

ANDRES JAANUS

Phytoplankton in Estonian coastal waters –
variability, trends and response
to environmental pressures



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Department of Botany and Ecology, Institute of Ecology and Earth Sciences,
Faculty of Science and Technology, University of Tartu, Estonia

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Supervisor: PhD Kalle Olli, University of Tartu, Estonia

Opponent: Dr. Norbert Wasmund, Leibniz Institute for Baltic Sea
Research, Warnemünde, Germany

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LIST OF ORIGINAL PUBLICATIONS

This thesis is based on the 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. Jaanus A., A. Andersson, I. Olenina, K. Toming & K. Kaljurand, 2011. Changes in phytoplankton communities along a north-south gradient in the Baltic Sea between 1990 and 2008. *Boreal Environment Research* 16 (Suppl. A): 191–208.
- II. Jaanus, A., K. Toming, S. Hällfors, K. Kaljurand & I. Lips, 2009. Potential phytoplankton indicator species for monitoring Baltic coastal waters in the summer period. *Hydrobiologia* 629: 157–168.
- III. Jaanus, A., S. Hajdu, S. Kaitala, A. Andersson, K. Kaljurand, I. Ledaine, I. Lips & I. Olenina, 2006. Distribution patterns of isomorphic cold-water dinoflagellates (*Scrippsiella*/*Woloszynskia* complex) causing ‘red tides’ in the Baltic Sea. *Hydrobiologia* 554: 137–146.
- IV. Jaanus, A. & K. Pellikka 2003. Does excessive phosphorus necessarily cause increasing biomass of diazotrophic cyanobacteria?. *Proceedings of the Estonian Academy of Sciences, Ecology* 52: 205–217.
- V. Ojaveer, H., A. Jaanus, B. MacKenzie, G. Martin, S. Olenin, T. Radziejewska, I. Telesh, M. Zettler & A. Zaiko, 2010. Status of Biodiversity in the Baltic Sea. *PLoS ONE* 5 (9):e12467.
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All papers in this thesis are co-authored with my principal contribution as following:

In papers **I–IV**, data assembling, data analysis and preparing the manuscripts were mainly my responsibilities. I was partly responsible for sample collection and phytoplankton analysis. In paper **V**, a review article, I was responsible for the chapters regarding phytoplankton. J. Kotta gave valuable advice for statistical analysis in papers **I** and **IV**.

I. BACKGROUND AND AIM OF THE THESIS

The Baltic Sea is one of the most intensively studied regional seas in the world; some continuous datasets go back to the early 1950s (V). Despite this, substantial gaps in knowledge still occur. Quantitative phytoplankton time-series data have been poorly published for most of the Baltic sub-basins. Wasmund et al. (2000) made the first trial to compile coastal data from the different countries of the south-eastern Baltic Sea. However, comprehensive attempts to present e.g. spatial phytoplankton distributions over large areas are mostly lacking. Analysis of historical and present day phytoplankton composition data shows that many taxa are now more frequent, and their seasonal dynamics have changed, in comparison to the early 1900s (Wasmund et al., 2008; Hållfors et al., 2008) or during the last decades (Olli et al., 2011).

One aim of my studies was to assess long-term changes in biomass of dominant summer phytoplankton taxa from class to species level in different sub-basins in the Baltic Sea (I). Yet more of the similar attempts are needed in order to be able to understand and explain the mechanisms that regulate the succession and thus what are the intrinsic or extrinsic forces that drive the whole system. In this thesis, the general patterns of seasonal dynamics in four areas of Estonian operational phytoplankton monitoring will be demonstrated together for the first time since the beginning of regular sampling in the early 1990s. This period coincides largely with my own experience in phytoplankton research.

In addition to phytoplankton sampled by conventional methods, intensive datasets collected by means of merchant vessels, hereafter referred as ships-of-opportunity (SOOP) have been analyzed (II–IV). Special attention has been devoted to dinoflagellates – the phytoplankton group dominating in the Baltic sea during the spring period and particularly to the medium-sized single-celled species causing blooms in the northern parts of the sea (III). All data are linked to spatial distributions of abiotic parameters (I–IV) and the results are discussed in relation to present and future environmental challenges to the Baltic Sea.

Data quality, especially the sampling frequency, has been considered as the main problem in elaboration of any ecological assessment. Measuring seasonal changes and inter-annual variability requires extensive sampling efforts. This has been achieved mainly within the framework of national monitoring programs. Inadequate sampling may provide misleading indications of the timing, performance and abundance of dominant phytoplankton taxa. The optimal sampling frequency for the northern parts of the Baltic Sea has been discussed (I, II) and alternative methods of phytoplankton monitoring introduced. Phytoplankton is also determined as one of the biological quality elements for the classification of the ecological status of surface waters. Phytoplankton biomass and bloom frequency are mostly assessed by means of a proxy (Chlorophyll *a*), taxonomic structure and abundance of species are, even if monitored, generally not taken into account. Based on high-frequency

observations, some potential eutrophication indicator species are proposed for the summer period (II).

And finally, phytoplankton constitutes only a part of overall biodiversity in the Baltic Sea (V). Nowadays, it is a common problem worldwide that professionals with extensive knowledge of different groups of aquatic organisms are becoming extinct (Costello et al., 2006). New techniques give opportunity to study large marine areas in more effective way, but the recognition of organism groups itself is receding into the background. It is necessary to keep professional staff with recruitment of younger generation to harmonize methods and to retain and improve skills for taxonomic identification in routine monitoring as well.

2. INTRODUCTION

Phytoplankton species are small (generally 10^{-3} – 10^{-7} m) and short-lived (10^4 – 10^7 s). As a consequence, many generations follow each other in a vegetation period (within a year) making the successional patterns highly dynamic (Padisák et al., 2010). Plankton communities may contain tens, hundreds and sometimes even thousands of species (e. g. Irigoien et al., 2004) with several interacting oscillations within multi-species food webs. In temperate fresh- and brackish-water bodies the environmental constraints for phytoplankton development are similar and can be divided basically into two groups: physical and biological. Physical constraints involve low insolation, cold temperatures, and deep mixing; conditions that commonly prevail between autumn and spring. In the southern Baltic Sea grazing (biological control) becomes of prime importance in breaking the spring bloom of phytoplankton and the spring grazer populations collapse rapidly because they overgraze their food supply. This scenario results in a clear-water phase (typically in May–July, depending on latitude) when neither physical nor biological control on phytoplankton is strong. In the northern parts of the Baltic Sea, where predators are less abundant, the fate of the spring phytoplankton bloom is sedimentation out of the mixed layer (e.g. Lignell et al., 1993; Heiskanen, 1998). During the summer period, competition for limiting nutrients (typically P and/or N) selects for those species that can obtain these resources with the highest efficiency. Parallel, antipredation features (such as large size), and mechanisms for overcoming sinking loss (mucilaginous colonies, buoyancy regulation, and flagellar movement) gain increasing importance (Sommer et al., 1986).

The species composition of plankton may vary markedly from year to year, usually thought to be driven by variation in weather conditions. However, Dakos et al. (2009) refer to mathematical models and laboratory experiments, which have shown that interactions between species may generate striking chaotic fluctuations in species abundances even without external forcing and interannual variability could be an intrinsic property of multi-species communities in seasonal environments. Moreover, the time factor itself may play a significant role – 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 (Olli et al., 2011). Though, the time factor is closely related to human factor. The identification skills are substantially upgraded; on the other hand, the taxonomic precision may be different by different phytoplanktologists or depending on the program requirements when analyzing routine monitoring samples.

Changes in phytoplankton composition may reflect structural and functional ecosystem shifts. For the functioning of the ecosystem it is important that not only key species and functional groups, but also rarer taxa are retained. Most factors affecting the Baltic biodiversity are of relatively recent concern and have localized impact, or information on their impact is poorly documented because

the stressors are relatively recent (V). In a species-poor environment like the Baltic Sea this is particularly critical as major ecosystem functions may be upheld by single species. Recent studies show that Baltic populations of dominant marine species are locally adapted, have lost genetic variation and are relatively isolated (Johannesson et al., 2011).

Previous case studies have resulted in the rough geographic subdivision of the Baltic Sea into the southern and eastern coastal waters, and the northern and western basins. Southern and eastern Baltic coastal waters are characterized by more extensive eutrophication, higher chlorophyll a concentrations and (in extreme cases) all-season dominance of cyanobacteria and green algae. In contrast, northern and western Baltic basins have distinct seasonal successions: diatoms/dinoflagellates–green algae/cyanobacteria–diatoms and summer dominance of dinoflagellates or N₂-fixing cyanobacteria (V; Schiewer 2008). The semi-enclosed ecosystem of the Baltic Sea has experienced a basin-scale shift in state and trophic structure during the 20th century, and especially since the early 1960s (Poutanen & Nikkilä, 2001; Österblom et al., 2007).

In the Baltic Sea, the main factors affecting the primary production are strong seasonality, specific overall hydrophysical features (water exchange, topographical characteristics), and local hydrodynamic variability (upwelling, eddy formation; Nömmann, 1990; Kononen, 1992). Hereto, long-term measurements with high temporal resolution are required to separate natural sources of variability from the effects of anthropogenic disturbance.

3. MATERIALS AND METHODS

3.1. Study areas

Estonian coastal waters belong to different sub-basins of the Baltic Sea area – the Gulf of Finland (GoF), the Gulf of Riga (GoR) and the northern (NBP) and central (CBP) parts of the Baltic Proper. A part of Estonian coastal waters – the Moonsund area (Väinameri) could be taken as a connecting link between the Gulf of Riga and the open Baltic Sea. About 85% of the water exchange of the Moonsund area passes through the straits of Muhu (Suur) Väin and Hari Kurk (Mardiste, 1974). According to the periodic assessment of the state of the Baltic Sea environment, the area north from the Muhu straits is considered to belong to the northern Baltic Proper (HELCOM, 2001a).

3.1.1. The Gulf of Finland

The western end of the GoF is a direct continuation of the NBP, whereas the eastern end receives the largest single fresh water inflow to the Baltic Sea from the discharge of the River Neva. Salinity has pronounced horizontal and vertical gradients in the entire gulf. The average salinity increases from east to west and, on a smaller scale from north to south. The surface salinity changes from 5–6.5 psu (practical salinity unit) in the west of the GoF to 0–3 psu at its easternmost end. A specific feature of the gulf is that horizontal gradients of salinity and temperature can occasionally be significantly large as a result of local upwellings (Soomere et al., 2008). The Gulf of Finland is regarded as one of the areas most affected by eutrophication in the Baltic Sea, with a nutrient load per unit water area 2–3 times higher than the average (Pitkänen et al., 2001a). The concentrations of TN and TP in the Gulf of Finland have been increasing since the 1990s, but stabilized during recent years (HELCOM, 2009).

The GoF comprises two areas of the Estonian coastal water operational monitoring program – Tallinn Bay and Narva Bay.

Tallinn Bay consists of the main basin and smaller bays – Kopli, Kakumäe and Paljassaare with total area of ~250 km². A deep trench (70–90 m) in the northern part of Tallinn Bay allows water from the western Gulf of Finland to enter. Salinity ranges between 4 and 7 psu. The large urban area affects the nutrient status of the surrounding waters, as Tallinn Bay receives most of the local municipal wastewaters. Minor part of pollution comes from ship traffic and Pirita River.

Narva Bay is situated in the south-eastern part of the GoF and reaches about 90 km from west to east. The area is wave-exposed and has good water exchange with the open parts of the GoF. Salinity varies between 3 and 6 psu. Narva Bay has the highest pollution load in the southern GoF due to the inflow from rivers (Narva, Purtse, Pühajõe) and leakage from residual deposits in Sillamäe area. The influence of outflow from Neva River is weak due to higher

stability of cyclonic (counter-clockwise) circulation along the southern coast of the GoF (Alenius et al., 1998).

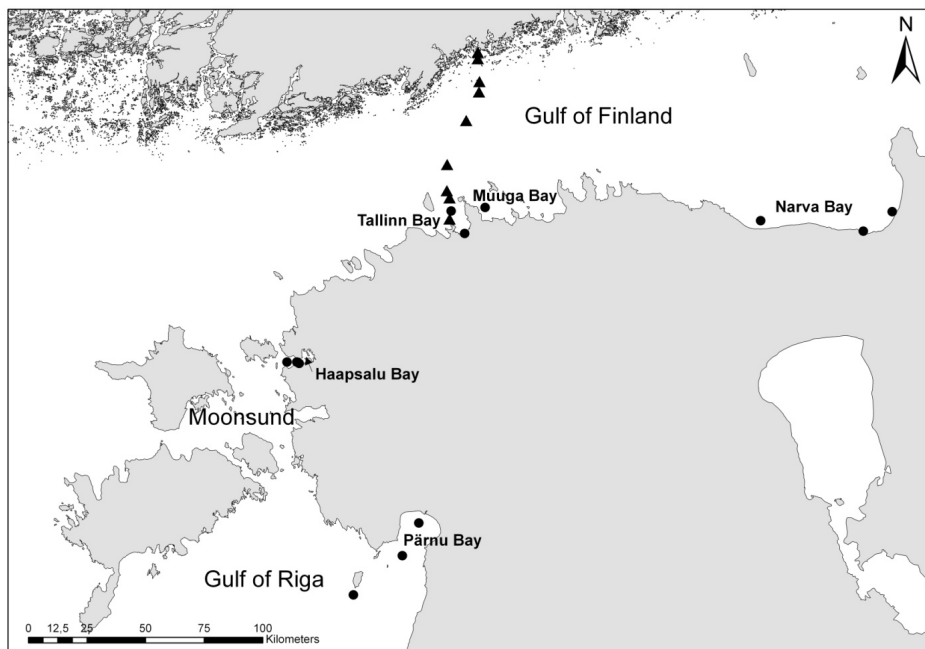


Figure 1. Locations of the sampling stations of Estonian operational coastal (black circles) and SOOP (triangles) monitoring.

3.1.2. The Gulf of Riga

The Gulf of Riga is a wide, shallow, semi-enclosed basin in the eastern Baltic Sea. Mean depth of the gulf is 30 m, the area of Estonian operational coastal monitoring is located in its shallow (< 10 m) north-eastern part. Mean salinity varies from 4.5 to 5.5 psu in the eastern and from 5.5 to 6 in the western parts of the GoR. Due to large riverine discharges to the gulf (drainage area 134 000 km²), the concentrations of nutrients are about twofold as compared to the Baltic Proper and similar to those in the GoF (HELCOM, 2009).

The salinity in Pärnu Bay varies between 3 and 5 psu. The town of Pärnu, with its 45 000 inhabitants, and the Pärnu River with about 10% of total riverine runoff to the GoR (Suursaar, 1995) are the major sources of pollution in the bay. Pärnu Bay was suffering from a heavy anthropogenic eutrophication in the 1970s and 1980s leading to an increase in concentrations of total nitrogen (TN), total phosphorus (TP), and primary production of phytoplankton (Ojaveer, 1995; Tenson, 1995). Since 1990, the wastewater of the Pärnu town is mechanically and biologically treated, but some minor outlets are still operating without wastewater treatment.

3.1.3. Haapsalu Bay

Sinuuous coast-line of West Estonia and the archipelago zone (Moonsund) with the outflow of several small rivers create variable hydrological conditions. Haapsalu Bay with its total area of about 50 km² extends deeply into the land in the western part of Estonia. The maximum depth of the bay is below 5 m and the mean depth is only 1.5–2 m. The inner part of the bay is very shallow with a maximum depth of approximately one meter. The bay is a typical brackish water body with limited water exchange between the inner part of the bay and the open Baltic Sea. The salinity varies between 1 psu in the inner part of the bay and up to 7 psu in Haapsalu Eeslaht – the mouth of the bay. During winter (December to April) the bay is normally covered with ice. The biggest settlement is the local administrative center Haapsalu with a population of approx. 11 500 inhabitants. The wastewater treatment plant in Haapsalu was thoroughly renovated during the late 1990s and early 2000s. In 2001 the nitrogen removal technology was introduced (HELCOM, 2001b).

3.2. Sampling

Under the European Water Framework Directive (EU WFD; European Communities, 2000) new monitoring and classification systems have developed. There are three types of monitoring required:

- 1) Surveillance monitoring – to validate the characterisation of pressure and impact assessments and to detect long-term trends,
- 2) Operational monitoring – to help classify those water bodies which are at risk of failing to meet ‘good ecological status’ and
- 3) Investigative monitoring – to ascertain the cause and effects or a failure to meet ‘good ecological status’ where it is not clear.

In this thesis, phytoplankton obtained from research vessels in the frame of operational monitoring and from merchant vessels, called as ships-of-opportunity (SOOP) are included (Table 1). The locations of the stations are shown in Fig. 1. Observations were generally made at regular intervals throughout the entire investigation period. At all monitoring sites, sampling regularity improved since the beginning of the 2000s, except Haapsalu Bay, where intensive monitoring started only in 2006. Sampling was generally conducted between 0 to 10 m depth using water samplers at discrete horizons (1, 5 and 10 m). In Haapsalu Bay, samples were taken from the surface layer (0.5 m). Samples for phytoplankton and chlorophyll a were obtained by pooling equal volumes (0.5–1 l) of water from different horizons, whereas nutrients were determined from discrete samples.

For SOOP samples, water was pumped through an inlet from a depth of about 5 m onboard the moving ship, but the sample was assumed to represent mixed surface water because of mixing caused by the ferry. Automatic

refrigerated water samplers (ISCO, WS316) conducted water sampling for chemical and phytoplankton analyses. Phytoplankton samples were taken twice a month during May–August and once a month in April, September and October within the frames of traditional monitoring and weekly or biweekly using SOOP sampling.

Phytoplankton samples (100–200 mL) were preserved with acid Lugol solution to a final concentration of 0.2–0.5 % and counted under the inverted microscopes Olympus IM, IMT-2, IX-51, CKX-41 and Leitz Fluovolt using 200–400× magnifications and the settling technique (Utermöhl 1958). All taxa were identified to the level achievable with routine methods. Some taxa, mainly dinoflagellates and nanoflagellates from different classes, cannot be identified to species or even genus level using Utermöhl techniques.

The volume and settling time varied between 3–50 ml and 4–48 h, respectively. Cell sizes were measured using an ocular scale and volumes were calculated from cell geometry (HELCOM, 1988; Hillebrand et al., 1999) or using standard size-classes (Olenina et al., 2006). Recent lists of biovolumes and fixed size-classes are recommended for use in the calculation of phytoplankton biomass in routine monitoring. Wet weight biomasses (mg per litre of seawater) were calculated for individual taxa and for the total biomass (http://www.helcom.fi/groups/monas/CombineManual/AnnexesC/en_GB/annex6).

The chlorophyll a concentration was measured spectrophotometrically (Yanaco UO 2000, Secomam S250I, Jenway 6400 and Libra S32) after extraction in ethanol (http://www.helcom.fi/groups/monas/CombineManual/AnnexesC/en_GB/annex4).

3.3. Data analysis

Raw sample data were treated in different ways before statistical analysis. Missing values in the SOOP samples time series were replaced by averages of neighbouring values in order to get weekly resolution (**II**). In case of traditional sampling, all studied time-series were transformed to monthly means (**I**). To obtain symmetric random deviations, the biomass data of the individual taxa were square-root transformed before the statistical analysis. R versions 2.8.1 and 2.11.1 (R project for statistical computing), PRIMER versions 5 and 6 (Clarke & Gorley, 2001 & 2006) and Statistica version 6 (StatSoft Inc., 2004) were used to conduct the analyses.

Welch two sample t-test was used to detect significant differences ($p < 0.05$) in the phytoplankton and environmental data to discriminate changes in time-series data (**I**). Relationships between environmental variables and the whole phytoplankton community or dominant phytoplankton groups were identified by BIOENV (**I**, **II**). Statistically significant differences in the biomass of different species among sampling stations and weeks were tested with an ANOSIM (analysis of similarity) procedure (**II**). Nonmetric multidimensional scaling (MDS) was used to examine temporal variation in phytoplankton (**II**).

Table 1. Availability of phytoplankton wet weight biomass (mg ww l^{-1}) data in the areas of Estonian operational coastal water and Ferrybox (SOOP) monitoring. X indicates at least one sampling event per month and area. * – Tallinn-Helsinki until April 2006, Tallinn-Stockholm since May 2006.

Area	Narva Bay										Tallinn Bay										Pärnu Bay										Haapsalu Bay										Ferrybox*									
Month	4	5	6	7	8	9	10	4	5	6	7	8	9	10	4	5	6	7	8	9	10	4	5	6	7	8	9	10	3	4	5	6	7	8	9	10														
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4. RESULTS AND DISCUSSION

4.1. Seasonal cycles and long-term variability of phytoplankton communities

Changes in phytoplankton biomass and species composition reflect not only the effects of eutrophication but also climatic change (e.g. Howarth et al., 2000; Neumann, 2010). It is, however, hard to prove trends statistically because of high variability due to natural patchiness and insufficiencies in sampling. Past studies of phytoplankton from the open Baltic Sea (Suikkanen et al. 2007) and the Kiel Bight (Wasmund et al. 2008) revealed an increase in total biomass (chlorophyll *a*), but the changes at the community level were more complex, showing both upward and downward trends. Wasmund and Uhlig (2003) have shown that the abundance of dinoflagellates generally increased in the central and southern parts of the Baltic proper in spring during the time period 1979–1999, whereas the abundance of diatoms decreased significantly. The reason for increased abundance of dinoflagellates is not yet clear, but both changes in climatic conditions and anthropogenic nutrient enrichment are factors that might be involved (Smayda, 1990; Kauppila & Lepistö, 2001). An increase in winter nutrient concentrations should theoretically cause changes in spring phytoplankton biomass. However, intensive measurements of chlorophyll *a* in the open Baltic Sea have not yet confirmed such an increase in spring phytoplankton biomass, although a slight tendency for the bloom to start earlier has been observed (Fleming & Kaitala, 2006). This earlier development of the spring bloom suggests that the summer phytoplankton communities will also develop earlier.

Various coastal environments experiencing increased nutrient loading have exhibited general trends of shifts in phytoplankton community dominance from larger to smaller cells (Cederwall & Elmgren, 1990; Cadee, 1992). A mesocosm experiment, in which seawater from the northern Baltic Sea was used, has also revealed that relatively small phytoplankton species appear to be favoured by nutrient loading and the average cell-size does not increase with nutrient enrichment (Andersson et al. 2006). The same trend has been observed in natural communities. Finni et al. (2001) found that small flagellates (crypto-, prymnesio-, chryso-, prasinophytes and the euglenoid *Eutreptiella* spp.) dominated moderately eutrophic coastal water bodies. The increased abundance of planktonic diatoms in the coastal waters of the Gulf of Finland, especially some fragile diatom (*Skeletonema marinoi*, *Cyclotella choctawhatcheeana* and *Chaetoceros minimus*) have also been attributed to increased eutrophication and turbidity (Finni et al. 2001; Weckström et al. 2007; II). The acceleration of eutrophication processes in different basins of the Baltic Sea took place since the beginning of the 1960s (Poutanen & Nikkilä, 2001). However, in the Gulf of Finland small flagellates considerably contributed to the primary production already then (Niemi, 1975).

Salinity gradient provides the basic difference between the southern and the northern as well eastern and western parts of the Baltic Sea. There are also significant environmental variations between the coastal areas and the open sea, being expressed by different trophic status and/or shifts from one to another limiting nutrient, usually from P to N-limitation besides different salinity conditions. In Estonian coastal waters, phytoplankton succession shows different timing patterns from both north to south and east to west. Both salinity gradient and nutrient conditions are important when comparing phytoplankton communities in different locations. Investigations of changes in biomass of summer (June–September) phytoplankton over the last two decades (1990–2008) along a north–south gradient in the Baltic Sea revealed increases in total phytoplankton biomass, particularly cyanobacteria, in the Gulfs of Bothnia and Finland (I). In these two areas over the study period cyanobacteria also became abundant earlier in the season.

The predominant taxa according to wet weight biomass differ between the areas of coastal water operational monitoring (Table 2). Devlin *et al.* (2009) have found that there is a substantive seasonal influence to the data, with common species reoccurring within the same calendar month over a 10-year time span. When the datasets are shorter in time, the ranking of dominant taxa by water bodies and months is to some extent affected by the magnitude of exceptional bloom events in single years. In that case, a single heavy bloom event captured in monitoring sample may be weighty to entire dataset. Wasmund and Uhlig (2003) suggest that a consistent time series of >20 years is required for reliable indications of long-term changes in phytoplankton biomass and community structure. Most plankton data that are currently available in marine areas are, however, unsuitable for trend analysis due to sparse sampling and natural inter-seasonal variability (McQuatters-Gollop *et al.* 2009). In addition, changes in methodology constitute the main problem for the comparability of historical data with recent data (Wasmund *et al.*, 2008). Estonian regular monitoring data date back to the early 1990s, in some areas (Narva and Haapsalu bays) only to the last decade (the 2000s). On this reason, all changes in phytoplankton biomass and community structure should be treated cautiously and variability or fluctuations would be more correct terms.

Table 2. Monthly predominant phytoplankton taxa according to mean wet weight biomass (1990–2010) in the areas of Estonian coastal water operational monitoring.

Month	Tallinn Bay	Narva Bay	Pärnu Bay	Haapsalu Bay
April	<i>Scrippsiella</i> complex <i>Thalassiosira levanderi</i> <i>Thalassiosira baltica</i>	<i>T. baltica</i> <i>Achnanthes taeniata</i> <i>Scrippsiella</i> complex	<i>T. baltica</i> <i>Achnanthes taeniata</i> <i>Peridiniella catenata</i>	<i>Diatoma tenuis</i> <i>Chaetoceros wighamii</i> <i>Melosira arctica</i>
May	<i>Scrippsiella</i> complex <i>Peridiniella catenata</i> <i>T. baltica</i>	<i>A. taeniata</i> <i>P. catenata</i> <i>T. baltica</i>	<i>P. catenata</i> <i>A. taeniata</i> <i>T. baltica</i>	<i>D. tenuis</i> thecate dinoflagellates <i>M. rubrum</i>
June	<i>Aphanizomenon</i> sp. <i>Mesodinium rubrum</i> <i>Dinophysis acuminata</i>	<i>Diatoma tenuis</i> <i>Aphanizomenon</i> sp. <i>M. rubrum</i>	<i>M. rubrum</i> <i>Aphanizomenon</i> sp. <i>Monoraphidium contortum</i>	thecate dinoflagellates <i>Pyramimonas</i> spp. Ullotrichales
July	<i>Aphanizomenon</i> sp. <i>Heterocapsa triquetra</i> <i>Nodularia spumigena</i>	<i>Aphanizomenon</i> sp. <i>Pseudanabaena</i> sp. <i>M. rubrum</i>	<i>Aphanizomenon</i> sp. <i>M. rubrum</i> <i>Pyramimonas</i> spp.	thecate dinoflagellates <i>Cylindrotheca closterium</i> pennate diatoms
August	<i>H. triquetra</i> <i>Aphanizomenon</i> sp. <i>N. spumigena</i>	<i>Aphanizomenon</i> sp. <i>Pseudanabaena</i> sp. <i>Dolichospermum</i> spp.	<i>Aphanizomenon</i> sp. <i>C. granii</i> <i>A. octonarius</i>	thecate dinoflagellates <i>Chrysochromulina</i> spp. <i>C. closterium</i>
September	<i>Aphanizomenon</i> sp. <i>Coscinodiscus granii</i> <i>M. rubrum</i>	<i>Aphanizomenon</i> spp. <i>Pseudanabaena</i> sp. <i>Dolichospermum</i> spp.	<i>C. granii</i> <i>Aphanizomenon</i> sp. <i>Cyclotella choctawhatcheeana</i>	<i>Chrysochromulina</i> spp. thecate dinoflagellates <i>M. rubrum</i>
October	<i>C. granii</i> <i>M. rubrum</i> <i>Actinocyclus octonarius</i>	<i>Aphanizomenon</i> sp. <i>Eutreptiella</i> spp. <i>M. rubrum</i>	<i>C. granii</i> <i>Aphanizomenon</i> sp. <i>Teleaulax</i> spp.	<i>M. rubrum</i> <i>H. triquetra</i> <i>C. granii</i>

4.1.1. Spring bloom

Typically to temperate water bodies, the spring and summer blooms are the most pronounced phenomena in seasonal succession of phytoplankton. The spring bloom in the Baltic Sea moves wavelike from the south to the north and usually develops in March, reaches peak abundances in April, and terminates in late May/early June in its northern parts (Hobro, 1979; Höglander et al., 2004). Diatoms generally prevail during the first phase of the succession in temperate and boreal coastal areas as they are generally adapted to more turbulent environments characterized by high nutrient concentrations (Margalef, 1978; Smayda & Reynolds, 2003).

The dominance of dinoflagellates in the Baltic Sea phytoplankton vernal communities, is rather exceptional in temperate coastal waters. The taxonomic affiliations of the involved medium-sized (15–30 μm) single-celled dinoflagellate species causing mass occurrences, beside easily identified *Peridiniella catenata*, have long been unclear (see references in III). From the late 1990s, the spring dinoflagellate blooms in the northern Baltic Sea had been attributed to a species with delicate thecal plates called *Scrippsiella hangoei* (Larsen et al., 1995). Recent molecular and SEM analyses of the dominant bloom species in the Gulf of Finland revealed considerable differences to the species description of Larsen et al. (1995) described from an isolated culture, implying that another more or less isomorphic species co-occurs with *S. hangoei*. This dinoflagellate was identified as *Gymnodinium halophilum* Biecheler (1952) and was transferred to *Woloszynskia* as *W. halophila* (Kremp et al., 2005). However, more recent studies have shown that thin-walled dinoflagellate species, known as woloszynskioids, fall into several taxonomic groups. Moestrup et al. (2009) considered it unlikely that the material studied by Kremp et al. (2005) represents Biecheler's organism, due to both ecological and morphological differences. The differences warranted the description of the organism isolated from the Baltic Sea as a separate, new species, *Biecheleria baltica* sp. nov. Yet another morphologically similar species is now described – *Gymnodinium corollarium* (Sundström et al., 2009).

When observed by conventional light microscopy, the vegetative cells of the abovementioned species cannot be distinguished. As the identification of *Scrippsiella*/*Biecheleria*/*Gymnodinium* to separate species is not reliable in preserved monitoring samples, these taxa are called *Scrippsiella* complex in the present thesis. As all species of the *Scrippsiella* complex have slightly different temperature and salinity preferences (Kremp et al. 2005; Sundström et al., 2009), they might exhibit different spatial and temporal distribution patterns in the Baltic Sea, although an overlap is expected to some extent (Sundström et al., 2010). Considering the window of survival for these species, with respect to salinity, the species of *Scrippsiella* complex could be expected to occur throughout the Baltic Sea with an exception of *Biecheleria baltica* in the north since it does not grow in salinities below 3. In late spring, *B. baltica* is also

restricted by temperatures below 6°C whereas the other two species can grow in temperatures up to 10°C (Sundström, 2010).

The bloom forming species *G. corollarium*, *S. hangoei* and *B. baltica* all have the ability to form resting cysts. Cysts can be relatively easily identified under the light microscope compared to vegetative cells, and field observations suggest *G. corollarium* to be abundant in the whole Baltic Proper (Sundström, 2010). Large abundances of *B. baltica* cysts have been observed in the Gulf of Finland, where encystment of this species accounted for 40% of the investigated dinoflagellate population (southwest coast of Finland; Kremp & Heiskanen, 1999), whereas cysts of *S. hangoei* appear to be less abundant (Kremp, pers. comm.). The treatment of sediment samples is, however, time-consuming and cannot be used routinely either.

4.1.1.1. The Gulf of Finland

The dinoflagellate *Scrippsiella* complex is predominant in spring phytoplankton of the central Gulf of Finland including Tallinn Bay. The species complex has a vegetative inoculum known to immediately exploit favourable growth conditions in early spring (Kremp, 2000). The *Scrippsiella* complex often made up to 75% of the total phytoplankton biomass already in March being the first dominant in the spring bloom development (Fig. 4 in **III**). Maximum cell densities of *Scrippsiella* complex in the water column have been mainly obtained in April or in the beginning of May at water temperatures <3°C prior to thermal stratification was formed. A second maximum at temperature >6°C may occur (**III**). Only in the second half of May *Scrippsiella* complex is gradually replaced by *Peridiniella catenata* and other species. It allows to conclude that medium-sized single-celled dinoflagellates are an essential components of the vernal phytoplankton community and that the *Scrippsiella* complex bloom is rather a yearly phenomenon at least in the Gulf of Finland (**III**).

Analysing the distribution of dinoflagellate cysts, Olli and Trunov (2010) found that all sampling locations with high cyst abundances were muddy with a high percentage of organic content. The number of observed living cells of *Scrippsiella* complex is very high near the Finnish coast (Fig. 2 & 3 in **III**). The Finnish coastline mainly consists of bedrock, but the sediments in the outer archipelago and open sea zone are mostly mudcovered. Kremp (2000) even suggested that the annual blooms of medium-sized dinoflagellates in the northern Baltic Sea are seeded by large coastal resting cyst populations and the offshore blooms likely originate from those coastal inocula transported to the central parts of the Baltic Sea by outflowing surface water.

The spring blooms usually peaks at the end of April in Tallinn Bay and in the first half of May in Narva Bay. The *Scrippsiella* complex is predominating in Tallinn Bay throughout the spring bloom period (April-May), while its biomass is decreasing towards the east. In Narva Bay diatoms – mainly *Thalassiosira baltica* and *Achnanthes taeniata* are dominating the spring communities

and *P. catenata* is the most abundant dinoflagellate species, especially in May. The deviations from the average spring bloom patterns in Tallinn Bay were recorded after severe winters 1994 and 1996 with dominance of arctic diatom *Achnanthes taeniata*, in 1990 and 2010, when the cold-water dinoflagellate *Peridiniella catenata* prevailed in the southern GoF and in 1997 with dominance of cold-water diatom *Chaetoceros wighamii*. After mild winters, especially in 2002, the nanoplanktic diatom *Thalassiosira levanderi* reached record abundance and biomass in Tallinn Bay. The mass development of low-salinity adapted diatom *Diatoma tenuis* like in May 1996 in Narva Bay may be considered as a deviation as well. Usually, the spring bloom terminated earlier after mild winters and post-bloom species like the autotrophic ciliate *Mesodinium rubrum* appeared among dominants already in May in the western and central parts of the GoF. The analysis with NAO indices showed that the overall magnitude of spring bloom increases after severe winters (see chapter 4.3.1).

4.1.1.2. The Gulf of Riga

The general succession of phytoplankton in Pärnu area is similar to that in Narva Bay, although with bloom peak approximately one month earlier. Monitoring observations made in the Gulf of Riga and in the adjacent areas to the central Baltic Proper in March–April indicate the clear dominance of diatoms, mainly *Thalassiosira baltica* and *Achnanthes taeniata*. The latter species has been also identified from under-ice blooms (Tenson, 1995). In the north-eastern part of the GoR, the dinoflagellate *Peridiniella catenata* adds to the dominants in April and persists high abundance in the water column until the end of May in some years. The dominant species have, however, been different in different years during the biomass maxima. The most prominent spring blooms during the recent decades have been dominated by *P. catenata* (in 1998 and 2001), *T. baltica* (2002), the diatom *Chaetoceros wighamii* (2005) or a mixture of all diatom species mentioned above (2009). The most striking difference in comparison to the Gulf of Finland is very low abundance of the diatom *Skeletonema marinoi* and the dinoflagellate *Scrippsiella* complex. The Gulf of Riga has approximately the same salinity range as the central GoF, where *Scrippsiella* complex is dominating the spring bloom (fig. 3 in III). Thus, salinity seems not to be the main factor governing the distribution of *Scrippsiella* complex. The organic-rich soft bottom, one possible precondition for *Scrippsiella* bloom (III; Olli & Trunov, 2010), is prevailing only in the middle deepest (40–55 m) part of the GoR (Stiebrinš & Väling, 1996) and a seed population of this species complex can be theoretically available at least there.

Yurkovskis et al. (1999) noticed an increase in the the percentage of dinoflagellates in the spring blooms at the end of 1980s and the beginning of the 1990s and attributed it to the increase in *Peridiniella catenata* biomass. Olli et al. (2008), analysing the long-term nutrient and phytoplankton time-series from

the GoR basin, however, found a high frequency of low after spring bloom dissolved silica (DSi) concentrations during the same period and associated it to preceding exceptionally intense diatom spring blooms dominated by the heavily silicified species *T. baltica*. Making DSi consumption and biomass yield experiments with cultured *T. baltica* they suggested that intense blooms can potentially exhaust the DSi stock of the water column and exceed the annual Si dissolution in the Gulf of Riga.

The spring chlorophyll *a* and phytoplankton biomass maxima can only be accidentally obtained by low frequency sampling. The bloom in Pärnu Bay starts most likely under the ice and the peak of the spring bloom has often past, when monitoring season begins. For that reason, the whole duration and succession of spring bloom in the GoR remains unclear.

4.1.1.3. Haapsalu Bay

Similarly to Pärnu Bay, the bloom in Haapsalu Bay starts under the ice or during the ice-break in March or in the beginning of April. Unlike the Gulf of Riga, the euglenophytes and cryptophytes constituted the initial communities in March 2000 in Haapsalu Eeslaht and euglenophytes with thecal dinoflagellates in Haapsalu Tagalaht. The monitoring activities have usually begun only when the basin is totally ice-free, i.e. in the second half of April. Due to this reason, the understanding about early succession of phytoplankton in Haapsalu Bay is inadequate. In April and May, the oligohaline diatom *Diatoma tenuis* prevails, accompanied with *Chaetoceros* spp., *Achnanthes taeniata* and *Melosira arctica*. The dinoflagellates from the order Peridiniales and the autotrophic ciliate *Mesodinium rubrum* become dominant in May. The peak biomasses are usually much higher in the semi-enclosed eastern part of the bay than in the open western part.

4.1.2. Summer communities

Depending on the severity of preceding winter and the conditions during the spring bloom, the transfer to summer phytoplankton communities occur from the mid of May in the Gulf of Riga and the Moonsund area to the end of June in the south-eastern Gulf of Finland.

4.1.2.1. The Gulf of Finland

The predominant taxa in the summer period are filamentous cyanobacteria (*Aphanizomenon* spp., *Dolichospermum* spp., *Pseudanabaena* sp. and *Nodularia spumigena*), dinoflagellates (*Heterocapsa triquetra* and *Dinophysis acuminata*) and the autotrophic ciliate *Mesodinium rubrum*. June is usually the period of summer minimum. The samples with higher biomass in June contain mainly spring species with dinoflagellates and diatoms dominating the

community. The autotrophic biomass peaks in July, when cyanobacteria, mainly filamentous taxa constitute over 50% of total biomass. Large cyanobacterial blooms in Tallinn Bay are, however, recorded only in 1997, 1999, 2002 and 2010, and in 2004 in Narva Bay. In 1998 and 2008 dinophytes, mainly *Heterocapsa triquetra*, briefly reached 70–90% of the total phytoplankton biomass. The estimated proportion of nanoplanktonic flagellates (eugleno-, prymnesio- and prasinophytes in July–August, and cryptophytes in August–September) of the total biomass is ~20% on average. In September, diatoms (mainly *Coscinodiscus granii*) reappear and become the dominant component of the phytoplankton, but in most years the phytoplankton biomass decreases 2–3 fold, compared to the maximum summer values. Exceptionally, the potentially toxic dinoflagellate *Prorocentrum minimum* reached bloom-like concentrations in autumn 1999 and 2003. *P. minimum* is considered to be the only reliably identified invasive alien phytoplankton species in the Baltic Sea causing a recognizable environmental effect (Olenina et al., 2010).

Temperature and salinity are the main factors shaping the summer phytoplankton communities in the Gulf of Finland. The salinity factor is expressed by gradual eastwards disappearance of some dominating or abundant taxa (*N. spumigena*, *H. triquetra*, *Chrysochromulina* spp.) and rise in relative importance of low salinity and freshwater species (*Dolichospermum* spp., *Pseudanabaena* spp.).

Analyzing spatially and temporally frequent samples from the northern GoF, Rantajärvi et al. (1998a) also revealed that the proportion of marine dinoflagellates decreases towards the east and the phytoplankton biomass is more evenly distributed between the different groups in the western areas.

Due to longer data series, temporal changes in summer phytoplankton are analyzed only in Tallinn Bay. Most of the statistically significant changes over the study period have been related to increases in the mean seasonal or monthly biomass values at different taxonomic levels (Fig. 4 and table 3 in I). Gasiūnaitė et al. (2005) suggested that cyanobacterial blooms are highly variable, due to their inhomogeneous distributions in time and space, which hinders the identification of steady trends. However, the most prominent rise in total biomass in Tallinn Bay in June between 1994–1998 and 1999–2003 has been accompanied by an increase in cyanobacterial biomass, especially *Aphanizomenon* sp. But, the last cyanobacterial mass developments in June were recorded in 1999, 2002 and 2005 (Fig. 2). After that, the blooms have been rather moderate and peaked in July–August.

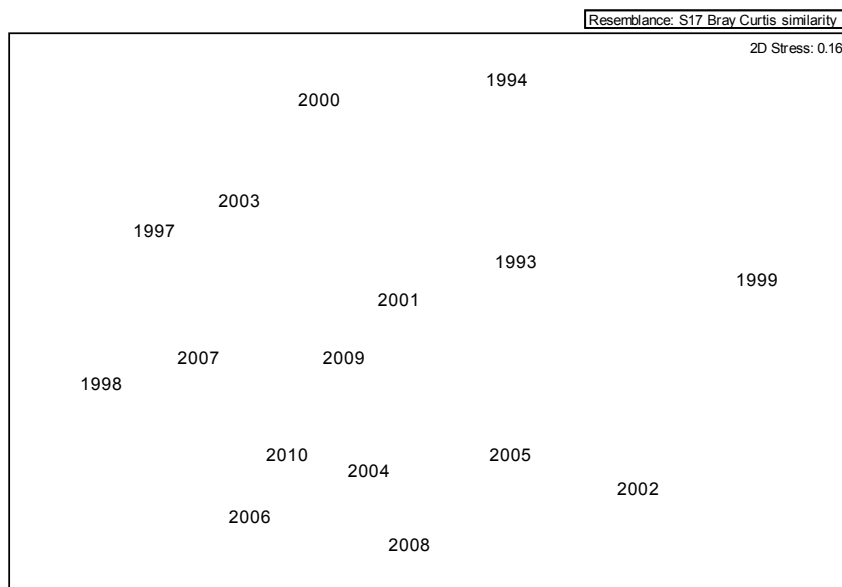


Figure 2. MDS ordination of phytoplankton biomass data collected in Tallinn Bay in June between 1993 and 2010. The distances between the year's numbers are proportional to dissimilarities in phytoplankton community structure. The years 1999, 2002 and 2005 represent heavy early summer cyanobacterial blooms.

Small biomass increases have been observed in case of the oscillatorean cyanobacteria *Pseudanabaena* sp. and the diazotrophic genus *Dolichospermum*. The autotrophic ciliate *Mesodinium rubrum* shows a steady increase in June. *M. rubrum* has reached its biomass peak after spring bloom also in another Baltic sub-basin – the Bothnian Sea (Andersson et al., 1996). The increasing biomass of this species together with *Aphanizomenon* sp. in June may have resulted from an earlier decline of spring communities and replacement by summer species. However, due to gaps in spring datasets, this cannot be confirmed yet for the southern GoF.

Substantially lower total phytoplankton biomass values during last years (2008–2010) have been observed in Narva Bay. One reason for that is decrease in biomass of diazotrophic cyanobacteria – the last bloom event of this group was recorded in 2004. On the other hand, an increase in the abundance of some nanoplanktic species (*Pyramimonas* spp., *Eutreptiella gymnastica*) has been noticed.

4.1.2.2. The Gulf of Riga

The transition to summer phytoplankton communities may occur already in the second half of May and the autotrophic ciliate *Mesodinium rubrum* usually prevails in the total biomass. In some years, the filamentous cyanobacterium

Aphanizomenon sp. has also grown intensively since the end of May, especially in the open parts of the Gulf, but almost never formed bloom-like densities or surface accumulations like in the Baltic Proper or in the Gulf of Finland. Olli (1996) attributes this early development of filamentous N₂-fixing cyanobacterium to very low inorganic N/P ratio, indicating nitrogen as a potentially limiting factor for phytoplankton growth. Yurkovskis et al. (1999) bring out the increasing role of dinoflagellates, green and blue-green algae in phytoplankton of the GoR since the 1990s and simultaneous decrease in diatom biomass. According to Estonian monitoring data diatoms have been dominant in late summer phytoplankton during last decades, at least in the north-eastern part of the GoR. A general feature of the summer phytoplankton in the GoR is the relatively low biomass (mostly below 1 mg l⁻¹) and only exceptional mass occurrence of any species. As an example, the mass occurrence of the nanoplanktonic diatom *Cyclotella choctawhatcheeana* in September 2002 might be brought on. Differently from the Gulf of Finland, the occurrence of some brackish-water species (the dinoflagellate *Heterocapsa triquetra*, prymnesiophytes) are of minor importance in summer phytoplankton.

Observations in Pärnu Bay have revealed an increase in both chlorophyll *a* concentrations and total phytoplankton biomass in the beginning of 2000s. The dynamics of chlorophyll *a* has been fluctuating during recent decades with moderate increase in the late 1980s and decline in the 1990s. The species composition has been monitored regularly since the end of 1990s and no clear trends can be demonstrated yet. However, the relative importance of filamentous cyanobacteria (mainly *Aphanizomenon* sp.) has been increasing during the last years and the mean abundance of this species in summer phytoplankton is now comparable to that in Narva Bay (Fig. 3). Similarly to Narva Bay, the abundance of nanoplanktonic prasinophytes *Pyramimonas* spp. has been on the increase during the second half of the 2000s. Moreover, the biomass maxima of *Pyramimonas* have been observed together with short-term TN pulses in 2004, 2005 and 2010. Kotta et al. (2004) attribute the strong decline of phytoplankton biomass in the early 1990s in Pärnu Bay to the lower loads of nutrients by better water treatment and lower intensity of agriculture in the catchment area. Both the concentrations of TN and TP in the Gulf of Riga have declined during the last decades (HELCOM, 2009).

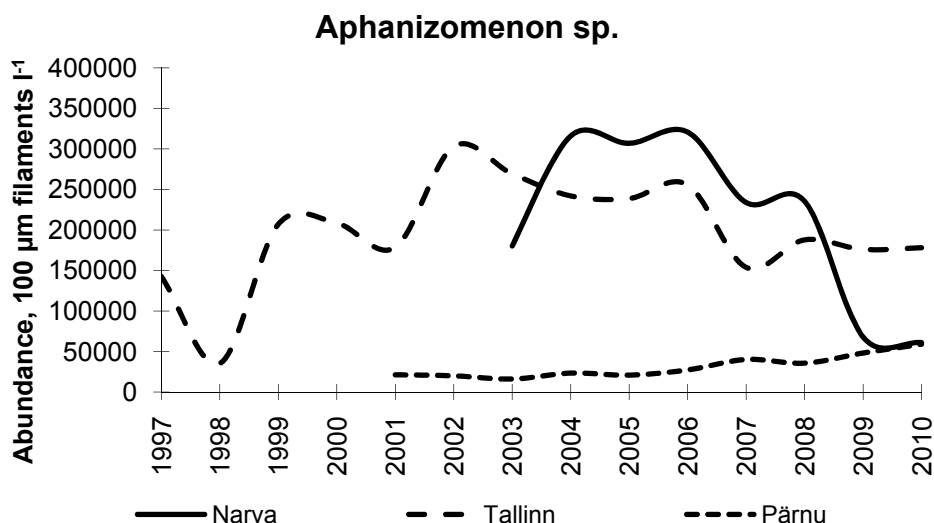


Figure 3. The dynamics of filamentous cyanobacterium *Aphanizomenon* sp. (100 µm filaments per litre) between June 15 and July 31 in areas of Estonian coastal operative monitoring during 1997–2010; 5-years moving average.

4.1.2.3. Haapsalu Bay

The semi-enclosed eastern parts of Haapsalu Bay are heavily eutrophied with about twofold concentrations of TP and 1.5-fold concentrations of TN compared to the gulfs of Finland and Riga. The eutrophic conditions are characterized by large biomass values increasing towards late summer and a sharp gradient in chlorophyll *a* concentrations and total phytoplankton biomass by a factor of 5–10 to 40 compared to the western open part of the bay. Strong and long-lasting blooms are yearly phenomena and the biomass drops only in October due to poor light conditions.

The dinoflagellates from the order Peridiniales have become predominant in summer phytoplankton, especially in the sheltered eastern part of the bay. The identification with calcofluor methods (Fritz & Triemer, 1985) suggests that the species with highest biomass are *Kryptoperidinium foliaceum* and *Durinskia baltica* (Kremp, pers. comm.). An alternative opinion from Guy Hällfors (pers. comm.) gives the names *Peridiniopsis borgei* or *P. polonicum* to the dominating taxa. G. Hällfors still admit that in the 1970s, *K. foliaceum* was identified from a living sample of an almost unialgal bloom in water then strongly affected by domestic waste and effluents from cellulose factory. He suggest *K. foliaceum* be strongly favoured by eutrophication and appears to prefer coastal and archipelago localities. The more precise identification methods like genetic examination of cultivated material and electron microscopy are needed.

A few samplings in Haapsalu Bay have been conducted already in the 1970s and 1980s, but phytoplankton has been frequently monitored only for five years. The diversity of higher taxa (at class level) which have belonged to the summer dominants is large – nostoco-, dino-, prymnesio-, diatomo-, prasino-, chloro-, charo- and conjugatophytes and the autotrophic ciliate *Mesodinium rubrum*. The most abundant or dominant species do mostly not coincide with those found in other areas of Estonian coastal monitoring or appear with unusual timing during the season (Table 2). For example the benthic diatoms from different genera (*Melosira*, *Amphiprora*, *Cocconeis*, *Stephanodiscus*, *Cyclotella*) and the conjugatophytes from the genera *Cosmarium* and *Closterium* notably contributed to total biomass in 2010, while the pennate diatom *Cylindrotheca closterium* was very abundant in summers 2006–2008. The general succession of phytoplankton communities in Haapsalu Bay has, however, not changed between 1970s and 1980s, and the biomass values obtained in the 2000s are similar to those calculated from the earlier samples (Jaanus, 2003).

4.2. Factors governing seasonal patterns

Year-to-year fluctuations in phytoplankton species compositions are governed by hydrographical and hydrochemical drivers. Physical constraints may be as important, if not more important, than biological ones in shaping the structure of phytoplankton assemblage.

The succession of phytoplankton has a rather regular pattern and the initial events like vernal blooms may also influence the formation of summer communities. Firstly, the dominance of either diatoms or dinoflagellates in spring period determines the rate of sinking organic matter and subsequent oxygen consumption in bottom sediments. The diatoms settle out quickly and cause oxygen depletion, which may in turn launch the release of phosphorus from sediments and favour the phytoplankton, which benefits by excessive P, especially diazotrophic cyanobacteria blooms (e. g. Eilola et al., 2009).

Both experimental results and models indicate that cyanobacteria respond more strongly to climate change than diatoms or green algae (De Senerpont Domis et al. 2007; Moore et al. 2008).

Although weather conditions and high nutrient loads were cited as an explanation for the mass development of cyanobacteria, their blooms have been recurrent as long as the Baltic Sea has been brackish (e.g. Bianchi et al., 2000). Finni et al., (2001), however, note that the blooms have been more frequent since the 1960s in the open sea in both the Baltic Proper and the Gulf of Finland.

4.2.1. Temperature and salinity

The statistical analysis of both high-frequency SOOP and traditional monitoring data showed that water temperature in combination with salinity has the strongest impact on the summer phytoplankton community structure in the Gulf of Finland (**I**, **II**). While water temperature has been found the most influential factor affecting the timing of blooms and the community structure of both spring (e. g. Lewandowska & Sommer, 2010) and summer phytoplankton, especially in the northernmost parts of the Baltic Sea (Gasiūnaite et al., 2005; Suikkanen et al., 2007; **I**), salinity has been considered to be the main factor influencing the species distribution (Wasmund et al., 2000). The highest number of phytoplankton taxa in Baltic sub-basins is recorded in the Gulf of Finland, where surface salinity varies from 0 to ~7 psu (Fig. 2 in **V**). Both salinity and temperature effects may, however, be associated or combined with the effects of nutrients (e. g. Table 5 in **I**). A decrease in summer salinity accompanied by an increase in cyanobacterial biomass in the Gulf of Finland (Suikkanen et al., 2007), and negative correlation between the increase in oscillatorean biomass and salinity (**II**) are likely combined with temperature. Notably, high water temperature has often been suggested as a prerequisite for intensive cyanobacterial bloom development, for example, the optimal temperature for *Aphanizomenon flos-aquae* ranges from 16 to 22°C (e.g. Pliński et al. 2007). Our study still indicate that *Aphanizomenon* sp. may become dominant already by the water temperature 10–12°C (**IV**). Oscillatoriales exhibited a positive correlation with temperature in our study in the Gulf of Finland (**II**). On the other hand, oscillatorean species are found to be sensitive to increasing nutrient loads (**II**). The combined effect of temperature and TN to the biomass of diatoms and small flagellates (especially prasinophytes) have been also revealed in the same area (**I**, **II**). Increasing air and sea surface temperatures in the late 1980s resulted in an extended growing season and increases in phytoplankton biomass (chlorophyll *a*) in both the North Sea and Baltic Sea (Alheit et al. 2005). Although monitoring data do not show any significant increase in surface water temperature during the last decades, it is possible that only a very small change may have occurred and further changes may cause major shifts in the dominant phytoplankton species.

4.2.2. Stability of water column

Non-motile (mainly diatoms) and motile algae (flagellates) have different preferences for environmental conditions owing to their different abilities. Diatoms prefer turbulent waters in order to keep suspended whereas flagellates need stratified waters in order to benefit from their ability to choose their optimum water depth. Some cyanobacteria may also accumulate at specific water depths by buoyancy regulation and therefore dislike mixing of the water (Thamm et al., 2004). The onset of the spring bloom is regulated by the

availability of light and onset of stratification (Smetacek & Passow, 1990) rather than by nutrients, which occur in excess throughout the winter. The water column in the Baltic Sea becomes stratified due to freshwater inputs from rivers (Eilola & Stigebrandt 1998). Although Smetacek & Passow (1990) and Wasmund et al. (1998) have considered the temperature gradient as a stabilizing mechanism for the initiation of the vernal bloom, the freshwater eddies stratify the water column and inhibit the convection that would otherwise take place until water warms above the temperature of maximum density of sea water (Stipa & Vepsäläinen, 2002). In calm conditions, after ice-free mild winters and during early development of shallow thermocline, dinoflagellates dominate over diatoms in the Baltic Sea (Heiskanen, 1998; Hajdu, 2002). However, the scenarios whether diatoms or dinoflagellates thrive, depend not only on the stability of the upper mixed layer, but also on the size of the inoculum's population of dinoflagellates and the relative abundance of co-occurring diatoms (Kremp et al., 2008). At the end of spring bloom, increased stability together with decrease in nutrient availability causes the diatoms to settle out of the euphotic zone (Wasmund et al., 1998; Höglander et al. 2004). The termination of the dinoflagellate spring bloom is mainly regulated by nutrient limitation and ends when their ability to exploit nutrients below the upper mixed layer is exhausted, but also with the rise of water temperature.

4.2.3. Atmospheric processes

Climatic oscillations in atmospheric modes such as North Atlantic Oscillation (NAO) are less perceptible in local environments, but may be seen as a proxy for regulating forces in both aquatic and terrestrial ecosystems (Ottersen et al., 2001). The NAO is primarily a winter phenomenon in the Baltic Sea area as its correlations with wind, temperature and precipitation are strongest during winter. During years with high NAO there is a substantial increase in rainfall and consequently the freshwater inflow into the Baltic Sea is higher (Hänninen et al., 2000). The analysis of long-term biological and environmental data in Pärnu Bay, the Gulf of Riga even indicated that NAO index explain better a large part of the interannual variation of the phytoplankton stock than the local environmental variables (Kotta et al., 2004).

The NAO values are likely to determine the timing and magnitude of phytoplankton spring peaks. The calculations made with regular datasets from Muuga Bay (southern GoF, 1993–2010) resulted in higher chlorophyll *a* and phytoplankton biomass values, when the NAO index was lower during the winter period (Fig. 4) The relationships were stronger between the averaged winter (December-February, January-March) or monthly (February) NAO indices and the concentrations of chlorophyll *a* in April ($R^2=0.30-0.45$, $p<0.05$). The same combinations with wet weight biomass in April gave weaker negative correlations ($R^2=0.12-0.13$, $p<0.1$). These results do not support a far-spread understanding that higher values of the NAO result in the warming of seawater

and, hence, prolong the growing season of the phytoplankton (e.g. Reid et al., 1998). There were neither clear relationships between the NAO indices and the biomasses of dominating phytoplankton groups (dinophytes and diatoms) or species. The only significant negative correlations were found between the winter (January–March or February) NAO indices and the biomass of the diatoms *Skeletonema costatum* ($R^2=0.47$, $p<0.01$) and the dinoflagellate *Scrippsiella* complex in April ($R^2=0.18$, $p<0.05$). Strong blooms of *Scrippsiella* complex in the central Gulf of Finland have been observed both after mild and harsh winters. The most pronounced blooms of *Scrippsiella* complex have been observed in 1992 and 2004 in Narva Bay, and in 2005, 2007 and 2010 in Tallinn Bay. The peak values of the *Scrippsiella* complex were found during a relatively short period (1–2 weeks). Only after the severe winter in 2003, the bloom persisted from the mid of April to the mid of May, i.e. almost a month (III).

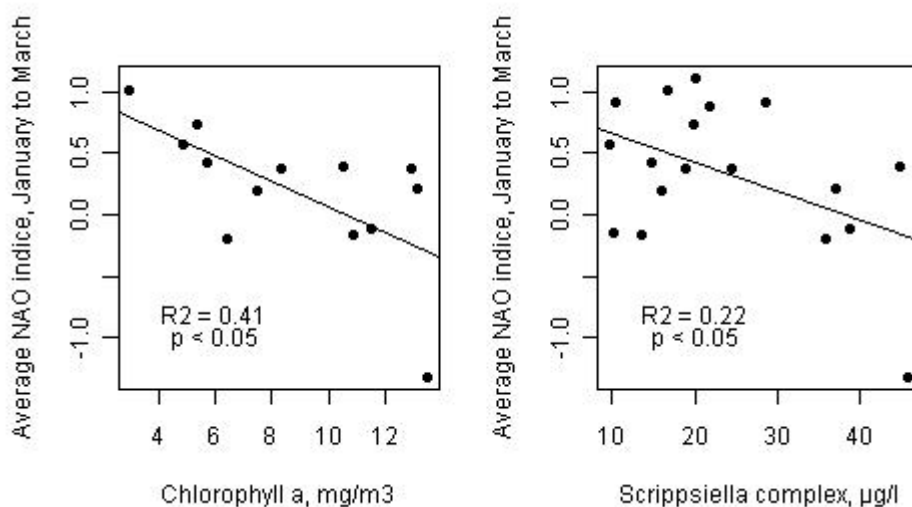


Figure 4. Linear regression between winter (January–March) NAO indices and chlorophyll *a* (mg/m³; left panel) and square-root transformed biomass of the dinoflagellate *Scrippsiella* complex (µg/ l; right panel) in April 1993–2010 in Muuga Bay (southern Gulf of Finland).

4.2.4. Role of nutrients

Nitrogen is generally considered to be the limiting nutrient for marine and coastal plankton communities (Ryther & Dunstan, 1971) and its depletion during the bloom is obviously a major cause of the rapid postbloom decline of planktonic biomass. Raateoja et al. (2011) have analyzed long-term high-frequency data from the Baltic Proper and found a declining trend for N:P ratio, suggesting that there is a pronounced wintertime stock of the potential excessive inorganic phosphorus (eDIP) and that this stock has lately increased in

magnitude. The most probable reason for this development was considered to be the acceleration of internal loading (Pitkänen et al., 2001b). Excessive phosphorus loading accompanying urban, industrial, and agricultural expansion, which started early in the 20th century, has often been related to the blooms of heterocystous cyanobacteria (e.g. Horstmann, 1975; Niemi, 1979; Janssen et al., 2004). Despite the decrease in loading, an increase in the phosphate-P concentrations was observed both in the surface and near-bottom layers around the mid-1990s. Mass release of phosphorus stored in oxic sediments occurs when the sediment becomes anoxic (e.g. Gunnars & Blomquist 1997) and the oxygen concentration in the bottom waters is in turn related to the vertical stratification of the water column, which limits wind-induced mixing and thermal convection. Excessive inorganic phosphorus released from bottom sediments in preceding autumn and winter as well as its incomplete utilization by the phytoplankton spring bloom have also been associated with the extremely vigorous blooms in the Gulf of Finland in July 1997 and 2002 (Pitkänen et al., 2003). It is different from the results presented in paper **IV**, where no strong relationships between cyanobacterial biomass and pre-bloom $\text{PO}_4\text{-P}$ concentrations or the N : P ratio were found. We suggested that the mass development of *Aphanizomenon* sp. was likely a response to short-time nutrient pulses accompanied with upwelling and/or other hydrodynamical forcing.

Earlier nutrient addition experiments with natural populations of cyanobacteria in the Gulf of Finland still indicated that the response is not clear, especially for phosphorus (e.g. Kononen et al., 1993). Phytoplankton blooms take up excessively DIP to DIN than calculated according to the uptake in the molar Redfield ratio, thus reducing the potential eDIP reserve (Raateoja et al., 2011). Moreover, some investigations in the Baltic showed that phytoplankton is able to exhaust nitrates and phosphates to the concentrations as low as $< 0.1 \mu\text{mol L}^{-1}$ (e.g. Wulff & Rahm, 1988). It is accordant to our study in the GoF – *N. spumigena* formed local short-time blooms only in 1999 and 2001, when the phosphorus concentration was at its lowest (**IV**).

The importance of stored nutrients as residual from spring bloom is greater for *Aphanizomenon* than for *Nodularia*, but in mesoscale blooms *Aphanizomenon* may also benefit from the short-term nutrient pulsing events (e.g. Kononen et al., 1996). The absence of intensive *Nodularia* blooms during the late 1980s and early 1990s have in turn been attributed to the increased nitrogen loading with accompanying increase in the N:P ratio (Kononen, 1992). Kahru et al. (2000), however, propose that the eastward expansion of *N. spumigena* blooms was triggered by the 1993 saltwater inflow into the Baltic. With the arrival of the saline and oxygen-depleted waters in the GoF in 1995, stratification in the bottom layers increased, oxygen concentrations decreased, and increased amounts of phosphate were released from the sediments.

High-frequency measurements in the Gulf of Finland have indicated that the time lag between a nutrient pulse and the response of phytoplankton is a few days (Rantajärvi et al., 1998a). Although rise in water temperature has been

suggested as main trigger for cyanobacterial intensive development, preceding favourable nutrient conditions (e. g. upwelling) substantially magnify biomass growth (IV; Lips & Lips, 2010). Raateoja et al. (2011) assert that in the Baltic Proper eDIP is typically exhausted in the time frame early June – early July, matching well the timing of the appearance of cyanobacteria in substantial numbers in the water-column. It is likely both stored and regenerated nutrients contribute to early summer phytoplankton blooms. Excessive phosphorus does, however, not fuel extensive late-summer blooms, except in the western Gulf of Finland, where eDIP remained detectable up to early August. Raateoja et al. (2011) conclude that the annual role of eDIP for cyanobacterial growth depends greatly on the weather of the late spring and the early summer: this may sometimes launch the cyanobacterial growth much earlier than is usually expected.

Our studies have also revealed positive biomass responses of other phytoplankton taxa to total nitrogen (*Pyramimonas* spp.) and total phosphorus (*Cylindrotheca closterium*, *Cyclotella choctawhatcheeana*) in natural communities in the Gulf of Finland (II).

Silicate is needed for the growth of diatoms. On the other hand, if dissolved silica limits the spring bloom, diatoms become replaced by non-siliceous forms, mainly flagellates (e. g. Radach et al., 1990; Smayda, 1990). A decrease in the ratio of SiO_4 to DIN was recorded in the northern Baltic during the period 1973–1999 (Kuparinen & Tuominen, 2001) and in the Gulf of Riga (Kotta et al., 2008). The change in the Si:N ratio has been also suggested to be enhanced by the eutrophication (Rahm et al., 1995; Paerl, 1997). In the Baltic Sea, dinoflagellates are a regular component of the spring phytoplankton assemblage, and recent evidence suggests that their proportion might be increasing relative to diatoms (Wasmund & Uhlig 2003). A concomitant decrease in terrestrial Si discharges and an increase in other nutrients have been considered as a possible cause of such development (Humborg et al., 2006), as they might lead to a weaker competitive position of co-occurring diatoms. Kremp et al. (2008) still confirm that variations in $\text{DSi}/(\text{N}+\text{P})$ do not have major effects on phytoplankton development and composition and the additions of N and P cannot alter the outcome of competition between diatoms and dinoflagellates when the latter are initially dominant.

4.3. Phytoplankton as a biological quality element

The implementation of the EU WFD requires the development of ecologically-based classification systems in all types of water bodies. On the other hand, the HELCOM Baltic Sea Action Plan sets a number of initial targets, as well as indicators to measure progress toward the commitment for achieving the agreed Ecological Objectives, and eventually a Baltic Sea in Good Environmental Status by 2021 (HELCOM, 2007). Any focus on status indicators should, where possible, have a link to pressures in order to be able to produce management

actions on pressures and to focus on the key problems to be solved in the Baltic Sea. During the last decade, numerous indicators are developed for various marine and coastal areas to quantify the degree of eutrophication. As the Baltic Sea is a heterogeneous water body, exact or uniform (chemical, biological or ecological) standards for water- and environmental quality are hard to define. The values change seasonally and depend on what the pristine or unaffected conditions were like (e.g. Rönnerberg & Bonsdorff, 2004).

No single indicator provides adequate information concerning the multiple, interrelated components of the ecosystem. On the other hand, whole-ecosystem experiments are not really possible in the study of coastal eutrophication, and thus, the understanding of how the various components of the ecosystem interact is incomplete (Cloern, 2001; Rogers & Greenaway, 2005). Biological indices might be suitable since they integrate the effects of increased nutrient loads and a state indicator is only useful if we know what is driving its changes. Phytoplankton is determined as one of the biological quality elements for the classification of the ecological status of surface waters. The EU WFD implies that the future water quality monitoring of coastal waters has to consider several ecological phytoplankton parameters, including the taxonomic structure, abundance and biomass as well as bloom frequency of phytoplankton community. Phytoplankton biomass and bloom frequency are mostly assessed by means of a proxy (Chlorophyll *a*), taxonomic structure and abundance of species are, even if monitored, generally not taken into account.

4.3.1. Phytoplankton as an indicator of eutrophication

A gradual decline of our environment is not easily noticed, but a comparison of water quality over decades would sometimes be shocking. In the Baltic Sea, anthropogenically induced eutrophication has been identified as the most important factor for degradation of the ecosystem, especially in the coastal areas (Wasmund & Uhlig, 2003). Increases in nutrient inputs lead directly to enhanced primary productivity, and phytoplankton may serve as an indicator of the trophic state. Eutrophication *per se* can be measured through the nutrient concentration, but in order to know if the actions taken (e.g. nutrient reduction) are having the desired effect on the system as a whole, it is purposeful to combine it with indicators of critical biological components of the system. The effects of eutrophication on phytoplankton may be expressed by shifts in species composition and increases in the frequency and intensity of nuisance blooms, which are often dominated by harmful cyanobacteria (Huisman *et al.* 2005; Carstensen *et al.* 2007). Paerl *et al.* (2006), however, recalled that seasonal hydrologic perturbations can overwhelm nutrient controls on the floral composition, underscoring potential difficulties in predicting the responses of phytoplankton production and species composition to nutrient input reductions. Moreover, active management to reduce nutrients from both diffuse and point sources may respond with delay in decline of marine nutrient concentrations

owing to large internal loading from the sediments (e. g. Carstensen et al., 2006). The nutrient effect on phytoplankton is rather multiple and a stochastic result of the combination of environmental factors (Hecky & Kilham, 1988; Reynolds et al., 2000).

The impact of nutrient enrichment on the phytoplankton community structure in the northern Baltic Sea has been recently discussed in several papers (e.g. Lagus et al., 2004; Vuorio et al., 2005; Kangro et al., 2007). Gasiūnaite et al. (2005) noted that only at the local level, the concentrations of inorganic nitrogen and phosphorus were among the significant factors shaping community structure and insignificant when data from different locations were combined. Olli et al. (2011) also revealed low association between total and mineral nutrients and phytoplankton communities in all Baltic sub-basins. Analyses of a large set of data obtained from different parts of the Baltic Sea found that phytoplankton composition changes with variations in nutrient levels, but the composition does not shift abruptly, and only small changes in the phytoplankton community occur in response to moderate increases in nutrient levels (Carstensen & Heiskanen 2007). Looking from the most pessimistic viewpoint, the long-term effects of increasing nutrient concentrations (eutrophication) on phytoplankton stocks could not be definitively determined, because of the overriding effect of hydrographic changes. All these are the reasons why time series documenting clear trends of change in the biomass of total phytoplankton or single taxa that coincide with trends of increasing nutrient concentrations are very few.

4.3.2. Biomass indicators

Various indices based on nutrient availability for aquatic primary producers in coastal waters have been established (Nixon, 1995; Karydis, 1996; Cloern, 2001). According to the widespread opinion, reference phytoplankton communities in all seasons are characterized by consistently low values of chlorophyll *a* coupled with relatively stable proportions of the taxonomic groups and low biomasses of key bloom-forming species (e.g. Buchanan et al., 2005). The concentration of chlorophyll *a* has been widely used in aquatic studies as a proxy of phytoplankton abundance (e.g. Devlin et al., 2007) or biomass (e.g. Gameiro et al., 2004). However, chlorophyll *a* concentration, biomass and abundance are three different variables. Abundance represents the number of cells per volume of water. Phytoplankton biomass, usually represented in carbon units, corresponds to the amount of organic carbon present in the phytoplankton cells per volume of water. Chlorophyll *a*, the key photosynthetic pigment, is present in all phytoplankton cells, but it only represents a fraction of the whole phytoplankton biomass.

Due to the time and cost-effective analysis methods, chlorophyll *a* concentration is extensively used to estimate phytoplankton biomass, usually through the application of a carbon/chlorophyll *a* ratio. However, the relationship

between carbon biomass and chlorophyll *a* (C:Chl) is highly variable on both intra- and inter-specific levels depending on the physiological state of the cell. It usually increases with increasing nutrient stress, and decreases with decreasing light (e.g. Zonneveld, 1998; Kruskopf & Flynn, 2005). Thus, the phytoplankton community in specific systems can exhibit a wide temporal and spatial variability in C:Chl values (e.g. 5–345 mg C mg Chl⁻¹; Putland & Iverson, 2007), which will complicate the estimation of phytoplankton biomass using chlorophyll *a* values. Diatoms usually exhibit a low, dinoflagellates and small cells a high C:Chl ratio. In the case of phytoplankton communities dominated by dinoflagellates, the use of average C:Chl ratios can lead to severe underestimation of the phytoplankton biomass (Domingues et al., 2008). In addition, high (bloom) and low (bust) biomass events within the impaired phytoplankton communities show strikingly different chlorophyll cell content (Buchanan et al., 2005). Chlorophyll *a* should be also used cautiously as an alternative for phytoplankton abundance and biomass, when pico- and nanophytoplankton are important components of the community. The relative contribution of pico-phytoplankton biomass to total biomass decreases with increasing chlorophyll *a* concentration, thus coastal and estuarine waters present low relative contributions of picophytoplankton, usually ranging between 10% and 20% (Bell & Kalff, 2001).

4.3.3. Species composition based indicators

The classification of eutrophic water conditions on the basis of phytoplankton composition is ambiguous. One problem with phytoplankton is that we are not able to identify all species with routine methods and therefore a big group of unidentified or identified only to genus or class level remains. This is blurring the real number of species, which is mostly needed for calculating of any diversity index and not applicable in coastal monitoring of Baltic Sea areas (Danilov & Ekelund, 2001). On the other hand, the lack of useful taxonomy-based evaluation systems for Baltic brackish coastal areas is probably caused by the high temporal and spatial variability of hydrological and geochemical parameters. Accordingly, phytoplankton eutrophication indices are also masked by their natural variability on a short and long term temporal scale (Wasmund & Kell, 1991). However, recent findings have suggested that large-scale diversity patterns are primarily driven by widespread species, while rare species are less important in this regard (Heino & Soininen, 2010).

Analyses with high-frequency data from the Gulf of Finland have revealed that none of the most common bloom-forming species (*Aphanizomenon* sp., *Nodularia spumigena*, and *Heterocapsa triquetra*) shows reliable correlations with enhanced nutrient (TN and TP) concentrations (II; Gasiùnaite et al., 2005; Vuorio et al., 2005). Moreover, *Aphanizomenon* sp. has shown negative correlation to TN in natural communities in the GoF (Rantajärvi et al., 1998a). This calls into question the indicative value of these species concerning the

trophic status of coastal waters. On the other hand, the sensitive species are rare in abundance in comparison with the omnipotent species and are therefore less suited from the statistical point of view.

At the moment there is neither phytoplankton species composition nor diversity related indicators accepted for the Baltic Sea. Sagert et al. (2008) have proposed seven phytoplankton indices on different taxonomical levels tested from a correlation analysis on a degradation vector: total phytoplankton biovolume, the percentage of diatoms and the biovolume of different size ranges of diatoms and one indicative species (*Woronichinia compacta*). These indices could be suitable in the southern Baltic Sea. For the northern parts of the Baltic Sea, the species suggested as reliable eutrophication indicators – oscillatorian cyanobacteria and the diatoms *Cyclotella choctawhatcheeana* and *Cylindrotheca closterium* – showed the best relationships with TP concentrations (II). Their maxima appear toward the end of July or in August-September when phytoplankton community structure is more stable, and less frequent observations may give adequate results (see chapter 4.4.1). Another diatom, *Skeletonema marinoi*, exhibited stronger correlations with dissolved inorganic and total nitrogen in June, during the period of the summer phytoplankton minimum.

Johansson and Wallström (2001) considered the oscillatorian cyanobacterium *Planktothrix agardhii* to be indicative of nutrient-rich conditions and Carstensen and Heiskanen (2007) proposed it to be the only species that characterizes eutrophic conditions in the northern part of the Baltic Sea, since it responds positively to increased TN levels. This species has been found during summer throughout the 20th century, when temperature conditions were stable until the 1990s in the coastal waters surrounding the cities of Stockholm and Helsinki (Johansson and Wallström 2001; Finni et al. 2001), but also in Kuressaare Bay (Trei & Piirsoo, 1996). These authors attributed the decrease in total biomass and change in phytoplankton dominance from *P. agardhii* to a more species-rich community to an effective reduction in nutrient load. And vice versa, *P. agardhii* has replaced *Aphanizomenon* sp. as the most abundant cyanobacterium in Neva Bay during the late 1980s and in the Curonian Lagoon during the 2000s (Basova & Lange, 1998; I). Both localities have suffered from gradual deterioration in environmental quality during the last few decades (Golubkov & Alimov, 2010; Alexandrov, 2010).

The opportunistic character of some species (*Heterocapsa triquetra*, *Eutreptiella gymnastica*, *Skeletonema marinoi*) to form biomass peaks in environments of short-term elevated nutrient levels makes relating such blooms to the background biogenic level ambiguous. Nonetheless, this does not exclude the possibility that the elevated biomass of opportunistic species may be a response to impairment of the ecological status in coastal waters.

4.4. Recommendations for phytoplankton monitoring in the Baltic Sea

Measurements of phytoplankton species abundance, composition and biomass are essential elements of most monitoring programmes. However, measuring seasonal changes and inter-annual variability requires extensive sampling efforts, inadequate sampling may provide misleading indications of the timing, performance and abundance of the dominant taxa. Substantial samples of phytoplankton from the Baltic Sea have been collected within the framework of national monitoring programs. HELCOM co-ordinated marine monitoring started in 1979. Evaluation of phytoplankton data from different laboratories requires the methods used and taxonomic expertise of the people analyzing the data to be comparable. Unfortunately, there is considerable heterogeneity among datasets from different countries, especially with respect to sampling methods and taxonomic precision, which limits the comparability of data and increases the level of uncertainty in the results of any comparative study. Sampling frequency appears to be the main factor hindering both proper assessment of temporal changes and evaluation of ecological status (see also 4.3.3). For example, phytoplankton data from different parts of the Baltic Sea have been collected with various intensity – 2 to 26 samplings per year, using different depth integrations (I; Heiskanen et al., 2005). Studies from before the 1960s and 1970s are even rarer, more fragmented and differ substantially with respect to the sampling and quantification methods used. This uncertainty increases further when biomass data are calculated from cell size measurements. The need to standardise collection methods, counting techniques and the identification of phytoplankton species was recognized in early phytoplankton studies, particularly through the framework of the Baltic Monitoring Programme in the late 1970s. This need was addressed by establishment of the HELCOM Phytoplankton Expert Group (PEG) and publication of standardized size-classes and biovolumes of phytoplankton species found in the Baltic Sea (Olenina et al. 2006).

Previous monitoring programs have focused mainly on open-sea areas and extensive, but seasonally rare sampling. Phytoplankton monitoring in the Baltic Sea is currently to a large extent coordinated through the HELCOM COMBINE (Cooperative Monitoring in the Baltic Marine Environment) protocol. This ensures that the methods of sampling and analysis are similar and that data are comparable. There are still differences in the spatial and temporal coverage of samples taken within the different monitoring programs. The optimum frequency of phytoplankton monitoring will be discussed in the following section.

4.4.1. Sampling frequency

Temporal variation must be accounted for – despite the factors of interest often being spatial, i. e. impacted versus control sites (Suthers et al., 2008). Papers I and II highlight the importance of regular, frequent phytoplankton monitoring in order to reliably detect trends and ecosystem shifts, especially over short-term spatio-temporal scales. The sampling frequency proposed by the WFD for surveillance monitoring of the phytoplankton composition, abundance, and biomass in lakes, rivers, transitional and coastal waters is every six months (EC, 2000). Ferreira et al. (2007) and Domingues et al. (2008) suggested that monthly phytoplankton monitoring should be feasible in restricted coastal and transitional waters. In reality, phytoplankton usually form communities which are highly complex and variable in terms of diversity and dynamics. The required monitoring efforts to ensure a precise classification of ecological status are considerably higher than predicted by the WFD. The proposed sampling frequencies will usually not provide sufficient precision, especially in the water bodies, where variations in hydrological conditions strongly affect natural succession (e.g. Rantajärvi et al., 1998b; Carstensen, 2007; Pilkaytite & Razinkovas 2007). Dubelaar et al. (2004) referred a minimum sampling frequency even of 5 to 6 days per week to follow some algal blooms, since many species may reach blooming conditions and start disappearing again within one week. Such high frequency is naturally not feasible within any phytoplankton monitoring program.

Most monitoring stations are sampled more frequently during summer. As the communities can change fundamentally on a weekly scale, proper assessment of phytoplankton community composition requires large investments in offshore sampling and experienced personnel for microscopic identification and quantification of phytoplankton. Recent phytoplankton monitoring in the Baltic Sea has directed emphasis toward intensive (weekly to bi-weekly) sampling at a few locations instead of extensive, but less frequent sampling covering larger sea areas. Due to economical reasons, intensive monitoring is preferably performable in coastal areas. Some alternative methods for monitoring mainly open sea areas are brought in 4.4.2.

Eutrophication assessments are often based on the calculation of mean or median values over the assessment period (year, season). This assumes that the monitoring data should be distributed approximately equidistantly over the period considered. Sampling frequency is determined by the variability, and optional increased sampling frequency in seasons with the main bloom events is recommended. Since traditional water quality monitoring is quite costly, it is very important to design properly the monitoring network so that the maximum amount of information can be extracted and forwarded to decision makers with moderate effort. One way could be to establish a joint environmental monitoring program covering pressures, state and impacts carried out by all Baltic Sea riparian countries. The monitoring program should be planned to provide

primarily data for indicator-based assessments covering spatial scales from local to Baltic Sea wide.

Nonmetric multidimensional scaling (MDS) was used to examine temporal variation in phytoplankton, as well as to modify sampling frequency in the future according to stability in summer communities (II). The results of analysis of similarity indicated that in the Gulf of Finland and probably in the whole northern Baltic Sea the most rapid seasonal changes, namely, mass development of phytoplankton caused mainly by the cyanobacterial species *Aphanizomenon* sp., *Dolichospermum* spp., and *Nodularia spumigena*, occur toward the end of June and in July. In the period of the most probable bloom events, the recommended frequency is 3–4 times per month. In August and September, when shifts in phytoplankton communities slow down, less frequent monitoring (1–2 times per month) could provide adequate information on both species composition and biomass. Thus, 7–8 observations for the period from June to September for surveillance and operational monitoring would be a minimum (II). There are no specific recommendations for the optimum sampling frequency during the spring phytoplankton bloom in the Baltic Sea. The onset and performance of the spring bloom is very variable, starting already in February in its southern parts and terminating in June in the Gulfs of Bothnia and Finland. However, taking into account the exponential nature of bloom development, at least two observations per month during the peak would be recommendable.

On the other hand, considering the labor expended in analyzing phytoplankton, the number of samples investigated can be increased by making selections in counting. Many species can be found in samples all year round, but their biomass values remain inconsiderable and peak only very briefly. The occurrence of a single phytoplankton species in the water column may be limited to only some weeks. For example in the GoF, the diatoms *Cyclotella choctawhatcheeana* and *Cylindrotheca closterium* are mostly absent in plankton before July, but *Skeletonema marinoi* usually disappears after June. This means that for some potential indicator species, the generally approved assessment period (usually June–September in the northern Baltic Sea) may not be adequate and some variations by reference to their appearance are requisite (II). Such decisions of selected analysis should, however, be done very carefully in order to maintain and continue the existing time series at whole community level. The indicator taxa could also be included in a multimetric index (e. g. Devlin et al., 2007), where the assessment period for each attribute is determined separately.

4.4.2. Alternative methods

To increase the number of sampling stations and the temporal frequency of conventional sampling is hardly realistic due to financial restrictions. Alternative methods for collecting data, such as pigment analysis (Millie et al., 1993; Ansotegui et al., 2003), ships-of-opportunity (Rantajarvi et al., 1998b) and remote sensing (e.g. Gordon et al., 1983; Platt & Sathyendranath, 2008; Barnes

et al., 2011) provide additional information to the traditional shipboard sampling. *In situ* instrumentation, with moorings for fluorescence measurements, can also provide early warnings for the occurrence of phytoplankton blooms. Submersible FlowCAM detects and images hundreds of particles and organisms per minute in real-time and can eliminate the need for labor-intensive analysis, yielding as accurate, actionable and statistically significant data as microscopy.

Taking into account spatial and temporal dimensions, all these methods should give more adequate information on plankton communities and dynamics than traditional monitoring only.

In the Baltic Sea area, satellite remote sensing has been used for detecting cyanobacterial blooms (e.g., Kahru et al., 1994; Kutser, 2004). The data collected from SOOP have been used in papers **II**, **III** and **IV** to analyze high-frequency spatio-temporal dynamics of phytoplankton. Such high spatial and temporal sampling frequencies are difficult to obtain by traditional methods and the use of unattended recordings on board SOOP may solve this problem.

However, despite the effectiveness of new techniques in covering large areas in a short time period, microscopy still remains the standard method for most detailed qualitative assessment. Moreover, phytoplankton pigment composition usually gives adequate information only at the class level, which is not sufficient for ecological assessment, as different species even from the same genus may occupy different ecological niches (e. g. Hällfors et al., 2011).

CONCLUSIONS

All areas of operational monitoring in Estonian coastal waters – the Gulfs of Finland (Tallinna and Narva Bay) and Riga (Pärnu Bay) and the Moonsund area (Haapsalu Bay) have differences in composition, biomass and seasonal dynamics of dominant phytoplankton taxa. The statistical analysis of both high-frequency ship-of-opportunity and traditional monitoring data showed that temperature and salinity are the main factors shaping the phytoplankton communities in the Gulf of Finland. The analysis with NAO indices showed that the overall magnitude of spring bloom increases after severe winters and the bloom terminates earlier after mild winters. Most of the statistically significant changes over the study period (1993–2010) have been related to increases in the mean seasonal or monthly biomass values at different taxonomic levels. The most prominent rise in total biomass in Tallinn Bay in June between 1994–1998 and 1999–2003 has been accompanied by an increase in cyanobacterial biomass, especially *Aphanizomenon* sp. It is likely both excessive nutrients left from spring bloom and short-term nutrient pulses followed by rise in water temperature contributed to early summer exceptional phytoplankton blooms in 1997 and 2002.

The salinity factor is expressed by gradual eastwards disappearance of some brackish-water abundant taxa (*Biecheleria baltica*, *Nodularia. spumigena*, *Heterocapsa triquetra*, *Chrysochromulina* spp.) and rise in relative importance of low salinity and freshwater species (*Dolichospermum* spp., *Pseudanabaena* spp.) in the Gulf of Finland. The phytoplankton biomass is more evenly distributed between the different groups in the western areas. Bloom formation of single-celled medium-sized vernal dinoflagellates – the *Scrippsiella* complex in the Baltic Proper and in the Gulf of Finland may not only be explained by optimum temperature and salinity, but also with other factors e.g. high nutrient concentrations and good seeding conditions from the sediments. The *Scrippsiella* complex bloom is rather a yearly phenomenon in the Gulf of Finland, but almost absent in the Gulf of Riga.

A general feature of the summer phytoplankton in the Gulf of Riga is the relatively low biomass and only exceptional mass occurrence of any species. The eutrophic conditions in Haapsalu Bay are characterized by large biomass values increasing towards late summer and a sharp gradient in chlorophyll *a* concentrations and total phytoplankton biomass by a factor of 5–10 to 40 compared to the western open part of the bay.

Sampling frequency appears to be the main factor hindering both proper assessment of temporal changes and evaluation of ecological status in the summer period (June–September). The periods of biomass peaks for single species have been defined and the rates of change in phytoplankton community structure during the summer period examined. Knowledge of the stability in summer communities allows modifications to be made to the sampling frequency and greater focus to be placed on certain periods and species that are

important in terms of assessing water quality. In the period of the most probable bloom events (end of June and July), the recommended frequency is 3–4 times per month. In August and September, when shifts in phytoplankton communities slow down, less frequent monitoring (1–2 times per month) could provide adequate information on both species composition and biomass. 7–8 observations for the period from June to September for surveillance and operational monitoring would be a minimum.

According to the results of intensive phytoplankton monitoring in the central Gulf of Finland, the diatoms *Cyclotella choctawhatcheeana* and *Cylindrotheca closterium* as well as the oscillatorean cyanobacteria with maxima in August and the diatom *Skeletonema costatum* with a maximum in June are the most reliable indicators in terms of eutrophication in the northern Baltic Sea.

Although phytoplankton biomass and species composition are influenced by different mechanisms, the impact of climate change may be overwhelming in the future and induce changes at higher trophic levels. Therefore it is important to maintain long-term biological monitoring programs to assess the biological response to both relatively slow processes and short-term events in water environment.

SUMMARY IN ESTONIAN

Eesti rannikuvete fütoplanktoni muutlikkus, trendid ja seosed keskkonnateguritega

Läänemere suhteliselt hea uurituse taseme juures on teadmised mõne organismirühma, sealhulgas fütoplanktoni esinemise ja dünaamika kohta senini lünklikud. Muutused fütoplanktoni kui mere ökosüsteemi ühe aluskomponendi koosseisus kutsuvad esile nii struktuurseid kui funktsionaalseid nihkeid toiduahela järgmistes lülides.

Valdavalt on fütoplanktoni liigilise koosseisu aastatevahelist varieeruvust seletatud ilmastikutingimustega, ent lühiajalised fluktuatsioonid võivad sesoonse iseloomuga kooslustes esineda ka ilma selgelt tuvastatava välismõjuta. Teisest küljest on üldteada, et fütoplankton reageerib esimesena toitainete juurdevoolu suurenemisele ja võiks olla seega heaks veekogu ökoloogilise seisundi indikaatoriks. Lühikesel ajaskaalal on looduslike ja inimtekkeliste protsesside osakaalu määramine fütoplanktoni dünaamikas keeruline, sest püsivama iseloomuga muutused leiavad aset järk-järgult ning isegi mõõdukas toitainetesisalduse kasv peegeldub liigilises koosseisus vähemärgatavalt.

Fütoplanktoni ajalis-ruumiline varieeruvus tingib, et sesooneid muutusi tuleb jälgida võimalikult väikese ajasammuga, ent samas vaatluste ja analüüsikulused mõistlikul tasemel hoides. Enamus fütoplanktoni pikaajalistest andmeridest on kogutud riiklike seireprogrammide raames, niisamuti käesolevate teeside jaoks. Lisaks traditsioonilisele seirele uurimislavadel on kasutatud kommertsalustele paigaldatud järelvalveta mõõtmis- ja proovikogumissüsteeme, mis võimaldavad suuremaid merealasid katvaid vaatlusi säästlikul viisil. Andmete kvaliteet, fütoplanktoni puhul peamiselt nende ebapiisav hulk, on keskkonnaseisundi hinnangute usaldusväärsuse suurim kõigutaja. Käesolevas töös on suure sagedusega kogutud andmed võimaldanud jälgida fütoplanktoni koosluste suktessiooni ja üksikute liikide ajalis-ruumilist dünaamikat kohati nädalase täpsusega, eriti suveperioodil. Selle põhjal saab anda soovitusi seiresageduse optimeerimiseks, arvestades vetikaõitsengute esinemise ajalisi mustreid ja õitsenguvaheliste perioodide suuremat stabiilsust koosluse struktuuris (II).

Fütoplanktonil on liigilise koosseisu pikaajaliste muutuste jälgimiseks vajalik minimaalne periood kirjanduse põhjal 15–20 aastat. Eesti rannikuvetes on see tingimus täidetud vaid Tallinna piirkonnas, kus enamus statistiliselt olulistest muutustest uurimisperioodi (1993–2010) jooksul on seotud kas sesoonse või kuukeskmise biomassi suurenemisega fütoplanktoni liigi kuni klassi tasemel (I). Ligikaudu 50% on suurenenud ka klorofüllil *a* sisaldus. Ülejäänud Eesti rannikumere operatiivseire piirkondades (Pärnu, Narva ja Haapsalu laht) on pidevad andmerekad 5–14 aastased. Käesolev töö fikseerib esmakordselt nende alade fütoplanktoni sesoonse dünaamika põhijooned koos biomassi dominantidega kogu vegetatsiooniperioodil, mis võib saada aluseks koosluste muutuste edasisele jälgimisele.

Erilist tähelepanu on pühendatud vaguviburvetikatele ehk dinoflagellaatidele, kelle õitsengud pole parasvöötme piirkonnas kevadperioodil tavalised, kuid Läänemeres on iga-aastaseks nähtuseks. Kogutud andmete põhjal on välja toodud need piirkonnad, kus üherakuliste keskmise suurusega dinoflagellaatide (*Scrippsiella* kompleks; 15–30 µm) massesinemised on kõige tõenäolisemad ning leitud seosed nii veekeskkonna parameetrite kui põhjasetete iseloomuga (III). Suviseid sinivetikaõitsenguid mõjutavad nii kevadõitsengust järele jäänud mineraalsed toitained, eelkõige fosfaadid, ent ka õitsengule vahetult eelnenud toitainepulsid. Viimaste esinemisega on seostatud tugevaid õitsenguid 1997. ja 2002. aasta varasuvel (IV).

Temperatuur ja soolsus on peamised tegurid, mis kujundavad Läänemere, sealhulgas Soome lahe fütoplanktoni koosluste struktuuri (I, II). Atmosfääri-protsessid nagu Põhja-Atlandi ostsillatsioonid (NAO) mõjutavad enam lokaalseid talviseid ilmastikutingimusi ja loovad selle kaudu tingimusi fütoplanktoni kevadõitsengu erinevateks stsenaariumideks. Selgus, et karmide talvede järel on vetikaõitsengute intensiivsus suurem ja õitsenguperiood pikem kui pehmete talvede järel. Soolsuse mõju on jälgitav mõnede riimveeliste liikide (*Biecheleria baltica*, *Nodularia. spumigena*, *Heterocapsa triquetra*, *Chrysochromulina* spp.) järk-järgulises kadumises ning vähesoolaste ja mageveeliikide (*Dolichospermum* spp., *Pseudanabaena* spp.) osatähtsuse kasvus Soome lahe idasuunalisel gradiendil.

Liivi lahe suvist fütoplanktonit iseloomustab suhteliselt väike biomass ning harv üksikute fütoplanktoni liikide vohamine. Haapsalu lahe eutroofsus väljendub fütoplanktoni biomassi hilissuvises kasvus ning järsus klorofüllil *a* ning biomassi väärtuste gradiendis lahe erinevate osade vahel. Nii on Haapsalu lahe poolsuletud kesk-ja idaosas vastavad näitajad keskmiselt 5–10 ning maksimaalselt 40 korda suuremad kui avatud lääneosas.

Soome lahe keskosast kogutud suure mõõtmissagedusega andmete analüüsi põhjal on leitud ka potentsiaalsed eutrofeerumise indikaatorliigid Läänemere põhjaosa jaoks. Nendeks on ränivetikad *Cyclotella choctawhatcheeana* ja *Cylindrotheca closterium* ning sinivetikad seltsist Oscillatoriales (II). Sobivaks osutus ka ränivetikas *Skeletonema costatum*, ent selle liigi puhul võib tegu olla ka oportunistiga lühiajaliste soodsate keskkonnatingimuste ärakasutamisel. Nimetatud indikaatoreid on tulevikus võimalik kasutada keskkonnaseisundi hindamise kriteeriumide väljatöötamisel kas eraldi või multimeetriliste indeksite osana.

Merekeskkonna seisundi uurimisel on viimastel aastakümnetel rakendatud alternatiivseid ja ühtaegu efektiivsemaid meetodeid (kaugseire, mõõtepoid, sukeldatavad osakeste loendurid/pildianalüsaatorid, pigmentanalüüs), samal ajal aga kahaneb nende spetsialistide hulk, kes objekti tunnevad. Uurimise ja seire järjepidevuse koha pealt on seega oluline ka traditsiooniliste meetodite nagu mikroskoopia jätkumine.

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PUBLICATIONS

CURRICULUM VITAE

Name: Andres Jaanus
Sünniaeg ja koht: 29.08.1963 Tallinn
Citizenship: Estonian
Address, E-mail: Koidu talu, Tammneeme küla, Viimsi vald, 74017 Harjumaal, andres@sea.ee
Position: University of Tartu, Estonian Marine Institute, researcher
Educational history: Tallinn 37th Secondary School, 1981
Tartu State University, BSc in biology and botany, 1989
Tallinn Pedagogical University, MSc in biology, 1997

Professional employment:

1989–1991 Tallinn University of Technology, Laboratory of Water Protection, technician
1991–1992 Institute of Ecology and Marine Research, junior researcher
1992 Viimsi commune administration, environmental specialist
1992–1995 Estonian Marine Institute, junior researcher
1995–2004 Estonian Marine Institute, researcher
2004–... Estonian Marine Institute, University of Tartu, researcher

Research history

Main research interests

- i) Short- and long-term dynamics of phytoplankton
- ii) Elaboration of ecological indicators
- iii) Distribution of alien species in the Baltic Sea

Publications

1. Tiselius, P., T. G. Nielsen, G. Breuel, A. Jaanus, A. Korshenko and Z. Witek, 1991. Copepod egg production in the Skagerrak during SKAGEX, May-June 1990. *Marine Biology* 111: 445–453.
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16. Ojaveer, H., J. Kotta, A. Põllumäe, M. Põllupüü, A. Jaanus and M. Vetemaa, 2011. Alien species in a brackish water temperate ecosystem: annual-scale dynamics in response to environmental variability. *Environmental Research*, xx–xx. [in press]

ELULOOKIRJELDUS

Ees- ja perekonnanimi: Andres Jaanus
Sünniaeg ja koht: 29.08.1963 Tallinn
Kodakondsus: eesti
Aadress, e-post: Koidu talu, Tammneeme küla, Viimsi vald, 74017
Harjumaa, andres@sea.ee
Haridus: Tallinna 37. Keskkool, 1981
Tartu Riiklik Ülikool, bioloog-botaanik, 1989
Tallinna Pedagoogikaülikool, M. Sc. bioloogia, 1997
Keelteoskus: eesti, inglise, vene, soome, rootsi

Teenistuskäik:

1989–1991 Tallinna Tehnikaülikool, Vetekaitse labor, insener
1991–1992 Ökoloogia ja Mereuuringute Instituut, nooremteadur
1992 Viimsi vallavalitsus, keskkonnainspektor
1992–1995 Eesti Mereinstituut, nooremteadur
1995–2004 Eesti Mereinstituut, teadur
2004–... TÜ Eesti Mereinstituut, teadur

Teaduslik ja arendustegevus

Peamised uurimisvaldkonnad

- i) fütoplanktoni sesoonse dünaamika lühi- ja pikaajaliste muutuste jälgimine Läänemeres seoses keskkonnateguritega
- ii) rannikuvete kvaliteedinormatiivide ja keskkonnaseisundi indikaatorite väljatöötamine
- iii) Läänemere võõrliikide leviku uurimine

Osalemine teadusprojektides ja grantides

Eesti haridus- ja teadusministeeriumi sihtfinantseeritav teema “Optiliselt keerukate ranniku- ja sisevete kaugseire ja optika” (2011–2016)
Eesti haridus- ja teadusministeeriumi sihtfinantseeritav teema “Ranna- ja sisevete optika ning kaugseire” (2005–2010)
Eesti haridusministeeriumi sihtfinantseeritav teema “Taimede evolutsioon, mitmekesisus ja levik ning funktsioon ökosüsteemides” (2003–2007)
EL projekt “Characterisation of the Baltic Sea Ecosystem: Dynamics and Function of Coastal Types” (CHARM) (2001–2005)
EL projekt “FerryBox” (2002–2005)
EL projekt “WFD Intercalibration”, Phase I (2004–2006), Phase II (2008–2011)
EL Life+ projekt “Innovative approaches for marine biodiversity monitoring and assessment of conservation status of nature values in the Baltic Sea” (MARMONI) (2010–2013)

Publikatsioonid

1. Tiselius, P., T. G. Nielsen, G. Breuel, A. Jaanus, A. Korshenko and Z. Witek, 1991. Copepod egg production in the Skagerrak during SKAGEX, May-June 1990. *Marine Biology* 111: 445–453.
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DISSERTATIONES BIOLOGICAE UNIVERSITATIS TARTUENSIS

1. **Toivo Maimets.** Studies of human oncoprotein p53. Tartu, 1991, 96 p.
2. **Enn K. Seppet.** Thyroid state control over energy metabolism, ion transport and contractile functions in rat heart. Tartu, 1991, 135 p.
3. **Kristjan Zobel.** Epifüütsete makrosamblike väärtus õhu saastuse indikaatoritena Hamar-Dobani boreaalsetes mägimetsades. Tartu, 1992, 131 lk.
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