DISSERTATIONES BIOLOGICAE UNIVERSITATIS TARTUENSIS
232

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Phytoplankton trends in the Baltic Sea

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The dissertation is accepted for the commencement of the degree of Doctor of Philosophy in environmental technology on September 24, 2012 by the Council of The Institute of Ecology and Earth Sciences, University of Tartu.

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Commencement: Room 218, 40 Lai Street, Tartu, on December 21, 2012,
                           at 10:15.

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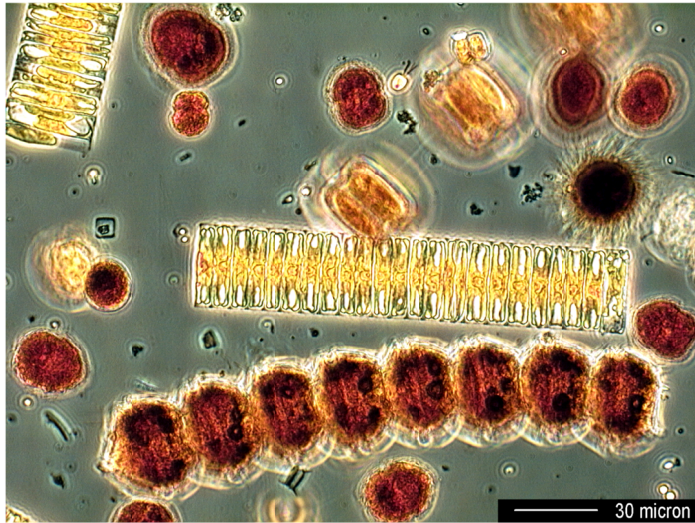
Main players of the spring blooms in the Baltic Sea (diatoms, *Peridiniella catenata, Biecheleria baltica*).

Pictured by renowned phytoplanktologist Seija Hällfors

CONTENTS

LIST OF ORIGINAL PUBLICATIONS

This thesis is based on following papers, which are referred to in the text by the relevant Roman numerals. All papers are reproduced by kind permission from the publishers.

I. Olli, K., O. Veresova, R. Klais, R. Ptacnik, T. Andersen, S. Lehtinen, T. Tamminen, 2012. Harmonizing large data sets reveals novel patterns in the Baltic Sea phytoplankton structure. In revision

II. Olli, K., R. Klais, T. Tamminen, R. Ptacnik, T. Andersen, 2011. Long term changes in the Baltic Sea phytoplankton community. Boreal Environment Research 16 (suppl. A): 3–14.

III. Klais, R., T. Tamminen, A. Kremp, K. Spilling, K. Olli, 2011. Decadal-scale changes of dinoflagellates and diatoms in the anomalous Baltic Sea spring bloom. PLos ONE 6(6): e21567.

IV. Klais, R., T. Tamminen, A. Kremp, K. Spilling, B. Woong An, S. Hajdu, K. Olli. Spring phytoplankton communities shaped by inter-annual weather variability and dispersal limitation: Mechanisms of climate change effects on key coastal primary producers. Submitted manuscript.

All papers in this thesis are co-authored with my contribution as following:

Papers III and IV, I performed the entire analysis, and was responsible for compiling the article text. In papers I and II, I was involved in the analysis, and preparation of the manuscript equally with other co-authors.

ABSTRACT

This thesis analyses long-term dynamics (1966–2008) and spatial patterns of the Baltic Sea phytoplankton. Over the four decades of observations, phytoplankton summer community composition has gone through a significant gradual change everywhere in the Baltic Sea. No abrupt or stepwise changes, in synchrony with the known regime shift at the top of the food web, could be detected. This implies relatively strong resistance of the phytoplankton community to the top down effect in the Baltic Sea food web. Proportion of spring bloom dinoflagellates has increased conspicuously over the decadal time scale to the disadvantage of diatoms in the central and northern Baltic Sea. Shifts in the diatom-to-dinoflagellate propotion can have ecosystem wide consequences, via the changes in sedimentation of organic material and benthic oxygen demand. Analysis was based on a phytoplankton data-set that was compiled from the data collected during routine monitoring programmes of many countries around the Baltic Sea. The data-set contains records from ca 15 000 phytoplankton field samples, covers the time period of 1966–2008 and the whole Baltic Sea, including the Danish Straits. We describe the spatio-temporal distribution of the data, evaluate the quality of the data between different data providers and estimate the extent and strength of spatial and temporal autocorrelation in the phytoplankton data. We found a significant positive autocorrelation at the spatial scale of 100 km and temporal scale of 30 days. Thus we suggest to use appropriate autocorrelation structures in statistical models with phytoplankton field data.

1. INTRODUCTION

Ecosystems worldwide are rapidly losing taxonomic, phylogenetic and functional diversity as a result of human appropriation of natural resources, modification of habitats and climate (Naeem et al. 2012). Coastal marine ecosystems are not an exception (Graig 2012). The beginning of the cultural eutrophication, i.e. increasing loads of mineral nutrients to coastal ecosystems due to human activities, dates back to the early 1900s (Dale 2009). Marked increase of nutrient loadings to the Baltic Sea, indicated by the increased sediment carbon content, took place around 1950–1960 (Poutanen and Nikkilä 2001).

Autotrophic phytoplankton at the base of the food web is the ecosystem component most immediately affected by increased nutrient availability (Cloern 2001). Phytoplankton variability is a primary driver of chemical and biological dynamics in the coastal zone. It affects directly water quality, biogeochemical cycling of reactive elements, as well as food supply to consumer organisms (Cloern and Jassby 2010). Phytoplankton species composition will affect the size distribution of food particles available for zooplankton and thereby potentially selecting for certain zooplankton species or groups (Hansen et al. 1994). Therefore structural changes in the phytoplankton community affect the abundance and composition of food for higher trophic levels of the marine food web.

The present thesis is based on analysis and statistical modeling of the Baltic Sea phytoplankton monitoring time-series. To elucidate the effects of climate change and eutrophication on the functioning and diversity of the phytoplankton community, it is of utmost importance to have access to decadal scale time series data with high temporal and spatial frequency. Phytoplankton monitoring data from the Baltic Sea are available already since 1966 (**I**). This data collection, in particular the species composition, abundances and biovolumes, represent a unique time series of the phytoplankton response to climate change and eutrophication from almost the whole temporal range since the beginning of increased nutrient loads to the Baltic Sea, not readily available from elsewhere in the world. Unfortunately I am not aware of the quantitative Baltic Sea phytoplankton data from the time period prior to the abrupt increase of eutrophication in the early 1960s (except for the few historical records from Kiel Bight, Wasmund et al. 2008). Therefore it is nearly impossible to compare the evolution of phytoplankton community structure during the past 4 decades with the pristine state of that ecosystem.

Decadal scale time-series of the biological variables from the marine ecosystems are rare (Edwards et al. 2010). Quantitative phytoplankton time series, i.e. data with species composition and the respective abundances or biomasses are even more rare. Probably, because the complex, intrinsically multivariate type of data collection is time consuming, and requires high level of expertise, both in microscopy and taxonomy. A few examples are the 'Helgoland Roads' time series from the south-eastern North Sea since 1962 (Franke et al. 2004), the San Francisco Bay monitoring program since 1979 (Cloern et al. 2007), the Western English Channel time series since 1992 (Widdicombe et al. 2010), the

Continuous Plankton Recorder time series from the NE Atlantic (Edwards et al. 2010). The value of these time-series has been shown to increase in time as new data are added (Edwards et al. 2010). The longer the data series, the more ecological patterns with different time scales can be elucidated. The long-term monitoring, in addition to assessing the status of the ecosystem has also improved our scientific understanding of marine ecosystem functioning (see Cloern 2001 for a review).

In the Baltic Sea region, phytoplankton monitoring has continued with almost unchanged methodology for > 40 years. However, the individual data sets were scattered among a multitude of academic institutions involved in the monitoring programs of many countries. Although the individual regional data series have great scientific value too, I believe the true potential of the phytoplankton monitoring data cannot be elucidated unless the isolated time-series are harmonized and combined in a joint coherent dataset. This rather tedious harmonization and joining was done prior to, and at the early phase of this PhD project. The data used in this thesis originate from nine different institutions around the Baltic Sea, with a number of different people being responsible in counting the samples and organizing the data. The main challenge in compilation of data from different providers is usually the vast amounts of time required for data inspection, correction and standardization, with taxonomic standardization and harmonization being the most demanding tasks (Moe et al. 2008). Ironically, although the monitoring data is collected and processed usually under the governmental financing paid by public tax-money, and the data by definition is public; it's nearly never a natural move for researchers to simply donate the data into a central repository for the benefit of the whole scientific community. This is unfortunate, as the data collection and processing has demanded many hours of highly qualified personnel's expertise and precious working time. With increasing spatial and temporal scales that one can easily utilize in analyses, more interesting patterns can be revealed, and this makes each single dataset combined more valuable than it was alone.

Subsets of Baltic Sea monitoring data have been used in studies describing the long-term trends and distribution of phytoplankton groups in different parts of the Baltic Sea (Jaanus et al. 2006; Jurgensone et al. 2011; Kononen and Niemi 1984), or in the detection of regime shifts in the ecosystem (Möllmann et al. 2009). Several of these studies describe significant time trends in phytoplankton groups (Suikkanen et al. 2007; Wasmund et al. 1998) but also delineate more general ecological mechanisms, which shape the phytoplankton community in the Baltic Sea (Kononen and Niemi 1984; Wasmund et al. 1998). E.g. Kononen and Niemi (1984) noted the high interannual variability in the relative proportions of diatoms and dinoflagellates in spring blooms at the entrance to the Gulf of Finland, northern Baltic Sea. Diatoms and dinoflagellates comprise on average > 90% of the spring bloom biomass, later on replaced gradually by a more diverse early summer community (Heiskanen 1998). Kononen and Niemi (1984) suggested that the diatom-to-dinoflagellate ratio in the northern Baltic Sea may be linked to the type of the winter. After harsh

winters with long lasting ice cover, diatoms were clearly dominating. In the mild winters, when ice cover was absent or disappeared already in March, dinoflagellates dominate. After this, the connection between winter-spring weather conditions and spring bloom composition has been found in a number of papers dealing with long-term trends and the variability of the Baltic Sea phytoplankton spring blooms in different parts of the Baltic Sea (Heiskanen 1998; Wasmund, Nausch et al. 1998; Wasmund and Uhlig 2003). However, the data sets behind these studies have been relatively restricted spatially and temporally.

The goal of this thesis was to harness the information content of the harmonized and joint Baltic Sea phytoplankton monitoring data set. The objective was to go beyond the constraints of restricted regional data, and analyze ecological patterns, which cannot be elucidated from single isolated data sets.

In the first paper (**I**) the details together with the pitfalls and recommendations of phytoplankton data compilation are given. This paper also highlights the value of joining the data-sets, demonstrating ecological patterns, which cannot be easily extracted from individual restricted data-sets.

The phytoplankton community structure in the temperate waters, including the Baltic Sea, has a strong seasonal pattern. Therefore the following papers focus separately either on the long term changes in the phytoplankton summer stage (**I, II**) or the Baltic Sea spring bloom (**III, IV**).

In these papers I specifically focus on the following questions:

i) what are the scales of spatial and temporal autocorrelation in the phytoplankton field data (**I**);
ii) are there visible long-term changes in the phytoplankton summer community composition, are they associated with known eutrophication patterns in the Baltic Sea (**II**),
iii) have the proportions of spring bloom diatoms and dinoflagellates changed on a decadal time scale, and are the changes explainable by eutrophication and/or climate variability (**III**), in particular the winter storminess and ice cover properties (**IV**); iii)

2. MATERIAL AND METHODS

"One undeniable fact of marine ecosystems is that they are complex, time variable, nonsteady state, nonlinear features, and need to be studied as such"
David M. Karl

2.1 Compilation of the data set

This thesis is based on analysis and statistical modeling of the Baltic Sea phytoplankton time-series compiled from a numerous external sources. Nine academic institutions around the Baltic Sea (**I**) provided the quantitative phytoplankton data analyzed from samples collected during the routine monitoring. With a few exceptions, most of the data were counted from fixed samples under an inverted microscope after settling for 24h (Edler 1979; Helcom 1988). 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). No qualitative or semi-quantitative samples were considered.

Compiling a master data-set from the original data provided by different institutions involved a demanding task of harmonizing and updating the taxonomy, described in detail in the methods section of paper **I**. The final joint data-set comprised of three interlinked tables: sample-table, species-table, and count-table, holding respectively essential information about individual samples, taxonomic data of the recorded taxa, and the actual abundances and biomasses of taxa in each sample (Table 2, **I**). In addition, environment table contained all the physical and chemical parameters, which were recorded by the data providers, or found from auxiliary sources, and were linked to the particular samples.

Overall the joint data-set included records from > 15000 quantitative Baltic Sea phytoplankton samples, with a total temporal range covering 1966 to 2008. The spatial distribution of the samples was aggregated, but the overall coverage of Baltic Sea sub-basins was reasonably good (Fig. 1 in **I**). Also, the sampling effort almost doubled in mid 1980s (Fig. 2A in **I**).

2.2 Statistical methods

Environmental monitoring usually collects observational data over time and space and without the immediate agenda to use it in testing of any particular ecological hypothesis, but to report the status and state of the observed ecosystem. This type of data does not fulfill the usual requirements of conventional parametric statistical models (normality, independence, homogeneity of error distributions). However, not meeting these requirements does not make the observational data less valuable (Brown et al. 2011). Methods better suited for handling the non-normality and non-linearity, like bootstrapping, non-metric multidimensional scaling, (Oksanen et al. 2012), generalized additive models,

(Wood 2006) were used. Spatial and temporal autocorrelations – were handled by employing the mixed effect models with auto-correlated error structures, (Zuur et al. 2009).

Analysis was done in the R computing environment (R Development Core Team 2012), so in the following text, all the functions and libraries mentioned are freely available in R.

2.2.1. Non-metric multidimensional scaling

Non-metric multidimensional scaling (NMDS) was preferred community ordination method (**II**) because the responses of species to environmental gradients could not assumed to be linear. NMDS is commonly considered as the most robust unconstrained ordination method in community ecology (Legendre and Legendre 1998). Instead of preserving the exact distances among objects (e.g. samples) in an ordination plot, NMDS tries to represent as well as possible the ordering relationships among objects in a small and specified number of axes (Borcard et al. 2011). It projects observed community dissimilarities nonlinearly onto low-dimensional ordination space and can handle nonlinear species responses (e.g. appearances/disappearances of the species over the time).

NMDS is an iterative process that minimizes distance between observed dissimilarities and ordination distance, but gets easily trapped into local minima instead of finding the overall global minimum. We used *metaMDS* procedure in R library *vegan,* which runs the NMDS from several random starts until finding two similar configurations with minimum stress, which is then taken as the best solution (Oksanen et al. 2012), thus providing some protection against local minima.

Ecological interpretation of the ordination results was done by fitting independent environmental parameters as gradients to the ordination surface (**II**). The strength of each environmental gradient was assessed by the square of the correlation coefficient between the ordination and the variable (R^2). The significance of the correlation, due to the non-metric nature of the ordination scores, was assessed by random permutations of the data: if a similar or better R^2 was frequently obtained with random permutations, the environmental gradient is insignificant. Both, the correlation coefficients and p-values were obtained with the function *envfit* from the *vegan* library.

2.2.2. Generalized additive models (GAM)

Things are not always linear. Neither can all functional responses be described with known non-linear parametric functions. For example, long-term dynamics of different species can take whatever arbitrary form, with no parametric relation between the year of the observation and the biological variable. Additive model fits a smoothing curve through the data and requires no prior decision on

the parametric form of the relationship between the response and predictor variables.

Although GAMs do not allow parameter estimations, this non-parametric technique appears to be useful in many specific cases and was utilized both for visualization (**III**, **IV**) as well as for detecting the possible significant non-linear relationships between the response and predictor variable (**IV**), or for removing the seasonality in the variables prior to analysis (**IV**). *gam* function allows inclusions of smooth terms and linear relationships simultaneously, so all the models where at least one effect was appeared to be non-linear, *gam* function was used, even if eventually simplified to linear model.

In R, there are two main packages for GAM: *gam* package written by Hastie and Tibshirani (1990) and the *mgcv* package produced by Wood (2006). We preferred the *mgcv* package as it can do cross-validation for the model selection. Cross validation is a process that automatically and objectively determines the optimal amount of smoothing.

2.2.3. Linear mixed effect models

Observational data, spatial and time-series, often are autocorrelated. A spatial structure in the response can result from two main origins: either from the forcing of external (environmental) factors that are themselves spatially structured (*induced spatial dependence*), or as the result of processes internal to the community itself (*spatial autocorrelation*).

In spatially correlated data, observations at any given site can be predicted, at least partially, from the values at nearby sites. Therefore the observed values cannot be considered stochastically independent. The assumption of independence of errors is violated in such cases. In statistical sense, each new observation does not add a full degree of freedom. While the correct degrees of freedom is difficult to estimate, the fact is that for a parametric test it is often overestimated, thereby biasing the test to the "liberal" side: the null hypothesis is rejected too often, and the probability of committing a type I error is higher than indicated by the p-value.

In modeling the effect of North Atlantic Oscillation index, a proxy for the overall weather conditions over the northeast Europe, including the Baltic Sea area, on the relative proportion of dinoflagellates in spring blooms (**III**), we accounted for the spatial autocorrelation in the data by first finding the basin wide weekly (biomass weighted) averages of dinoflagellate proportion and then treating the basin as a random component in the mixed effect model. Within each spatial group, we incorporated the temporal autocorrelation structure, which takes into account that the weekly averages following each other are more similar than those further apart. We accommodated the correlation structure based on the variogram model, estimating the distance decay of similarity with increasing number of weeks between two values. Variogram-based correlation structures are usually intended for modeling the spatial autocorrelation

(Zuur et al. 2009). In our case, we treated the week as a univariate coordinate. The sequence of the weeks was decoded to monotonously increase over the years, instead of start over with '1' every year.

2.2.4. Permutations and re-sampling methods

Methods based in a way or another on the re-sampling or bootstrapping were extensively used in papers **I** and **II**. First, to test the robustness of the temporal shift found for the phytoplankton community (**II**), we conducted a bootstrap analysis. The presence of temporal shift was detected with temporal pattern in the NMDS scores. The first critical question was whether the temporal pattern in ordination scores represents a major significant shift in the community, or is it due to changes in a few peculiarly behaving species only. In bootstrapping, a random set of species (columns from a community matrix) was drawn, subjected to detrended correspondence ordination (due to the high computational cost of NMDS), 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 community matrix size (with a step of 1) to finally include all the taxa, with 10 random selections from the community matrix at each step. Also, the function *envfit* (*2.2.1*) is using the random permutations to estimate the significance of the correlation between the ordination scores and environmental variables.

In paper **I** we use ***rarefaction*** to estimate the total taxon richness, which is based on re-sampling method. Rarefaction procedure re-samples randomly an increasing sub-set of samples from a pool of samples multiple times, and calculates the average number of taxa as a function of the number of samples. In paper (**I**) we estimated the total number of phytoplankton taxa that could be revealed in routine microscopy by fitting the asymptotic species accumulation curve on the smooth rarefaction curve, using the asymptote of the model as the estimate of taxon richness.

2.2.5. Geographically weighted regression

To describe the spatially non-stationary changes in time, or more generally the relationship between 2 variables that is believed to vary over space, a geographically weighted regression is a useful method (Fotheringham et al. 2007). The function applies the weighting function to each of the observations, calculating a weighted regression for each point. The results may be explored to see if and how coefficient values vary over space. We modeled the decade-long (1995-2004) change of spring bloom dinoflagellate proportion, i.e. linear regression between dinoflagellate proportion and year of observation as a spatially non-stationary process over the Baltic Sea (**III**). In each unique spatial sampling station in the data, a slope between the dinoflagellate proportion and year was found, where the data at the proximity of that point was weighed up

compared to more distant points. The slope parameters estimated for each spatial point were eventually interpolated (ordinary kriging) over the Baltic Sea to show the coarse spatial patterns in the change (Fig. 5 in **III**).

2.3. Phytoplankton seasonality and sample selection

Phytoplankton species composition and total biomass in the Baltic Sea show strong seasonality. A typical high biomass spring bloom community, consisting mostly of diatoms and dinoflagellates is switching to a more diverse summer community around the end of May – beginning of June in the northern Baltic Sea (Heiskanen 1998). Because of this prior known seasonality, the analyses mostly focused on the data from either spring (**III**, **IV**) or summer (**I,II**). Summer community, i.e. July, August, September, is seasonally more coherent and stable, and was therefore used in assessment of the extent of spatial and temporal autocorrelation (**I**), as well as in the study of long-term shifts in the whole community composition (**II**). During the spring blooms that account for the major part of the annual new production in the northern Baltic Sea, algal biomass is dominated only by a few 'key' species of diatoms and dinoflagellates. We were interested in the long-term trends in the relative proportions of these two groups (**III**), and the links of the changes to the environmental factors, such as variability in ice cover and storminess (**IV**).

2.4. Physical models of the Baltic Sea

There are several model calculations available for the Baltic Sea system, reconstructing the development of sea surface temperatures, salinities, wind speed, ice cover etc, with a different level of temporal and spatial resolution. We used the data from two of them: the PROBE-Baltic model (Omstedt and Axell 2003) and Baltix ice model (Finnish Meteorological Institute) in **IV**. In the PROBE-Baltic, the Baltic Sea is divided into a number of natural subbasins (see Fig. 1 in Omstedt and Axell 2003) and all the time-series, spanning 1958–2010, are calculated at the spatial resolution of basin (i.e. one number per basin). Variables include the water temperatures, salinity, air temperature, wind speed at 10 m, ice concentration and thickness, with a temporal resolution of 1 hour or 1 day. In **IV** we used the wind speed time-series from PROBE-Baltic model as the proxy to the winter storminess and bloom time turbulence. Winter storminess was calculated as an average wind speed in January, bloom time turbulence was the average wind speed during the 2 weeks period prior to sampling. Baltix ice model has a higher spatial resolution (2 nautical miles), hence the ice thickness time-series (mean ice thickness in March), was extracted for the closest model point to the respective cluster centres of phytoplankton sampling stations.

Both models are hind-cast models, forced by the meteorological data (the gridded database and ERA40 downscaled reanalysis, developed at Swedish Meteorological Insitute).

3. RESULTS AND DISCUSSION

In the following sections I'll recall and discuss the main findings of my research in the following order: first, I describe and discuss the long-term changes in the Baltic Sea summer phytoplankton community (**II**). Secondly, I analyze some dramatic long-term shifts in the dinoflagellate and diatoms proportions at group level during the Baltic Sea spring blooms (**III**). Although the spring bloom diatoms seem to form a coherent guild in the Baltic Sea, as well as worldwide, the cold water bloom dinoflagellates in the Baltic Sea apparently have a very different, often contrasting strategies to compete with each other, as well as with diatoms. In the follow-up study I search for mechanistic explanations to the dramatic increase of dinoflagellates in the northern Baltic Sea (**IV**). Last, I discuss and comment the data-set and data availability in general, the compilation and harmonization, quality of the data, and ecological facets with relevance for the statistical inferences (e.g. autocorrelation). Also, the estimation of the phytoplankton taxon richness in the Baltic Sea is shortly described at the end (**I**).

3.1. Baltic Sea phytoplankton community in a gradual shift

Analysis of the long-term trends in phytoplankton species composition indicates that phytoplankton community in the Baltic Sea has gone through gradual and long-term changes over the 4 decades of observational records, with seasonal and spatial differences in the direction, nature and rate of the changes. This applies to the both, the summer phytoplankton community, as well as the spring bloom dominant groups and species. The main conclusion from these findings is that the phytoplankton community, forming the base of the Baltic Sea food web, is not in a steady state, but in a measurable and continuous shift. The phytoplankton community today in the Baltic Sea is not the same what it was 20 or 30 years ago.

Summer phytoplankton
During the past 40 years, the Baltic Sea phytoplankton summer community composition has changed gradually and continuously, without clearly notable abrupt alternations in community composition (Figures 3 and 4 in **II**). The NMDS ordination of the whole Baltic Sea summer community (7272 samples, 815 taxa) revealed the two primary environmental gradients that correlated significantly with the ordination scores: the spatial salinity gradient (squared correlation coefficient R^2=0.77, p< 0.001) and the sampling year (R^2=0.41, p< 0.001; Table 1 in **II**). With no spatial constraints, the phytoplankton communities involved in whole Baltic Sea analysis were necessarily very heterogeneous, ranging from almost full ocean salinity Kattegat to very low salinity

environments in the Bothnian Bay and eastern Gulf of Finland. Therefore the high correlation between community structure and salinity came as no surprise. However, the surprisingly strong correlation with sampling year was astounding. Only in the southwestern Baltic Sea the steep salinity gradient obscured the long-term temporal effect, while in the northeastern Baltic Sea the time trend had an extraordinary strong association with the community composition (R^2=0.88. p < 0.001). 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.

For the time being the exact nature of the observed summer community change is not clear. Multiple mechanisms could explain a gradual drift in the community composition: i) turnover of community composition – continuous appearance and disappearance (local invasions and extinctions) of the species, ii) changing species richness, iii) demographic processes like shifting relative abundances (evenness) at the sample level. Many such changes have been demonstrated as long-term shifts in large taxonomic groups as a response to gradually changing climate or eutrophication pressure (Suikkanen et al. 2007).

The true extent of the phytoplankton invasions is largely unknown in the Baltic Sea. Gomez (2008) argues that when it comes to phytoplankton, identifying true invaders is an arduous task. Low detection level of rare species during routine phytoplankton counting may give a false impression of invasion, when species increases to detectable levels during favorable climatic episodes or eutrophication. Doubling the overall biomass doubles also the biomass of rare species that can suffice to cross the detection limit in routing phytoplankton monitoring analysis, leaving a false impression of invasion.

The gradual nature of the phytoplankton community change observed in our studies deserves discussion in light of the recently reported regime shifts in the Baltic Sea ecosystem. Ecological observations sustained over decades have revealed several past occurrences of abrupt shifts in the marine ecosystems, manifested by the major reorganizations in the trophic structure and functioning of the biological communities (Cloern et al. 2007; Edwards et al. 2010). Such shifts often appear to result from large-scale state changes in the nearest ocean-atmosphere system, although increasingly combining with the anthropogenic pressures, like eutrophication and overfishing. Möllmann et al (2009) describe a major reorganization in the central Baltic Sea ecosystem in the late 1980s and early 1990s, simultaneously with the similar events detected in many North Pacific (Cloern et al. 2007; Hare and Mantua 2000) and North Sea ecosystems (Alheit et al. 2005; Beaugrand 2004). Until mid 1980s the Baltic Sea ecosystem was characterized by the dominance of the Atlantic cod (*Gadus morpha*) as a top predator and high abundance of herring (*Clupea harengus membras*), together with a copepod zooplankton *Pseudocalanus acuspes*. Within approximately 5 years, the system shifted into a state where the planktivorous sprat (*Sprattus sprattus balticus*) became dominating, together with the copepods *Acartia* spp. and *Temora longicornis* (Möllmann et al. 2009). Casini et al (2008) proposed that the Baltic Sea phytoplankton community is mainly top-

down driven in the summertime and has gone through a reduced grazing pressure due to the dominance of the sprat. They suggest that the zooplankton community could potentially suppress the blooms of cyanobacteria, unless weakened by heavy control from sprat. Even more, they claim that sprat dominance could hence explain the increased cyanobacterial blooms after the regime shift, exemplifying a trophic cascade all the way from the top predator to the primary producers (Casini et al. 2008).

Notably, we didn't observe any sudden changes in the Baltic Sea summer phytoplankton community at the late 1980s and early 1990s. Lack of comparable abrupt alternation in the phytoplankton community structure simultaneously with the observed regime shifts in the Baltic Sea (Alheit et al. 2005; Möllmann et al. 2009) can arise from a number of reasons, both ecological as well as methodological in this case.

First, the abrupt ecosystem shifts reported by Möllmann et al (2009) mostly involved higher trophic levels, i.e. changes in dominating copepod zooplankton and fish species. Despite of the trophic cascade effect in the Baltic Sea summer communities found by Casini et al (2008), actual changes in the phytoplankton composition contributed only modestly to the results in the regime shift as reported by Möllmann et al (2009), with the only difference before and after the shift being the increased dinoflagellate proportion in spring blooms. This agrees with our finding of no abrupt changes in the summer phytoplankton community. Casini et al (2008) note the elevated chl *a* values after the regime shift in the central Baltic Sea. Also Suikkanen et al (Suikkanen et al. 2007) report the chl *a* increase after 1990, in the late summer observations from the northern Baltic Proper and Gulf of Finland, and increasing abundances of cyanobacteria and dinophytes after 1990. However, also these changes were gradual, in line with the smooth patterns in our findings. In summary, it becomes likely that ecosystem regime shifts in the Baltic Sea, driven by top predators, do not cascade down to the base of the food web. This is in line with our perception of the web type architecture of trophic connections, buffering against simple Lotka-Volterra prey-predator type cascading.

Further studies on the essence of temporal changes, for example the changes in the taxon richness and relative abundance of the dominant species, functional diversity and the assembly of the community, are in progress and should shed light on the mechanisms and nature of the observed long-term community change. Knowing more of the entity of the community shifts can help us to identify the drivers of the change, e.g. the adaptation to the elevated nutrient levels after 1950s, warming climate and enhanced dispersal through intensified ship traffic, all potentially contributing to the gradual alternation of the phytoplankton composition.

Spring phytoplankton
The annual phytoplankton successional cycle in temperate to boreal coastal waters classically begins with a winter-spring diatom bloom that is seasonally replaced by summer communities dominated by flagellates (Smayda and

Trainer 2010). The phytoplankton spring blooms in the Baltic Sea is anomalous in the sense that the bulk biomass of the spring blooms, especially in the central and northern Baltic Sea, is often dominated by the cold-water dinoflagellates. Several species are involved – the arctic species *Peridiniella catenata,* and a group of morphologically similar medium sized dinoflagellates assigned to *Biecheleria baltica, Scrippsiella hangoei* and *Gymnodinium corollarium*. Due to the difficulties in differentiating between the latter three species, we refer to them as 'the *B. baltica* complex' hereafter. However, the proportion of dinoflagellates remains unpredictable in any particular year, with a marked interannual variability (Kononen and Niemi 1984). As for the long-term trends in the southern Baltic Sea, Wasmund and Uhlig (2003) found a long-term increase of dinoflagellates and a negative trend of diatoms between 1979–1995.

We provide the most comprehensive picture of the temporal trends and spatial patterns of the diatoms and dinoflagellates in the Baltic Sea to date, using all the available monitoring data (Fig. 4 & 5 in **III**). Most dramatic increase of the dinoflagellate proportion in spring blooms, from 0.2 to 0.8 occurred in the Gulf of Finland between 1970s and 2006. Proportion of dinoflagellates was increasing also in the northern Baltic Proper (Landsort Deep, west from island Gotland) (from 0.4 to 0.6), and in Gulf of Bothnian (from 0.1 to 0.4). Further towards southwestern Baltic Sea, the long-term change is leveling off. The linear slope estimated only for the latest decade of observations (1995–2004) reveals positive trend in the Gulfs of Finland and Bothnian, and negative change in dinoflagellate proportion in the central and southern Baltic Sea and in the Gulf of Riga (Fig. 5 in **III**). Presently, dinoflagellates dominate the spring blooms in the Gulf of Finland and central Baltic Sea, and diatoms in Gulfs of Bothnia and Riga and southwestern Baltic Sea, including the Danish Strait.

Mild winters in Baltic Sea region, the most common explanation to the high dinoflagellate proportion (Kononen and Niemi 1984) are to a large extent determined by large-scale atmospheric processes over Atlantic, such as North Atlantic Oscillation (Hänninen et al. 2000). However, the spring bloom dinoflagellate proportion has changed with a spatially varying rate as well as direction in different basins (**III**), indicating that mechanisms driving the change have a strong regional and fine-scaled component, characteristic to coastal ecosystems in general (Cloern and Jassby 2010). Accordingly, we found a positive relation between of North Atlantic Oscillation index and dinoflagellate proportion in the Gulf of Finland and northern Baltic Proper (**III**), but not in the Gulfs of Bothnian, Riga and southwestern Baltic Sea.

Similarly to NAO, there was no apparent association between the spring bloom biomass and dominance patterns of dinoflagellates or diatoms (Fig. 4 in **III**), as diatoms hold a strong position both in the oligotrophic northern basins (Bothnian Bay) as well as in eutrophied Gulf of Riga, Kattegat, Danish coastal waters and in the Southern Baltic Sea, where the spring bloom biomass is relatively high (3–4 mg L^{-1} wet weight), particularly in the Bay of Kiel (ca. 6 mg L^{-1}). Analogously, dinoflagellates dominate the spring blooms both in the highly eutrophied Gulf of Finland as well as in the least eutrophied offshore

waters of the northern Baltic Proper (>0.8), which shows moderate to low average spring bloom biomass values (ca. 1.5 mg L^{-1}). This supports the functionally surrogate role of these phylogenetic groups in system-wide biogeochemical cycles and undermines the hypothesis that anthropogenic nutrient enrichment favors universally the fast-growing diatoms.

The decreasing dissolved silica (DSi) availability and lowering DSi:N ratios, associated with eutrophication (Papush and Danielsson 2006; Rahm et al. 1996) and decreasing riverine DSi inputs (Humborg et al. 2006), have been suggested to limit diatom growth in the Baltic Sea, and thus indirectly support the expansion of dinoflagellate blooms. Even though most common Baltic spring diatoms are well adapted to low DSi concentrations and not directly affected by decreased surface levels during the growth period (Spilling et al. 2010), some spring bloom diatoms in the Baltic Sea rely on benthic resting stages to survive the warm summer, and require large amounts of DSi when the spores are formed (Mcquoid and Hobson 1996). At the late phase of the bloom, low DSi may thus lead to poor sporulation and subsequently compromise the seeding and competitive success of the next generation of these diatoms. Therefore, in specific cases, low DSi may set the upper limit to the diatom spring bloom magnitude. Long-term data analysis showed that the semi-enclosed Gulf of Riga went through a DSi depletion event culminating in 1993 (Olli et al. 2008), coinciding with the significant increase of dinoflagellate abundance (Fig. 2 in **III**). The likely cause was the exceptionally strong blooms of heavily silicified diatom species. Given the slow dissolution of biogenic silica, the net result was a drawdown of DSi stocks for several years. Since 1995, the DSi concentrations and the proportion of diatoms in the Gulf of Riga have recovered and dinoflagellate proportion decreased rapidly. Significant link between potential silica limitation and higher spring dinoflagellate proportion in Gulf of Riga was also confirmed by Jurgensone et al (2011).

To elucidate the mechanism of the association between spring bloom composition and winter-spring weather conditions, we designed a statistical model study combining the phytoplankton field observations and the meteorological time-series reconstructed by physical models of the Baltic Sea system (**IV**). We used the phytoplankton observations from three locations in the Baltic Sea, each representing one out of the following conditions: i) a coastal area with the highest proportion and recent expansion of dinoflagellates (Helsinki archipelago, the central Gulf of Finland); ii) an open-sea area where dinoflagellate proportion increase was less pronounced (Landsort Deep, northern Baltic Sea) and iii) a coastal area, where dinoflagellate proportion decreased recently (Gulf of Riga). It should also be noted here that these three locations are connected by the dominant surface currents in the same order as listed, i.e. the water masses flow from Gulf of Finland over the Landsort Deep and, after passing through the southern Baltic Sea, turn first to east and then back to north, eventually reaching the Gulf of Riga. Dinoflagellates were resolved to species level in this study, i.e. as *Peridinella catenata* and the *B. baltica* complex, as we had good reasons to expect significant species-specific differences in the dinoflagellate response,

as discussed already in **III**. We suggested that the medium-sized cold-water dinoflagellate species comprising the *B. baltica* complex are responsible for the observed trends in dinoflagellate abundance. We further hypothesized that the success of the *B. baltica* complex was related to winters conditions, requiring a specific sequence of weather events – strong storms in January followed by thin ice cover in March.

Based on the analysis, the biomass of the *B. baltica* complex was highest when ice thickness in March was between 10–20 cm, decreasing both, towards the absence of ice as well as with the increasing ice thickness. Wind speed in January had a positive, and bloom-time wind (the direct turbulence) a negative effect on the *B. baltica* complex success. The negative effect of the direct turbulence was also apparent on the other spring dinoflagellate, *Peridiniella catenata*. Somewhat surprisingly, diatoms did not benefit from the bloom time turbulence, as is usually expected (Smyda 2002), but their biomass showed a positive relation to ice thickness (**IV**).

The *B. baltica* complex has life cycle properties, which fit particularly well to the local hydrography and changing climate. These include massive production of resting cysts that are very efficiently re-suspended by winter storms and ready to germinate already at winter, when exposed to light (Kremp 2001). This was in line with the positive effect of the winter storms that we found. However, being re-suspended to the water column does not yet secure the dominance over much faster growing diatoms. Diatom resting cells are also shown to be always present in the plankton, ready to seed the spring bloom as soon as the physical conditions become permissive (Wasmund et al. 1998). The key factor leading to the dominance of the *B. baltica* complex is probably the timing and properties of the ice cover in spring. The 'right' ice should be thin enough to let the light go through and present around March, when there is already enough sunlight for the algal growth. Ice, however thin, promotes the strong salinity stratification, created by ice melt and/or spreading of freshwater plumes from nearby rivers. Diatoms are not able to keep themselves in the strongly stratified illuminated thin lenses under the ice and sink out to deeper layers where light is growth limiting. This segregation leaves a window of opportunity for the *B. baltica* complex to build an abundant inoculum before the onset of the spring bloom. Such dense under-ice blooms have been frequently observed in the Gulf of Finland in March (Spilling 2007). When mixed into the water column after the ice break-up, these patches provide the decisive head start in competition with diatoms. Six years of mesocosm experiments with natural phytoplankton communities demonstrated that the singlemost important condition leading to the dominance of *B. baltica* complex is a strong head start of the species at the early phase of the bloom (Kremp et al. 2008).

With increasing ice thickness, as well as with the snow cover on the ice, the light conditions under ice become less favorable for growth, explaining the right hand side of the unimodal response in Fig. 2 in **IV**.

As far as can be concluded from the analysis of monitoring data, *Bicheleria baltica* complex has not truly expanded to the northwestern Baltic Sea or to

Gulf of Riga. Although the spring bloom dinoflagellate proportion increased also in the northwestern Baltic Proper (station Landsort Deep, west from the island Gotland), an area well connected to the waters of Gulf of Finland by major surface currents, the modest increase of *B. baltica* complex abundances constitute only a minor part of that change (Fig. 4 in **IV**). Even more, I do believe that majority, if not all, of the *B. baltica* complex in the offshore northwestern Baltic Sea are in fact the expatriates from the Gulf of Finland.

Most of the observed increase in the dinoflagellate proportion in the northwestern Baltic Proper seems to result rather from the phenological advancement of the spring bloom events in general. In the northwestern Baltic Proper, the spring bloom is composed of sequential biomass peaks of diatoms and dinoflagellates (**III, IV**). Comparison of the data prior and after 1990 (Fig 4. in **IV**) revealed that the peaks of both, the diatoms and dinoflagellates, shifted about 10 days earlier in the northwestern Baltic Proper. Also, along with this shift the bloom window of diatoms has shortened, leaving potentially more nutrients for the following dinoflagellate bloom (mainly *P. catenata*) and resulting in an overall higher proportion of dinoflagellates over the spring bloom.

The conspicious absence of *Biecheleria baltica* complex from Gulf of Riga (Jurgensone et al. 2011) is rather surprising, given that the Gulf of Riga, seasonally ice covered and relatively shallow, should provide equally good conditions for the species as the Gulf of Finland. Also, because of the high dispersal capacity of microscopic organisms (Finlay 2002). We propose that the expansion of *B. baltica* complex to the Gulf of Riga is hindered by dispersal limitation, resulting from a combination of the surface currents in the Baltic Sea and the life-cycle of the species. When progressing southwards, following the main currents in the Baltic Sea, the vegetative *B. baltica* complex populations from the Gulf of Finland are exposed to incrementally warmer surface water invoking rapid encystment and sedimentation off the surface waters at ca. 6°C (Kremp and Heiskanen 1999; Kremp et al. 2009) before reaching the entrance to the Gulf of Riga. A combination of a founder effect, low connectivity between basins, and a threshold in cyst accumulation in sediments, before a hangaround species is able to build the necessary head-start under supportive physical conditions, and thus to secure future success in the habitat, seems a plausible hypothesis for the observed spatial distribution of *B. baltica* complex, both its temporal expansion in Gulf of Finland, as well as absence from Gulf of Riga.

3.2. Importance of the spring bloom composition on the biogeochemistry of the Baltic Sea

Shifts from diatom to dinoflagellate-dominated spring bloom have major consequences on important basin-wide biogeochemical cycles, like the vertical transport of organic matter and benthic oxygen consumption. Termination and sedimentation of spring bloom biomass, within about 2-week time period,

accounts for ca. 50% of the annual organic matter input to the benthos in the northern Baltic Sea (Heiskanen 1998).

Diatoms mostly sink rapidly as intact cell aggregates, while the bulk of dino-flagellate biomass disintegrates in the water column and sinks slowly as refrac-tory phytodetritus (*Peridiniella catenata*) or massively in the form of resistant resting cysts (*Biecheleria baltica*) (Heiskanen 1993; Spilling et al. 2006). The quality of the settling material as a food source for benthic food-web, as well as the subsequent benthic oxygen demand increases rapidly on a gradient of *B. baltica -> P. catenata ->* diatom dominated blooms (Spilling and Lindstrom 2008), with consequences on the spreading of anoxic deep water in the Baltic Sea (Conley et al. 2011).

Projections of climate change suggest that water temperature and wind speed will increase and ice cover will decrease in the future Baltic Sea (Meier et al. 2004; Neumann 2010). The positive relationship between the ice-cover thick-ness and diatom success suggests decreasing diatom abundance with the future climate in the Baltic Sea area. The narrow ice thickness range favoring the *Biecheleria baltica* complex indicates that with evolving changes in ice cover, the geographical distribution could shift, but a necessary precondition for major changes is gradual overcoming of the current dispersal limitation to adjacent basins (Gulf of Riga and Bothnian Sea). The role of accumulating seeding po-tential from sediments appears critical for this. The present dominance of the species in the Gulf of Finland developed over several decades, well within the projected climate change pace.

It is necessary to resolve the complex interplay between weather forcing of the spring bloom composition, species-specific ecophysiological responses and life cycles, and spatial dispersal dynamics, in order to predict the overall climate change effects on the Baltic Sea ecosystem.

3.3. The Baltic Sea phytoplankton data set – technical aspects

Joining a large part of the publicly available data to a joint data set is a de-manding, but revealing exercise. The various background and traditions in dif-ferent countries add a degree of heterogeneity when compiling and harmonizing the data. We found notable data provider specific differences in the proportion of phytoplankton biomass identified to species or genus level, indicating a ten-dency to ignore unknown and unidentified taxa in the sample counting practice of some countries (**I**). An opposite subjective tendency was to more frequently record species that are easy to identify. This was reflected in the top frequency list of all records, which was dominated by taxa, which are morphologically easily recognized even by inexperienced analysts. Both of the tendencies create bias in the microscopic phytoplankton monitoring, implying qualitative differ-ence when microscopy based phytoplankton monitoring will be compared to, or replaced by metagenomics based approaches in the future.

Despite the potential biases, compiling a large multi-source data set enables to ask questions and do analysis, which are not possible with regional or smaller scale data. As an example the strength and scale of spatial and temporal autocorrelation in phytoplankton field data can only be analyzed when sufficient spatio-temporal data coverage is available. We found a statistically significant, but ecologically modest spatial and temporal autocorrelation in the phytoplankton monitoring data (**I**). The univariate Moran correlogram (using the total biomass as a variable) revealed positive autocorrelation up to 400 km distance at the extent of the whole Baltic Sea. This can be seen as the induced spatial dependence, via the general patterns of productivity in the Baltic Sea, determining the overall biomass level but not necessarily the species composition. A multivariate Mantel correlogram (using the species composition as a variable) showed a positive spatial autocorrelation up to a scale of 100 km, and this can be considered as the true intrinsic autocorrelation of the phytoplankton community. Additionally, there was a strong temporal autocorrelation between samples taken within less than 30 days time window, but overall the similarity between samples was modest and decreased rapidly in time (Figure 8 in **I**). As a conclusion, since the positive autocorrelation was present, effect of the autocorrelation on the degrees of freedom in the analyses using the present data set must be considered. Also, since the extent and strength of the autocorrelation depends on the variable of interest (e.g. total biomass vs. species composition) as well as on the level of the data averaging before analysis, one solution is to involve the correlation structures in statistical models, as was done in our paper **III** in the analysis of NAO impact on spring bloom dinoflagellate proportion. Useful and easy to follow instructions to handling the spatial and temporal autocorrelation can be found from the book by Zuur et al (2009).

Estimating the taxon richness
One of the general characteristics of ecological communities is that the number of species accumulates with increasing sampling effort (Gotelli and Colwell 2001). Accumulation rates of new species over the sampled area is described by the species accumulation curve. Initially many species are found as sampling effort increases and a plot of accumulated number of species against sampling effort rises steeply at first and then more slowly as the increasingly rare species are added (Colwell and Coddington 1994).

The species-accumulation curve may approach an asymptote for data-sets of species that can be identified easily, such as large mammals or breeding birds, where it is possible to obtain a count of all the species present. For other habitats or organism groups, like the microbial field communities, one cannot expect to count all the species. All that can be done is to estimate total species richness and the sampling effort needed to obtain reliable estimates of taxon richness.

In **I** we focus on fitting widely used asymptotic models to species-accumulation curves for one of these difficult habitats that we have extensive data of – quantitative phytoplankton data from monitoring programmes.

A common justification of the chosen model relies on the R^2 values close to 1 while fitting the curves, or some other goodness of fit parameter; the assumption being that if the model approximates the observed accumulation curve, its extrapolation must be quite close to the true species richness.

Good fit of a model with the existing data, however, is intrinsically weak test for the appropriateness of the model. Extrapolating beyond the data availability is always a dangerous business. Even more, for a given data, more than one model may give a close to perfect fit, making the final model selection a subjective decision.

By using the sheer amount of data at hand, we offer a complete new logical method to follow and an approach to be considered by others. We assume that the sampling from a region can be increased infinitely. For phytoplankton field samples, this is certainly true within any realism. All we expect is that the estimated taxon richness, described by the asymptote of the species accumulation curve, remains stable as the sampling effort increases. By simulating a range of sampling efforts, we tested this simple expectation on a variety of commonly used asymptotic species accumulation models.

Apparently all the tested models showed increasing species richness at a low range of sampling effort, and the asymptotes of most models kept increasing with increasing sampling effort, but notable exceptions – Lomolino and Weibull 4 parameter models, revealed remarkable asymptote stability after a modest sampling effort (Fig. 10 in **I**). We thus pay tribute to George E. P. Box: *All models are wrong but some are useful* (Box and Draper 1987).

Based on visual inspection of the asymptote stability, and the AIC based goodness of fit measure, we preferred the Weibull model from the set of tested models. There are two caveats to be pointed out, though. First – our preferred model is by no means the best from all asymptotic models possible. However, the logical method of model testing can be used with any asymptotic model. Second, our preferred model appeared best by using phytoplankton data; any other organism type may have resulted in a different conclusion. Even more, habitat and sample heterogeneity may well influence the model fit. Therefore, a careful model testing seems to be an unavoidable step in taxon richness estimates, and a wealth of available data seems to a prerequisite of such testing.

4. CONCLUSIONS

To see the forest for the trees

1. While the management objective of monitoring programs is to assess the status and trends in the environment, can monitoring data also constitute a wealth of information advancing our knowledge on the ecosystem functioning and its response to both, human-mediated and natural changes in climate and environment. Gathering and unifying the data that is often aggregated among a number of sources into a large and comprehensive data-set is time consuming and demanding, yet well rewarded effort. We've demonstrated here only a few of the kinds of questions that can be asked and answered by analyzing the data spanning increasing spatial and temporal scales.

2. Baltic Sea phytoplankton community is relatively resistant to sudden changes in the ecosystem, but nevertheless has remained in a constant continuous drift during the 1966–2008. While the higher trophic levels in the Baltic Sea went through a sudden regime shift in the end of 1980s and beginning of 1990s, we didn't notice any abrupt stepwise alternations in the phytoplankton composition, even if the analysis was based on the observations during the summer months. In the Baltic Sea, the top-down effects are believed to be strongest during summer months, where the changes in the top of the food web cascade down to primary producers. Our findings undermine that belief and imply the resistance and inertia of the primary producers to sudden changes in the ecosystem structure.

3. Spring bloom composition, during which up to 70% of the annual primary production takes place, has shifted towards higher contribution of dinoflagellates mainly in the northern and eastern areas of the Baltic Sea, and especially so in the last decades. Much of that change is due to recent expansion of *Biecheleria baltica* complex spring blooms. The *B. baltica* complex has a life cycle that fits particularly well to the hydrometeorological setting of the winter-spring period in the shallow and seasonally ice-covered Gulf of Finland. For what can be concluded from the monitoring data, the *B. baltica* complex has not yet expanded to the basins that are connected to the Gulf of Finland by the surface currents (northwestern Baltic Proper, Gulf of Riga), in northwestern Baltic Sea, and possibly also southern Baltic Sea, increasing dinoflagellate proportion can be mainly related to the phenological shift in the spring bloom succession. In Gulf of Riga, only explanation to the temporal dynamics of spring bloom composition is the availability of dissolved silica.

4. Although the phytoplankton samples show high variability and low predictability, both spatial and temporal autocorrelation was detectable from the data. We recommend to always incorporate the autocorrelation structures in the models to obtain realistic p-values, when using that particular data-set or phytoplankton field data.

SUMMARY IN ESTONIAN

Läänemere fütoplankton muutuste keerises

Viimase paari aastakümnega on inimkond oluliselt muutnud maailma nägu – elukeskkonda, elurikkust, ökosüsteemide toimimist, aine- ja energiavooge ning, lühemas perspektiivis ka kliimat. Ranniku- ja sisemered ei ole selles mõttes erand, ehkki muutusi neis on, võrreldes maismaakooslustega, vähem uuritud ja kirjeldatud, ning sellevõrra vähem on teada ka nende muutuste põhjustest ja tagajärgedest.

Käesolev töö uurib ja kirjeldab Läänemere fütoplanktonikooslsust viimase poole sajandi jooksul kogutud vaatlusandmete põhjal. Fütoplankton koosneb peamiselt mikroskoopilistest fotosünteesivatest ainuraksetest organismidest. Nagu taimed maismaal, asub fütoplankton toiduahela alusel ning on mootoriks biogeokeemilisele aineringele veeökosüsteemides. Fütoplankton on ühtlasi hea ökoloogiline indikaator, peegeldades toitainete (lämmastik ja fosfor) üleüldist kättesaadavust ja herbivooride (zooplanktoni) aktiivsust.

Viimase poolsajandi jooksul, s.o. alates 1950ndatest, on Läänemeri muutunud kunagisest vähetoitelisest üheks maailma eutrofeerunumaks sisemereks. Püsiv toitainetekoormus kujutab endast ajas süvenevat kroonilist stressi, mis nõrgestab veeökosüsteemide võimet puhverdada järske lühiajalisi muutusi keskkonnas. Sagedamini on seda täheldatud järvedes, kuid järjest rohkem ka ranniku- ja sisemeredes. Läänemere ökosüsteemi haprust peegeldavad näiteks järsud muutused 80ndate lõpus, kui sisuliselt kadus tursa ja kasvas järsult räime asurkond. Järsud ümberkorraldused toiduahela tipus võivad teatud tingimustel kanduda alumiste astmete ja esmastootja arvukusteni. Väidetavalt juhtus see ka Läänemeres – tursa langus põhjustas räime populatsiooni kasvu, mis omakorda nõrgestas zooplanktonit ja viis suvise fütoplanktoni biomassi suurenemiseni. Samas minu töö tulemused räägivad fütoplanktonikoosluse sujuvatest ja muutustest ning 1980ndate lõpu ökosüsteemi nihke fütoplanktoni dünaamikas silmnähtavalt ei kajastu. Fütoplanktonikoosluse pidev muutumine on tõenäolisemalt tingitud muudest teguritest kui tippkiskja vahetumine. Kohanemine eutrofeerumisega, soojemate talvedega, liikide juhuslik saabumine ja kohalik väljasuremine, muutused dominantliikide suhtelises arvukuses – on kõik võrdselt võimalikud seletused liigilise koosseisu järgjärgulisele muutusele.

Läänemere, nagu kogu parasvöötme- ja boreaalse kliimavööndi veeökosüsteemide fütoplanktonit, iseloomustab tugev sessoonsus, nii liikide kui biomassi osas. Sessoonset käiku reguleerib peamiselt valguse erinev kättesaadavus eri aastaegadel. Talvel, kui valgust napib, on primaarproduktsioon minimaalne. Kevadeks on suur osa eelnenud aastal toodetud biomassist regenereeritud ning anorgaaniliste toitainete kontsentratsioonid vees kõrgeimad, millele lisandub ka talvel jõgedega juurde toodu. Kevadel, niipea kui valgus lubab, algab vetikate kevadõitseng, milles globaalselt domineerivad *ränivetikad*[*]. Ränivetikate

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[*] Ainuraksed autotroofsed protistid, kelle eripäraks on peamiselt ränist moodustunud rakukestad. Sellest ka rühma nimetus.

kevadõitsengud on enamasti liigirikkad ning õitsengu ja toitainete lõppedes vajub suurem osa rakkudest kiiresti veesambast välja, vältimaks herbivoore. Seetõttu on ränivetikate kevadõitsengud oluliseks energiaallikaks põhjaelustikule. Veekogude toiteainetekoormuse tõustes põhjustavad massilised ränivetikaõitsengud sageli hapnikupuudust veekogude põhjas, värskelt toodetud biomassi lagundamise käigus.

Läänemere kevadõitsengud on erandlikud. Kõrvuti ränivetikatega, kuigi aastati väga varieeruva edukusega, domineerivad Läänemere kevadõitsengutes vaguviburvetikad. Vastandina ränivetikatele on vaguviburvetikate hulgas kevadeti edukad vaid üksikud liigid. *Peridiniella catenata*, muidu pigem arktiline liik ja meil siin tõenäoliselt relikt ajast, mil Läänemeri oli viimati ühenduses Põhjamerega (ca 7500–4000 aastat tagasi), moodustab põhiosa biomassist kevadõitsengute lõpusfaasis, enne suveperioodi, kui toitained on lõppemas ja veesammas tasapisi kihistumas. *P. catenata* arvukus ja õitsengute dünaamika ei ole ajas eriti muutunud. *Biecheleria baltica*, keda enne 1975 pole seireandmetesse märgitud, kas vähese arvukuse või siis taksonoomilise teabe puudumise tõttu, on olnud ajas dünaamilisem, vastutades vaguviburvetikate viimase aja tõusutrendi eest. Soome lahes domineerib *B. baltica* kevadõitsengu biomassis tavaliselt õitsengute algusfaasis, aprilli alguses. Koos *B. baltica* arvukuse tõusuga on ränivetikate biomass aastate lõikes langenud. Mujale, isegi aladele, kuhu valdavad pinnahoovused võiks *B. balticat* Soome lahest transportida, pole liik silmnähtavalt veel laienenud. *B. baltica* edu on seotud ilmselt tema elutsükliga, mis sobib erakordselt hästi Soome lahe kevadtalve tingimustega.

Kevadõitsengu liigiline koosseis on oluline õitsengu käigus toodetud biomassi omaduste määraja. Kui ränivetikate biomass settib kiirelt peale õitsengut ja hakkab veekogu põhjas lagunema, siis vaguviburvetikad, sõltuvalt liigist, lagunevad veesamba ülemises osas (*Perdiniella catenata*) või settivad lagundamisele vastupidavate puhkerakkudena (*Biecheleria baltica*). Mõlemal juhul on hapnikutarve põhjakihtides oluliselt väiksem kui valdavalt ränivetikatest koosneva kevadõitsengu puhul. Settelähedaste põhjakihtide hapnikupuudus reguleerib setetesse kogunenud fosofri liikuvust, ja on oluline Läänemere ökosüsteemi seisundit mõjutav tegur. Laiaulatusliku anoksia (hapnikupuuduse) korral on täheldatud sinivetikaõitsengute võimendumist (lekkiva fosfori tõttu), lisaks on tursa kudemisalade suurus seotud Läänemere keskosa põhjakihtide seisundiga. Anoksiliste alade suurenemine soodustab ökosüsteemi seda tasakaalupunkti, kus domineerib räim. Ränivetikate osakaalu vähenemine kevadõitsenguis, leevendades põhjakihtide hapnikupuudust, on Läänemere keskkonnaseisundile pigem positiivse mõjuga.

ACKNOWLEDGMENTS

The true value of life, I learned, is the precious people you find and keep. During the years, I have found some to keep. I'm pretty thankful to Moa, for being there and sharing with me her insights to life and love, during many late hours in coffee room, at Gothenburg. It's not always easy to be alone in a place far away from home, but she kept me standing up. I would also like to express my gratitude to Sirpa, for trying to teach me to have fun and relax. Was a nice try! Sometimes I felt, with a smile and a clever look, we exchanged more thoughts than with many words. You definitely made some of my best days in Helsinki! Thank you Karolin, for, providing me a home, good advice and always, always listening my endless troubles. Marko, my dear – can't remember a single time, when you would have said "no" to an invite for a beer or hanging out. I can't even remember the time when I didn't have you as a default part of my life.

In a professional sense I gained significantly from working together with Anke Kremp, Kristian Spilling, Timo Tamminen, Anders Omstedt and Anna Godhe.

Then there are these people, who, in some point on this long trip had an important effect on me, just by being who they are, though they probably don't even know it! Peter Drent, Katherine Richardson, Angela Wulff – I took something from every one of you – be it an attitude or a sense of future and perspective.

Saamuel, Maribel – I never gave you a good answer to why I always wanted to work (not 'had to', but 'wanted to'), I hope you'll understand when the time comes. And one day, in case you should happen to read this – I want you to know that you certainly did your best to cope with my ways of working and living. It's a great privilege and will always remain my sole greatest achievement to have you in my life.

Kalle the Supervisor – thank you, for the last 12 years, for getting me going in the first place, for the inspiration, encouragement, for making me believe that I can, if I just want, for all the wisdom you shared with me. Without you – I would be different, and definitely elsewhere.

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Publications
Olli, K.; Wassmann, P.; Reigstad, M.; Ratkova, T.; Arashkevich, E.; Pasternak, A.; Matrai, Patricia; K., Johan; T., L.; Klais, R.; Jacobsen, A., 2007. The fate of production in the central Arctic Ocean – top-down regulation by zooplankton expatriates? Progress in Oceanography, 72, 84-113

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mete analüüs, statistiline modelleerimine.

Publikatsioonid
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    A.; Matrai, Patricia; K., Johan; T., L.; Klais, R.; Jacobsen, A., 2007. The fate
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