

# Long term changes in the Baltic Sea phytoplankton community

Kalle Olli<sup>1)\*</sup>, Riina Klais<sup>1)</sup>, Timo Tamminen<sup>2)</sup>, Robert Ptacnik<sup>3)</sup> and Tom Andersen<sup>4)</sup>

<sup>1)</sup> Institute of Ecology and Earth Sciences, University of Tartu, Lai 40, EE-51005 Tartu, Estonia  
(\*Corresponding author's e-mail: kalle.oli@ut.ee)

<sup>2)</sup> Marine Research Centre, Finnish Environment Institute, P.O. Box 140, FI-00251 Helsinki, Finland

<sup>3)</sup> ICBM, University of Oldenburg, Schleusenstrasse 1, DE-26382 Wilhelmshaven, Germany

<sup>4)</sup> Department of Biology, University of Oslo, P.O. Box 1066, Blindern, N-0316 Oslo, Norway

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During the last four decades the Baltic Sea phytoplankton went through a significant and gradual change in community composition. An analysis of several thousand quantitative samples from 1966 to 2008 reveals significant changes in the phytoplankton summer community in most parts of the Baltic Sea. By using community gradient analysis methods (NMDS, DCA), we found a strong correspondence between sample ordination scores and sampling year ( $R^2 > 0.5$ ). The association was stronger when the samples were geographically more confined and the temporal range sufficiently large ( $R^2 > 0.8$ ). Only in the southern Baltic Sea and the Kattegat had the salinity gradient stronger associations with the phytoplankton community composition as compared with the time effect over four decades. Eutrophication-related parameters (total and mineral nutrients) revealed low association with the phytoplankton community composition in all Baltic Sea sub-basins ( $R^2 < 0.2$ ). Also, known eutrophication gradients in the Baltic Sea had low association with phytoplankton community. The phytoplankton community in the Baltic Sea is not in a steady state or equilibrium, and is not the same today as it was decades ago.

## Introduction

The Baltic Sea is a shallow semi-enclosed estuarine brackish water body ( $422 \times 10^3 \text{ km}^2$ ), endangered by large nutrient inputs from the more than four times larger (ca. 2 million  $\text{km}^2$ ) and highly populated (ca. 80 million people) drainage area (Elmgren and Larsson 2001). The Baltic Sea reveals relatively stable north–south and east–west gradients of salinity, nutrient availability and nutrient limitation patterns (Tamminen and Andersen 2007). Its northern basins (the Gulf of

Bothnia) have low salinity and remain relatively pristine, while southern basins suffer from consequences of eutrophication. The Gulf of Finland is one of the most eutrophicated estuarine areas worldwide, directly connected to the Baltic Proper at its western end and under the influence of the river Neva at the eastern end.

Changes in the phytoplankton community may reflect major structural and functional shifts in the ecosystem. Previous data analyses detected significant long-term trends in the phytoplankton community structure (Wasmund and Uhlig 2003,

Suikkanen *et al.* 2007). Changes in the phytoplankton community composition have taken place both at species (Hajdu *et al.* 2000) and functional group level (Wasmund *et al.* 1998).

The Baltic Sea has a long history of eutrophication, with clear signs from the late 19th century (Finni *et al.* 2001). In the 1970s and 1980s, the increasing loadings of nitrogen and phosphorus to the Baltic Sea led to accelerated eutrophication and increased phytoplankton biomass (Elmgren 2001, Kuparinen and Tuominen 2001). Ongoing eutrophication and changing nutrient ratios seemed to have led to silicate limitations in some Baltic Sea basins in the mid-1990s (Olli *et al.* 2008). Decreasing trends in primary production in the Kattegat and Belt Sea region after 1980 (Rydberg *et al.* 2006) and a slower increase in nutrient levels during the last decades, as compared with the 1970s–1990s (Papush and Danielsson 2006), are signs of ecosystem recovery, possibly in response to reduced point sources and agricultural pollution. On the other hand, enhanced internal sources may counteract efforts to reduce external nutrient loading (Pitkänen *et al.* 2001, Conley *et al.* 2002). Eutrophication may lead to self-sustaining, feedback loops, with N-fixing cyanobacterial blooms being part of a “vicious circle”, and a tight coupling between the internal nutrient cycling and the phytoplankton community composition (Kangro *et al.* 2007, Tamminen and Andersen 2007, Vahtera *et al.* 2007).

The aim of the present paper was to study a large set of summer phytoplankton samples with coherent community analysis methods. For the first time, several thousand quantitative phytoplankton samples from all over the Baltic Sea could be analyzed simultaneously. As the data spans over four decades, we were interested in potential shifts in the community composition and if these shifts have visible relation to known eutrophication patterns in the Baltic Sea (e.g. Elmgren 2001, Finni *et al.* 2001).

## Methods

### Origins of the data

The spatial and temporal distributions of phy-

toplankton, as well as hydrochemical and nutrient data were obtained from monitoring datasets provided by various national environmental monitoring agencies around the Baltic Sea (*see* Acknowledgements). Hydrochemical data were supplemented by matching the phytoplankton samples with corresponding entries extracted from the Baltic Environmental Dataset (Sokolev *et al.* 1997). The original data tables from national agencies were structurally unified. The naming of taxa was carefully harmonized between different sources, particularly for changes in nomenclature, differences in taxonomic practices, and taxon names were checked against synonyms. The taxonomy and nomenclature follows Hällfors (2004).

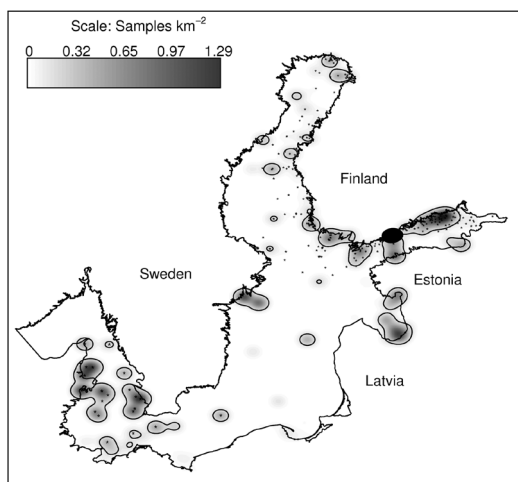
The historic phytoplankton data were counted from Lugol fixed samples under an inverted microscope after settling for 24h as suggested by Edler (1979). In the late 1960s and early 1970s Keefe preservation was used by the City of Helsinki Environment Centre (Finni *et al.* 2001). Older samples (1975–1992) provided by the Institute of Aquatic Sciences, University of Latvia, were formalin fixed and counted using a settling method. No semi-quantitative or plankton net samples were included in our data set. Phytoplankton sampling involved pooling discrete surface samples from pre-defined depths, or taking an integrated sample with a sampling hose. Species-specific cell volumes were used to calculate the total phytoplankton biovolume (Edler 1979) from the surface samples. The species-specific biovolumes and size classes were matched and compared with the suggestions of the HELCOM Phytoplankton Expert Group (Olenina *et al.* 2006), but the changes in the analysis results were minor and are not presented here.

### Data structure

In the Baltic Sea, transition from the spring bloom to summer stage corresponds to a major change in the phytoplankton composition and biomass. In order to avoid the effect of this known change, our analysis focused on the summer community only. The switch to phytoplankton summer community changes with

latitude in the Baltic Sea. To account for the latitudinal gradient, we gradually constrained the data selection from 1 May in the Sound and Belt Sea to 4 July in the Gulf of Bothnian in the north, and up to the end of September at all latitudes. Within this period, we extracted data for 7272 surface samples from the unified dataset, including 1122 taxonomic units (819 identified to species level, 31 to below species, 228 to genus and 44 to higher rank level). Taxonomically most diverse groups were diatoms and chlorophytes (285 taxa both), followed by dinoflagellates (179 taxa) and cyanobacteria (160 taxa). The geographic distribution of the samples is uneven (Fig. 1), with strong clusters in intensively sampled areas around the cities of Helsinki and Stockholm, the Danish straits, Gulf of Riga and the Gulf of Finland. The temporal range of the data is from 1966 to 2008, with increased sampling frequency since the late 1980s (Fig. 2).

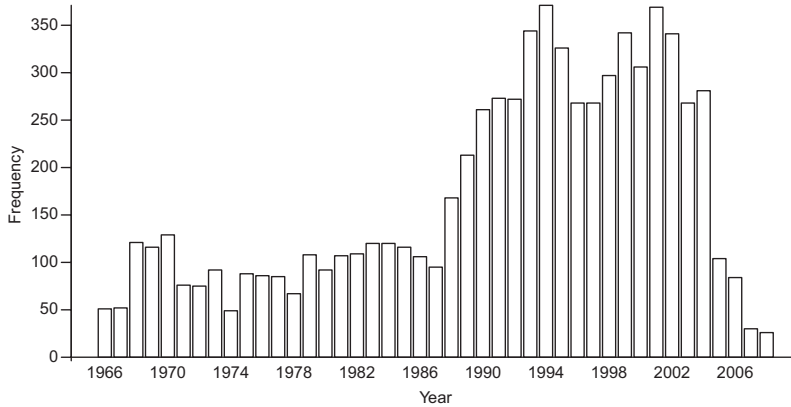
The phytoplankton community data matrix was split by data providers. Although ecologically arbitrary, this ensures maximum methodological homogeneity within a data subset and minimizes potential human factors and variability due to taxonomic practices, which we are unable to control *a posteriori*. The amount of data varies between providers and we chose three well represented data subsets with large temporal range as case studies: the City of Helsinki Environment Centre, the Danish National Environmental Research Institute (NERI) and the Finnish Environment Institute (SYKE). Helsinki data comprise 2220 samples from 1968 to 2008. The data are geographically constrained, with a maximum latitudinal and longitudinal range of 20 and 30 km, respectively, minimizing spatial salinity and eutrophication gradients. The majority of the Helsinki samples were counted by only four persons, and we have interviewed the personnel to assure that there were no major changes in the methodology. The NERI data subset comprises 1574 samples from 1979 to 2004, is geographically constrained (Fig. 1), but encompasses a strong salinity gradient (7 to 32 psu) through the Danish straits. The SYKE data subset has 1383 samples from 1966 to 2005, has a large geographic span from the eastern Gulf of Finland to the northern part of the Gulf of Bothnian (Fig. 1). This geographic span involves sub-



**Fig. 1.** Kernel density estimate of the frequency of summer phytoplankton samples in the Baltic Sea used in this study. Note that samples are spatially not homogeneously distributed. Regions of high sampling frequency are in the Sound, the Belt Sea, the Gulf of Finland, the Gulf of Riga and close to the cities of Stockholm and Helsinki. The gray scale shows quantitatively the spatial distribution of the sampling frequency (estimated samples  $\text{km}^{-2}$ ). The sampling frequency of the Helsinki data subset exceeds the color scale and the region is shown as a black polygon. The contour line delineates sampling density of  $1.9 \times 10^{-2}$  samples  $\text{km}^{-2}$ . The contours enclose 6748 (93%) of the total 7272 samples. Sample locations of the NERI and SYKE data sets are marked with small symbols.

stantial salinity (1 to 6.7 psu) and eutrophication gradients, as well as changes in N to P limited summer communities (Tamminen and Andersen 2007).

Aggregating the samples by data providers reduces potential variability caused by taxonomic and procedural practices in different institutions, but is otherwise less justified. To clarify if and how the association between community ordination and external environmental variables changes geographically we defined more natural grouping of samples based on spatial proximity (Fig. 1). We used two dimensional kernel density estimation of the spatial sampling frequency. Choosing an arbitrary cut-off ( $1.9 \times 10^{-2}$  samples  $\text{km}^{-2}$ ) we defined 30 spatially confined groups of stations with high sampling frequency. The Helsinki data subset was not included in the kernel density estimate due to very high sampling frequency in a small spatial region, but was added as



**Fig. 2.** Sampling frequency of the 7272 summer samples per year. The frequency distribution pattern is not the same for all the Baltic Sea sub-regions and for all data providers.

a natural entity to the above delineated groups in its own right. Out of the 7272 summer samples, 6748 were in these geographic groups. The rest (524) were single samples with a wide spatial distribution and were left out at this stage of the analysis. We expect the procedure to yield more homogeneous natural groups of samples where the geographic span of association with environmental variables can readily be demonstrated.

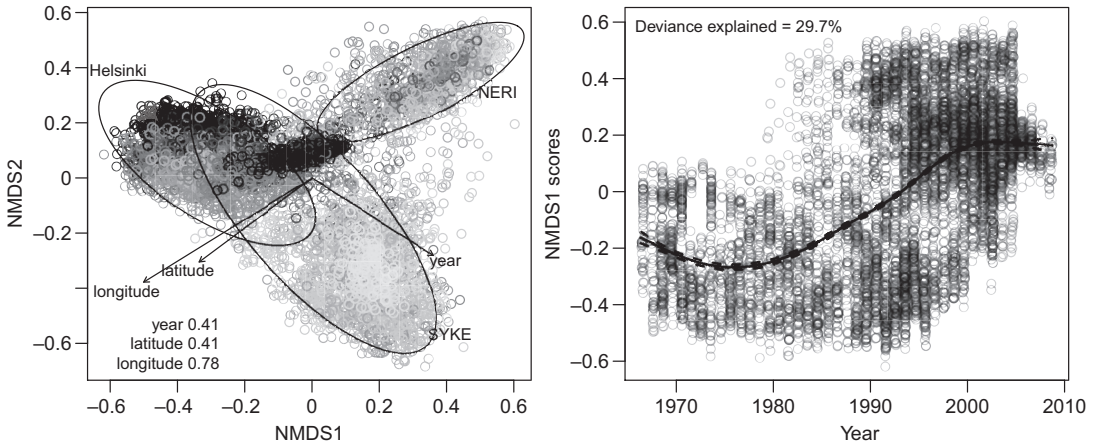
## Statistical methods

We constructed a community data matrix (samples in rows and taxa in columns) from the phytoplankton biovolume values. After deletion of rare species (present in fewer than three samples), the data was square root transformed to stabilize variability followed by Wisconsin double standardization (first species divided by their maxima, second samples divided by sample totals). From the standardized community matrix a Bray-Curtis dissimilarity matrix was calculated and subjected to non-metric multidimensional scaling. Non-metric multidimensional scaling (NMDS) is commonly considered as the most robust unconstrained ordination method in community ecology (Legendre and Legendre 1998). NMDS projects observed community dissimilarities nonlinearly onto 2-dimensional ordination space and it can handle nonlinear species responses. The method minimizes distance between observed dissimilarities and ordination distance (expressed by a stress statistic  $S$ ). NMDS is an iterative process, which gets easily trapped into local optima instead of find-

ing a global solution. Therefore, we used a procedure with several random starts until finding two similar configurations with minimum stress, which was taken as the best solution (metaMDS procedure in the vegan library of the R software; Oksanen *et al.* 2009).

Ecological interpretation of the ordination results was done by using independent environmental parameters. Environmental variables were fitted onto the unconstrained ordination to show the direction of the most rapid change in the environmental variable within the ordination space (the direction of the gradient) and the strength of the correlation between the ordination and environmental variable (the strength of the gradient). In contrast to the constrained ordination methods, the environmental fitting is independent of the ordination procedure and the number of environmental parameters fitted. This allows independent fitting of arbitrary number of environmental variables. The strength of each environmental gradient can be assessed by the square of the correlation coefficient between the ordination and the variable ( $R^2$ ). The significance ( $p$  values) of the environmental variables can be assessed by random permutations of the data: if a similar or better  $R^2$  is frequently obtained with random permutations, the environmental gradient is insignificant.

To test the robustness of the association between phytoplankton community and sampling year we conducted a bootstrap analysis. For the bootstrap analysis we used the Helsinki data subset, which we considered as the most homogeneous, spatially restricted and with a strong time trend. A random selection of species was



**Fig. 3.** Left-hand-side panel: NMDS ordination plot of the 7272 summer samples, using 815 phytoplankton taxa. The ellipses show the position of samples from the Helsinki, NERI and SYKE data subsets (surrounding ca. 85% of the samples). The color scale is proportional to the sampling year (dark grey: older samples, light grey: more recent samples). Due to the high number of samples there is a substantial symbol overlap and the clustering of samples according to time should be treated as a first glimpse. The arrows show the direction and strength (proportional to the length of the arrow) of external gradients superimposed on the ordination. The numerical values on the lower left section of the plot show the squared correlation coefficient ( $R^2$ ) of the external factor with the ordination. Right-hand-side panel: relationship between the scores of the first ordination axis (from left panel), and sampling year. The smooth line shows GAM fit with standard errors (dashed lines). The symbols show the actual data and are plotted with 20% transparency so that regions with many overlapping symbols appear darker. Note that symbols are not continuously located with respect to x-axis, which reflects the selection of summer samples only.

drawn from the community matrix, subjected to ordination, followed by assessing the correlation between the ordination and the sampling year (the independent variable). We started from a minimum of three random taxa, and incrementally increased the sample size to finally include all the taxa. At each sample size we drew ten random samples for analysis. The bootstrap analysis was done on the original Helsinki data subset (2220 samples, 349 taxa), and also on a modified community matrix, where the species (columns) were collapsed to the taxonomic level of a genus (2220 samples, 156 taxa). It is reasonable to assume that recognizing and naming of phytoplankton taxa at the genus level is less variable as compared with that at the species level and thus analyzing the genus-level community matrix will give a more conservative result. Because of the high computational cost of NMDS, in the bootstrap simulation study we used detrended correspondence analysis (DCA) with downweighting of rare species (decorana procedure in the vegan library of the R software; Oksanen *et al.* 2009). As an eigenvector method, DCA makes a linear

mapping of the samples onto the ordination plane as opposed to the non-linear response in NMDS.

All calculations were carried out using the R computing environment (R Development Core Team 2009), with extensive use of the vegan library (Oksanen *et al.* 2009).

## Results

### Whole Baltic Sea phytoplankton community ordination

The NMDS ordination of the whole Baltic Sea summer phytoplankton community (7272 samples) reveals a strong structure in the data (Fig. 3). The samples provided by NERI stand apart from the rest, due to the substantial distinction of the phytoplankton community in the more saline part of the Baltic Sea. The strong correlation between the ordination and latitude ( $R^2 = 0.41$ ) and particularly longitude ( $R^2 = 0.78$ ) support the prominent effect of salinity ( $R^2 = 0.77$ ; Table 1) on the community composition.

Both, latitude and longitude point to the same direction, suggesting the impact of increasing salinity in the southwestern part of the Baltic Sea. Clearly, the cluster of the NERI samples is spread along this gradient on the ordination plane. However, outside the waters with strong salinity gradient, the phytoplankton community tends to spread perpendicularly with the latitude–longitude gradient, along another gradient, which correlates well with the sampling year. The gray shades, depicting the sampling year in Fig. 3, reveal a clear grouping along the time gradient, which has equally high correlation with the ordination ( $R^2 = 0.41$ ) as has latitude.

The ordination (first axis) and time relationship shows considerable scatter (Fig. 3), and if we fit a Generalized Additive Model (GAM) to the ordination sample scores *versus* time, the model explains ca. 30% of the deviance in the data. This is a conservative estimate, as it only shows the association between the sampling time and the first ordination axis, while the time gradient (Fig. 3) has a strong component along both axes. Notably, eutrophication related environmental parameters had only a weak correlation with the ordination, either when all samples were included, or when data subsets were analyzed separately (Table 1).

### Case studies by data providers

The NMDS ordination results and time trends in community composition are presented in Fig. 4. The geographically rather compact NERI data

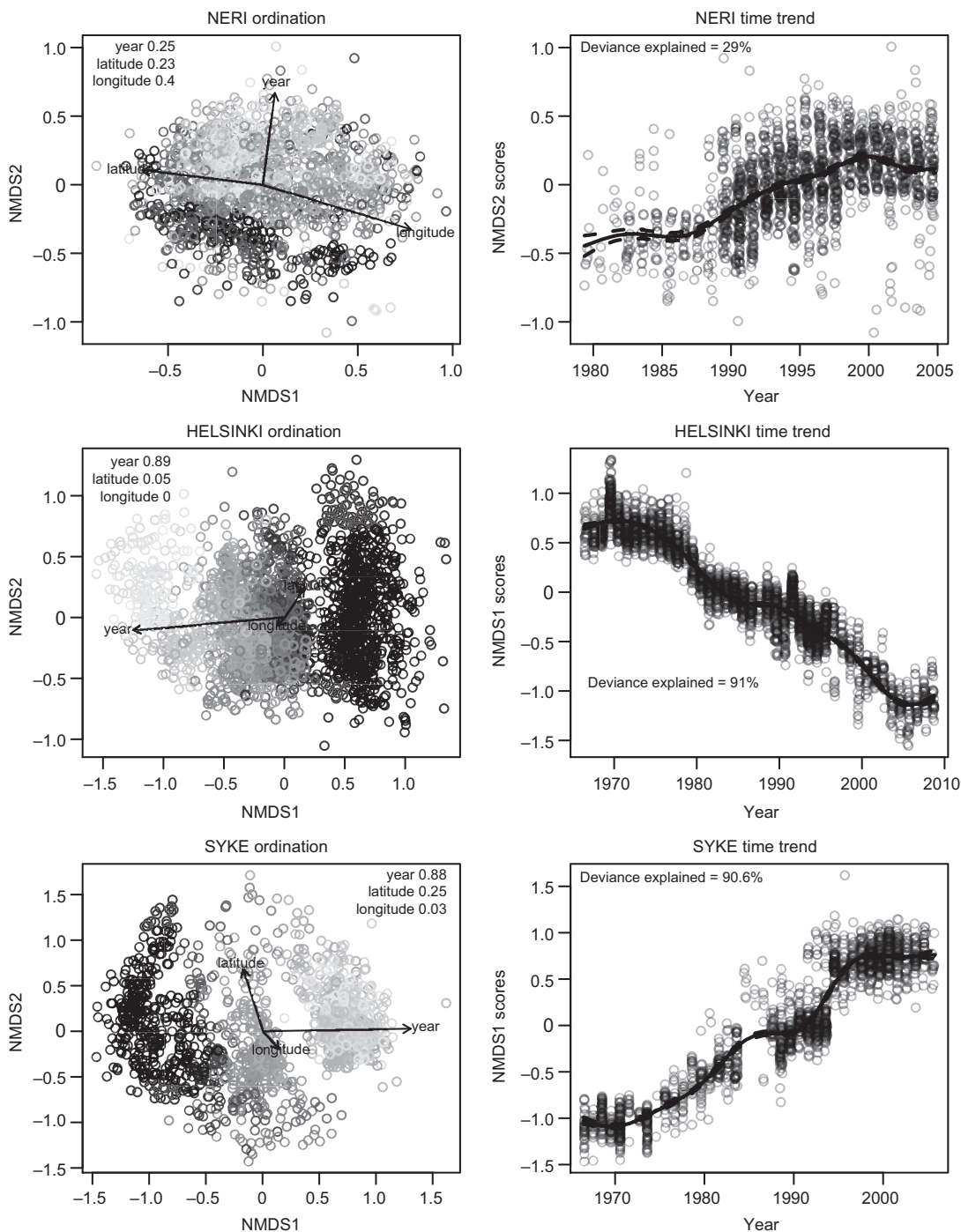
subset shows a well resolved ordination. The first ordination axis reflects changes on the salinity scale, which decreases with longitude and increases with latitude. However, the influence of time on the community ordination is almost equally important and is best explained by the second ordination axis. The relatively large scatter in the 2nd ordination axis and time relationship, and only 29% deviance explained by time, indicate the prominent effect of salinity on the phytoplankton community composition in the southwestern part of the Baltic Sea.

The NMDS analysis of the geographically compact Helsinki data subset shows a very clear time gradient in the ordination ( $R^2 = 0.89$ ). Also, the direction of the time gradient is almost parallel to the first ordination axis. The limited geographic span minimizes potential impact of the salinity gradient. There is a weak ( $R^2 = 0.05$ ) correlation with latitude, probably reflecting changes in community composition along the coastal–offshore axis, while the correlation with longitude is  $< 0.01$ . The association between sampling time and the first ordination axis shows relatively little scatter and an almost continuously monotonous trend, with the fitted GAM model explaining 91% of the deviance.

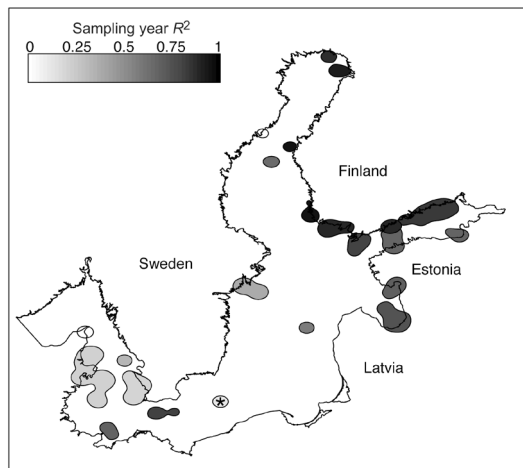
The NMDS ordination of the SYKE data subset reveals a very strong correlation with time ( $R^2 = 0.88$ ) along the first ordination axis, a substantially weaker correlation with latitude ( $R^2 = 0.25$ ) and only a very weak correlation with longitude. Sampling time explains almost 91% of the deviance in the data along the first ordination axis.

**Table 1.** Correlation coefficients ( $R^2$ ) between the NMDS ordinations of all the samples, and Helsinki, NERI, and SYKE data subsets and external factors: sampling year, latitude, longitude, salinity, temperature, julian day (season), distance from shore, dissolved inorganic nitrogen, phosphate, total phosphorus, total nitrogen, nitrite + nitrate. The statistical significance tends to be very high due to the high amount of data and the ecological significance is best expressed by the  $R^2$  values. All  $p$ 's are  $< 0.001$ , unless indicated as follows: \*  $p > 0.001$ ; °  $p > 0.01$ ; #  $p > 0.1$ .

	Year	Lat	Lon	Salinity	Temp	Julian day	Distance from shore	Dissolved inorganic N	PO <sub>4</sub>	P <sub>tot</sub>	N <sub>tot</sub>	NO <sub>x</sub>
All	0.41	0.41	0.78	0.77	0.02	0.02	0.07	0.06	$< 0.01^{\#}$	$< 0.01^{\#}$	0.10	0.03
HELSE	0.89	0.05	$< 0.01^*$	0.11	0.17	0.29	0.06	0.17	0.07	0.01 <sup>#</sup>	0.02 <sup>#</sup>	0.02 <sup>#</sup>
NERI	0.25	0.23	0.40	0.57	0.01 <sup>°</sup>	0.10	0.05	0.01 <sup>°</sup>	0.05	0.08	0.04	0.03
SYKE	0.88	0.25	0.03	0.15	0.11	0.07	$< 0.01^{\#}$	0.07	0.04	0.07	0.02	0.05



**Fig. 4.** NMDS ordination and relationship between the ordination scores and sampling year (time trends) of specific data subsets. The interpretation of the grey scale, the direction and length of axes, the numeric values of external factors, and the smooth lines are as in Fig. 3. The NERI subset has 1574 samples and 289 taxa, Helsinki 2220 samples and 349 taxa, SYKE 1383 samples and 406 taxa. Note that in time trend plots, the 2nd ordination axis is used in the NERI data and 1st axis in the Helsinki and SYKE data.



**Fig. 5.** Sampling regions (as in Fig. 1) shaded according to the correlation coefficient between the NMDS ordination and sampling year. Only those 21 sampling regions are plotted which have a temporal range of at least 10 years and more than 40 samples. The sampling region in the Bornholm basin marked with the asterisk has the lowest  $R^2$  (0.1) and the lowest significance level ( $p = 0.064$ ). In all the other regions  $p < 0.001$ .

### Analysis of spatial sample groups

The spatial grouping of samples yielded 30 sampling regions (enclosed contour lines in Fig. 1) with the number of samples ranging from 28 to 845, and the temporal range from 2 to 41 years, and the Helsinki region with 2220 samples and a temporal range of 42 years. Out of the total 31 sampling regions, we filtered out 10, which had fewer than 10 years of temporal span and/or fewer than 40 samples. We calculated the NMDS ordination for each of the data subsets and fitted external gradients onto the ordination. On average there is a strong correlation between the sampling year and community ordination

throughout the Baltic Sea (Fig. 5), although the association appears to be stronger in the northern and eastern basins ( $R^2 > 0.6$ ) and moderate in the Danish coastal waters ( $R^2 = 0.2$ – $0.3$ ), but also off Stockholm ( $R^2 = 0.38$ ). In all but one region (marked with asterisk in Fig. 5) the statistical significance of the correlation between sampling year and ordination is high ( $p < 0.001$ ).

Compared with other external factors that can potentially influence the phytoplankton community (Table 2), sampling year had by far the highest importance, followed by other abiotic factors: salinity, temperature, season (early to late summer), longitude and distance from shore of the sampling site. Notably, the residual concentrations of dissolved mineral nutrients (DIN,  $\text{NO}_x$ ,  $\text{PO}_4$ ) had very low influence on the phytoplankton community, but also the total nutrients ( $\text{P}_{\text{tot}}$ ,  $\text{N}_{\text{tot}}$ ).

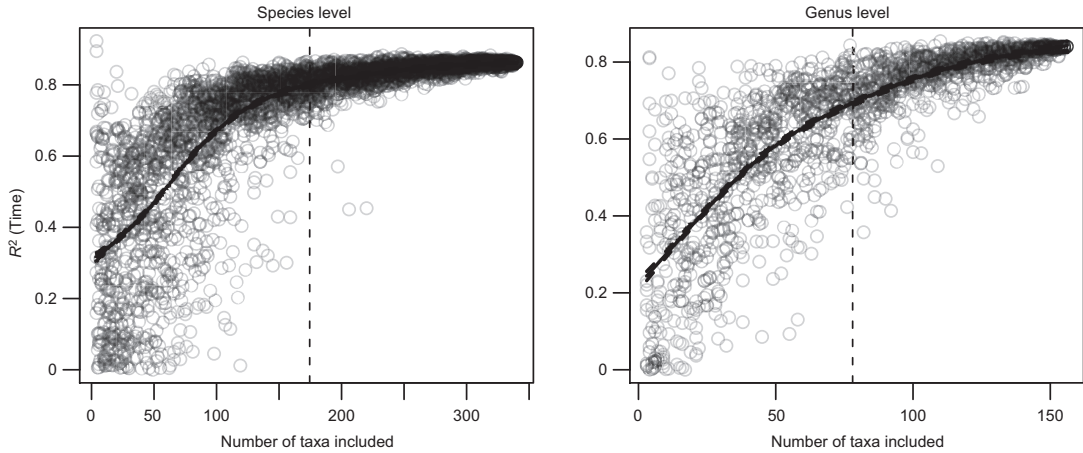
### Sensitivity analysis

In order to test whether the observed time-trend emerges from a few taxa or whether it represents a change of the entire community, we performed a bootstrap analysis in which a varying number of taxa was randomly selected. The bootstrapping analysis showed that when the sample size of taxa is low (below 1/3 of the total amount of taxa), the correlation between the ordination result and sampling time has a high variability (Fig. 6). Increasing the sample size increases the correlation, until it gradually approaches the asymptotic value of ca. 0.8. With only 50% of the community considered, the  $R^2$  reached already  $> 0.65$  at the genus level and close to 0.8 at the species level. As we used a different ordination technique in the bootstrap analysis

**Table 2.** Median (50th percentile) and interquartile range (25th and 75th percentiles) of the correlation coefficients ( $R^2$ ) between NMDS ordinations of sampling regions (as in Fig. 1) and external factors (as in Table 1). 23 regions with  $> 40$  samples were included. Columns are arranged according to decreasing median values.

	Year	Salinity	Temp.	Julian day	Long.	Distance from shore	Dissolved inorganic N	Lat.	$\text{PO}_4$	$\text{P}_{\text{tot}}$	$\text{N}_{\text{tot}}$	$\text{NO}_x$
25%	0.57	0.07	0.04	0.06	0.07	0.07	0.09	0.04	0.05	0.04	0.02	0.03
50%	0.69	0.21	0.18	0.17	0.17	0.15	0.12	0.11	0.1	0.08	0.08	0.06
75%	0.86	0.27	0.26	0.29	0.24	0.49	0.19	0.31	0.17	0.19	0.21	0.14





**Fig. 6.** Robustness analysis of the time trend in the Helsinki data subset. Correlation coefficients ( $R^2$ ) between DCA ordination scores and sampling year, as a function of increasing number of randomly sampled taxa. The dashed vertical lines show where half of the taxa are included. As the taxon number increases, the correlation coefficient approaches 0.8. The pattern remains unchanged when taxa are taken at the species level (left panel) or collapsed to the genus level (right panel). Note that as there are more taxa in the species level community matrix, the x-axis scales are different, but the general pattern remains perpetually unchanged.

(detrended correspondence analysis), the final correlation coefficient does not need to exactly match the one obtained with NMDS (Fig. 4). The results obtained by bootstrapping the genus or species level community matrix are very similar.

## Discussion

Our analysis shows that in most parts of the Baltic Sea the phytoplankton summer community went through significant and gradual changes during the past decades, without any clear association with eutrophication. The change has been smooth, without abrupt or step-wise alterations. This contradicts the reported regime shift type changes, which have been detected based on the fish stocks analyses and the consequent impact of the trophic cascade (Möllmann *et al.* 2008, Casini *et al.* 2009). The temporal change in the phytoplankton community appears to be a robust general phenomenon. The pattern is evident to varying degree across all Baltic Sea sub-basins, and from the data coming from different institutions and personnel. The changes are more clearly demonstrated in regions where long time series are available (e.g. several decades Helsinki and SYKE data subsets). Only in the southwestern Baltic Sea,

where the salinity gradient is strong over short distances (e.g. Paavola *et al.* 2005: fig. 2), has salinity apparently equal or stronger impact on the phytoplankton community than the temporal change.

It is noteworthy but expected that the eutrophication related parameters (dissolved and particulate nutrients) correlated poorly with the phytoplankton community composition. Growth season concentrations of both inorganic N and P are generally low, often close to or even below the detection limits of standard analyses (Tamminen and Andersen 2007), so that assessment of association between phytoplankton community composition and the inorganic nutrient concentration on the basis of monitoring nutrient data is uncertain. Changes in community composition were only poorly associated with known eutrophication gradients in the Baltic Sea. For example, the east–west eutrophication gradient in the Gulf of Finland correlates only weakly with the phytoplankton community (Fig. 4) and the gradual change in the phytoplankton community does not confirm the known temporal pattern of anthropogenic eutrophication (Elmgren 2001, Finni *et al.* 2001, Papush and Danielsson 2006).

The absence of a clear relationship with temperature should not be interpreted as a

lacking relationship with climatic change. We limited our analysis to readily-available data, including water temperature at the time of sampling. Climatic factors would involve numerous parameters such as mixing patterns and onset of summer stratification, changes in winter and spring bloom conditions and other factors, which are beyond the scope of this study.

The exact nature of the phytoplankton composition change is not easy to quantify and is currently under investigation. Our initial results indicate multiple mechanisms: appearance of new and disappearance of existing taxa, changes in the overall taxonomic diversity, and changes in the proportion of large taxonomic groups. In this context, the sensitivity analysis points out that the results do not depend on single taxa, but reflect an overall change in composition, involving changes in dominance patterns among taxonomic groups.

Suikkanen *et al.* (2007) showed long-term changes in the biomass and proportions of large taxonomic groups of phytoplankton in the late summer community of the northern Baltic Sea (northern Baltic Proper and the Gulf of Finland). They admit notable differences between the basins, but acknowledge long term monotonous increasing biomass of certain groups (e.g. chrysophytes and chlorophytes), while several other groups show non-monotonous long-term changes in biomass (e.g. dinoflagellates, cyanobacteria). However, their study is spatially restricted, and based on a total of 90 quantitative phytoplankton samples from 1979 to 2003. We believe that restricted number of samples leads to relatively wide confidence intervals of the inherently noisy phytoplankton data, and makes it difficult to separate with confidence true trends in the biomass and proportions of phytoplankton groups from random noise.

Wasmund *et al.* (2008) thoroughly studied long-term trends in both the spring and summer phytoplankton community and the relevant environmental parameters in the southern Baltic Sea. They reported increasing biomass of dinoflagellates and decreasing biomass of diatoms, but note substantial differences between sub-basins and seasons.

Apart from changes in biomass and relative proportion of larger taxonomic groups, changes in

species composition (invasions and local extinctions) alter the community structure and have an impact on the ordination results. The Baltic Sea has inherently low species diversity, canonically believed to be so due to the prevalent salinity levels occupying the diversity minimum on the Remane curve (Remane 1934). Paavola *et al.* (2005) argued that European brackish seas host ca. 100 well established non-indigenous species. However, of the ca. 100 documented non-indigenous species only a handful belong to phytoplankton. For example, Hajdu *et al.* (2000) reported that *Prorocentrum balticum* was common until 1990, but disappeared after that and was replaced by the potentially toxic *P. minimum*. Apart from the toxic or otherwise harmful species, we believe that the true extent of phytoplankton invasions is probably largely unknown in the Baltic Sea. Gómez (2008) argues that when it comes to phytoplankton, distinction between indigenous species and true newcomers is increasingly difficult. The intrinsically low detection level of rare species during routine phytoplankton counts may give a false impression of invasion, when a species increases to detectable levels during climatic episodes or eutrophication. Moreover, marginal dispersion, occasional advances or withdrawals of species at the frontiers of its native range should not be considered invasions (Gómez 2008), but such processes nevertheless shape the outcome of community analysis.

## Conclusions

During the last four decades a significant, gradual change in the phytoplankton summer community composition took place in most parts of the Baltic Sea, with no clear association with the known eutrophication patterns. The temporal change in the phytoplankton community seems to be a robust feature, which does not depend on the occurrence or abundance pattern of a particular species or group, but seems to be inherently embedded into the data. The phytoplankton species community in the Baltic Sea today is not the same what it was decades ago. Consequently, the whole Baltic Sea plankton community is not in a steady state or equilibrium, but rather in a continuous change.

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