5.2 ± 10.8	7.4 ± 10.5		0.9 ± 1.6	2.9 ± 7.4
	III	59	6.1 ± 8.4	8.2 ± 11.8	**36.5 ± 31.7**	21.1 ± 17.2		13.6 ± 16.8	14.5 ± 15.1
	IV	27	1.7 ± 1.3	2.5 ± 5.6	1.2 ± 0.8	**89.4 ± 7.2**		3.9 ± 4.9	1.3 ± 0.8
7	I	88	**73.3 ± 21.2**		14.4 ± 16.5	1.6 ± 3.0	5.0 ± 7.9		5.4 ± 7.1
	III	28	5.4 ± 6.4		**71.5 ± 20.9**	2.5 ± 4.7	9.6 ± 13.5		10.0 ± 10.5
	IV	13	14.3 ± 11.5		5.6 ± 5.4	**35.1 ± 24.6**	7.2 ± 5.7		**34.5 ± 23.2**
	V	36	6.7 ± 11.2		5.6 ± 5.3	3.3 ± 5.3	**71.6 ± 21.1**		12.1 ± 10.5
8	I	96	**81.9 ± 17.0**		4.9 ± 9.1	1.9 ± 5.1	6.8 ± 11.6		4.4 ± 5.4
	III	19	11.6 ± 10.9		**80.6 ± 16.5**	2.1 ± 4.6	1.4 ± 4.9		4.3 ± 4.4
	V	24	14.3 ± 8.9		10.3 ± 13.2	3.8 ± 5.8	**58.5 ± 19.9**		13.2 ± 13.9
	VIII	16	25.6 ± 17.3		10.1 ± 9.3	5.0 ± 5.6	4.7 ± 4.8		**54.6 ± 21.5**

diatoms and dinophytes (VII) or a pool of other species (VIII) (Table 2).

Using the clusters identified at the different locations, seasonality was analysed by plotting their relative occurrence along the temporal axis (Fig. 2). This monthly relative occurrence was calculated as the ratio between the number of samples representing particular cluster type and the total number of samples in a given month.

The succession in the Eastern Gulf of Finland at salinity 3.5 starts with co-dominance of dinophytes and diatoms (cluster type VII) until the biomass peak in May. Afterwards the dominance shifts to cyanophytes (July–September) and cryptophytes (October–November).

The structural changes in the phytoplankton community at salinity 6.0 in the Western Gulf of Finland are more complex. The dominance of ciliates or diatoms is common in winter–early spring; dinophytes appear in late spring and subsequent follow by several shifts between ciliates, cyanophytes and diatoms until the end of year. The maximum biomass values are observed in April–May (Fig. 2).

The succession in the Gulf of Riga (salinity 5.2) starts with dominance of diatoms (cluster type I), continued with cyanophytes from June to September (cluster type II) and returned to diatoms again in the late autumn. The biomass is peaked in April–May (Fig. 2).

The dominance of diatoms (cluster type I) in winter and late autumn is characteristic for the phytoplankton succession near the Lithuanian coast (salinity 6.8). The dominance of dinophytes (cluster type III) coincides with the biomass peak in April, whereas cyanophytes (cluster type II) dominate in July–August (Fig. 2).

In the Curonian lagoon (salinity 0), the succession starts with dominance of diatoms (cluster type I from Table 2 and Fig. 2) from January until June, and follows by the dominance of cyanophytes (cluster type II) or co-dominance of cyanophytes and diatoms (cluster type VI) until the biomass peak is generally reached in August–September. The diatoms are again abundant in late autumn.

Cryptophytes (cluster type IV) and dinophytes (cluster type III) dominate in winter in Greifswalder

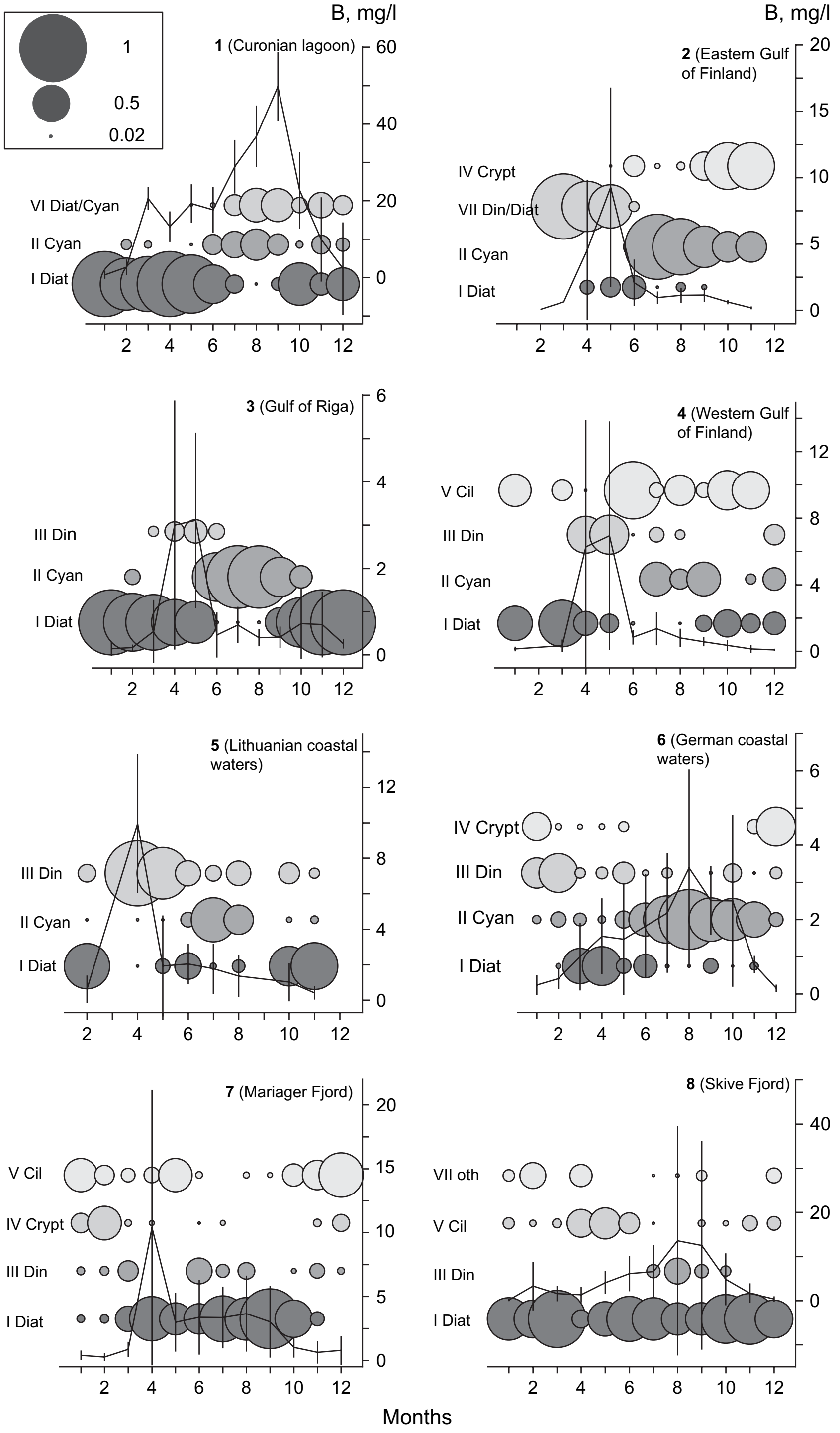

Fig. 2. The sequence of phytoplankton seasonal succession for each salinity regime. The size of the sphere represents monthly ratio of number of samples, belonging to the particular seasonal group and total number of samples (see legend). Solid line represents monthly means (±1SD) of the total phytoplankton biomass (mg wet weight/l; secondary *Y* axis). Location numbers, cluster type numbers and abbreviations correspond to those in Table 2.

Bodden (Fig. 2; salinity 7.4). The dominance of diatoms (cluster type I) is most likely in March–April; cyanobacteria (cluster type II) dominate in the phytoplankton during June–November. The biomass peak is usually observed in August–September.

Ciliophora (cluster type V) and cryptophytes (cluster type IV) dominate during winter in the Mariager Fjord (salinity 16.0). Diatoms (cluster type I) dominate in spring, summer and autumn with the biomass peak in April (Fig. 2).

Diatoms (cluster type I) dominate year round in the Skive Fjord, at salinity 25.5; with a biomass peak in August–September (Fig. 2).

3.2. Trophic status indication

The maximum summer biomass (MSB) showed the best correlation to both winter DIN and winter phosphate concentration ($r = 0.71$ and $r = 0.51$, respectively, significant at $p < 0.05$). For other expected indicators (maximum spring biomass, mean spring biomass, mean summer biomass), the correlations with both winter DIN and winter phosphate were not significant at $p < 0.05$. Therefore the MSB were selected as an indicator of the trophic status on each location. According to the MSB, all sampling sites could be ranked from Gulf of Riga (lowest) to Western Gulf of Finland, Eastern Gulf of Finland, Lithuanian coastal waters, German coastal waters, Mariager Fjord, Skive Fjord and Curonian lagoon (highest).

3.3. Factor analysis at community level

Cluster types I–IV represented more than 82% of all analysed samples, thus they were selected for further redundancy analysis (RDA).

The results of the RDA for cluster type I (diatom-dominated community) are shown in Fig. 3. All explanatory variables were responsible for 42% of the variability in the biomass values. The significant predictors for this group were salinity and MSB (Table 3).

The RDA plot for cluster type II (cyanophyte-dominated community) is presented in Fig. 3. Forty-two percentage of the variability was explained by explanatory variables; the significant predictor was MSB. GI and salinity were followed by temperature, all of them still significant at $p < 0.005$ (Table 3). In this cluster, the relationship between cyanophytes and nutrients was positive, whereas dinophytes and ciliates were negatively related with cyanophytes, nutrients and MSB.

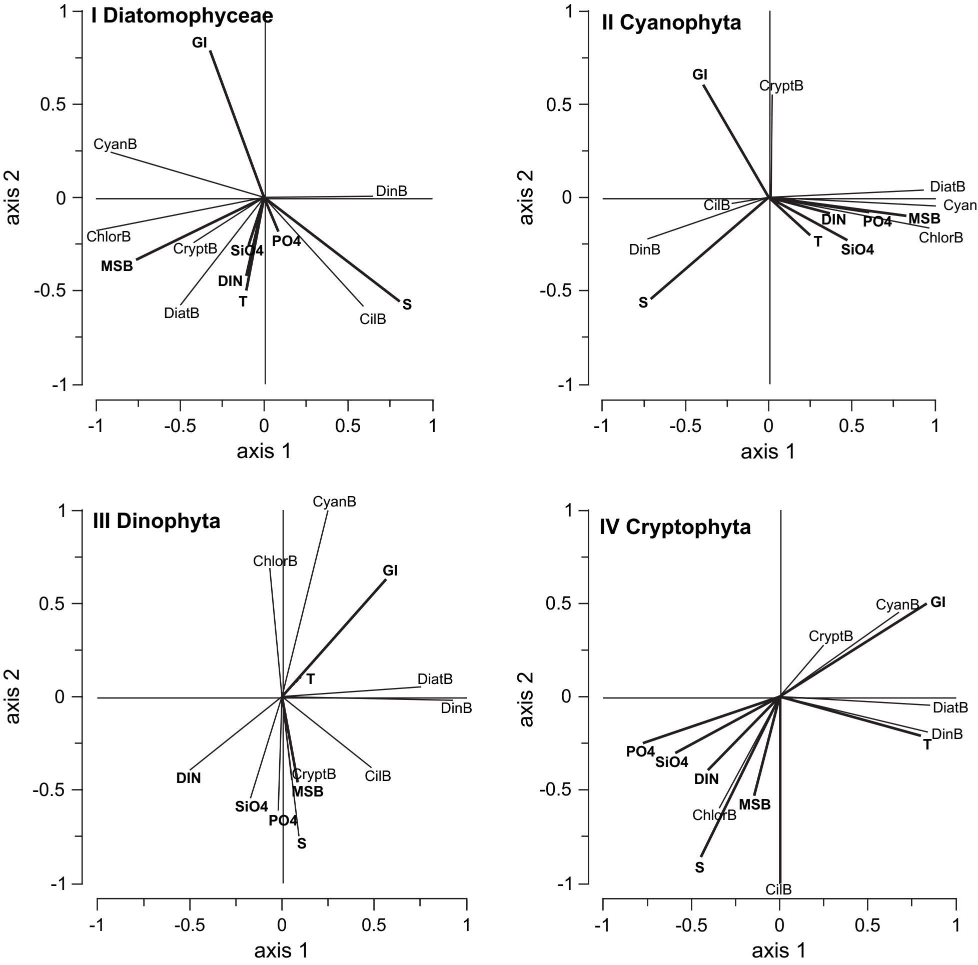

Fig. 3. RDA for I–IV cluster types. GI – geographic index; S – salinity; T – temperature; MSB – maximum summer biomass. Thin lines represent response variables, thick lines represent explanatory variables.

Table 3
Numerical output of the RDA for main cluster types. Cluster type number as in Table 2; GI – geographic index; MSB – maximum summer biomass. Marked values are significant at $p < 0.005$

Cluster type	% of variability described by predictors	Contribution to the total sum of eigenvalues				
		GI	t (°C)	Salinity	MSB	Others
I	42	0.01	0.03	0.24*	0.12*	0.04
II	42	0.10*	0.02*	0.10*	0.23*	0.00
III	30	0.11*	0.05*	0.11*	0.02*	0.08
IV	58	0.32*	0.12*	0.20*	0.01	0.07

The explanatory variables were responsible for 30% of the variability in the cluster type III (dinophyte-dominated community; Fig. 3). The significant predictors were GI and salinity. Biomass of dinophytes was positively related with diatoms, however, there was no clear relationship between the dinophytes and abiotic factors.

The explanatory variables described 58% of the variability in cluster type IV (cryptophyte-dominated community; Fig. 3), whereby GI salinity and temperature were the significant predictors. This cluster includes more than 50% of winter samples characterised by high cryptophyte biomasses and reflected the climatic gradient very well, in contrast to the other community types (compare Table 3), however, strong positive relation was observed between GI and cyanophytes. Almost all nutrient parameters were negatively related to the GI.

3.4. Factor analysis at location level

The results of RDA at the location level are presented in Fig. 4 and Table 4. The percentage of variability explained by selected predictors varied from 42 to 54% in Gulf of Finland and Gulf of Riga to only 17% in the Pomeranian Bay (Table 4). Temperature appeared to be the most significant factor shaping the phytoplankton community structure at all locations and was positively related with cyanophytes, chlorophytes and cryptophytes and negatively with diatoms (except in the Curonian lagoon, Pomeranian Bay and Danish waters). Inorganic nutrient concentrations were significant factors, but their importance varied in different locations. Silicate was a significant predictor in all locations except in the Eastern Gulf of Finland and the Pomeranian Bay. Phosphate concentration was significantly important in all locations except the Curonian lagoon and the Western Gulf of Finland. Dissolved inorganic nitrogen was only a significant predictor in the Curonian lagoon, Lithuanian coastal waters and the Western Gulf of Finland (Table 4).

4. Discussion

The cluster analysis of the data set, which consisted of more than 1200 samples distributed throughout the Baltic Sea coastal area, resulted in eight phytoplankton community types. These phytoplankton community types were characterised by different taxonomic composition and considered as separate stages of seasonal succession. Further RDA revealed the hierarchy of explanatory variables that best predict the community types dominated either by diatoms, cyanophytes, cryptophytes or dinoflagellates (Table 4).

In temperate and boreal coastal areas diatoms generally prevail during the first phase of the succession (spring bloom), they are generally adapted to more turbulent environments characterised by high nutrient concentrations (Margalef, 1978; Smayda, 1980). Diatoms are one of the largest taxonomic groups of phytoplankton of the Baltic Sea (Snoeijs and Balashova, 1998; Snoeijs, 2001), and are the dominant spring phytoplankton in all analysed locations. The common species are *Stephanodiscus* spp. (Curonian lagoon, Lithuanian coastal waters), *Thalassiosira* spp. and *Achnanthes taeniata* (Gulf of Finland, Gulf of Riga, and Pomeranian Bay), *Coscinodiscus granii* (Lithuanian coastal waters, Gulf of Riga) and *Skeletonema costatum* (Western Gulf of Finland, Pomeranian Bay, Danish fjords). Overall diatom biomass and the salinity are not related statistically, however, salinity appeared to be the most important factor shaping the structure of diatom-dominated communities (see Fig. 3). Development of diatom communities is also governed by other physical factors like stratification, mixing depth, and turbidity (resulting in light limitation), which were not considered in this study. Diatom-dominated spring blooms with clear biomass peaks appeared in all locations, where sampling sites were generally deeper than 10–15 m, and where either temperature or salinity stratification is temporarily established during the course of the seasonal development. While in very shallow stations (Curonian lagoon, Pomeranian Bay, and Skrive Fjord) establishment of spring bloom diatom biomass peak may be limited by turbidity, either caused by high freshwater flow or wind mixing and resuspension during the spring period.

Diatom biomass was well related to the MSB (Fig. 3), while the structure of the diatom-dominated community appeared to be less important as an indicator of the trophic status of the location (Table 3). Diatoms, like other dominant phytoplankton groups, did not have a significant relationship with ambient nutrient conditions, which may have been due to the limitation of other factors (such as light) as discussed above. Diatoms have high growth rate, they often emerge as pioneer species of the succession, and rapidly consume inorganic nutrients, and sink out from the water column after

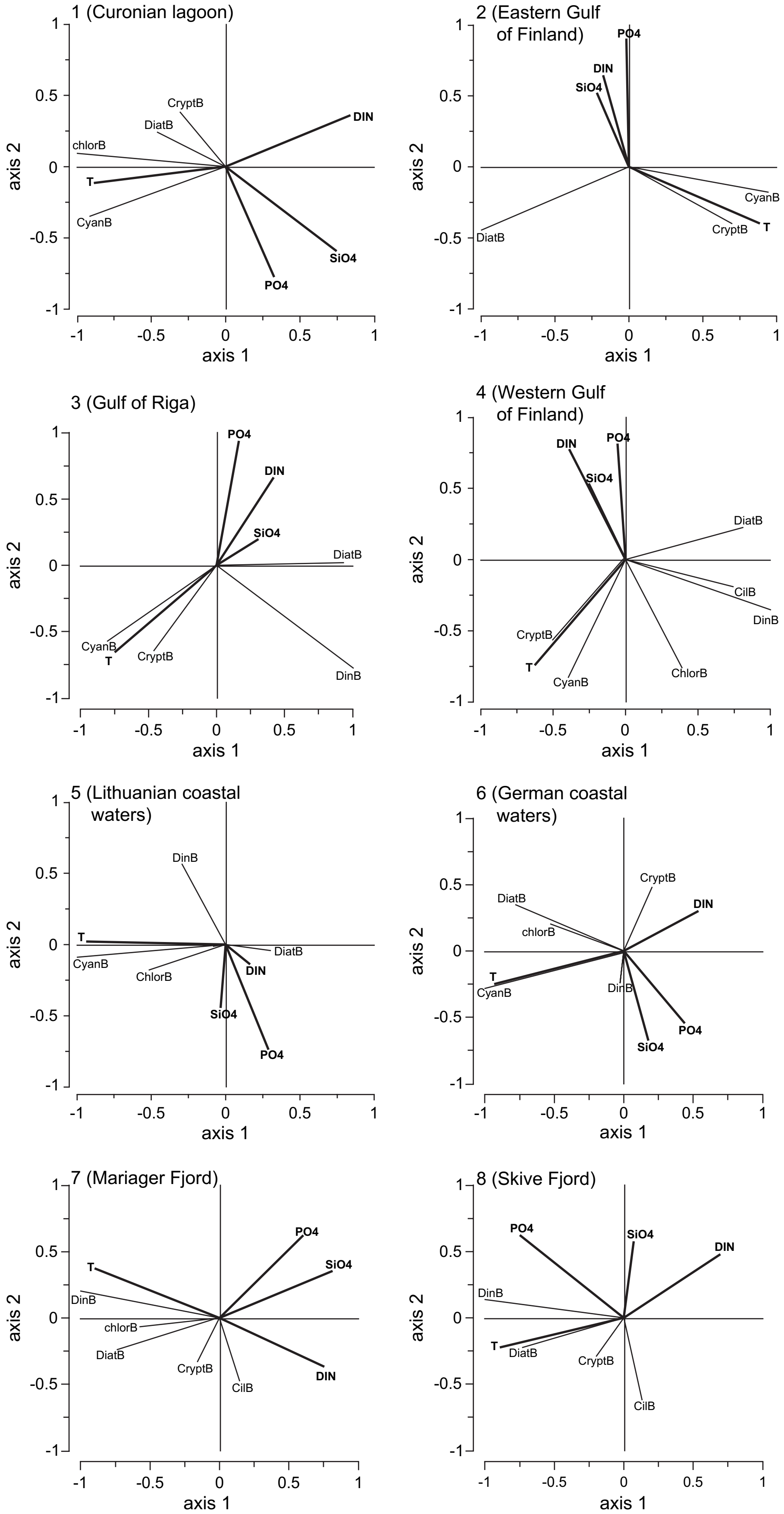

Fig. 4. RDA for locations. Thin lines represent response variables, thick lines represent explanatory variables.

Table 4
Numerical output of the RDA for locations. Location numbers (No.) as in Table 1. Marked values are significant at $p < 0.005$

No.	% of variability described by predictors	Contribution to the total sum of eigenvalues			
		t (°C)	PO_4	DIN	SiO_4
1	31	0.2*	0.05	0.18*	0.16*
2	53	0.37*	0.06*	0.05	0.04
3	42	0.21*	0.13*	0.11	0.03*
4	54	0.24*	0.14	0.17*	0.08*
5	24	0.16*	0.04*	0.01*	0.01*
6	17	0.11*	0.04*	0.04	0.02
7	28	0.18*	0.1*	0.13	0.14*
8	27	0.15*	0.13*	0.10	0.03*

termination of their vegetative life cycle (Kilham and Kilham, 1980). During the Baltic spring bloom, diatom biomass peak generally appears at the time when nutrients are already bound to phytoplankton biomass, whereafter their bloom is terminated by rapid sinking (Heiskanen, 1998). During autumn blooms, another set of diatom species appear, probably governed by their species-specific life cycles linked to the breakage of the summertime stratification and subsequent availability of nutrients at the surface layer.

Cyanophyte-dominated communities were found at all stations except at the two Danish sites that represented the highest salinities. Cyanobacteria did not appear in significant amounts in Danish phytoplankton samples from analysed fjords, whereas the genera *Nodularia* and *Aphanizomenon* were common in summer samples from the adjacent areas with lower salinities (e.g. Belt Sea and Sound). While the growth of *Aphanizomenon* ceases at salinities above 10, *Nodularia* could grow in these two Danish fjords (Lehtimäki et al., 1997). However, rates of growth and primary production are severely reduced with increasing salinities (Lehtimäki et al., 1997; Wasmund, 1997; Henriksen unpubl. results) and thus these genera may be competitively excluded under the prevailing physical conditions in analysed areas. On the other hand, some cyanobacteria species are tolerant of a wide range of salinities (Wasmund et al., 1999), so the main separation of species composition actually exists between fresh and brackish waters more than within brackish water.

In the nutrient rich, shallow water locations (Curonian lagoon and Pomerian Bay) cyanobacteria were generally dominating the bloom peaks during summer (Fig. 2). Thus it appeared that on these two locations, cyanobacterial biomass comprised most of the prevalent summer blooms, therefore being strongly indicative for the trophic status proxy MSB (Table 3). In the other deep open water locations (deeper than 10 or 15 m), cyanobacteria-dominated communities were the most prevalent during summer, but the biomass levels were generally lower than during the spring bloom (Fig. 2).

Due to their ability to fix gaseous nitrogen, heterocystic cyanophytes are very successful competitors during N-limitation periods (e.g. Paerl, 2000). N-limitation prevails in most of the Baltic coastal areas during late spring and summer periods (Tamminen et al., 1985; Graneli et al., 1990), thus allowing development of cyanobacteria dominated blooms during late summer in the Baltic (Niemi, 1979; Kononen, 1992). For example, in the easternmost Gulf of Finland, the nutrient ratios and hydrographical conditions determine which one of the cyanophytes – the heterocystic *Aphanizomenon* sp. or non-N fixing *Planktotrix agardhii*, achieves dominance in the phytoplankton community (Kauppila et al., 1995; Kauppila and Lepistö, 2001). However, recurrent cyanobacterial blooms are natural phenomena in the Baltic Sea (Bianchi et al., 2000), although the intensity of blooms may have increased during last century (Finni et al., 2001). Therefore simply the dominance of cyanobacteria as such, would not be an appropriate indicator of high trophic conditions. Whereas the current results suggest that high summer phytoplankton biomass in combination with cyanobacteria-dominated communities could be a potential indicator of elevated trophic conditions in shallow coastal waters.

Dinophyte-dominated communities appeared in locations with salinity above 5 and were generally most frequent during spring in the Gulf of Finland (dominated by *Peridiniella catenata* and *Scrippsiella hangoei*), Gulf of Riga (*Peridiniella catenata*), Lithuanian coastal waters (dominated by *P. catenata* and *Gymnodinium* sp.) and Pomeranian Bay (*Amphidinium crassum*, *Heterocapsa rotundata*). Dinophyte communities, dominated by other species than during spring period (*Heterocapsa triquetra* in the Gulf of Finland and Lithuanian coastal waters; *Dinophysis acuminata* in the Gulf of Riga; *Prorocentrum* spp. in Pomeranian Bay) also appeared during summer in all of those locations as well as in Danish coastal waters (*Prorocentrum minimum*).

The RDA did not predict the dinoflagellate-dominated community well, suggesting that it is affected by factors not included in the current analysis. Many of the common dinoflagellates may potentially be mixotrophic species, partly independent on ambient nutrient conditions (Jacobson and Andersen, 1994). Many dinoflagellate species also migrate vertically and are able to use sub-pycnocline nutrients during the stratified period, thus are independent of ambient nutrient conditions of the surface layer (Passow, 1991; Olli et al., 1998). Dinophytes are often preferred food items and thus are grazed on heavily by meso- and microzooplankton grazers (Kleppel, 1993). Some dinoflagellates may also be limited by availability of trace metals that are bound in the humic substances (Graneli et al., 1985).

Cryptophytes could be found in all analysed locations, but dominated in only three of them: Eastern Gulf of Finland, Pomeranian Bay and Mariager Fjord. In contrast to the other groups, this community appeared in late autumn–winter (November–February) samples in more than 50% of the cases. The sensitivity of the cryptophytes to the geographic index and the dominance of this group in only three different locations suggest that other site-specific factors (e.g. hydrodynamics, ice cover) are more likely to predict these communities than salinity or trophic status indicators. Cryptophytes have a relatively low affinity for light and often dominate in the deeper part of the stratified water column (Sommer, 1985; Stewart and Wetzel, 1986). Moreover, lack of winter sampling might influence the finding that cryptophyte-dominated communities were not detected in all locations. Therefore the factors that resulted in appearance of cryptophyte-dominated communities in these three geographically separate and hydrodynamically different areas are not clear. Potentially species-specific analysis could shed some light on the regulation. However, based on the current results the indicative value of cryptophytes for trophic conditions seems to be limited.

The RDA at the location level reveals that temperature is the most important factor that shapes phytoplankton community structure at all locations. This relationship is the strongest in the northernmost locations (Gulf of Finland) and much weaker in the southernmost location (Pomeranian Bay). The importance of temperature reflects the strong seasonal differences characteristic of boreal and temperate coastal waters. Further, inorganic nitrogen and phosphorus concentrations were also significantly linked to different phytoplankton community structures at different locations. Silica availability appeared to be a significant factor shaping phytoplankton communities at all locations except Eastern Gulf of Finland and Pomeranian Bay.

It is important to note that nutrients were not among the most significant factors that shaped previously defined community types when data from all locations were combined. This proves the feasibility of formal statistical methods to derive seasonal community types. While the analysis of phytoplankton community structure covering all seasonal succession stages confirmed it to be sensitive to nutrient concentrations at the location level.

It could be concluded that irrespective of the limitations in database compiled from different national sources, it was possible to identify phytoplankton community types, indicative of climatic conditions, salinity and trophic status of the locations. It is clear, that cyanophyte abundance alone cannot be used as an eutrophication indicator in the brackish Baltic Sea where such blooms occur also naturally. Also, the structure of both diatom- and cyanophyte-dominated communities is governed by salinity, and thus the abundances of these groups cannot be directly used as an indicator across the whole Baltic Sea.

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