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Changes in phytoplankton communities along a north–south gradient in the Baltic Sea between 1990 and 2008

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Evaluation of changes in Baltic Sea phytoplankton communities has been hampered by a lack of quantitative long-term data. We investigated changes in biomass of summer (June–September) phytoplankton over the last two decades (1990–2008) along a north–south gradient in the Baltic Sea. The areas were characterized by different temperature, salinity and nutrient conditions. Thirty taxonomic groups were selected for the statistical analysis. Increases in total phytoplankton, particularly cyanobacterial, biomass were observed in the Gulfs of Bothnia and Finland. In these two areas over the study period cyanobacteria also became abundant earlier in the season, and in the Curonian Lagoon *Planktothrix agardhii* replaced *Aphanizomenon flos-aquae* as the most abundant cyanobacterium. In general, water temperature was the most influential factor affecting the summer phytoplankton communities. Our data suggest that temperature increases resulting from climate change are likely to cause basin-specific changes in the phytoplankton communities, which in turn may affect overall ecosystem functioning in the Baltic Sea.

Introduction

Changes in phytoplankton composition may reflect structural and functional ecosystem shifts, and changes in the seasonal succession patterns of phytoplankton species are thought to be better predictors of long-term environmental change than the more commonly used parameters of biomass (chlorophyll *a*) and productivity (e.g. Moline and Prézelin 1996). However, long-term measurements with high temporal resolution are required to separate natural sources of variability from the effects of anthropogenic disturbance. Two of the most consistent effects of eutrophication on phytoplankton are shifts in species composition and increases in the frequency and intensity of nuisance blooms, which are typically dominated by harmful cyanobacteria (Huisman *et al*. 2005, Carstensen *et al*. 2007). Unfortunately, most plankton data that are currently available are unsuitable for trend analysis due to sparse sampling and natural inter-seasonal variability (McQuatters-Gollop *et al*. 2009).

Measurements of phytoplankton species abundance, composition and biomass are essential elements of most monitoring programmes. However, measuring seasonal changes and interannual variability requires extensive sampling efforts, and inadequate sampling may provide misleading indications of the timing, performance and abundance of the dominant taxa. Ferreira *et al*. (2007) suggested that monthly phytoplankton monitoring is appropriate for restricted coastal and transitional waters, but this level of sampling may not be sufficient to identify changes in more complex systems, where variations in hydrological conditions strongly affect natural succession (e.g. Pilkaytitė and Razinkovas 2007).

Furthermore, evaluation of phytoplankton data from different laboratories requires the methods used and taxonomic expertise of the people analyzing the data to be comparable. Unfortunately, there is considerable heterogeneity among datasets from different countries, especially with respect to sampling methods and taxonomic precision, which limits the comparability of the data and increases the level of uncertainty in the results of any comparative study. This uncertainty increases further when biomass data are calculated from cell size measurements. The need to standardise collection methods, counting techniques and the identification of phytoplankton species was recognized in early phytoplankton studies, particularly through the framework of the Baltic Monitoring Programme in the late 1970s. This need was addressed by the establishment of the HELCOM Phytoplankton Expert Group (PEG) and publication of standardized size-classes and biovolumes of phytoplankton species found in the Baltic Sea (Olenina *et al*. 2006).

Year-to-year fluctuations in phytoplankton species compositions are governed by hydrographical and hydrochemical drivers. For example, increases in salinity and nutrient concentrations in the Baltic Proper during the 1970s caused a general increase in phytoplankton biomass, especially during spring (Kononen and Niemi 1984). In addition, increasing air and sea surface temperatures in the late 1980s resulted in an extended growing season and increases in phytoplankton biomass (chlorophyll *a*) in both the North and Baltic Seas (Alheit *et al*. 2005). Long-term observations indicate that from the 1960s until the 1990s nearly a four-fold increase occurred in the winter inorganic nitrogen concentration in the northern Baltic Proper and the Gulf of Finland, and almost a two-fold in the Bothnian Sea (HELCOM 2009). The concentration of inorganic phosphorus followed a similar pattern, rising three-fold from the 1970s to the beginning of the 1990s in the northern Baltic Proper and the Gulf of Finland, and increasing by 30% in the Gulf of Bothnia. A slight decrease in phosphorus concentrations has been reported since the 1990s across the entire Baltic Sea, except in the Gulf of Finland (Fleming-Lehtinen *et al*. 2008). An increase in winter nutrient concentrations should theoretically cause changes in spring phytoplankton biomass. However, intensive measurements of chlorophyll *a* in the open Baltic Sea have not yet confirmed such an increase in spring phytoplankton biomass, although a slight tendency for the bloom to start earlier has been observed (Fleming and Kaitala 2006). This earlier development of the spring bloom suggests that the summer phytoplankton communities will also develop earlier.

Wasmund and Uhlig (2003) suggest that a consistent time series of > 20 years is required for reliable indications of long-term changes in phytoplankton biomass and community structure. However, there have been few long-term phytoplankton studies, especially of changes in species composition and abundance, even in such well-studied ecosystems as the Baltic Sea. Studies from before the 1960s and 1970s are even rarer, more fragmented and differed substantially with respect to the sampling and quantification methods used. Comparisons of historical data with recent data are always problematic and have to be treated cautiously (e.g. Finni *et al*. 2001b, Wasmund *et al*. 2008). Nevertheless, past studies of phytoplankton from the open Baltic Sea (Suikkanen *et al*. 2007) and the Kiel Bight (Wasmund *et al*. 2008) revealed an increase in total biomass (chlorophyll *a*), but the changes at the community level were more complex, showing both upward and downward trends.

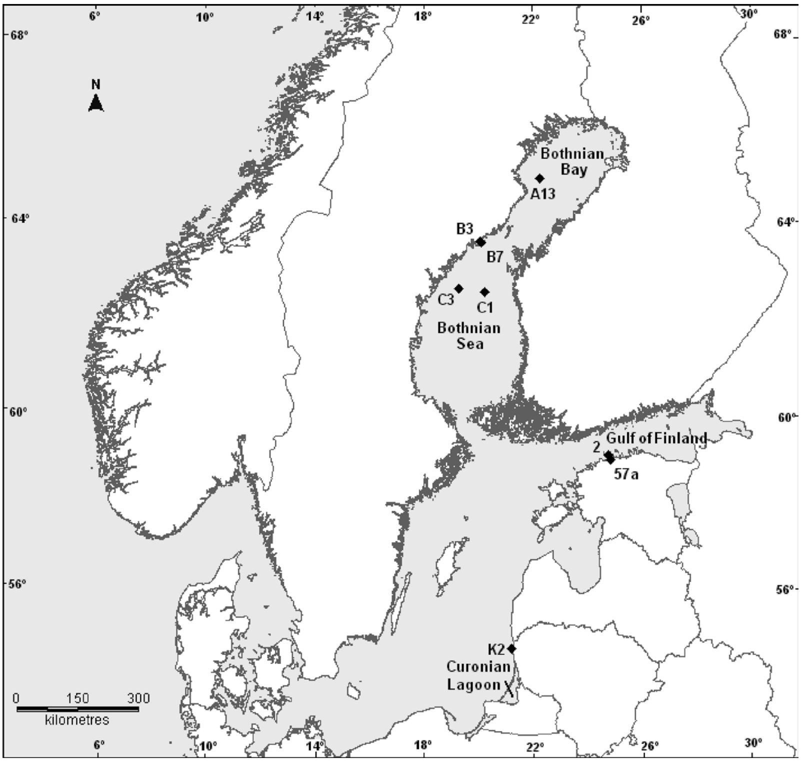

Fig. 1. Locations of the sampling stations in the Baltic Sea.

Quantitative phytoplankton time-series data have not been collected, or are of poor quality, for most of the Baltic sub-basins. The aim of this study was to assess long-term changes in the dominant phytoplankton along a north–south gradient in the Baltic Sea, including the Gulf of Bothnia, southern Gulf of Finland (Tallinn Bay) and Curonian Lagoon. Summer data from high frequency monitoring programmes that began in the 1990s and continued until 2008 were used in the analysis. A statistical method (BIOENV) was used to identify the most influential environmental factors affecting the phytoplankton communities in each of the major Baltic Sea basins. The results are discussed in relation to present and future environmental threats to the Baltic Sea.

Material and methods

Study area

We analyzed monitoring data from five basins: Bothnian Bay — station A13 (64°42´49´´N, 22°03´93´´); Bothnian Sea — stations C1 (62°35´22´´, 19°58´41´´) and C3 (62°39´22´´, 18°57´06´´); Öre Estuary, western Gulf of Bothnia — stations B3 (63°29´´98´´, 19°49´18´´) and B7 (63°31´48´´, 19°48´47´´); Tallinn Bay, southern Gulf of Finland — stations 2 (59°32´20´´, 24°41´30´´) and 57a (59°27´00´´, 24°47´30´´); and Curonian Lagoon, southeast Baltic Sea — station K2 (55°55´50´´, 20°58´50´´) (Fig. 1).

The Bothnian Bay is the northernmost sub-basin of the Baltic Sea, and accounts for ca. 10% (36 260 km^2) of the total Baltic Sea surface area. This bay has a mean water depth of 43 m, low salinity (2–3 practical salinity units, psu) and surface water that is typically covered with ice during the winter months (January–April). Light availability is lower than in other regions of the Sea due to high contents of humic substances in the water. Through a shallow (20 m) sill area called the Quark, the bay is connected to the deeper (mean depth 68 m, maximum 147 m) parts of the Bothnian Sea (HELCOM 1996). The Öre estuary is situated just south of the northern Quark.

Tallinn Bay is located in the southern part of the Gulf of Finland and consists of four smaller bays and a more open part. A deep trench (70–90 m) in its northern part allows water from the western Gulf of Finland to enter Tallinn Bay. The large urban area affects the nutrient status of the surrounding waters, as Tallinn Bay receives most of the local municipal wastewaters. At a broad scale, the Gulfs of Finland and Bothnia could be considered large estuaries because they are strongly influenced by river waters (Kauppila 2007).

The Curonian Lagoon is a shallow (mean depth 3.7 m), mostly freshwater, semi-enclosed estuary. The lagoon is connected to the Baltic Sea at its northern end, while the main inflow is from freshwater discharge from the Nemunas River, which is the third-largest contributor (after the Vistula and Oder) of total nitrogen and phosphorus to the southeast Baltic Sea (Stålnacke *et al*. 1999).

Time-series data

The data used in this study date back to the early 1990s when national monitoring programmes were established in all of our study areas. Three laboratories in three countries contributed to our study and all analysts were members of PEG, providing us with confidence that the data are reliable and comparable.

Samples were taken between 1990 and 2007 from the Curonian Lagoon, 1993 and 2008 from Tallinn Bay, and 1995–2008 from the Gulf of Bothnia. We focused on the summer period (from June to September) for which the phytoplankton datasets were most representative. Depending on the location and year, sampling frequency varied from 1 to 14 observations per season and basin. The average frequencies of sampling events per season were four in the Curonian Lagoon, five in the open Gulf of Bothnia and six in the Öre Estuary. It should be noted that samples were always taken simultaneously at the two monitoring stations in Tallinn Bay that contributed data, at a similar sampling frequency (6–7 per season) to the frequency in other areas. Observations were generally made at regular intervals throughout the entire investigation period, except that the sampling intensity was lower between 2004 and 2008 in the open Gulf of Bothnia and Curonian Lagoon (Table 1). In Tallinn Bay, only one sample was collected in both 1995 and 1996.

Sampling was generally conducted between 0 to 10 m depth using either a plastic hose (in the Gulf of Bothnia) or water samplers at discrete horizons (1, 5 and 10 m; the Gulf of Finland). In the Curonian Lagoon, samples were taken from the surface layer (0–0.5 m) using a 5-litre plastic water sampler. In Tallinn Bay, samples for phytoplankton and chlorophyll *a* were obtained by pooling equal volumes (0.5–1 l) of water from different horizons, whereas nutrients were determined from discrete samples. In the Gulf of Bothnia, samples for determining total phosphorus (P_{tot}) and total nitrogen (N_{tot}) were obtained from discrete depths (e.g. 0, 1, 2, 4, 6, 8 and 10 m) using a water sampler.

Samples collected from the Curonian Lagoon were divided into sub-samples for determining phytoplankton biomass and community composition, and chlorophyll *a* and nutrient concentrations. Temperature and salinity were measured using CTD probes. Data for chlorophyll *a* were not provided from the Gulf of Bothnia.

Table 1. Numbers of sampling events by sub-area, period and month.

	Bothnian Bay	Bothnian Sea	Öre Estuary	Tallinn Bay	Curonian Lagoon	Total
June	23	21	26	50	19	139
July	14	17	16	57	19	123
August	19	17	24	50	23	133
September	17	16	20	30	16	99
Before 1999	31	26	31	58	38	184
1999–2003	25	25	28	62	23	163
2004–2008	17	20	27	67	16	147
Total	73	71	86	187	77	494

Biological and chemical analyses

Phytoplankton samples were preserved with acid Lugol solution (0.5–1 ml per 200 ml sample) and analyzed using inverted microscopes (Gulf of Bothnia samples — Zeiss and Nikon Eclipse TE 300; Gulf of Finland — Olympus IM, IMT-2 and Leitz Fluovert FU; Curonian Lagoon — Leitz Fluovert FU and Olympus IX-51) and the sedimentation technique (Utermöhl 1958). The sediment volume and sedimentation time varied between 5 and 50 ml and 4 and 48 h, respectively. For the samples from the Gulf of Bothnia, 50% of the sedimentation chamber was scanned at the 100× magnification when counting large cells (> 10 μm), while small cells (< 10 μm) were counted at the 400× magnification along one diagonal. For phytoplankton from Tallinn Bay, the 200× magnification was used for larger cells and cells along one or two diagonals were counted, depending on the density of the sample. The abundance of smaller cells was estimated by examining 20 or 30 objective fields using the 400× magnification. Phytoplankton samples from Curonian Lagoon were counted using the 100× magnification and scanning 50% of the sedimentation chamber for large, rare species and 400× magnification along one diagonal or in 10 objective fields for common species. Cell sizes were measured using an ocular scale and volumes were calculated from cell geometry (HELCOM 1988, Hillebrand *et al.* 1999) or using standard size-classes (Olenina *et al.* 2006). Recent lists of biovolumes and fixed size-classes are recommended for use in the calculation of phytoplankton biomass in routine monitoring. Wet weight biomasses (mg per litre of seawater) were calculated for individual taxa and for the total biomass (http://www.helcom.fi/groups/monas/CombineManual/AnnexesC/en_GB/annex6).

The chlorophyll-*a* concentration was measured spectrophotometrically (Gulf of Finland — Yanaco UO 2000 and Jenway 6400; Curonian Lagoon — Specol 21 and Jenway 6300) after extraction in ethanol according to the HELCOM COMBINE manual (http://www.helcom.fi/groups/monas/CombineManual/AnnexesC/en_GB/annex4).

N_{tot} and P_{tot} were analyzed with Braan & Luebbe GmbH TRAACS 800 and Skalar San Plus autoanalyzers using standard seawater methods (Grasshoff *et al.* 1983; EVS-EN ISO 15681:2005 and EVS-EN ISO 11905-1:2003). Average concentrations in the upper 10-m layer were calculated for each sampling occasion using depth integrations.

Statistical analyses

Thirty taxonomic groups were used in the phytoplankton analysis, ranging from class to species level depending on the resolution of the method. The taxa were selected on the basis of their common appearance in all sub-basins, with some exceptions for species that were dominant in only one area (Table 2). To avoid probable misidentifications by different analysts and due to recent changes in nomenclature, especially for small-sized flagellates and colonial cyanobacteria, these organisms were aggregated into higher taxonomic groups. For example, the colonial cyanobacterium *Microcystis reinboldii* (Pankow 1976, Tikkanen and Willén 1992) includes several species from the genera *Aphanocapsa* (Hällfors 2004). Due to taxonomic changes and identification difficulties we merged several species and genera into class (crypto-, prymnesio-, chryso-, eugleno and prasinophyceae), order (Chroococcales) or subfamily (Gomphosphaerioideae) levels before further analysis. Total autotrophic biomass, chlorophyll-*a* content, water temperature and salinity, and the concentrations of total nitrogen (N_{tot}) and total phosphorus (P_{tot}) were used in our analyses as explanatory variables.

For statistical analyses, we divided the datasets into three periods: (1) before 1999, (2) 1999–2003 and (3) 2004–2008, for which the total numbers of samples were 184, 163 and 147, respectively. The data from the offshore and coastal stations in the Gulf of Bothnia were treated separately. To obtain symmetric random deviations, the biomass data of the individual taxa were square-root transformed before the statistical analysis. Temperature, salinity and nutrient concentrations were averaged over 0–10 m depth. R version 2.8.1 (R project for statistical computing) was used to conduct the Welch two sample *t*-test to detect significant differences

($p < 0.05$) in the phytoplankton and environmental data between the periods within a sub-area. In these tests, the data were compared across all seasons and for single months. Relationships between environmental variables and the whole phytoplankton community or dominant phytoplankton groups were identified by BIOENV. We computed all possible combinations for each environmental variable separately and for all possible combinations simultaneously. Spearman correlation coefficients (ρ_s) were calculated to compare the similarity matrices generated for the community and environmental data to examine the ecological significance of each measured environmental variable on the dynamics of selected groups. This analysis was conducted using PRIMER version 5 (Clarke and Warwick 2001).

Table 2. Phytoplankton taxa included in the statistical analysis. Nomenclature according to Hällfors (2004).

Taxon name	Comments
Nostocophyceae	
Chroococcales*	excl. Gomphosphaerioides
Gomphosphaerioides**	
Pseudanabaena spp.	
Planktothrix agardhii	Curonian Lagoon
Anabaena spp.	
Aphanizomenon sp.	*A. flos-aquae* in Curonian Lagoon
Nodularia spumigena	
Cryptophyceae	
Dinophyceae	
Dinophysis acuminata	
Gymnodiniales	
Heterocapsa rotundata	
Heterocapsa triquetra	
Prymnesiophyceae	
Chrysophyceae	
Diatomophyceae	
Chaetoceros wighamii	
Actinocyclus normanii	Curonian Lagoon
Cyclotella choctawhatcheeana	
Skeletonema costatum	
Skeletonema subsalsum	Curonian Lagoon
Cylindrotheca closterium	
Eutreptiella gymnastica	
Prasinophyceae	
Chlorophyceae	
Monoraphidium contortum	
Oocystis spp.	
Planctonema lauterbornii	Curonian Lagoon
Mesodinium rubrum	no data from Curonian Lagoon

* Chroococcales comprise the genera *Aphanocapsa, Aphanothece, Chroococcus, Coelosphaerium, Cyanodictyon, Lemmermanniella, Merismopedia* and *Microcystis.*

** Gomphosphaerioides comprise the genera *Coelomoron, Snowella* and *Woronichinia.*

Results

Variability and environmental trends

Seasonal temperature variations were similar in all study areas, with the minimum temperature at the beginning of June and the maximum at the end of July or beginning of August (1.4–18.9 °C in the Bothnian Bay, 1.9–20.7 °C in the Bothnian Sea, 3.3–20.8 °C in the Öre Estuary, 4.0–22.6 °C in Tallinn Bay and 6.6–25.8 °C in the Curonian Lagoon). However, some anomalies were correlated with upwelling events in coastal areas, the most pronounced occurring in August 1995 (Öre Estuary; mean surface layer temperature 6.0–7.5 °C, long-term mean ± SD 14.0 ± 3.3), July 1997 (Tallinn Bay; 7.8 °C, 16.3 ± 2.6 and Curonian Lagoon; 6.6 °C, 20.1 ± 4.2) and August 2006 (Tallinn Bay; 7.5 °C, 16.4 ± 3.0). The variation in salinity was higher, as expected, in the Curonian Lagoon where conditions alternated between nearly freshwater (minimum 0.05 psu) and brackish water (maximum 8.61 psu). The only statistically significant decreasing trend in mean salinity in the summer was observed in Tallinn Bay between 1993 and 1998, and 1999 and 2003 (from 5.89 to 5.67 psu; $p < 0.01$).

There were only small differences in the concentrations of N_{tot} between the Gulf of Bothnia (average 16.6, range 7.1–23.1 μM) and Tallinn Bay (20.5 and 6.4–39.3 μM, respectively). However, the concentrations of P_{tot} in the Gulf of Bothnia (0.24 and 0.09–0.61 μM), and especially the Bothnian Bay (0.17 and 0.09–0.47 μM), were markedly lower than those in Tallinn Bay (0.78 and 0.28–1.73 μM). The Curonian Lagoon was characterized by large variations in both variables and extremely high maximum values (average 85.5 μM, range 10.7–204.9 μM for N_{tot}; average 2.85 μM and range 0.42–9.98 μM for P_{tot}). In brackish-water conditions, when the salinity was > 5 psu, the concentration of both nutrients was markedly lower (average 53.5 μM, range 21.4–84.2 μM for N_{tot}; average 1.75 μM and range 0.42–4.20 μM for P_{tot}), but these values were still higher than corresponding average values from the other study sites by factors of 2.5 for N_{tot} and 2–10 for P_{tot}.

In Tallinn Bay, the mean concentrations of N_{tot} and P_{tot} increased between periods 1 and 3 (16.7 to 23.4 μM, $p < 0.001$, and 0.67 to 0.85 μM, $p < 0.001$, respectively). In the same area, the mean summer chlorophyll-*a* concentration increased by 50% over the entire study period (3.2 to 4.8 mg m^{-3}, $p < 0.001$) (Fig. 2).

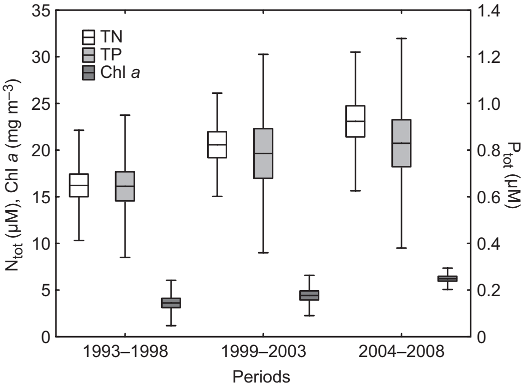

Fig. 2. Variations in the concentrations of total nitrogen (N_{tot}, μM), total phosphorus (P_{tot}, μM) and chlorophyll *a* (Chl *a*, mg m^{-3}) in Tallinn Bay between 1993 and 2008. Standard errors are shown as vertical boxes and standard deviations as vertical lines.

Seasonal phytoplankton patterns

Phytoplankton succession showed different timing patterns from north to south. In the Gulf of Bothnia, the spring bloom often lasted until the end of June and mainly consisted of diatoms and dinoflagellates (up to 3.67 mg l^{-1}). Nanoplanktonic (< 20 μm) flagellates were usually represented by crypto-, prasino- and prymnesiophytes, the last being dominant in the open Bothnian Sea. In July, phytoplankton biomass dropped to the summer values and remained low until September (median 0.11–0.25, maximum 0.30–1.86 mg l^{-1}). Cyanobacteria (mainly *Aphanizomenon* sp.) were briefly dominant, but only in July and August in the open Bothnian Sea, while small-sized flagellates and the autotrophic ciliate *Mesodinium rubrum* formed 40%–60% of the total phytoplankton biomass in all sub-areas of the Gulf of Bothnia. However, *Aphanizomenon* sp. had relatively low maximum biomass values (0.3 mg l^{-1}) in the open Bothnian Sea and was rare in samples from the Bothnian Bay. In the Öre Estuary, diatoms (mainly *Thalassiosira baltica*) were the second largest contributors to the total biomass in July and August after *M. rubrum*. The percentage of unidentified taxa in the total phytoplankton biomass remained relatively high throughout the season (5%–16% on average).

In Tallinn Bay, the total biomass in June varied from 0.05 to 2.63 mg l^{-1}. Samples with higher biomass contained mainly spring species with dinoflagellates and diatoms dominating the community. The most frequent taxa in summer were *Aphanizomenon* sp., the dinophyte *Dinophysis acuminata,* chrysophytes and prymnesiophytes. The autotrophic biomass peaked in July (median 0.88, maximum 3.54 mg l^{-1}) when cyanobacteria constituted over 50% of total biomass. However, large cyanobacterial blooms in Tallinn Bay were only recorded in 1997 and 2002. In some years (1996, 2003, 2004 and 2008) dinophytes, mainly *Heterocapsa triquetra*, briefly reached 70%–90% of the total phytoplankton biomass. The estimated proportion of nanoplanktonic flagellates (eugleno-, prymnesio- and prasinophytes in July–August, and cryptophytes in August–September) of the total biomass was on average ~20%. In September, diatoms reappeared and became the dominant component of the phytoplankton, but in most years the phytoplankton biomass decreased 2–3 fold as compared with the maximum summer values.

Phytoplankton dynamics in the Curonian Lagoon differed substantially from the other study areas. Cyanobacteria, diatoms and chlorophytes already dominated in June and the total median biomass was 4.93 mg l^{-1} (maximum 18.4 mg l^{-1}). In eutrophic water bodies, phytoplankton biomass typically increases towards late summer and remains high until the end of the season. The calculated median biomass for July–September ranged from 11.39 to 18.11 mg l^{-1} and the

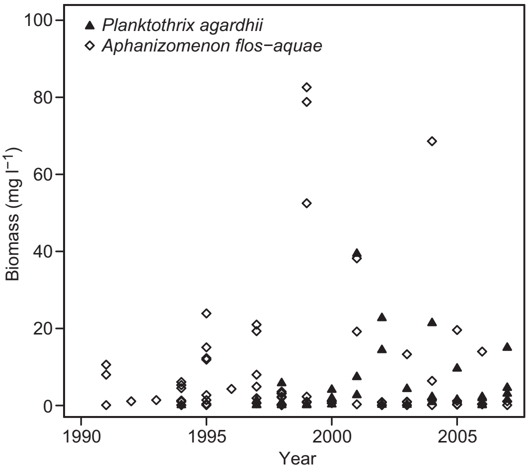

Fig. 3. Wet weight biomass (mg l^{-1}) of the filamentous cyanobacteria *Aphanizomenon flos-aquae* and *Planktothrix agardhii* in the Curonian Lagoon between 1991 and 2007.

maximum values from 98.74 to 152.63 mg l^{-1} (in July–September 1999 and August 2001). Only one extremely high value (90.5 mg l^{-1}) was recorded between 2004 and 2007. Both the nutrient concentrations and the total phytoplankton biomass were markedly lower when brackish-water conditions prevailed (salinity > 5 psu), ranging from 0.54 to 13.5 mg l^{-1}, with a median of 3.0 mg l^{-1}. However, salinity variation did not change the relationships between the dominant algal groups.

Among the cyanobacteria, *Aphanizomenon flos-aquae*, *Planktothrix agardhii*, *Anabaena* spp., gomphosphaerioids and chroococcalean species constituted most of the biomass. *Aphanizomenon flos-aquae* was replaced by *P. agardhii* as the dominant cyanobacterium in the 2000s (Fig. 3). *Actinocyclus normanii* was the dominant diatom species, constituting > 20% (maximum 65%) of the total phytoplankton biomass in freshwater conditions. In addition, *Skeletonema costatum* made a major contribution (mean 6.6%, maximum 44%) to the total biomass in June. Under brackish-water conditions, the dinoflagellate *Heterocapsa triquetra* constituted up to 65% (11% in average) of the total phytoplankton biomass in July and August. In some cases the chlorophytes *Pediastrum boryanum* var. *boryanum, P. duplex* var. *duplex* and *Oocystis lacustris* (10%–52%) contributed significantly to the summer phytoplankton. The most abundant green algal species, *Planctonema lauterbornii,* whose abundance was constant during the summer, did not make a major contribution to the total biomass (2% on average, maximum 13%).

Changes in the biomass of the dominant phytoplankton taxa

We observed a significant increase in the average total summer autotrophic biomass in the Bothnian Bay (0.11 to 0.34 mg l^{-1}; $p < 0.01$) and Tallinn Bay (0.58 to 0.87 mg l^{-1}, $p < 0.05$) between the periods 1994–1998 and 1999–2003. The rise in total biomass in Tallinn Bay was most prominent in June (0.25 to 0.98 mg l^{-1}, $p < 0.001$). Different phytoplankton groups comprised the autotrophic component of the phytoplankton biomass. Most of the statistically significant changes over the study period were related to increases in the mean seasonal or monthly biomass values at different taxonomic levels. In this section, we mainly focus on the dynamics of the cyanobacteria.

Cyanobacteria were the dominant group in the Curonian Lagoon (all seasons, up to 87% of the total phytoplankton biomass) and Tallinn Bay (July to September, up to 74%). In the Bothnian Sea, cyanobacteria also contributed 36%–57% at their peak, which occurred from July to September, but they usually only constituted ~20% of the total biomass. Increases in cyanobacterial biomass were observed in the Gulfs of Bothnia and Finland between periods 1 and 2. In addition, in the coastal Bothnian Sea, statistically significant increases were observed between periods 2 and 3. An increase in the cyanobacterial biomass in June was common in both the open and coastal sites in the Bothnian Sea and Tallinn Bay (Fig. 4). The main cyanobacterial species responsible for these biomass changes was *Aphanizomenon* sp. (maximum biomass in the Bothnian Sea and Tallinn Bay, 0.3 and 1.5–2.0 mg l^{-1}, respectively). The changes between July and September were insignificant in all sub-areas. Small biomass increases of the oscillatorean cyanobacteria *Pseudanabaena* sp. and the diazotrophic genus *Anabaena* were observed in the Gulf of Finland.

The autotrophic ciliate *Mesodinium rubrum* showed a steady increase in June in Tallinn Bay, and August in the Gulf of Bothnia between periods 1 and 2. Similarly to the changes observed in Tallinn Bay, the biomass of *M. rubrum* continued to increase in the Bothnian Sea throughout the season between periods 2 and 3. A decrease in cryptophycean biomass was first observed in Tallinn Bay (from period 1 to 2) and the Gulf of Bothnia thereafter (from period 2 to 3). All other biomass changes of the selected taxa were basin-specific (*see* Tables 3 and 4).

Relationships between phytoplankton and environmental factors

The BIOENV analysis showed that water temperature had the strongest impact on the summer phytoplankton community structure, in combination with either salinity (Tallinn Bay and the Curonian Lagoon) or nutrients (the Gulf of Bothnia) (Table 5). A similar pattern, but with weaker significance, was detected for cyanobacteria in the Bothnian Bay and Öre Estuary. The biomass of diatoms had stronger relationships with temperature and N_{tot} in Tallinn Bay and the Gulf of Bothnia, but salinity largely explained the variation in the Curonian Lagoon. Small flagellates were abundant in the summer phytoplankton in both the Gulf of Bothnia and Tallinn Bay, showing the best match with temperature in both areas, but with P_{tot} in the Gulf of Bothnia and N_{tot} in Tallinn Bay. The biomass of dinoflagellates had no clear correlation with any of the measured environmental variables.

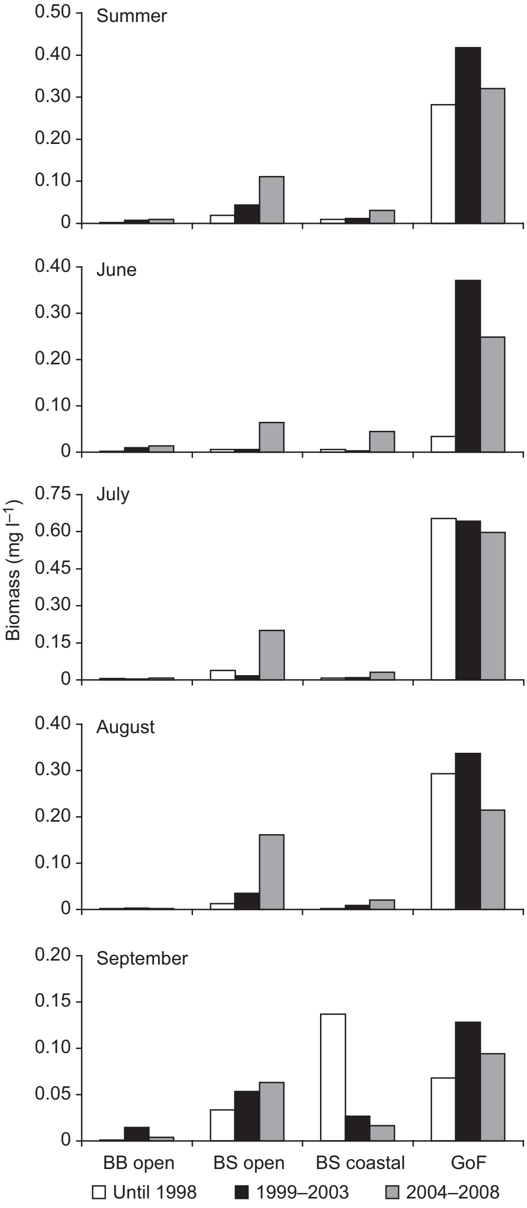

Fig. 4. Seasonal and monthly mean cyanobacterial biomass values (mg l^{-1}) in different sub-areas (BB = Bothnian Bay, BS = Bothnian Sea, GoF = Gulf of Finland) during the study period. Note the different scales.

Discussion

Previous case studies have resulted in the rough geographic subdivision of the Baltic Sea into the southern and eastern coastal waters, and the northern and western waters. Southern and eastern Baltic coastal waters are characterized by more extensive eutrophication, higher chlorophyll-*a* concentrations and (in extreme cases) all-season dominance of cyanobacteria and green algae. In contrast, northern and western Baltic waters have distinct seasonal successions: diatoms–green algae/cyanobacteria–diatoms and summer dominance of dinoflagellates or N-fixing cyanobacteria (Schiewer 2008). Our study sites covered the range of these environmental conditions, from heavy eutrophication in the Curonian Lagoon to (largely) oligotrophy in the Gulf of Bothnia. As compared with the Gulf of Bothnia, Tallinn Bay

Table 3. Significant increasing trends for selected phytoplankton and environmental variables, analyzed using the Welch two-sample *t*-test ($p < 0.05$). Division of periods: 1 = before 1999, 2 = 1999–2003, 3 = 2004–2008. Roman numerals indicate the months with significant changes, "+" and Roman numerals indicate that changes are valid both for all seasons and the marked month.

Bothnian Bay	Bothnian Sea (open)	Bothnian Sea (coast)	Gulf of Finland	Curonian Lagoon
Increase between periods 1 and 2				
Nostocophyceae	Nostocophyceae	Chroococcales, VIII	Nostocophyceae, VI	Chroococcales
Gomphosphaerioides, IX	Chroococcales, VII	Dinophyceae	*Pseudanabaena*, +VI &VIII	Gomphosphaerioides
Prymnesiophyceae	Dinophyceae, IX	*D. acuminata*, +VIII	*Anabaena*, +VIII	*P. agardhii*, +IX
Prasinophyceae	*M. rubrum*, VIII	Chrysophyceae	*Aphanizomenon*, VI	
M. rubrum, VIII		*C. closterium*	*C. closterium*, VIII, IX	
Total biomass			*M. contortum*, +VI & VIII	
			P. lauterbornii, VIII	
			Total biomass, VI	
			Total nitrogen, +VIII & IX	
			Total phosphorus, +VI	
Increase between periods 2 and 3				
	Nostocophyceae, VI	Nostocophyceae, +VI	*Pseudanabaena*, VII	Cryptophyceae, VII
	Gomphosphaerioides	Chroococcales, +VI	*C. choctawhatcheeana*, +IX	
	Aphanizomenon, +VI	Gomphosphaerioides	*C. closterium*, VII	
	M. rubrum	*Aphanizomenon*, +VI	*M. contortum*, VII	
		Diatomophyceae, IX	*M. rubrum*, VII & VIII	
		Oocystis, VI	Total nitrogen, VI	
		M. rubrum, +VI	Chlorophyll *a*, VII	
Steady increase from period 1 to period 3				
			M. rubrum, VI	
			Chlorophyll *a*	

Table 4. Significant fluctuations and decreasing trends for selected phytoplankton and environmental variables, analyzed using the Welch two-sample *t*-test ($p < 0.05$). Division of periods: 1 = before 1999, 2 = 1999–2003, 3 = 2004–2008. Roman numerals indicate the month with significant changes, "+" and Roman numerals identify that changes are valid for all seasons and the marked month.

Bothnian Bay	Bothnian Sea (open)	Bothnian Sea (coast)	Gulf of Finland	Curonian Lagoon
Higher values during period 2				
Diatomophyceae Total biomass, IX		Total nitrogen, VI	Chroococcales, +VI Cryptophyceae Gymnodiniales Prasinophyceae P. lauterbornii, VIII	Prymnesiophyceae Chrysophyceae
Decrease between periods 1 and 2				
Cryptophyceae, +VIII	Cryptophyceae Gymnodiniales		Gomphosphaerioides, IX *C. wighamii*, +VI Salinity	
Decrease between periods 2 and 3				
			Gomphosphaerioides *D. acuminata*, VI Diatomophyceae, VI Chlorophyceae, VII–IX	

in the southern Gulf of Finland may be regarded as a transitional water body between these two extremes, showing either dominance of N-fixing cyanobacteria or dinoflagellates, mainly *Heterocapsa triquetra*, but considerably higher phytoplankton biomass during the summer period.

Changes in phytoplankton — Bothnian Bay

We observed increases in total phytoplankton biomass between 1994–1998 and 1999–2003 in the Bothnian Bay (0.11 to 0.29 mg l^{-1}). High phytoplankton biomass is a common indicator of eutrophication and increased phytoplankton biomass may correspond to an increase in available nutrients. However, we did not detect any significant changes in N_{tot} and P_{tot} contents in the Bothnian Bay over the study period. Slight increases in N_{tot} and P_{tot} were observed at this site in the 1970s, but they subsequently stabilized and have decreased since that time (HELCOM 2009). In addition, the chlorophyll-*a* concentrations have remained at a roughly constant level (1.7–1.8 μg l^{-1}) during the past 30 years (Fleming-Lehtinen *et al*. 2008). Hence, the increases in total phytoplankton biomass are difficult to explain. There was no shift in monitoring activities between these two periods, thus the potential error of unbalanced weighting for a certain month within the season can be excluded. We conclude that the phytoplankton biomass was very low level during the whole summer period.

Open Bothnian Sea

The statistical analysis revealed an increase in cyanobacterial biomass between 1994–1998 and 1999–2003. The cyanobacteria responsible included the filamentous species *Aphanizomenon* sp. in June. Similarly to the observed changes in the Bothnian Bay, the biomass of *M. rubrum* first increased in August and the species became abundant over the whole season in later years.

Our data demonstrated that the spring bloom often lasted until the end of June. Andersson *et al*. (1996) observed a *M. rubrum* peak in the Bothnian Sea after the spring bloom, thus the increasing biomass of this species together with *Aphanizomenon* sp. in June may have resulted from an earlier decline of spring communities and replacement by summer species during the last decade. In contrast, in a study of the Gulf of Finland, the ciliate *M. rubrum* showed a strong positive correlation with salinity and a negative correlation with temperature (Rantajärvi *et al.* 1998).

As in the Bothnian Bay, we did not detect any trends in N_{tot} and P_{tot} contents, but observed significant changes in the total phytoplankton biomass over the study period in the open Bothnian Sea. For comparison, the summer concentrations of chlorophyll *a* had increased until the end of the 1990s and declined thereafter (Fleming-Lehtinen *et al.* 2008, HELCOM 2009). Observations from the beginning of the 1990s indicate that the total biomass (wet weight) was ca. two times lower in the Bothnian Bay than in the Bothnian Sea during the summer period (June–September) (Andersson *et al.* 1996). Our data generally confirm these observations, despite the increasing trend in the Bothnian Bay at the beginning of the 2000s, which has *inter alia* reduced the difference in biomass bewteen the two areas in July.

Coastal Bothnian Sea — Öre Estuary

The concentrations of N_{tot} have followed the same trends in the coastal zone of the Bothnian Sea as in the open sea, with an increase during the 1970s and a decline thereafter. Both the increase and decline in P_{tot} were larger in the coastal zone, magnifying the overall pattern in

Table 5. The results of BIOENV analyses. The best combination of environmental variables and the strength of their relationships with the biomass of the total phytoplankton community and selected groups in different sub-areas of the Baltic Sea using Spearman's rank correlation (ρ_s). *n* = number of observations.

	Best combination of variables				ρ_s	*n*
All phytoplankton						
Bothnian Bay	T °C	N_{tot}			0.278	73
Bothnian Sea	T °C	P_{tot}			0.32	66
Öre Estuary	T °C	P_{tot}			0.232	81
Tallinn Bay	T °C	Sal			0.247	138
Curonian Lagoon	Sal	T °C			0.565	72
Cyanobacteria						
Bothnian Bay	Sal	T °C			0.072	73
Bothnian Sea	T °C	P_{tot}			0.286	66
Öre Estuary	T °C				0.075	81
Tallinn Bay	T °C	Sal			0.246	138
Curonian Lagoon	T °C	P_{tot}	N_{tot}	Sal	0.462	72
Dinoflagellates						
Bothnian Bay	T °C				0.055	73
Bothnian Sea	T °C				0.158	66
Öre Estuary	N_{tot}	T °C			0.039	81
Tallinn Bay	Sal	T °C			0.116	138
Curonian Lagoon	Sal	T °C			0.051	72
Diatoms						
Bothnian Bay	N_{tot}				0.173	73
Bothnian Sea	T °C	N_{tot}			0.079	66
Öre Estuary	T °C	N_{tot}			0.202	81
Tallinn Bay	N_{tot}	T °C			0.115	138
Curonian Lagoon	Sal				0.466	72
Small flagellates (crypto-, prymnesio-, chryso-, eugleno- and prasinophytes						
Bothnian Bay	T °C	P_{tot}			0.198	73
Bothnian Sea	P_{tot}	T °C			0.186	66
Öre Estuary	P_{tot}	T °C			0.193	81
Tallinn Bay	T °C	N_{tot}			0.171	138
Curonian Lagoon	Sal	P_{tot}			0.361	72

this region (HELCOM 2009). The N_{tot} values we obtained were similar across the entire Gulf of Bothnia. However, the P_{tot} concentrations were markedly higher in both the coastal and open parts of the Bothnian Sea as compared with those in the Bothnian Bay, marking a switch from P limitation to N limitation. In contrast, the concentration of dissolved inorganic phosphorus (DIP) was markedly lower in the coastal zone of the Bothnian Sea than in open waters, and bioassays have shown that this area is still P-limited. Such conditions do not favour the dominance of N-fixing cyanobacteria (Andersson *et al*. 1996).

The changes in the phytoplankton community varied significantly in the coastal waters, as compared with those in the open waters. We also observed an earlier appearance of cyanobacteria, especially *Aphanizomenon* sp., in both areas after the spring bloom. However, the overall increase in cyanobacterial biomass occurred later in the coastal waters (between 1999–2003 and 2004–2008) than in the open Bothnian Sea. A common feature in this region was the increased biomass of *M. rubrum* and gomphosphaerioids during the last period. Increases in the biomass of the dinophyte *Dinophysis acuminata*, chrysophytes and the diatom *Cylindrotheca closterium* were observed from 1994 to 1998 and from 1999 to 2003, and for Chroococcales between 2004 and 2008; these features were typical of coastal waters. Chrysophytes also increased in summer phytoplankton communities in the northern Baltic Proper and the Gulf of Finland (Suikkanen *et al*. 2007). According to mesocosm experiments described by Kangro *et al*. (2007), some species of chroococcales (*Cyanodictyon* sp.) and chrysophytes (mainly *Pseudopedinella* spp.) are favoured by N addition, while *D. acuminata* and *C. closterium* respond positively to P enrichment. The positive biomass response of *C. closterium* to an increase in P has also been demonstrated in natural communities in the Gulf of Finland (Jaanus *et al*. 2009). The latter species does not yet dominate in the coastal phytoplankton of the Bothnian Sea, but its presence is a sign of a changing environment. *Cylindrotheca closterium* has been proposed as an indicator of eutrophication in the northern Baltic Sea (Jaanus *et al*. 2009). The coastal waters of the Bothnian Sea had relatively stable nutrient conditions in recent decades. Analyses of a large set of data obtained from different parts of the Baltic Sea indicated that phytoplankton composition changes with variations in nutrient levels, but the composition does not shift abruptly, and only small changes in the phytoplankton community occur in response to moderate increases in nutrient levels (Carstensen and Heiskanen 2007).

The Gulf of Finland — Tallinn Bay

The Gulf of Finland is regarded as one of the areas most affected by eutrophication in the Baltic Sea, with a nutrient load per unit of water area 2–3 times higher than the average (Pitkänen *et al*. 2001). Consequently, the higher cell abundancies of phytoplankton as compared with those in the Gulf of Bothnia are likely to be due to eutrophication. However, the growing season is also longer in the Gulf of Finland, which may also contribute to this pattern. As compared with the other study sites, the changes in both environmental variables and phytoplankton have been more dynamic at this site and have included both upward and downward trends.

Previous studies have shown that trends in concentrations of N_{tot} and P_{tot} differed in recent decades, but overall they have been increasing since the 1990s (HELCOM 2009). We found the same trends for both nutrients in the southern Gulf of Finland, but while significant increases of both nutrients occurred at the start of the 2000s, they only continued for N_{tot} in June. In addition, the summer chlorophyll-*a* concentrations have been continuously increasing in Tallinn Bay (by ~50% since 1993), which is consistent with the results of Fleming-Lehtinen *et al*. (2008), who found an increase of more than 150% in the surface chlorophyll-*a* concentrations in the open parts of the Gulf of Finland from the 1970s to the present. Nevertheless, the total phytoplankton biomass in Tallinn Bay increased significantly only in June between 1994–1998 and 1999–2003, accompanied by an increase in cyanobacterial biomass, especially *Aphanizomenon* sp.

Finni *et al*. (2001a) showed that cyanobacterial blooms have been common in the Gulf of Finland for many years, but Gasiūnaitė *et* *al*. (2005) suggested that cyanobacterial blooms are highly variable, due to their inhomogeneous distributions in time and space, which hinders the identification of steady trends. Accordingly, the only trends we found in this respect were that the dominance of cyanobacteria changed, and they became more abundant earlier in the year, although we sampled as frequently as every second to third week and hence expected to detect almost all bloom events. The lack of clear trends may be due to the effects of temperature, which has been shown to be one of the most important contributors to variations in cyanoprokaryote assemblages in various parts of the Baltic Sea (Laamanen 1997, Pliński *et al*. 2007). Notably, high water temperature has often been suggested as a prerequisite for intensive bloom development, for example, the optimal temperature for *A. flos-aquae* ranges from 16 to 22 °C (e.g. Pliński *et al*. 2007). However, in 2002, a cyanobacterial bloom in the southern Gulf of Finland had already peaked by the end of June at a surface water temperature of 14–16 °C (Jaanus and Pellikka 2003). The earlier appearance of cyanobacteria and the decline of the cold-water diatom *Chaetoceros wighamii* in summer phytoplankton may represent an earlier succession towards summer communities as a result of the rise in surface water temperature. Increased temperature can even have a greater stimulatory effect on phytoplankton than excess nutrients. For instance, long-term phytoplankton studies in the discharge area of power plant effluents have shown a decrease in the biomass of *C. wighamii* caused by the rise in water temperature (Ilus and Keskitalo 2008). The preference of *C. wighamii* for more saline and cold-water conditions has also been found in a previous study in the Gulf of Finland (Rantajärvi 1998). Although our results do not show any significant increase in surface water temperature, it is possible that only a very small change may have occurred and further changes may cause major shifts in the dominant phytoplankton species.

Our statistical analysis revealed that some other filamentous cyanobacteria (*Anabaena* spp. and *Pseudanabaena* sp.) have become more abundant in Tallinn Bay since the late 1990s. These changes correlated with the decrease in surface water salinity. Suikkanen *et al*. (2007) also observed a decrease in summer salinity accompanied by an increase in cyanobacterial biomass in the Gulf of Finland, and an analysis of extensive phytoplankton datasets from the same area confirmed that oscillatorean biomass is negatively correlated with salinity, but positively correlated with temperature and P_{tot} (Jaanus *et al*. 2009). In recent decades, the biomass of Oscillatoriales also increased in the eastern part of the Gulf of Finland (Nikulina 2003). P_{tot} concentrations had been low in the 1970s, increased to much higher levels in the 1980s, then declined but have subsequently further increased since 1990 (HELCOM 2009).

The Curonian Lagoon

Finni *et al*. (2001b) identified the intensive growth of phytoplankton communities during the entire vegetation period and very high late summer total wet weight biomass (> 10 mg l^{-1}) as indicators of hypereutrophic conditions. The total phytoplankton biomass estimated in the Curonian Lagoon exceeded 100 mg l^{-1} in July and August in 1999 and 2001. As only one extremely high value (90.5 mg l^{-1}) was recorded during 2004–2007, we did not observe any clear trends in total biomass in this area. However, *Planktothrix agardhii* appeared to competitively exclude *Aphanizomenon flos-aquae* from dominating filamentous cyanobacterium in this region.

Johansson and Wallström (2001) considered *P. agardhii* to be indicative of nutrient-rich conditions and Carstensen and Heiskanen (2007) proposed it to be the only species that characterizes eutrophic conditions in the northern part of the Baltic Sea, since it responds positively to increased N_{tot} levels. This species was surveyed during summer throughout the 20th century, when temperature conditions were stable until the 1990s in the coastal waters surrounding the cities of Stockholm and Helsinki (Johansson and Wallström 2001, Finni *et al*. 2001b). These authors attributed the decrease in total biomass and change in phytoplankton dominance from *P. agardhii* to a more species-rich community to an effective reduction in nutrient load. Despite the water quality improvement in some Lithuanian rivers, the Nemunas (the main river discharging into the Curonian Lagoon) is still affected by municipal and industrial wastewater from Russia and accounts for half of the total nutrient loading (Cetkauskaite *et al*. 2001).

In the Curonian Lagoon, the concentrations of inorganic nutrients are too high to limit total plankton biomass, which is mostly controlled by the ambient physical factors (Pilkaytitė and Razinkovas 2007). For example, high rates of freshwater discharge reduce both salinity and residence time. These conditions generally favour fast-growing phytoplankton, such as chlorophytes (green algae) and various flagellates, members of which have been shown to grow optimally under low salinity conditions (Pinckney *et al*. 1999). In locations with highly turbulent mixing, freshwater diatoms may start to dominate summer phytoplankton communities rather than cyanobacteria (Rehbehn *et al*. 1993, Pilkaitytė 2007). However, cyanobacteria and diatoms formed a large overall component of the total phytoplankton biomass in the Curonian Lagoon and chlorophytes were only the third largest contributors. Although small flagellates were abundant, their relative importance in terms of total biomass remained low throughout the season.

Salinity best explained the variation in phytoplankton biomass, especially that of diatoms. A gradual increase in salinity, due to mixing of river plumes with sea water, has been associated with reductions in nutrient concentration and phytoplankton biomass. Dilution of the high biomass of riverine phytoplankton, however, does not result in a steady decrease in all components, but in the successive disappearance of different freshwater species (Wasmund *et al*. 1999). In the Curonian Lagoon, cyanobacteria, diatoms and chlorophytes were still the dominant groups when brackish-water conditions prevailed, but the median total biomass was ca. 5-fold lower in comparison to the entire dataset of the same area. As the phytoplankton biomass, the mean concentrations of N_{tot} and P_{tot} also decreased by a factor of 1.6 when surface water salinity was > 5 psu.

Phytoplankton species composition as an indicator of eutrophication

Classification of eutrophic water conditions on the basis of phytoplankton composition is ambiguous. The likely long-term effects of increasing nutrient concentrations (eutrophication) on phytoplankton stocks could not be definitively determined, because of the overriding effect of hydrographic changes. Finni *et al*. (2001b) characterized moderately eutrophic coastal water bodies by the presence of only modest amounts of cyanobacteria and gomphosphaerioids rather than oscillatorialean species. These authors also found that small flagellates (crypto-, prymnesio-, chryso-, prasinophytes and the euglenoid *Eutreptiella* spp.) dominated coastal water bodies and that summer algal blooms are unusual where there is moderate eutrophication. Such a community structure is more characteristic of the Gulf of Bothnia, which is considered to be non-eutrophic unlike the other surveyed regions. The increased abundance of planktonic diatoms in the coastal waters of the Gulf of Finland, especially some fragile diatom (e.g. small centrales, *Skeletonema* spp., and *Chaetoceros minimus*) have also been attributed to increased eutrophication and turbidity (Finni *et al*. 2001b, Weckström *et al*. 2007). Some small diatoms (e.g. *Cylindrotheca closterium* and *Cyclotella choctawhatcheeana*) have become more common in the Gulf of Finland and already appear in the phytoplankton of the Bothnian Sea. Thus, the hypothesis that nutrient-rich conditions promote the growth of relatively large planktonic species (e.g. Thingstad and Sakshaug 1990) might not be valid for much of the Baltic Sea. A mesocosm experiment, in which seawater from the northern Baltic Sea was used, has revealed that relatively small phytoplankton species appear to be favoured by nutrient loading and the average cell-size does not increase with nutrient enrichment (Andersson *et al*. 2006). However, Niemi (1975) reported that small flagellates had considerably contributed to the primary production in the Gulf of Finland since the 1960s, when eutrophication processes were not yet occurring, at least in offshore waters.

Overall changes in the phytoplankton communities

Significant differences were found in phytoplankton biomass from class to species level in all basins during the study period. Tallinn Bay was the most dynamic according to observed changes in both environmental factors and phytoplankton. Observations at Tallinn Bay have been made with similar intensity throughout almost all of the study period, while the frequency of sampling has decreased in the open Gulf of Bothnia and Curonian Lagoon. The differences in mean biomass of the dominant taxa between periods should be interpreted with caution, as the data sets were less homogeneous for the Gulf of Bothnia and the total number of sampling intervals was relatively low in the Gulf of Bothnia and Curonian Lagoon. This probably explains the high interannual variation and fewer significant changes (trends) observed over the study period in these regions than in the Gulf of Finland. Our results highlight the importance of regular, frequent phytoplankton monitoring in order to reliably detect ecosystem shifts, especially over short-term spatio-temporal scales, which is essential for detecting natural variations.

Changes in phytoplankton biomass and species composition reflect not only the effects of eutrophication but also climatic change. Seasonal temperature variation may markedly influence the performance and succession of phytoplankton over the year (Andersson *et al*. 1994). Temperature was the key physical factor shaping the phytoplankton communities, especially the total wet weight biomass and the biomass of cyanobacteria in all of the sub-areas we studied. Both experimental results and models indicate that cyanobacteria respond more strongly to climate change than diatoms or green algae (De Senerpont Domis *et al*. 2007, Moore *et al*. 2008). We did not detect any significant differences in seasonal or monthly water temperature over the study period. However, a positive summer sea-surface temperature trend was found across the entire Baltic Sea, particularly in the north, with a maximum > 0.3 K y^{-1} in the Bothnian Sea (Siege *et al*. 2006). The cited authors reported that the number of warm summers has increased in recent decades, particularly in the northern Baltic. Since cyanobacteria, especially the dominant species in the Baltic Sea (*Aphanizomenon* sp.), form large blooms only when the surface water temperature exceeds 16 °C (Pliński *et al*. 2007), any rise in the sea surface layer temperature may influence the northernmost area, particularly the Gulf of Bothnia, most strongly. We found that cyanobacterial biomass increased over time in this region, but the biomass values of *Aphanizomenon* were still far from strong blooms (maximum 0.3 mg ww l^{-1} compared with 1.5–2.0 mg ww l^{-1} in the Gulf of Finland). Biomass of the potentially toxic cyanobacterium *Nodularia spumigena*, which favours water temperatures > 20 °C (Lehtimäki *et al*. 1997), did not show any clear trends in our study. Although phytoplankton biomass and species composition are influenced by different mechanisms, the impact of climate change may be overwhelming in the future and induce changes at higher trophic levels.

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