



Long-term changes in summer phytoplankton communities of the open northern Baltic Sea

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Abstract

Changes in the biomass and species composition of phytoplankton may reflect major shifts in environmental conditions. We investigated relationships between the late summer biomass of different phytoplankton taxa and environmental factors, and their long-term (1979–2003) trends in two areas of the Baltic Sea, the northern Baltic proper (NBP) and the Gulf of Finland (GF), with statistical analyses. An increasing trend was found in late summer temperature and chlorophyll *a* of the surface water layer (0–10 m) in both areas. There was also a significant decrease in summer salinity and an increase in winter dissolved inorganic nitrogen to phosphorus (DIN:DIP) ratio in the NBP, as well as increases in winter DIN concentrations and DIN:SiO₄ ratio in the GF. Simultaneously, the biomass of chrysophytes and chlorophytes increased in both areas. In the NBP, also the biomass of dinophytes increased and that of euglenophytes decreased, whereas in the GF, cyanobacteria increased and cryptophytes decreased. Redundancy analysis (RDA) indicated that summer temperature and winter DIN concentration were the most important factors with respect to changes in the phytoplankton community structure. Thus, the phytoplankton communities seem to reflect both hydrographic changes and the ongoing eutrophication process in the northern Baltic Sea.

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1. Introduction

Phytoplankton form the energetic basis of open sea food webs, and because of their relatively high growth rates and direct dependency on both hydrographic factors and dissolved nutrients, phytoplankton species are important indicators of water quality in pelagic areas. However, due to both natural and methodological reasons, phytoplankton species composition and abundance data are highly variable, and consequently their use as water quality indicators is usually restricted and only chlorophyll *a* concentrations are monitored. Also, due to development in taxonomical classification and methodology, sufficiently long comparable time series of phytoplankton are rare.

Due to concern over the pollution of the Baltic Sea, the surrounding states signed the Convention on the Protection of the Marine Environment of the Baltic Sea Area in 1974. To improve the knowledge on the long-term changes in the factors related to eutrophication and pollution of the sea, the Baltic Marine Environment Protection Commission (Helsinki Commission, HELCOM) has been coordinating a joint monitoring programme of the Baltic Sea (BMP, later COMBINE) since 1979. Data on physical, chemical and biological parameters of the open sea have now been collected for over 25 years. According to the latest assessment of the state of the Baltic Sea, covering years 1994–1998 (HELCOM, 2002), eutrophication is still a major problem in most sub-areas, despite the successful reductions in point-source nutrient loading.

The typical annual phytoplankton succession in the open northern Baltic Sea is characterised by a winter biomass minimum stage, a vernal bloom of diatoms and dinoflagellates that depletes the inorganic nutrients in the euphotic layer and leads

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to a summer minimum stage, a late summer maximum, mainly formed by cyanobacteria, and a late autumn biomass decline (Niemi, 1973). This paper focuses on the nutrient-poor late summer (July–August) period, when high water temperatures and stable weather conditions favour the development of nitrogen-fixing cyanobacteria, and mass-occurrences formed by *Aphanizomenon flos-aquae*, *Nodularia spumigena* and *Anabaena* spp. occur frequently. In addition to the filamentous and colonial cyanobacteria, the late summer community also typically contains several species of cryptophytes, dinoflagellates, chrysophytes, euglenophytes and chlorophytes (Kononen, 1988).

The aim of our study was to use the HELCOM monitoring data to determine if long-term changes in hydrography and nutrient conditions are reflected in the late summer phytoplankton community. We evaluated the 1979–2003 data set for the late summer period, consisting of quantitative phytoplankton observations, as well as several environmental factors in two sub-areas of the northern Baltic Sea; the northern Baltic proper (NBP) and the Gulf of Finland (GF). In a recent analysis, Wassmund and Uhlig (2003) used the BMP data in an investigation of phytoplankton trends in the southern and central Baltic Sea. In contrast, long-term phytoplankton community analyses have not been made since the end of the 1980s for the northern Baltic Sea (Kononen and Niemi, 1984; Kononen, 1988).

2. Materials and methods

2.1. Study area

The Baltic Sea is a semi-enclosed, brackish water sea (ca. 422 000 km², mean depth 55 m), with a very restricted connection to the North Sea via the Danish straits. It is characterized by strong seasonal temperature variation, as well as a north-south surface salinity gradient, with surface water salinities decreasing from ca. 20 in the Kattegat to 1–2 in the northern and eastern areas. The northern Baltic proper comprises an area of 29 100 km² (Fig. 1). Connected to the NBP without a sill, the Gulf of Finland (29 500 km²) is situated between Finland and Estonia. It has a surface water salinity gradient ranging from about 7 in the west to freshwater conditions in the Neva Bay, Russia. GF has a large catchment area (421 000 km²) and is heavily influenced by nutrient loading

from the surrounding agricultural and urban areas, especially from the city of St. Petersburg by the run-off from the River Neva. The nutrient reserves of the GF are also affected by the phosphorus-rich Baltic Sea deep waters flowing freely into the gulf due to the sill-free connection to the Baltic proper. The GF receives two to three times the average Baltic Sea external nutrient inputs relative to its surface area (HELCOM, 2002), and it is thus considered as one of the most eutrophicated sub-basins of the Baltic Sea.

The study area is stratified, with a deep, permanent halocline (at a depth of ca. 60–80 m) and a summer thermocline (10–20 m). Our data originated from five HELCOM monitoring stations (Fig. 1): three in the northern Baltic proper; H3 (58° 35' 00" N, 18° 14' 00" E; bottom depth 450 m), H2 (59° 02' 00", 21° 05' 00"; 166 m) and H1 (59° 29' 00", 22° 54' 00"; 82 m), and two in the Gulf of Finland; F3 (59° 51' 06", 24° 50' 03"; 77 m) and F1 (60° 04' 01", 26° 21' 00"; 66 m).

2.2. Data

The original data collected by the BMP since 1979 consist of observations of biological and environmental parameters made in different times of the year. The monitoring programme focuses on quantification of summer phytoplankton, which is why the current paper deals with the nutrient deficient late summer period, between the end of July and the beginning of September, 1979–2003. Data from years 1982 (GF) and 1998–1999 (both sub-regions) are lacking, as the samples were taken outside the time period of interest during those years.

The phytoplankton data consisted of 90 quantitative observations (50 from the NBP and 40 from the GF), resulting in up to three observations per year at each of the sub-regions. In 1979–1997, the sampling days were distributed between 29 July and 3 September, whereas in 2000–2003, samples were taken between 30 July and 20 August each year, due to a change in the sampling schedule. Integrated samples of the upper water layer (0–10 m) were preserved with acid Lugol solution, and analysed using an inverted microscope (Utermöhl, 1958). During most of the study period (1982–2003), only one person (Maija Huttunen) was responsible for species identification and counting, which ensured the comparability

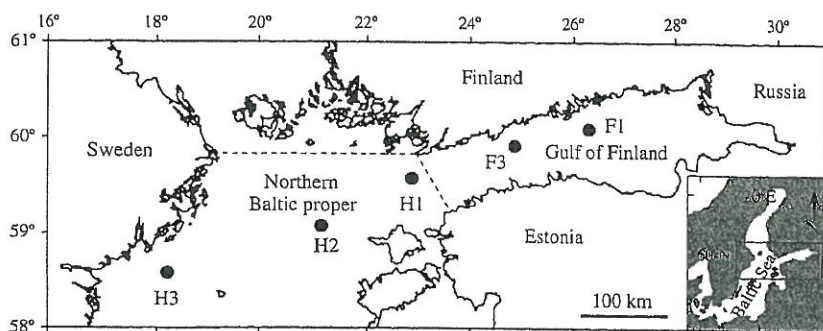


Fig. 1. Location of the monitoring stations in the Baltic Sea. The dashed line represents the borders of the two sub-areas studied.

of the data. Altogether ca. 200 taxa, mostly identified to species level, were found in the samples. The species nomenclature is according to Hällfors (2004). The biomass calculations were made according to the Manual for Marine Monitoring in the COMBINE Programme of HELCOM (Annex C-6; <http://sea.helcom.fi/Monas/CombineManual2/contents.html>). Chlorophyll *a* concentration in samples taken from discrete depths was measured spectrophotometrically according to HELCOM (1988), and averaged over 0–10 m.

The environmental data consisted of simultaneous measurements of temperature and salinity, as well as concentrations of inorganic nutrients (phosphate-phosphorus, nitrate, nitrite and ammonium-nitrogen and silicate-silicon) measured at the same stations during the preceding winter (November–January). As there were often several nutrient measurements per station and winter, these were averaged for the analysis. Long-term trends in surface water nutrient concentrations are most reliably detected in winter samples because in winter season the least amount of nutrients are bound to biological material. In summer, concentrations of inorganic nutrients, especially that of nitrogen, are often below the detection limits. However, variability may be great due to e.g. organic aggregates and sporadic events such as upwelling. We also examined early summer nutrient concentrations in samples taken before the phytoplankton sampling, but the large variability of these data, due to the reasons mentioned above, prevented their inclusion in the analysis. The rationale for comparing wintertime nutrient concentrations with summer phytoplankton data was that winter nutrient trends can be expected to be linked to summer communities in a long time scale. The water chemistry parameters were determined according to Koroleff (1979), and each value represents the mean for the 0–10 m water layer. The limit of detection in the nutrient measurement was 0.01 μM . Salinity was measured using the Practical Salinity Scale.

2.3. Statistical analyses

Both the phytoplankton and the environmental data were analysed for the presence of monotonic increasing or decreasing trends by the non-parametric Mann–Kendall test using the MAKESENS 1.0 application (Salmi et al., 2002). A non-parametric trend test was used, because all data were not normally distributed. In the Mann–Kendall procedure, the data need not conform to any particular distribution and missing values are allowed (Gilbert, 1987).

Relationships between the phytoplankton composition and the environmental factors were assessed using redundancy analysis (RDA), which is a linear method of direct ordination (ter Braak, 1994). For the analysis, we selected phytoplankton species or wider taxonomic groups which were identified consistently over most of the study period (at least from 1983 onwards), and which occurred in more than seven samples in each sea area (Table 1). The final number of taxa in the analysis was 32 in the NBP and 28 in the GF. 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), with forward selection to identify the environmental variables that best explained the phytoplankton species composition. The significance of the variables and the first ordination axis was determined using Monte Carlo permutation testing (9999 permutations), implemented in CANOCO.

3. Results

3.1. Long-term trends in environmental factors and phytoplankton

In the northern Baltic proper, significant (Mann–Kendall test, $p < 0.05$) increasing trends were observed for summer temperature and chlorophyll *a* concentration, and winter dissolved inorganic nitrogen to phosphorus (DIN:DIP) ratio, whereas summer salinity showed a decreasing trend (Table 2, Fig. 2A). In the Gulf of Finland, increasing trends were found for summer temperature and chlorophyll *a*, and winter DIN concentration and DIN:SiO₄ ratio (Fig. 2B). In the analysis of early summer nutrient concentrations (data not shown), no significant trends were observed due to a large variance (Mann–Kendall test, $p > 0.05$). However, there was a decreasing tendency in DIN concentrations in both sub-areas, but especially in the GF.

In the phytoplankton biomass data (Fig. 3), significant increasing trends were found for dinophytes, chrysophytes and chlorophytes in the northern Baltic proper (Table 2, Fig. 3A), and for cyanobacteria, chrysophytes and chlorophytes in the Gulf of Finland (Fig. 3B). Negative trends were observed for euglenophytes in the northern Baltic proper and for cryptophytes in the Gulf of Finland.

3.2. Relationships between phytoplankton and environmental factors

The phytoplankton taxa selected for the RDA and the species included in each combination taxon are listed in Table 1. The 32 combination taxa used in the RDA consisted of 11 dinophytes, 6 cyanobacteria, 6 diatoms, 4 chlorophytes, 2 chrysophytes and 1 taxon of cryptophytes, euglenophytes and zooflagellates, i.e. *Ebria tripartita* (Table 3). Most of the included species are typical of warm brackish water, but some of the taxa also contain lacustrine or cold-water species. Some of the species use mixo- or heterotrophic nutrition, although they are traditionally regarded as phytoplankton species (Table 3). The most common taxa in the material, occurring in all samples, were *Aphanizomenon* spp. and *Pyramimonas* spp. Cryptomonads were also found in all samples in the GF. *Aphanizomenon* spp. and cryptomonads had the highest mean biomass in both sea areas (87.9 and 68.1 $\mu\text{g l}^{-1}$ in the NBP, and 103.7 and 99.3 $\mu\text{g l}^{-1}$ in the GF, respectively). The third highest biomasses were formed by picocolonial cyanobacteria in the NBP and the toxic cyanobacterium *Nodularia spumigena* in the GF (Table 3). *Gonyaulax* spp., *Dinobryon faculiferum*, *Cylindrotheca closterium* and *Nitzschia* spp. were encountered frequently enough in the NBP only, and thus they were excluded from the analysis of the GF data.

Table 1

The phytoplankton taxa present in more than seven samples per sea area, and occurring at least from 1983 onwards; the codes used in the RDA and the species included in each taxon. Nomenclature is according to Hällfors (2004)

Code	Name: species included
Picocolo	Picocolonial cyanobacteria: <i>Aphanocapsa</i> spp. Nägeli, <i>A. reinboldii</i> (<i>Microcystis reinboldii</i>) (P. Richter) Komárek & Anagnostidis <i>Aphanothece</i> spp. Nägeli, <i>A. clathrata</i> W. & G.S. West <i>Chroococcus</i> spp. Nägeli, <i>C. microscopicus</i> Komárková-Legnerová & Cronberg <i>Coelosphaerium kuetzingianum</i> Nägeli, <i>C. minutissimum</i> Lemmermann, <i>C. subarcticum</i> Komárek & Komárková-Legnerová <i>Cyanodictyon</i> spp. Pascher, <i>C. imperfectum</i> Cronberg & Weibull, <i>C. planctonicum</i> Meyer <i>Cyanonephron</i> spp. Hickel, <i>C. styloides</i> Hickel <i>Lemmermanniella</i> spp. Geitler, <i>L. pallida</i> (Lemmermann) Geitler, <i>L. parva</i> Hindák <i>Merismopedia tenuissima</i> Lemmermann, <i>M. warmingiana</i> (Lagerheim) Geitler <i>Microcystis</i> spp. Kützing ex Lemmermann <i>Synechococcus</i> spp. Nägeli
Gomphosp	Gomphosphaerioids: <i>Coelomoron</i> spp. Buell, <i>C. pusillus</i> (van Goor) Komárek <i>Snowella fennica</i> Komárek & Komárková-Legnerová, <i>S. lacustris</i> (<i>Gomphosphaeria lacustris</i>) (R. Chodat) Komárek & Hindák <i>S. litoralis</i> (Häyryén) Komárek & Hindák, <i>S. septentrionalis</i> Komárek & Hindák <i>Woronichinia</i> spp. Elenkin, <i>W. compacta</i> (<i>Gomphosphaeria compacta</i>) (Lemmermann) Komárek & Hindák, <i>W. elorantae</i> Komárek & Komárková-Legnerová, <i>W. karelica</i> Komárek & Komárková-Legnerová
Anablem	Anabaena lemmermannii:
Anabaena	<i>Anabaena flos-aquae</i> (Lyngbye) Brébisson in Brébisson & Godey ex Bornet & Flahault, <i>A. lemmermannii</i> P. Richter in Lemmermann
	Anabaena spp.:
	<i>Anabaena</i> spp. Bory ex Bornet & Flahault, <i>A. baltica</i> J. Schmidt, <i>A. cylindrica</i> Lemmermann, <i>A. inaequalis</i> Kützing ex Bornet & Flahault, <i>A. spiroides</i> Klebahn
Aphanizo	Aphanizomenon spp.: <i>Aphanizomenon</i> spp. Morren ex Bornet & Flahault, <i>A. flos-aquae</i> (L.) Ralfs ex Bornet & Flahault, <i>A. gracile</i> (Lemmermann) Lemmermann, <i>A. sp.</i> ("baltica" nom. ined.)
Noduspu	Nodularia spumigena: <i>Nodularia</i> spp. Mertens ex Bornet & Flahault, <i>N. baltica</i> Komárek et al., <i>N. spumigena</i> Mertens ex Bornet & Flahault
Cryptomo	Cryptomonads: <i>Cryptomonas</i> spp. Ehrenberg <i>Hemiselmis</i> spp. Parke, <i>H. virescens</i> Droop <i>Plagioselmis</i> spp. Butcher ex Hill, <i>P. prolonga</i> Butcher <i>Teleaulax</i> spp. Hill, <i>T. acuta</i> (Butcher) Hill, <i>T. amphioxeia</i> (Conrad) Hill
Dinoacu	Dinophysis acuminata Claparède & Lachmann
Dinonor	Dinophysis norvegica Claparède & Lachmann
Dinorot	Dinophysis rotundata Claparède & Lachmann
Amphidin	Amphidinium spp.: <i>Amphidinium</i> spp. Claparède & Lachmann, <i>A. crassum</i> Lohmann, <i>A. elenkinii</i> Skvortzow, <i>A. longum</i> Lohmann, <i>A. sphenoides</i> Wulff
Gymnodin	Gymnodinium spp.: <i>Gymnodinium</i> spp. Stein, <i>G. galatheanum</i> Braarud, <i>G. gracile</i> (<i>G. abbreviatum</i> , <i>G. lohmannii</i>) Bergh, <i>G. helveticum</i> Pénard, <i>G. sanguineum</i> Hirasaka, <i>G. simplex</i> (Lohmann) Kofoid & Swezy, <i>G. vestificii</i> Schütt
Gyrodini	Gyrodinium spp.: <i>Gyrodinium</i> spp. Kofoid & Swezy, <i>G. fusiforme</i> Kofoid & Swezy, <i>G. cf. pepo</i> (Schütt) Kofoid & Swezy, <i>G. spirale</i> (Bergh) Kofoid & Swezy
Glenodin	Glenodinium spp. Ehrenberg
Oblerot	Oblea rotunda complex <i>Oblea rotunda</i> (Lebour) Balech ex Sournia
Protoper	Protoperidinium spp.: <i>Protoperidinium</i> spp. Bergh emend. Balech, <i>P. bipes</i> (Paulsen) Balech, <i>P. brevipes</i> (Paulsen) Balech, <i>P. granii</i> (Ostenfeld) Balech, <i>P. pellucidum</i> Bergh
Gonyaula	Gonyaulax spp.: <i>Gonyaulax</i> spp. Diesing, <i>G. spinifera</i> Claparède & Lachmann, <i>G. verior</i> Sournia <i>Peridiniella catenata</i> (<i>Gonyaulax catenata</i>) (Levander) Balech
Protret	Protoceratium reticulatum: <i>Protoceratium reticulatum</i> (<i>Gonyaulax grindleyi</i>) (Claparède & Lachmann) Bütschli
Dinofac	Dinobryon faculiferum: <i>Dinobryon faculiferum</i> (<i>D. petiolatum</i>) (Willén) Willén
Pseudope	Pseudopedinella spp.: <i>Pseudopedinella</i> spp. N. Carter, <i>P. elastica</i> Skuja, <i>P. tricostata</i> (<i>Pedinella tricostata</i>) (Rouchijajnen) Thomsen
Actioct	Actinocyclus octonarius Ehrenberg
Chaedan	Chaetoceros danicus P.T. Cleve
Chaetoce	Chaetoceros spp.: <i>Chaetoceros</i> spp. Ehrenberg, <i>C. ceratosporus</i> Ostenfeld, <i>C. minimus</i> (<i>Rhizosolenia minima</i>) (Levander) Marino et al., <i>C. subtilis</i> P.T. Cleve, <i>C. tenuissimus</i> Meunier, <i>C. thronsenii</i> (Marino et al.) Marino et al., <i>C. wighamii</i> Brightwell

(continued on next page)

Table 1 (continued)

Code	Name: species included
Thalassi	<i>Thalassiosira</i> spp.: <i>Thalassiosira</i> spp. P.T. Cleve emend. Hasle, <i>T. baltica</i> (Grunow in P.T. Cleve & Grunow) Ostenfeld, <i>T. guillardii</i> Hasle, <i>T. lacustris</i> (Grunow in P.T. Cleve & Grunow) Hasle in Hasle & G. Fryxell, <i>T. levanderi</i> van Goor, <i>T. pseudonana</i> (Hustedt) Hasle & Heimdal
Cylico	<i>Cylindrotheca closterium</i> : <i>Cylindrotheca closterium</i> (Ehrenberg) Reimann & J. Lewin <i>Nitzschia acicularis</i> v. <i>closterioides</i> Grunow, <i>N. longissima</i> (Brébisson in Kützing) Ralfs in Pritchard
Nitzschi	<i>Nitzschia</i> spp.: <i>Nitzschia</i> spp. Hassall, <i>N. palea</i> (Kützing) W. Smith, <i>N. paleacea</i> (Grunow) Grunow in van Heurck
Eutrepti	<i>Eutreptiella</i> spp.: <i>Eutreptiella</i> spp. da Cunha, <i>E. gymnastica</i> Throssen
Pyramimo	<i>Pyramimonas</i> spp.: <i>Pyramimonas</i> spp. Schmarla, <i>P. grossii</i> Parke emend. Manton, <i>P. orientalis</i> McFadden, Hill & Wetherbee, <i>P. virginica</i> Pennick
Monocon	<i>Monoraphidium contortum</i> : <i>Koliella longiseta</i> Hindák, <i>K. spiculiformis</i> (Vischer) Hindák <i>Monoraphidium contortum</i> (Thuret in Brébisson) Komárková-Legnerová
Oocystis	<i>Oocystis</i> spp.: <i>Oocystis</i> spp. A. Braun, <i>O. borgei</i> Snow, <i>O. lacustris</i> R. Chodat, <i>O. submarina</i> Lagerheim
Planlau	<i>Planctonema lauterbornii</i> Schmidle
Ebriiri	<i>Ebria tripartita</i> (Schumann) Lemmermann

The results of the RDA are displayed in two ordination plots for both sea areas (Fig. 4). For more detailed interpretation of the triplots, see ter Braak (1994). In both areas, the RDA with forward selection yielded two significant environmental variables explaining the variability in the phytoplankton biomass: temperature (NBP: $F = 3.02$, $p = 0.0001$; GF: $F = 2.85$, $p = 0.0002$) and DIN concentration (NBP: $F = 1.93$, $p = 0.011$; GF: $F = 2.06$, $p = 0.008$). In the NBP, the effect of SiO_4 concentration ($F = 2.09$, $p = 0.006$) was also significant. Although in the NBP, the length of the salinity vector in the ordination plots (Fig. 4A,B) also indicated a high co-variance with the phytoplankton data, the relation was not significant ($F = 1.52$, $p = 0.061$). In the GF (Fig. 4C,D), the effects of salinity, SiO_4 concentration and DIP concentration were not significant ($p > 0.05$). Together, all environmental

variables (and all canonical axes) accounted for 16.4% of the variation in the phytoplankton biomass data in the NBP, and 20.0% in the GF. In the NBP, DIP was omitted from the RDA because of its negligible variance.

In the RDA ordination (Fig. 4), the first two axes explained 12.7% (NBP) and 15.0% (GF) of the total variance in the phytoplankton biomasses (NBP: axis 1: 7.5%, axis 2: 5.1%; GF: axis 1: 9.2%, axis 2: 5.8%). The first RDA axis was significant in both areas (NBP: $F = 3.67$, $p = 0.0001$; GF: $F = 3.45$, $p = 0.029$), and it described a gradient from a relatively higher silicate concentration and salinity towards higher temperature and DIN concentration. When plotted against the environmental variables (Fig. 4A,C), the samples (fitted with the phytoplankton biomasses and environmental variables) from the different decades formed loose clusters, indicating a transition in the environmental conditions during the study period. In general, samples from the late 1970s and 1980s were associated with higher silicate concentrations and salinity than samples taken in the 1990s and early 2000s, which were characterised by higher temperatures and DIN concentrations.

Similarly, the phytoplankton taxa could be classified according to their association with the environmental variables (Fig. 4B,D). The vector length indicates the goodness of fit of each taxon's biomass to the displayed ordination, and acute angles between two vectors indicate a high positive correlation. Thus, the biomass of e.g. *Pseudopedinella* spp. was strongly related to a high DIN concentration and a high temperature, but also to a low salinity and low silicate concentration in both sub-areas (Fig. 4B,D). In general, the phytoplankton taxa could be divided into two main groups according to their correlation with the environmental factors. The first group was formed by taxa whose biomass was highest in either low temperatures and low DIN concentrations (e.g. gomphosphaerioids, cryptomonads, *Dinophysis norvegica*, *Ebria tripartita*), or in high salinity and high silicate

Table 2

Results of the Mann–Kendall test for detection of long-term trends in the environmental factors and the phytoplankton biomass data (Z = test statistic, p = significance, n = number of sampling years)

	Northern Baltic proper			Gulf of Finland		
	Z	p	n	Z	p	n
Temperature	3.02	<0.01	20	2.63	<0.01	20
Salinity	-3.41	<0.001	20	-1.07	>0.05	20
Chlorophyll <i>a</i>	2.82	<0.01	20	2.95	<0.01	20
DIN	0.23	>0.05	20	2.17	<0.05	19
DIP	-1.85	>0.05	20	0.21	>0.05	19
SiO_4	-1.01	>0.05	20	-1.75	>0.05	19
DIN:DIP	2.43	<0.05	20	1.47	>0.05	19
DIN: SiO_4	1.78	>0.05	20	3.92	<0.001	19
Cyanobacteria	0.85	>0.05	23	2.03	<0.05	22
Cryptophyceae	-1.74	>0.05	23	-3.10	<0.01	22
Dinophyceae	2.32	<0.05	23	-0.62	>0.05	22
Chrysophyceae	3.20	<0.01	23	3.10	<0.01	22
Diatomophyceae	-1.11	>0.05	23	-0.39	>0.05	22
Euglenophyceae	-3.09	<0.01	23	-1.17	>0.05	22
Chlorophyta	2.38	<0.05	23	2.26	<0.05	22
Ebriidea	-0.48	>0.05	23	-1.44	>0.05	22

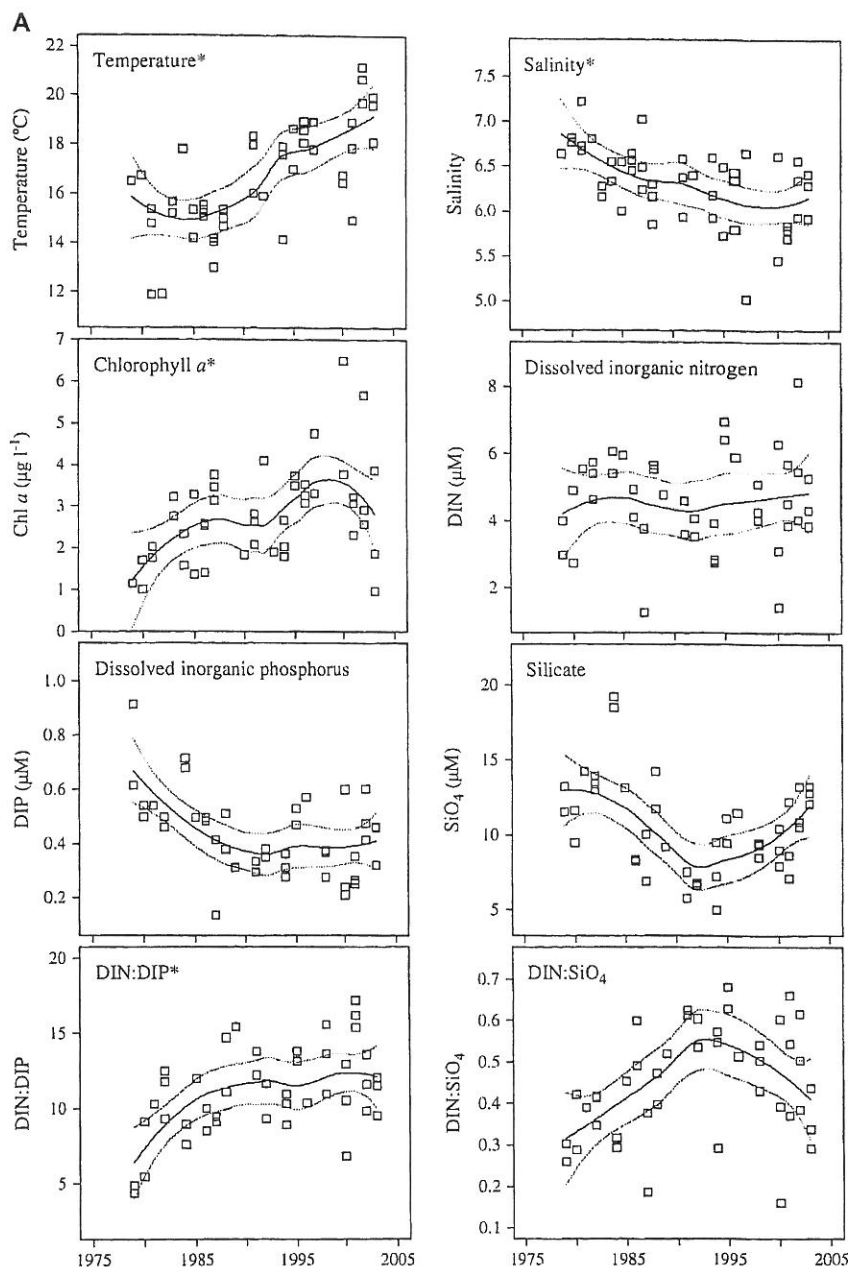


Fig. 2. Summer temperature, salinity and chlorophyll a , winter concentrations of inorganic nutrients (DIN, DIP and silicate), and molar ratios of DIN:DIP and DIN:SiO₄ from 1979 to 2003 (mean 0–10 m). A Loess curve (span = 0.75) (solid black lines) with 95% confidence intervals (dashed lines) is fitted to describe the long-term variation. Asterisks indicate statistically significant trends (Mann–Kendall test, $p < 0.05$). (A) Northern Baltic proper, (B) Gulf of Finland.

concentrations (mainly *Eutreptiella* spp. and the diatoms *Actinocyclus octonarius*, *Chaetoceros danicus*, *Chaetoceros* spp. and *Thalassiosira* spp.). All but one diatom taxon in the whole study area belonged to this group.

The second group included taxa generally preferring a high temperature and DIN concentration, and a low silicate concentration and salinity (picocolonial and filamentous cyanobacteria: *Anabaena lemmermannii*, *Aphanizomenon* spp. and *Nodularia spumigena*, the dinoflagellates *Dinophysis*

rotundata, *Amphidinium* spp., *Gymnodinium* spp. and *Oblea rotunda* complex, *Pseudopedinella* spp. and *Pyramimonas* spp.). Most of the dinoflagellate taxa in the whole study area, and, additionally, both chrysophyte taxa in the NBP, and most of the cyanobacterial taxa and all chlorophytes in the GF could be assigned to this group. The biomass of the former group generally decreased, whereas that of the latter group increased, simultaneously with the change in environmental conditions throughout the study period.

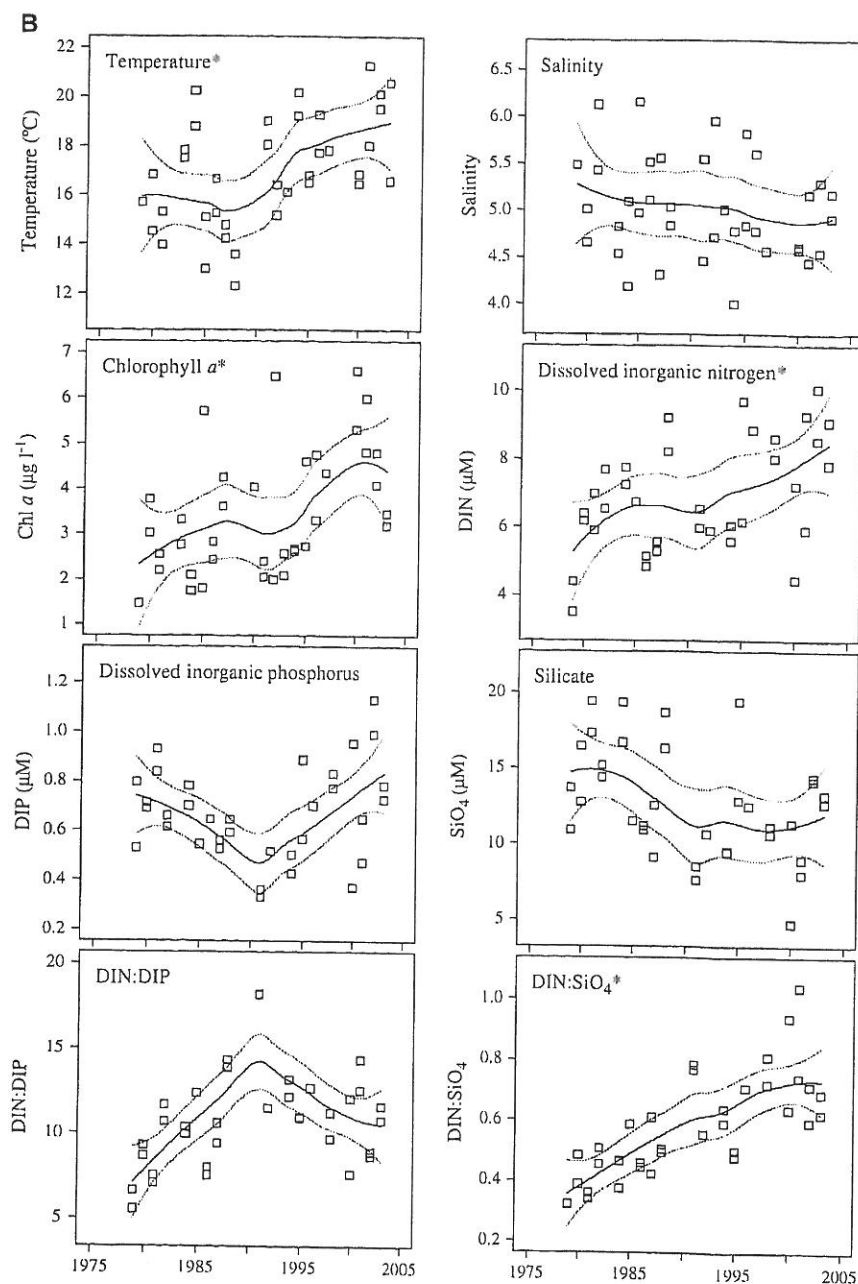


Fig. 2 (continued).

4. Discussion

During the past 25 years, the pelagic ecosystem of the Baltic Sea has undergone drastic changes both due to climate-driven changes in hydrography and to anthropogenic influence. The present study indicates that in the northern Baltic Sea, a transition has occurred in environmental conditions in 1979–2003, from more saline summer conditions, with higher silicate concentrations in winter, towards higher summer temperatures and higher winter DIN concentrations and DIN:DIP and DIN:SiO₄ ratios. At the same time, the summertime chlorophyll

a concentration of the surface water has significantly increased, indicating an ongoing eutrophication process of the open sea. Changes in environmental factors, especially increased summer temperature and winter DIN concentration, seem to be reflected in the late summer phytoplankton community structure.

4.1. Long-term changes in hydrography and nutrients

The decreased frequency and duration of salt water inflows from the North Atlantic since the 1970s and simultaneous increase in rainfall and river runoff, controlled by climatic

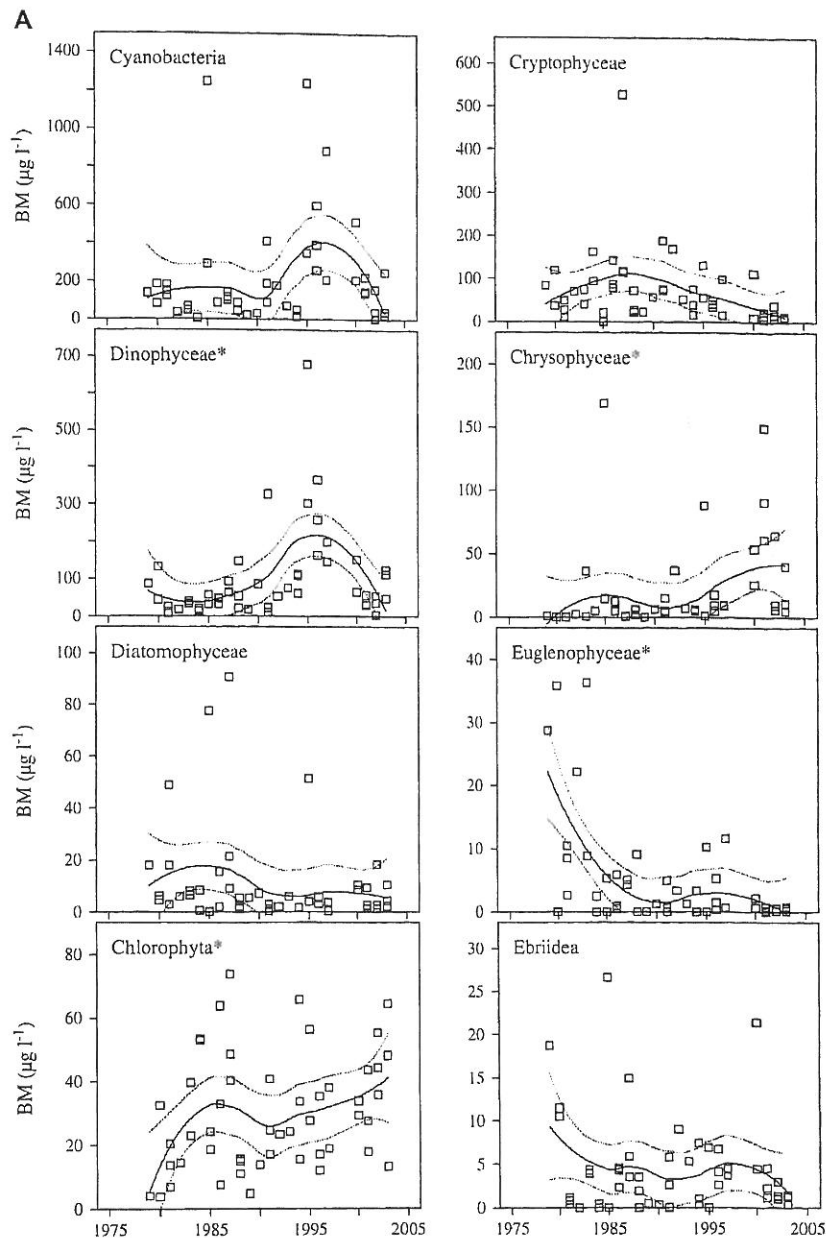


Fig. 3. Biomass of the major phytoplankton groups ($\mu\text{g l}^{-1}$) from 1979 to 2003 (mean 0–10 m). A Loess curve (span = 0.75) (solid black lines) with 95% confidence intervals (dashed lines) is fitted to describe the long-term variation. Asterisks indicate statistically significant trends (Mann–Kendall test, $p < 0.05$). (A) Northern Baltic proper, (B) Gulf of Finland.

factors in the Atlantic, have contributed to a general decrease in Baltic Sea salinity and deep layer dissolved oxygen concentrations (HELCOM, 2002). Consequently the coverage of oxygen deficient near bottom areas has increased (Pitkänen et al., 2003). In the northern Baltic Sea, salinity has decreased since the early 1980s (Flinkman et al., 1998; Rönkkönen et al., 2004). This trend was also found in the northern Baltic proper in the present study, whereas only a slight decrease was observed in the Gulf of Finland. Instead, the data suggests a notable increase in summer temperature in 1979–2003 in both areas. However, in the end of the study period (2000–2003),

the samples were generally taken earlier during August than in 1979–1997, which may thus partly explain the observation. On the other hand, some warming may have occurred, corresponding to a general atmospheric heating during the last century: Rönkkönen et al. (2004) also reported an increase in summer temperature in the northern Baltic Sea in 1950–1999. In the southern Baltic Sea, intermediate winter water temperatures and summer temperature maxima in the surface mixed layer have increased since the late 1980s, connected with a change in the North Atlantic Oscillation index from a negative to a positive phase (Alheit et al., 2005).

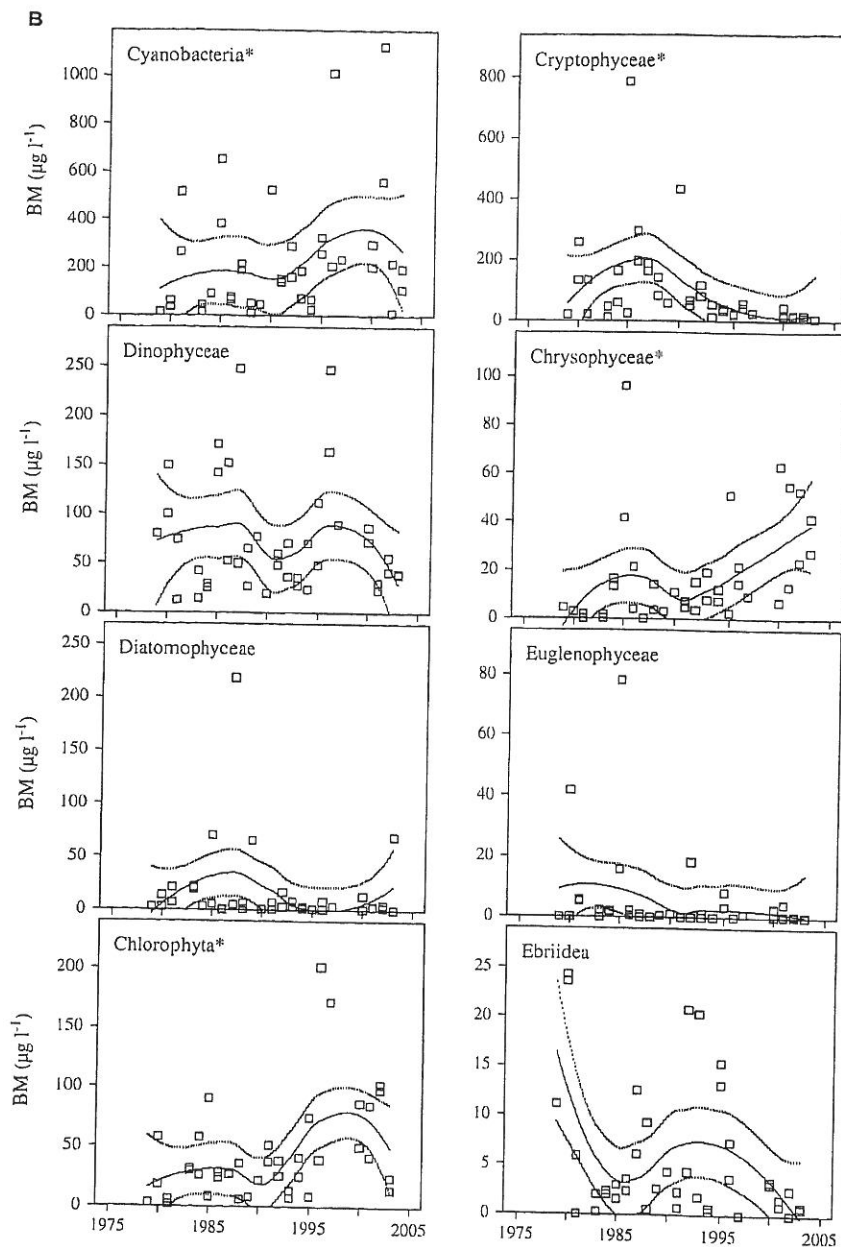


Fig. 3 (continued).

Statistically significant increases in total N and P, as well as DIN and DIP have been recorded from most of the Baltic Sea since the late 1960s (Wulff and Rahm, 1988; Sandén and Rahm, 1993; HELCOM, 1996). To a large part, the high nutrient content of the surface water is due to the heavy anthropogenic nutrient loading: N concentrations have been attributed to riverine and atmospheric load, whereas P mainly originates from the riverine load and anoxic sediments (Sandén and Rahm, 1993; Pitkänen et al., 2001). Especially in the GF, nutrient levels are high and eutrophication continues due to internal nutrient loading (Pitkänen et al., 2001, 2003). In the present data set, there was a slight decreasing tendency in winter surface water DIP concentration in the NBP, but no decrease was observed in the

GF. Instead, the DIP concentration in the GF seems to have increased since the beginning of the 1990s. Furthermore, DIN concentration significantly increased in the surface water of the GF during the study period. This is most likely the result of a combination of N loading and increased N accumulation in the Gulf. In addition to P releases, bottom anoxia leads to weakening of the denitrification capacity of the sediment and accumulation of ammonium, which is oxidized into nitrate when transported to the surface water (Kuparinen and Tuominen, 2001). The amount of DIN in relation to the other inorganic nutrients (DIP, SiO_4) was also found to generally increase in the study area, which may have had consequences for the phytoplankton community (discussed below).

Table 3

List of phytoplankton taxa included in the RDA (Code: see Table 1 for included species), their systematic group, nutrition, the number of non-zero observations (Northern Baltic proper, total $n = 50$; Gulf of Finland, total $n = 40$), mean biomasses and standard deviations in the analysed data

Code	Group ^a	Nutrition ^b	Northern Baltic proper		Gulf of Finland	
			Obs.	Mean \pm SD $\mu\text{g l}^{-1}$	Obs.	Mean \pm SD $\mu\text{g l}^{-1}$
Picocolo	Cyano	A	26	48.6 \pm 168.2	16	18.5 \pm 110.5
Gomphosp	Cyano	A	35	3.3 \pm 6.3	36	19.9 \pm 62.6
Anablem	Cyano	A	26	1.6 \pm 3.9	32	7.3 \pm 11.6
Anabaena	Cyano	A	17	11.7 \pm 77.8	17	8.4 \pm 28.4
Aphanizo	Cyano	A	50	87.9 \pm 76.9	40	103.7 \pm 75.2
Noduspu	Cyano	A	38	25.1 \pm 35.8	29	54.1 \pm 154.2
Cryptomo	Crypto	A/H	49	68.1 \pm 81.8	40	99.3 \pm 143.9
Dinoacu	Dino	A/H	39	3.6 \pm 4.9	38	18.4 \pm 17.9
Dinonor	Dino	A/H	31	9.6 \pm 23.6	10	4.3 \pm 22.9
Dinorot	Dino	H	29	2.0 \pm 3.7	17	0.8 \pm 1.6
Amphidin	Dino	A/H	22	2.0 \pm 5.0	12	2.4 \pm 7.7
Gymnodin	Dino	A/H	45	30.0 \pm 86.8	37	11.7 \pm 14.0
Cyrodini	Dino	A/H	16	2.1 \pm 7.7	14	1.0 \pm 1.9
Glenodin	Dino	A/H	14	4.8 \pm 14.5	12	2.7 \pm 4.9
Oblerot	Dino	H	8	4.9 \pm 32.8	10	0.4 \pm 1.1
Protoper	Dino	H	8	0.6 \pm 2.1	8	0.3 \pm 0.9
Gonyaula	Dino	A	13	0.8 \pm 2.4	2	0.0 \pm 0.2
Protret	Dino	A	31	3.1 \pm 6.1	19	6.3 \pm 13.3
Dinofac	Chryso	A	10	0.2 \pm 0.8	5	0.1 \pm 0.4
Pseudope	Chryso	A	39	13.8 \pm 27.9	32	11.3 \pm 15.3
Actioct	Diatom	A	28	2.0 \pm 4.3	20	7.5 \pm 34.4
Chaedan	Diatom	A	21	0.6 \pm 1.3	11	0.5 \pm 1.3
Chaetoce	Diatom	A	20	1.2 \pm 3.2	16	2.1 \pm 10.9
Thalassi	Diatom	A	23	4.4 \pm 13.9	12	0.4 \pm 0.9
Cyliclo	Diatom	A	9	0.1 \pm 0.2	1	0.0 \pm 0.1
Nitzschi	Diatom	A	10	0.2 \pm 0.6	6	0.2 \pm 1.3
Eutrepti	Eugleno	A	39	4.8 \pm 8.5	24	4.9 \pm 14.0
Pyramimo	Chloro	A	50	25.8 \pm 16.5	40	39.1 \pm 42.6
Monocon	Chloro	A	24	0.1 \pm 0.3	29	0.4 \pm 0.7
Oocystis	Chloro	A	35	3.4 \pm 6.7	27	3.3 \pm 6.1
Planlau	Chloro	A	10	0.1 \pm 0.4	9	0.0 \pm 0.0
Ebri tri	Ebri	H	43	4.2 \pm 5.7	35	5.3 \pm 6.9

^a Cyano = Cyanobacteria, Crypto = Cryptophyceae, Dino = Dinophyceae, Chryso = Chrysophyceae, Diatom = Diatomophyceae, Eugleno = Euglenophyceae, Chloro = Chlorophyta, Ebri = Ebriidea.

^b A = autotrophy, H = heterotrophy.

We found slight decreases in wintertime silicate concentration in the whole study area and a distinct increase in DIN:SiO₄ ratio in the GF. In the surface waters of the whole Baltic Sea, there have been significant decreases in silicate concentration and SiO₄:DIN ratio since the late 1960s (Sandén and Rahm, 1993; Rahm et al., 1996; Kuparinen and Tuominen, 2001). This has been attributed to increased sedimentation of biogenic silica as a result of increased diatom production due to eutrophication in the marine environment (Wulff et al., 1990; Conley et al., 1993), and already in the catchment area, leading to drastic reductions in riverborne silicate loads to the Baltic Sea (Humborg et al., 2000). Silicate limitation of spring bloom diatoms may also lead to changes in the summer phytoplankton communities, as more inorganic nutrients are left in the surface mixed layer for their use (Rahm et al., 1996; Kuparinen and Tuominen, 2001). The relationship between dinoflagellates and diatoms during spring bloom has actually changed in favour of dinoflagellates in the southern Baltic Sea (Wrzolek, 1996; Wasmund et al., 1998) and in the Baltic proper (Wasmund and Uhlig, 2003), and since the 1990s, the late summer phytoplankton biomasses have

increased in relation to the spring bloom in the GF (Raateoja et al., 2005).

4.2. Phytoplankton community changes in relation to environmental factors

Biological effects of eutrophication of the open sea include increases in primary productivity, chlorophyll *a* concentrations, algal blooms, deposition of organic matter and oxygen deficiency of bottom waters, and reductions in water transparency and bottom fauna (Cloern, 2001). All of these have been documented in the Baltic Sea; e.g. water transparency has decreased (Sandén and Håkansson, 1996) and phytoplankton production and biomass have increased since the end of 1960s, especially in summer (HELCOM, 2002). Significant increasing chlorophyll *a* trends were also documented in the present study in both sub-regions. In the GF, the increase was more pronounced than in the NBP, probably reflecting the severe internal nutrient loading. Furthermore, our results indicate that major changes have also happened in summer phytoplankton communities.

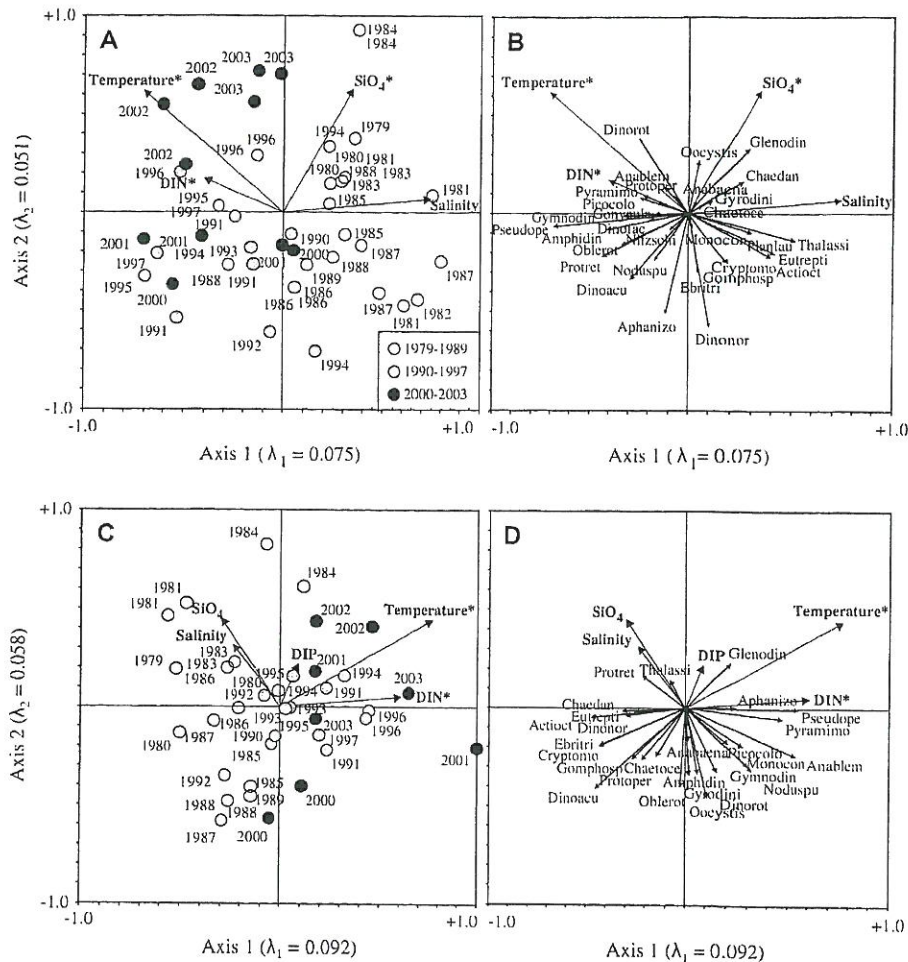


Fig. 4. Correlation plots of the redundancy analysis (RDA) for the northern Baltic proper (A, B) and the Gulf of Finland (C, D), on the relationship between (A, C) the environmental variables and sample years, with the periods 1979–1989, 1990–1999 and 2000–2003 indicated with different colours, and (B, D) the biomass of phytoplankton taxa (small vectors) and environmental variables (large vectors). The plots display 12.7 and 15.0% of the variance in the phytoplankton biomass in the NBP and GF, respectively, and eigenvalues of the first two axes are indicated by λ_1 and λ_2 . Codes of the phytoplankton taxa are as in Table 1. Asterisks indicate statistical significance ($p < 0.05$) of environmental variables.

Temperature and DIN concentration were the most important environmental factors modifying the late summer phytoplankton community. In the NBP, silicate concentration also played an important role. Temperature has been found to be the most significant factor affecting the phytoplankton community structure throughout the Baltic Sea, being positively related with the biomass of e.g. cyanobacteria and chlorophytes and negatively with diatoms (Laamanen, 1997; Alheit et al., 2005; Gasiūnaitė et al., 2005). Salinity, which is the key factor affecting the balance between species of marine and freshwater origin in the Baltic Sea, was not found to be a significant factor in the present study, but its decrease may have affected some taxa.

Some of the observed trends in the phytoplankton group biomasses 1979–2003 may be explained by the results of the RDA. In the whole study area, the biomasses of chrysophytes and chlorophytes increased. The chrysophytes mainly consisted of *Pseudopedinella* spp., which in the RDA were

highly associated with high DIN concentrations and a high temperature. The increasing trends observed in these parameters thus seem to be associated with the increase in chrysophytes. Chrysophytes shared these preferences with *Pyramimonas* spp., which formed the bulk of the chlorophyte biomass. *Pyramimonas* spp. have been found to correlate positively with temperature in the GF (Rantajärvi et al., 1998), and increases in their summer biomass have also been documented in the southern Baltic Sea since 1979 (Wrzotek, 1996). The increase in chlorophytes may, on the other hand, be associated with the decrease in salinity, as many of the common chlorophytes (e.g. *Monoraphidium contortum* and *Oocystis* spp.) are of lacustrine origin (Niemi, 1973).

The intensity and frequency of cyanobacterial blooms has increased in the Baltic Sea during the last half a century (Kahru et al., 1994; Finni et al., 2001), and several extensive cyanobacterial blooms occurred in the late 1990s and early 2000s in the GF (Pitkänen et al., 2003). Despite the high

variability in the biomass data, we observed a significant increase in cyanobacterial biomass, mainly formed by *Aphanizomenon flos-aquae* and *Nodularia spumigena*, in the GF during 1979–2003. Using the BMP data, Wasmund and Uhlig (2003) also found an autumn increase in cyanobacteria in the Baltic proper in 1979–1999, but in the samples from 2000–2003, this trend seemed to have levelled off. The increase in the GF was possibly associated with the increase in temperature and inorganic nutrients: in the RDA, gomphosphaerioids were the only cyanobacterial taxon not associated with high temperatures and high DIN concentration. In the GF, gomphosphaerioids are most abundant during the cool, well-mixed spring and autumn periods (Laamanen, 1997). Temperature (>16 °C) is the main factor determining the onset and intensity of blooms dominated by *N. spumigena* in the Baltic Sea (Wasmund, 1997; Kanoshina et al., 2003), whereas the biomass of *Aphanizomenon* spp. may be strongly related to DIN concentration (Jaanus and Pellikka, 2003). Also the slight decrease in salinity, combined with the increased temperature, may have favoured e.g. the picocolonial cyanobacteria, *Anabaena* spp. and *Aphanizomenon* spp. (Laamanen, 1997; Hällfors, 2004).

On the other hand, we found no strong association between winter DIP concentration and the nitrogen-fixing cyanobacterial biomass, although increased cyanobacterial blooms in the GF have often been attributed to increasing DIP concentrations and decreasing DIN:DIP ratios, originating from the sediment efflux (Pitkänen et al., 2003). Instead, the biomass of both *Aphanizomenon* spp. and *Nodularia spumigena* correlated positively with winter DIN concentration. It has been stated, however, that cyanobacterial blooms in the GF have an association with the amount of excess DIP left over from the spring bloom (Kiirikki et al., 2001), and not so much with the nutrient concentrations during mid-winter, when the samples for this study were taken. As discussed above, the vernal biomass has decreased (Raateoja et al., 2005), possibly leaving a greater amount of DIP for the use of summer communities, including the cyanobacteria, which have increased in biomass. Increased nitrogen-fixing cyanobacteria may, on the other hand, have contributed to the increased DIN level in the winter surface water (Kononen and Niemi, 1984). Moreover, in both sub-areas, there was a decreasing tendency in early summer DIN concentrations, which may have favoured the cyanobacteria over other species unable to fix atmospheric N.

The biomass of cryptophytes decreased in the GF, which may be connected with the increase in temperature: in the RDA, the cryptophytes were associated with low temperatures. Interestingly, the decrease in cryptophytes coincided with the increase in cyanobacteria in the GF. Extracts of the most common Baltic cyanobacteria (*Aphanizomenon flos-aquae*, *Nodularia spumigena* and *Anabaena* spp.) have recently been found to inhibit the growth of cryptophytes in laboratory experiments employing a natural Baltic Sea plankton community (Suikkanen et al., 2005).

In the NBP, many of the dinophytes (e.g. *Dinophysis rotundata*, *Gymnodinium* spp., *Oblea rotunda* complex) may have

been favoured by the increasing water temperature and/or DIN concentration (cf. Niemi, 1973; Kononen, 1988; Hällfors, 2004). Also, the general increase of small-celled species (chrysophytes, chlorophytes), aggregates of ageing cyanobacteria with associated bacteria and excreted DOM may have benefited the dinoflagellates, many of which are mixo- or heterotrophs. Wasmund and Uhlig (2003) also reported an increase in spring and summer dinophyte biomass in the NBP in 1979–1999, coinciding with a decrease in diatoms. Increasing dinoflagellates may be a cause of concern, as some Baltic dinoflagellate species are also potentially toxic (HELCOM, 1996).

In spite of the rather low sampling frequency and the high variability in some variables, we believe that the BMP data gives a reliable picture of the general changes in the pelagic ecosystem of the Baltic Sea. The rather low percentage of variance in the phytoplankton data explained by the environmental variables in the RDA is quite common in complex ecological monitoring data (ter Braak and Šmilauer, 1998), and is partly due to other factors, not considered in this study, influencing phytoplankton populations (e.g. grazing, sedimentation, micronutrients, inhibitory substances, light conditions).

To conclude, the long-term development of the late summer phytoplankton communities in the northern Baltic Sea seems to reflect the combination of ongoing eutrophication and climate-driven changes in hydrography. The significant increase of phytoplankton biomass, indicated as chlorophyll *a* concentration, is due to a considerable increase in cyanobacteria, various flagellates and chlorophytes. Our results agree with those of Kononen (1988), who also noticed an increase in nanoplanktonic flagellates, chlorophytes, picocolonial cyanobacteria and heterotrophic species in the GF in 1972–1985, suggesting an increase of the relative importance of regenerated production and the microbial loop. A cyanobacteria-flagellate dominated community is generally poor food for many grazers (Officer and Ryther, 1980), but the large-scale consequences of the changes in phytoplankton for higher trophic levels and their connections with observed long-term changes in e.g. zooplankton, benthic and fish communities are yet unknown.

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