

**ABIOTIC FACTORS CONTROLLING THE
CYANOBACTERIAL BLOOM OCCURRENCE
IN THE GULF OF FINLAND**

INGA LIPS



TARTU UNIVERSITY
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Institute of Zoology and Hydrobiology, Faculty of Biology and Geography,
University of Tartu, Estonia.

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Opponent: Prof. Geoffrey A. Codd, Faculty of Life Sciences,
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LIST OF ORIGINAL PUBLICATIONS

This thesis is based on the following papers, which will be referred to in the text by their Roman numerals.

- I **Kanoshina, I.**, Lips, U. & Leppänen, J.-M. 2003. The influence of weather conditions (temperature and wind) on cyanobacterial bloom development in the Gulf of Finland (Baltic Sea). *Harmful Algae*, 2: 29–41.
- II **Lips, I.** & Lips, U. An analysis of factors controlling the development of cyanobacterial blooms in the Gulf of Finland (Baltic Sea) (manuscript).
- III Laanemets, J., Lilover, M.-J., Raudsepp, U., Autio, R., Vahtera, E., **Lips, I.** & Lips, U. 2005. A fuzzy logic model to describe the cyanobacteria *Nodularia spumigena* bloom in the Gulf of Finland, Baltic Sea (accepted by *Hydrobiology*).
- IV **Lips, I.**, Lips, U., Kononen, K. & Jaanus, A. 2005. The effect of hydrodynamics on the phytoplankton primary production and species composition at the entrance to the Gulf of Finland (Baltic Sea) in July 1996. (accepted by *Proc. Est. Acad. Sci.*)
- V Kononen, K., Huttunen, M., **Kanoshina, I.**, Laanemets, J., Moisander, P. & J. Pavelson. 1999. Spatial and temporal variability of a dinoflagellate-cyanobacterium community under a complex hydrodynamical influence: a case study at the entrance to the Gulf of Finland. *Mar. Ecol. Prog. Ser.*, 186: 43–57.

AUTHORS CONTRIBUTIONS:

- I Inga Lips was responsible for half of the microscopic analysis (Andres Jaanus was responsible for the other half), for the data analysis and paper writing. Prof. Urmas Lips supervised the work.
- II Inga Lips was responsible for part of the microscopic analysis (Andres Jaanus and Kaire Kaljurand were responsible for the rest), for the data analysis and paper writing. Prof. Urmas Lips supervised the work.
- III Inga Lips was helping in defining the membership functions and knowledge rules for the fuzzy logic model. Dr. Jaan Laanemets and Dr. Madis-Jaak Lilover were responsible for model development and paper writing.
- IV Inga Lips was helping in experiment designing, was partly responsible for chlorophyll *a*, primary productivity and phytoplankton laboratory analysis (Andres Jaanus was responsible for the other part), was responsible for the data analysis and paper writing. Prof. Urmas Lips and Dr. Kaisa Kononen supervised the work.

V Inga Lips was responsible for sampling, chlorophyll *a* and primary productivity analysis, and partly of the microscopic analysis (Mrs. Maija Huttunen did most of the microscopic work), helped in data analysis and paper writing. Dr. Kaisa Kononen supervised the work.

ABBREVIATIONS

DIN	dissolved inorganic nitrogen
DIP	dissolved inorganic phosphorus
eP	excess phosphorus
N	nitrogen
P	phosphorus
PAR	photosynthetic active radiation
SOOP	ship-of-opportunity
PP	primary productivity
Chl <i>a</i>	chlorophyll <i>a</i>

ABSTRACT

Increasing public concern on degradation in environmental quality of coastal waters demands also a scientific assessment of the apparently increasing intensity of cyanobacterial blooms in the Baltic Sea. These blooms are a recurrent phenomenon but the spatial extension, duration, intensity and species composition varies widely between years. The occurrence of blooms has been traditionally related to the low nitrogen/phosphorus ratio, resulting from the high concentrations of phosphorus in the low-oxygen or anoxic bottom layers. During the last decade the late-summer cyanobacterial blooms have been observed in the Gulf of Finland every year. The blooms are dominated by *Aphanizomenon* sp., *Nodularia spumigena* and *Anabaena* spp. These different species are able for co-blooming, but the scales of the blooms are different.

Regular high frequent investigations of cyanobacterial blooms in the near-surface layer of the Gulf of Finland have been conducted along the ferry route between Tallinn and Helsinki since 1997. These studies revealed several important aspects of bloom dynamics of different cyanobacterial species in conditions of low nitrogen/phosphorus ratio established in the Gulf of Finland since 1996. The formation of cyanobacterial blooms takes place in late June-early July. The water temperature is controlling the initiation of the bloom, in general, but vertical stratification appears to be the critical factor determining the intensity of the bloom in species level. Strong vertical stratification favours the accumulation of *N. spumigena* filaments at depth optimal for growth. Mixing events may almost wipe *N. spumigena* out while the mixed conditions can favour the *Aphanizomenon* sp. growth.

Analysis of eight year biomass data as well as weather service and marine monitoring data have demonstrated that the difference between bloom and non-bloom years is explained with 96% by PAR and upwelling intensity index variations. The variation of these two environmental parameters can explain with 46% likelihood the dynamics in cyanobacterial bloom intensities. There is a clear indication that the intensity of *Aphanizomenon* sp. blooms is largely determined by the surplus of phosphorus related mainly to the pre-bloom upwelling events. In the sea areas where coastal upwelling is not so important in bringing nutrients from the lower layers to the upper layer the upwelling of nutrients along inclined isopycnals related to different meso-scale phenomena — eddies and fronts — can be important. The outcome of *N. spumigena* bloom is highly dependent on weather conditions like photosynthetic active radiation and water temperature. Absence of a direct relationship between surplus of phosphorus and *N. spumigena* biomass suggests that this species could grow mainly on the regenerated phosphorus pool during summer.

Upwelling events during bloom periods do not favour cyanobacterial growth because of intensive vertical mixing and low water temperature in these areas. The observed upwelling events during the bloom periods determine the spatial

distribution of cyanobacterial blooms in the Gulf of Finland by the wind-forced advection.

After all the analysis in this study it is suggested that the measures which, in long-term, could reduce the cyanobacterial bloom intensities in the Gulf of Finland must be directed to the overall abatement of primary production and related accumulation of organic matter in the sediment.

1. INTRODUCTION

Cyanobacterial blooms have become almost every year features in the Baltic Sea in recent decades and are one of the main public concerns. Although the phytoplankton blooms in general are a natural phenomenon occurring in pelagic marine ecosystems, the increasing frequency, intensity and spreading of toxic and non-toxic phytoplankton blooms could be attributed to human activities, like the discharge of excess nutrients to coastal waters (GEOHAB, 2001; Hallegraeff *et al.*, 2003). On the other hand, physical variability is fundamental in affecting the pelagic environments. Weather-driven events cause variations in temperature, irradiance, precipitation, run-off, nutrient loading, mixed layer depth, etc. Variance in the physical habitat leads to variance in plankton cycles, ecosystem structure, and productivity (Smayda, 1998).

Different hydrographical features can change nutrient and light availability. Vertical mixing and advection are crucial to the structure and dynamics of primary production in the sea (Marra, 1980; Dealgadillo-Hinojosa *et al.*, 1997). There are several examples in which mixing processes or various hydrodynamic events are shown to affect the structure of phytoplankton populations and their spatial heterogeneity — e.g. upwelling (e.g. Talpsepp *et al.*, 1994), fronts (e.g. Kahru *et al.*, 1984; Kononen and Nõmmann, 1992), and eddies (Nelson *et al.*, 1989).

The areal extension, duration, intensity and species composition of cyanobacterial blooms in the Baltic Sea vary widely between years. Much research has been conducted to explain the role of different ecological variables in bloom development and cyanobacterial physiological characteristics, and to explain the ecological significance of filamentous cyanobacteria in the Baltic Sea (N-fixation as the source of “new” nitrogen to the water column). For the Baltic Sea, Kononen (1992) has shown the importance of autecological differences of the two main bloom forming species — *Aphanizomenon* sp. (earlier identified as freshwater species *Aphanizomenon flos-aquae* (L) Ralfs, Janson *et al.*, 1994) and *Nodularia spumigena* Mertens — in structuring the summer phytoplankton community. Depending on the meteorological conditions and hydrophysical background, different species abundance relationships can be observed. In addition, other phytoplankton groups (dinoflagellates or diatoms) can bloom in certain conditions at the same time.

The major purpose of this thesis is to investigate the influence of varying meteorological conditions and meso-scale hydrophysical processes on the development and spatio-temporal pattern of summer cyanobacterial blooms in the Gulf of Finland. Most of the previous studies have been based on the long-term fragmentary data and information (historical records back 7000 years before present or fluctuations during the last 50 years) or short-term investigations (one to two week field or laboratory experiments). The intention of this study was to follow the seasonal and inter-annual variations in summer

cyanobacterial biomass seen in high-frequency (weekly) sampling in the Gulf of Finland and relate this to different environmental variables. These data were complemented with some results obtained during two-week interdisciplinary field studies at the Gulf entrance area in July 1996 and 1997. Such high resolution temporal and spatial scale data is used for the first time in the statistical analysis carried out to link the biomass data with multivariate environmental variables to explain the occurrence of cyanobacterial mass development. The results obtained during the eight year study (1997–2004) and the statistical analysis incorporating different environmental parameters allowed us to distinguish the most important controlling factors for the bloom development of different cyanobacterial species and to give some suggestions in regard to the future perspectives of the Gulf of Finland.

The description and map of the study area and sampling transects are presented in Section 2. In Section 3 the different research strategies, their main advantages and disadvantages are described. The species composition and historic data on cyanobacterial blooms are briefly described in Sections 4 and 5 respectively. The role of factors controlling the development and intensity of blooms are outlined and the statistical analysis given in Section 6. The influence of meso-scale hydrophysical processes on the phytoplankton growth and bloom distribution are described in Section 7. Future perspectives are analysed in Section 8 and conclusions of the studies follow in the Section 9. The main results of the work are presented in more detail in five attached papers (denoted by Roman numerals **I** to **V**). The authors' contributions are outlined after the publication list.

2. STUDY AREA

The Baltic Sea is one of the largest brackish water areas in the world. It has very restricted water exchange with the North Sea via the narrow Danish Straits. At irregular intervals, major inflows from the North Sea supply large volumes of saline and oxygen-rich water to the Baltic Sea. These inflows are the only mechanism to renew the stagnant bottom water of the deep basins of the Baltic Proper (e.g. Carstensen *et al.*, 2002).

The Baltic Sea is divided into five sub-basins of which the Gulf of Finland is the easternmost (Fig. 1). Gulf of Finland is geomorphologically a direct continuation of the Baltic Proper without any sills. The line between the Hanko peninsula and the island of Osmussaar is often treated as the western boundary of the Gulf of Finland. Mean depth in the Gulf of Finland is 37 m and maximum depth is 123 m. The central Gulf of Finland is quite deep (over 60 m) up to longitude 28°E. The southern coast of the Gulf is rather steep, whereas the northern coast is shallower and more broken, with small islands. Due to the Coriolis effect and prevailing wind directions, the average circulation of surface water in the Gulf is anticlockwise, the inflow of the saltier northern Baltic Proper water occurs along the Estonian coast and the outflow of the fresher Gulf water occurs along the Finnish coast (Alenius *et al.*, 1998). The sea temperature and salinity have both horizontal and vertical gradients. In the western Gulf of Finland a permanent halocline exists throughout the year between depths 60–80 m and the existence of the halocline prevents vertical mixing of the water body down to the bottom. In summer, a thermocline exists at 10–20 m depth and it is strongest in July–August when the temperature difference between the warm upper mixed layer and the cold intermediate layer varies by 12–20°C (Laanemets *et al.*, 2004). The overall horizontal distribution of the surface temperature in the Gulf of Finland during summer is usually quite homogeneous. However, horizontal gradients can be locally intense due to upwelling.

The Gulf of Finland is the most loaded part of the Baltic Sea in relation to its water volume — total volume is 1103 km³ (5% of the volume of the whole Baltic Sea) and drainage area is 420 990 km² (20% of the total drainage area in the Baltic Sea; Myrberg, 1998). Anthropogenic inputs of phosphorus to the Gulf of Finland have decreased since the 1980s, but as the reserves in the bottom sediments are high (Lehtoranta *et al.*, 1997). Oxygen-deficiency in near bottom layer causes internal loading by a flux of phosphate from the sediment (Pitkänen and Välipakka, 1997).

A seasonal variation is observed in the upper layer nutrient concentration: from the winter maximum values to the minimum in summer. During autumn the water column is mixed down to the bottom in shallow areas or down to the halocline in deeper areas. The winter concentrations of inorganic nutrients are high because the vertical mixing and remineralisation, also deep vertical mixing and low light levels prevent phytoplankton growth. The winter level of

inorganic nutrients directly controls the intensity of the spring phytoplankton bloom following the formation of stratification. After the spring bloom the inorganic nutrients are almost depleted in the upper layer and strong stratification (formation of seasonal thermocline) prevents mixing between the nutrient depleted upper layer and the nutrient rich lower layers. Wind-induced vertical mixing and upwelling are the important processes in bringing nutrient-rich waters from deeper layers to the surface. Due to the elongated shape of the Gulf of Finland upwelling events could impact on the phytoplankton growth in the entire Gulf.

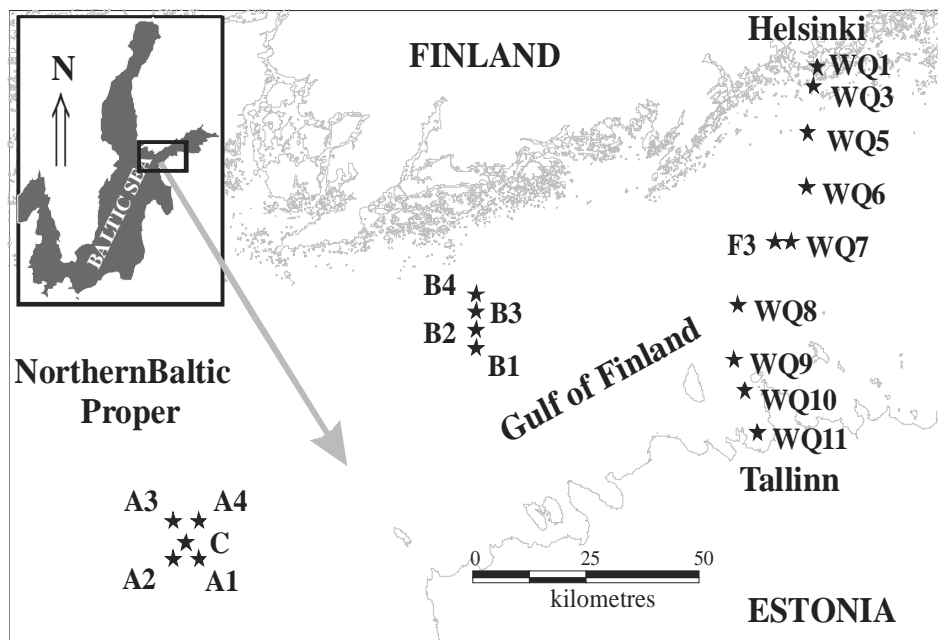


Figure 1. Map of the study areas in the Gulf of Finland, Baltic Sea.

There is a clear seasonal dynamics of phytoplankton species composition and biomass values in the Gulf of Finland. After the establishment of stratification in March-April the spring bloom — dominated by diatoms and dinoflagellates — develops. The peak time of the spring bloom and its species composition may vary from year to year. After the decline of the vernal bloom a summer minimum in phytoplankton biomass can usually be observed until the end of June. From late June-early July the dominating phytoplankton group in the Gulf of Finland is cyanobacteria which in some years may form extensive surface accumulations. After the summer cyanobacterial bloom diatoms may have a second peak in autumn if there are enough nutrients in the upper water layer. Seasonal mixing in autumn will bring a second minimum to the phytoplankton

biomass until the following spring. The main cyanobacteria, which form late-summer blooms and surface accumulations in the Gulf of Finland, belong to the genera *Aphanizomenon*, *Nodularia* and *Anabaena* (henceforth called after genera). Occasionally other phytoplankton species (e.g. dinoflagellates) may also form intensive blooms during some summers.

3. STUDY APPROACHES

The dynamics of the pelagic ecosystem is difficult to study because of its high temporal and spatial heterogeneity (Dybern and Hansen, 1989) and the multitude of spatio-temporal scales involved. Investigations of phytoplankton growth and bloom development have been carried out in the Gulf of Finland in recent decades using different approaches: routine monitoring at fixed stations, autonomous measurements on commercial ferries, multi-disciplinary meso-scale surveys by research vessels and remote sensing. The data analysed in my thesis are mainly from autonomous measurements and multi-disciplinary surveys. Analysis of routine monitoring (mainly nutrient data) data and satellite images were used as complementary information.

3.1. Routine monitoring

Monitoring of changes in the pelagic ecosystem of the Baltic Sea has been carried out under the HELCOM umbrella since 1970s. This traditional monitoring strategy is based on temporally sparse sampling at a few fixed stations. The non-linear response of a pelagic ecosystem to eutrophication appears in rapid changes in the pelagic community. These changes often remain unobserved using the traditional sampling methods. On the other hand, routine monitoring can provide very long data series, which are useful for describing the long-term changes in the particular sea area. In the assessments of the state of the Baltic Sea (e.g. HELCOM, 2002; 2003) the recent changes in the pelagic ecosystem are described at least on the level of tendencies.

3.2. Ships-of-opportunity

One possibility for obtaining high resolution multi-scale data of changes in the pelagic ecosystem is the use of commercial ferries for autonomous measurements. The Baltic Sea has a dense network of passenger ferries and cargo ships following regular schedules. The ships-of-opportunity (SOOP) technique (Rantajarvi and Leppänen, 1994) thus allows to observe the upper layer dynamics from meso- to basin wide scale with high spatial and temporal frequency and to cover large areas of the sea synoptically at low cost (Leppänen and Rantajarvi, 1995). This research strategy is useful *inter alia* for studying the generation of phytoplankton blooms (**I**). Using this kind of technique for many years, high frequent and hence more detailed long-time data series will be produced. Obtained data may be combined for example with meteorological (air temperature and wind speed/direction, **I** or photosynthetic active radiation, **II**) or biochemical (N:P ratio or excess phosphorus values, **II** and **III**) data to find

out the causative processes in phytoplankton growth and distribution. The main disadvantage of the SOOP technique used in the Baltic Sea is the fixed sampling depth (4–5 m). For example, during a cyanobacterial bloom *Nodularia* filaments accumulate at the surface during calm and sunny days and therefore may remain unobserved (I). Despite this the bloom initiation phase is clearly detectable (Fig. 8 in I) and the probability of formation of intense surface accumulations can be predicted in advance. Therefore these kind of observations can be used within the early warning systems.

The SOOP technique was first used in the Gulf of Finland between Tallinn and Helsinki in 1990 (on board “Georg Ots”). Since 1997, the regular observations on board passenger ferries plying between Tallinn and Helsinki (first “Wasa Queen”, since September 1999 — “Finnjet” and since April 2004 — “Romantika”) are carried out (I, II and III).

The water is constantly pumped onboard of the moving ship from a fixed depth (4–5 m). Temperature and salinity are recorded with a spatial resolution of about 150 m using an Aanderaa thermosalinograph. Simultaneous *in vivo* fluorescence of chlorophyll *a* is measured using a Turner AU-10 fluorometer. Measurement locations are determined with a GPS navigator. Water samples for analyses of phytoplankton species composition, nutrient concentration and chlorophyll *a* are obtained using an automated water sampler (ISCO). Water is sampled on a weekly basis at nine fixed locations (Stations WQ1-WQ11, Fig. 1) and is kept refrigerated (4°C) in the dark until analysis. Phytoplankton samples are preserved with acid Lugol solution and analysed using the inverted microscope technique (Utermöhl, 1958). Wet weight biomass of phytoplankton is calculated from cell geometry using cell volumes (Phyto, Software Kahma Ky).

3.3. Multi-disciplinary measurements

The regulatory and cycling processes of the ecosystem can best be studied on research vessels. The main advantage here is the wide range of measurements which can be conducted simultaneously. On the other hand, the time scales of pelagic biological processes are short and they cause practical difficulties in arranging field-measuring campaigns. For example wind forcing induces a variety of physical processes which may alter within a few days. As a result, it is difficult to carry out sampling with the temporal and spatial coverage and resolution needed to link phenomena of pelagic biology to hydrophysical phenomena. Sampling at fixed stations (Eulerian approach) is widely used during multidisciplinary studies. Using the Eulerian approach, the variability in measured parameters is always affected by the advection. The other possibility to study the changes in the ecosystem is the Lagrangian approach,

when the changes in the defined water mass are followed (for example using a floating buoy).

To describe the changes in the pelagic ecosystem at a fixed position on a short scale, a new measuring strategy has been introduced, which combines the sampling at a fixed station during day time and the meso-scale hydrophysical-biological surveys during night time (Kononen *et al.*, 1996). This strategy is used within the present study as well (**IV**, **V**). It gives a better picture about the hydrophysical conditions around the sampling point and helps later explain the observed changes in pelagic biology. The methods employed are described in detail in the papers **IV** and **V**. The disadvantages of conducting multi-disciplinary measurements on board research vessels should be mentioned; these are the high expenses and the large commitment of time required.

3.4. Satellite imagery

The traditional technique used to study phytoplankton is microscopic examination of water samples collected on board research vessels or samples collected unattended onboard commercial ferries. This methodology is often limited in temporal and spatial scope because due to the enormous amount of time involved in analyzing the samples. Visible satellite imagery provides a synoptic perspective, but is not effective during inclement weather (Kahru, 1997). Visible and infrared satellite images are blocked by all but the thinnest cloud cover, and time series of events will therefore be intermittent and may be missed altogether (Gower, 1997). The concentration of chlorophyll *a* as a general indicator for phytoplankton biomass can be assessed using imagery from a wide range of air- and spaceborn sensors. Recent advances in spaceborn remote sensing technology broaden the perspectives of studies toward the identification and quantification of plankton groups (Simis *et al.*, 2005).

Satellite remote sensing has been used in the Baltic Sea area for detecting phytoplankton blooms and it also gives valuable information on water masses and surface layer dynamics (e.g. Kahru *et al.*, 1994, 1995; Kutser, 2004). The detection of cyanobacteria surface accumulations in satellite imagery is probably the best tool available to map changes in the distribution of this ecologically important and environmentally sensitive phytoplankton group in the Baltic Sea (Kahru, 1997). Despite the uncertainties in the interpretation of images, during cloud-free periods they provide helpful information about the regional coverage of the cyanobacterial surface accumulations (Fig. 2).

The real cyanobacterial bloom actually starts before the accumulations appear at the surface, and therefore remains undetected by AVHRR (Advanced Very High Resolution Radiometer) imagery. Thus, the combination of, for example, SOOP technique and satellite imagery will help explain the different bloom forming mechanisms and patterns. This kind of combination has been used in recent years in the Baltic Sea within the Alg@line project (**I**, **II**) and it has proved to be very

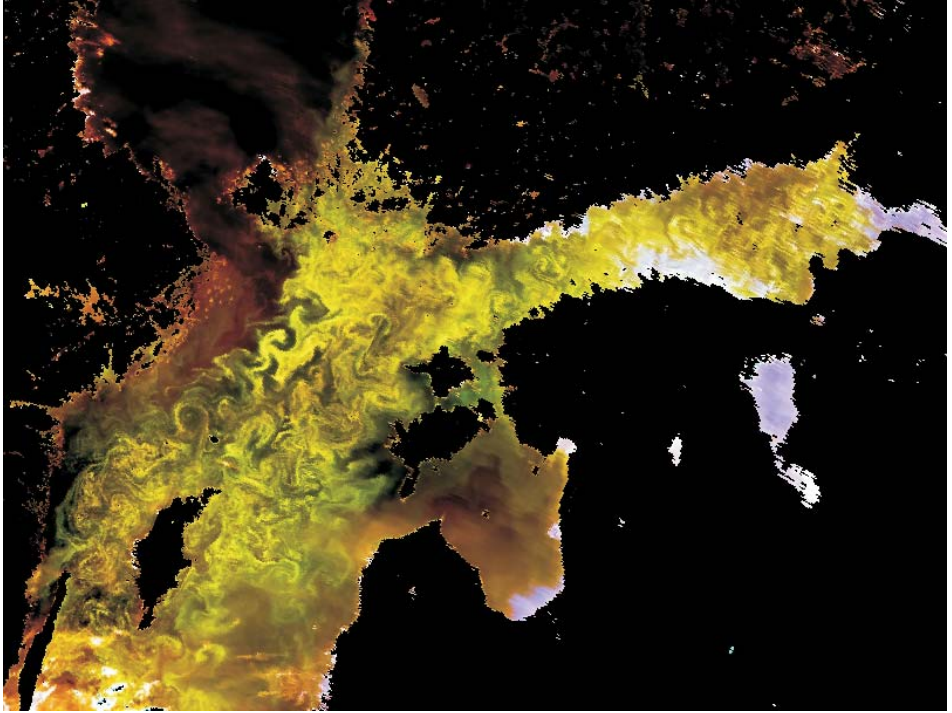


Figure 2. MODIS 1 km resolution image of cyanobacterial bloom in the Baltic Proper and Gulf of Finland on July 17, 2002 (© Tiit Kutser).

effective in giving the operational information to the public for example via the Baltic Sea Portal web page (www.fimr.fi/en/itametikanta.html).

3.5. Bloom definition and estimates of bloom intensities

Phytoplankton blooms are transient departures from quasi-equilibrium when the primary productivity temporally exceeds the losses and transports and the population grows rapidly and reaches exceptionally high biomass (Paerl, 1988). Phytoplankton blooms usually are not single discrete events but rather are a series of fluctuations in which the biomass and the species composition of the phytoplankton population change rapidly.

Blooms can be very generally classified into three types (Cloern, 1996): (1) recurrent seasonal events that usually persist over periods of weeks, (2) aperiodic events that often persist for periods of days and (3) exceptional events that are typically dominated by a few species and persist for months. Cyanobacterial blooms in the Gulf of Finland fall into the seasonal bloom type (1).

The considerations of bloom threshold have been different in different studies in the Baltic Sea. When analysing satellite images the bloom has been defined usually as surface accumulations of cyanobacterial filaments (e.g. Kahru *et al.*, 1994) and the intensity of bloom is characterised by spatial coverage. When microscopic analysis is conducted the biomass of species or group of species is used. Bloom intensity can be described as the maximum biomass observed (e.g. III) or as integrated biomass over a period at the single station or set of stations (e.g. II).

Wasmund (1997) took the biomass value 0.2 mg l^{-1} as a threshold in his analysis as this “differences from ‘normal’ levels of species abundance” and because at that concentration aggregated cyanobacteria became visible in the water and appeared as a “bloom” to the beholder. In our studies we used the value 0.5 mg l^{-1} as a threshold because it enables us to better differentiate the “bloom” years.

The intensity of cyanobacterial blooms in this study is characterised by integrated biomass values of *Nodularia*, *Aphanizomenon* and *Anabaena* over the bloom period. The bloom period is defined as the period when cyanobacterial biomass exceeds 0.5 mg l^{-1} at one or more sampling points along the transect. It means we are looking at the total intensity of bloom in the upper water layer rather than surface accumulations or biomass peak values.

4. SPECIES COMPOSITION OF CYANOBACTERIAL BLOOMS

Summer cyanobacterial blooms in the Gulf of Finland consist mainly of diazotrophic (they are capable of using atmospheric N₂ as a source of nitrogen), filamentous species belonging to genera *Aphanizomenon*, *Nodularia* and *Anabaena*. All these genera have gas vesicles which make them buoyant and enable them to control their position in the water column. *Nodularia* has been proved to be toxic in the Baltic Sea environment (Sivonen *et al.*, 1989) but so far no toxic *Aphanizomenon* or *Anabaena* strains have been isolated in the Baltic.

Aphanizomenon forms straight densely packed colonies that are often a few millimetres in length. *Nodularia*, on the other hand, forms colonies of about the same size but as the filaments are usually curled these are far less densely packed and may also form aggregates as large as 10 cm across (Stal *et al.*, 2003). Diatoms, zooplankton and bacteria colonize aggregates of *Nodularia*, particularly when they are old and close to decaying. Different species of *Anabaena* also present in lower numbers as compared to the two previously described genera. *Anabaena* species can occur as single trichomes or as aggregates formed by curled filaments.

Due to the possession of gas vesicles and the formation of aggregates, *Nodularia*, *Anabaena* and *Aphanizomenon* float to the water surface during periods of calm weather (Walsby *et al.*, 1997), and may form thick surface scum (Fig. 3). This surface scum is mostly formed by potentially toxic *Nodularia* and in smaller number of *Anabaena* filaments; non toxic *Aphanizomenon* is usually more evenly distributed in the upper mixed water layer (Niemistö *et al.*, 1989). The ability to regulate buoyancy and form surface accumulations is the factor what makes cyanobacterial blooms nuisance. Surface accumulations can be concentrated along coasts and in bays by wind and currents (Niemistö *et al.*, 1989). Blooms of cyanobacteria are usually patchy over a wide range of spatial scales (Moisander *et al.*, 1997; Kahru *et al.*, 2000). There is a large inter-annual variation in the mean and maximum biomass of different bloom forming cyanobacterial species.



Figure 3. Surface scum of cyanobacteria in the Gulf of Finland (© Inga Lips).

5. HISTORIC DATA ON CYANOBACTERIAL BLOOMS

Records of large cyanobacterial blooms in the Baltic Sea first occur in the 19th century (Finni *et al.*, 2001). Recent studies on pigment analysis from sediments indicate that nitrogen-fixing cyanobacterial blooms are nearly as old as the present brackish water phase of the Baltic Sea (Bianchi *et al.*, 2000). The sediment pigment data obtained by Poutanen and Nikkilä (2001) show increased intensity of cyanobacterial blooms in the Baltic Sea since 1960s coinciding with the human-induced increased nutrient concentrations (Finni *et al.*, 2001). The spatial extension, duration, intensity and species composition of cyanobacterial blooms vary widely between years (Kononen, 1992). In the central and eastern Gulf of Finland, surface blooms of cyanobacteria were reported in the 1970s and early 1980s (Kononen & Niemi, 1984; Niemistö *et al.*, 1989), but between 1982 and 1994 no accumulations were detected east of approximately 24° 30' E, in contrast to the massive accumulations elsewhere (Kahru, 1997). This was probably due to the absence of *Nodularia* which is mainly responsible for the formation of surface accumulations. At the same period *Aphanizomenon* was frequently observed in high numbers in the upper water column in this area (Kononen, 1992). Since 1995, massive floating blooms containing *Nodularia* have occurred on a smaller or larger scale every summer and over the whole Gulf of Finland, including its eastern part. The main differences between years have been in the intensity of these blooms and the species composition during different years. The potential controlling factors for bloom development are discussed in the next chapter.

6. FACTORS CONTROLLING THE OCCURRENCE AND INTENSITY OF BLOOMS

6.1. Nutrients

Bloom forming cyanobacteria in the Baltic Sea are capable of fixing atmospheric N_2 making them less dependent of the amount of dissolved inorganic nitrogen (DIN) in the upper water column. Cyanobacteria can store surplus phosphorus (as polyphosphate granules and sugar phosphate) for later use until very low cellular phosphorus content inhibits further growth (e.g. Rapala, 1998). There are also suggestions that *Nodularia* makes more efficient use of low ambient concentrations of phosphorus than *Aphanizomenon* (Wallström, 1991) i.e. a higher concentrations of phosphate is needed for *Aphanizomenon* to be able to take up it efficiently. In case of higher phosphorus concentrations in the upper water column *Aphanizomenon* is able to store it in the cells. *Nodularia*, at the same time, is able to use the regenerated phosphorus pools during summer (Paerl, 1996).

Larsson *et al.* (2001) have found during field measurements that in the Northern Baltic Proper a significant increase in *Aphanizomenon* biomass occurred 4 to 6 weeks after inorganic nitrogen was depleted in the upper mixed layer, but with phosphate still present. On the other hand *Nodularia* and *Anabaena* were often only found when phosphate was severely depleted. Different competitive ability for phosphorus is a probable reason for differences in spatial distribution of these two species. *Nodularia* is most common in the nutrient deficient areas of the open Baltic Proper whereas *Aphanizomenon* is more common in coastal areas (Wallström, 1991) and in frontal zones (Konninen, 1992) where the phosphorus concentration is higher.

The initiation of cyanobacteria blooms in the Baltic Sea has been traditionally related to the low N:P ratio (Niemi, 1979), resulting from the high concentrations of phosphorus in the low-oxygen or anoxic bottom layers (Niemistö *et al.*, 1989). Low N:P ratios in the surface waters occur generally in summer after the spring bloom of diatoms and dinoflagellates. Because of the stratification of the Baltic Sea and the sedimentation of organic matter, waters below the halocline are often oxygen depleted. There, denitrification removes inorganic nitrogen from the system while the anoxic conditions promote the flux of phosphate from the bottom sediments (Fonselius, 1976). During the last decade the oxygen conditions have worsened in the lower layers of the Gulf of Finland (e.g. HELCOM, 2003) and due to that the dissolved inorganic nitrogen and dissolved inorganic phosphorus ratio (DIN:DIP) has been lowered continuously after the mid 1990s (Fig. 4).

DIN:DIP

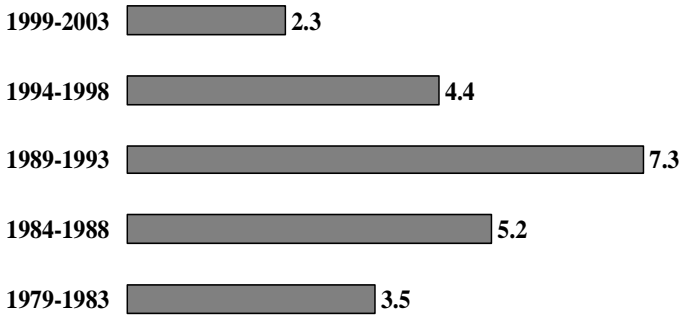


Figure 4. 5-year average values of molar DIN:DIP ratio in the near bottom layer (70–77 m) at station F3 in 1979–2003.

6.1.1. Wintertime DIN:DIP ratio

As the shortage of DIN inhibits the growth of phytoplankton that does not fix nitrogen, low DIN:DIP is a good indicator that a bloom of N_2 -fixing cyanobacteria is likely to develop. During recent decade the inorganic N:P-ratio has decreased in the Gulf of Finland (Pitkänen *et al.*, 2001; Lips *et al.*, 2002) and at the same time cyanobacterial blooms in the Gulf have become more extensive (Kahru *et al.*, 2000). These considerations point to the phosphorus availability as to the main factor triggering the blooms.

A low winter time DIN:DIP ratio should, theoretically, lead to an excess amount of phosphate phosphorus (eP) in the surface waters after the spring bloom of diatoms and dinoflagellates. In this study (III) correlation between peak values of *Nodularia* and eP (estimated on the basis of wintertime DIN and DIP concentrations in the upper layer) was suggested. The time series of study (III) involve years before 1996 (1992–1995) when the eP values were low (less than 0.3 mmol m^{-3}) and years after 1996 with changes in the Gulf of Finland bottom layer waters (1996–2003) when the eP concentrations were high enough to support cyanobacterial bloom development. This major changes in the ecosystem — the increase of eP from less than 0.3 to greater than 0.5 mmol m^{-3} — could support the high correlation found between *Nodularia* peak biomass and eP ($r^2 = 0.61$, $p < 0.05$, $n = 8$) if the summers with the surface layer temperature less than the chosen threshold ($\sim 16^\circ\text{C}$, Huber, 1984) were excluded.

Statistical analysis of data from 1997–2004 when biomass data are collected in a weekly basis at 4–5 m depth onboard commercial ferries gave different results to the previous study. There was no correlation found between eP and summer cyanobacterial biomass (if data from all eight years were treated). For years when temperature conditions were favourable for cyanobacteria (tempe-

rature above 16°C) some correlation of eP with total cyanobacterial bloom-forming species biomass was found but it was insignificant ($r^2 = 0.53$, $p < 0.2$). Similar correlation was found with *Aphanizomenon* biomass ($r^2 = 0.48$, $p < 0.2$), whereas it was very weak with *Nodularia* biomass ($r^2 = 0.20$, $p < 0.45$) and there was no correlation with *Anabaena* biomass ($r^2 = 0.03$, $p < 0.8$). Thus we may conclude that bloom forming cyanobacteria in the Gulf of Finland may store some of the surplus DIP left in the upper water column after the spring bloom (Larsson *et al.*, 2001) but this is not the triggering factor for bloom initiation. As the study period is characterised by relatively high eP values every spring (compared with the period 1992–1995) there might already be sufficient phosphorus concentrations in the water, so the measured relatively small differences in eP during different springs do not affect the cyanobacterial bloom formation significantly. The absence of correlation between integrated *Nodularia* biomass during the bloom period and eP (II) may indicate that *Nodularia* is not storing phosphorus in the cells but instead is able to use the regenerated phosphorus pools during summer. Another explanation may be the absence of *Nodularia* filaments in the water column after the spring bloom. Only a few cells per millilitre were found at the beginning of June in the water samples. Even if these short filaments are able to store a lot of phosphorus in the cells the initial biomass is too low to support the high biomass formation in the late summer.

Even when there is weak correlation between winter time eP and summer cyanobacterial biomass, the importance of low inorganic N:P ratio in the lower layers in cyanobacterial bloom development will be demonstrated in the following parts of this chapter.

6.1.2. Vertical transport of nutrients

Upwards transport of nutrients from below the seasonal thermocline could also create favourable conditions for the growth of cyanobacteria due to the low DIN:DIP ratio there and location of the phosphocline in the upper part of the thermocline (Laanemets *et al.*, 2004). The major process responsible for the vertical transport of nutrients in such an elongated basin as the Gulf of Finland in summer time is the coastal upwelling (Myrberg and Andrejev, 2003). At the same time the low water temperature associated with upwelling events inhibits the growth of cyanobacteria (reported in paper I), thus the transport of nutrients only by pre-bloom upwelling events must be looked at more carefully.

The pre-bloom upwelling events and related transport of nutrient rich waters from deeper layers with low DIN:DIP ratio has been found to be a major trigger for extensive cyanobacterial bloom formation dominated by *Aphanizomenon* in the Gulf of Finland during this study (II). Very high correlation between the *Aphanizomenon* biomass and upwelling index ($r^2 = 0.83$, $p < 0.002$; upwelling index calculation method is introduced by London and Lips, 2003) was found in the Gulf of Finland. Data analysis shows that the correlation benefits from the

very intense upwelling events observed in 2002 (see also Fig. 2d in paper II), which led to the high biomass of *Aphanizomenon*. Correlation between *Anabaena* or *Nodularia* biomasses and upwelling index was weak and insignificant. The exclusion of 2002 data does not affect these conclusions. Thus, *Aphanizomenon* can out-compete *Nodularia* and *Anabaena* when relatively high inorganic phosphorus concentration in the upper water layer exists.

Also, turbulent vertical mixing has been considered as one possible mechanism bringing the nutrients from lower layers to the upper layer. Lilover *et al.* (2003) have demonstrated a considerable input of phosphate to the surface layer via turbulent mixing and they have suggested that this could support the cyanobacterial biomass elevation in the phosphorus deficient upper layer waters in the Gulf of Finland in late summer. However, usually the energy barrier is too high for wind-induced turbulence to mix nutrients directly from below the pycnocline into the upper mixed layer. Also Lilover *et al.* (2003) showed that strong wind events (over 10 m s^{-1}) were needed to generate relatively large phosphate fluxes into the upper mixed layer.

During this study we could not confirm this hypothesis with real measurements for cyanobacteria, but significant correlation between the preceding day wind speed and the phytoplankton primary production was found at the entrance area to the Gulf of Finland during the multidisciplinary measurements in 1996 and 1997 (for example in 1997 $r^2 = 0.63$ at $p < 0.005$; Fig. 5). However, in both cases, stratification of the water column was too strong to allow nutrients to reach the upper layer via wind-induced vertical turbulent mixing and another explanation of the observed relationship has to be found (see section 7 of this thesis).

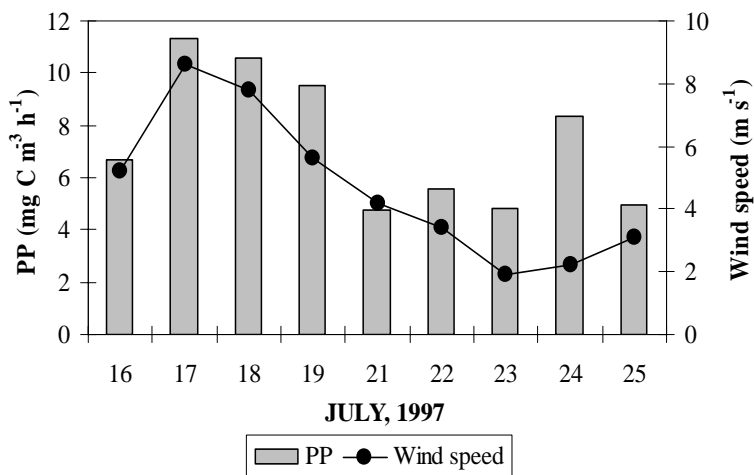


Figure 5. Daily mean potential phytoplankton primary production (bars) and preceding 24 hour mean wind speed (black circles) on 16–25 July 1997.

6.2. Solar irradiance

Light is another important factor that determines the formation of diazotrophic cyanobacterial blooms in the Baltic Sea. In general, most cyanobacteria are considered as shade-adapted organisms but they can tolerate a wide range of irradiance. Some species survive at irradiance of only a few $\mu\text{mol m}^{-2} \text{s}^{-1}$, but others can tolerate direct sunlight (Rapala, 1998). Experimental work with laboratory cultures and mesocosms has revealed several basic differences in the autecological characteristics of the two main bloom forming species in the Baltic Sea. The near surface occurrence of *Nodularia* distinguishes it from *Aphanizomenon*, which is usually more evenly distributed throughout the water upper mixed layer (Niemistö *et al.*, 1989). Lehtimäki *et al.* (1997) showed with laboratory experiments that *Aphanizomenon* grew best at low irradiance (25 to 45 $\mu\text{mol m}^{-2} \text{s}^{-1}$), but *Nodularia* preferred higher irradiance (45 to 155 $\mu\text{mol m}^{-2} \text{s}^{-1}$). Galat and Verdin (1989) have shown in lake experiments that *Nodularia* biomass is very dependent of the amount of photosynthetic active radiation (PAR) and there is also an opinion that solar irradiance is the main factor controlling the growth of *Nodularia* in the Baltic Sea (Stal *et al.*, 2003).

Analysis of last 50 year PAR data (Russak and Kallis, 2003) and historical records of cyanobacterial bloom occurrences (Finni *et al.*, 2001; Kahru *et al.*, 1994) show that the inter-annual variations of PAR are in good accordance with the occurrences of extensive cyanobacterial blooms in the Baltic Sea (II). For the first time, in this study the relatively long-term (eight years) measurements of cyanobacterial biomasses of high temporal and spatial scale have been correlated with the PAR values and a high and significant correlation was found ($r^2 = 0.69$, $p < 0.01$; see also Fig 2b in paper II). At a single species level the highest correlation was found between PAR and *Nodularia* biomass ($r^2 = 0.78$, $p < 0.004$, II). The lower and insignificant correlation values were found for *Aphanizomenon* ($r^2 = 0.39$, $p < 0.1$) which is in accordance with lower light demands compared to *Nodularia*.

6.3. Water temperature

Cyanobacteria have generally a higher optimum temperature for growth than other phytoplankton taxa, and water temperature has been considered the most important factor contributing to cyanobacterial dominance (Sellner, 1997). Wasmund (1997) has found that in the Baltic Sea the biomass of *Nodularia* exceeded 1 mg l^{-1} only if the temperature was higher than 16°C and that of *Aphanizomenon* if the temperature exceeded 17°C. During the studies in the Gulf of Finland the same critical temperature value for *Nodularia* was found, but for *Aphanizomenon* the temperature seemed not to be so important (see also Table 1 in paper I and Fig 2a in paper II). The highest correlation with water

temperature was found for *Nodularia* biomass ($r^2 = 0.63$, $p < 0.02$) but the correlations for *Aphanizomenon* ($r^2 = 0.24$, $p < 0.2$) and *Anabaena* ($r^2 = 0.11$, $p < 0.4$) were insignificant. There was no correlation between maximum values of *Aphanizomenon* and *Anabaena* biomasses and average temperature during the bloom period (Fig. 6). This may indicate that temperature is not so critical for *Aphanizomenon* and *Anabaena* growth enhancement, but is one of the main factors determining the intensity of *Nodularia* bloom.

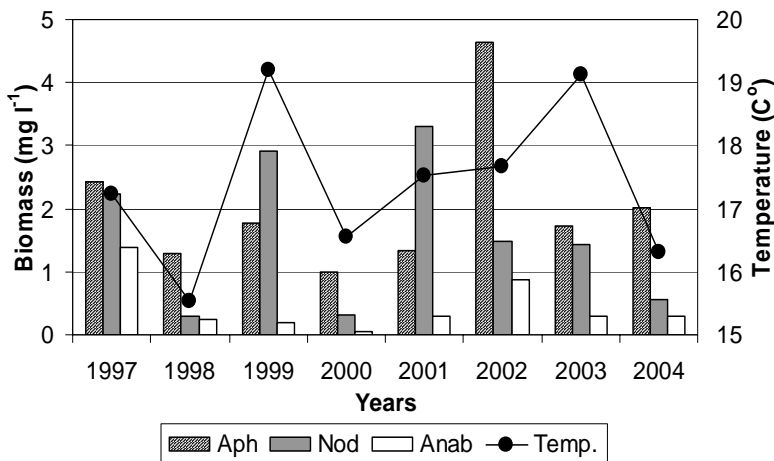


Figure 6. Time-series of the maximum measured biomass of *Aphanizomenon* (striped bars), *Nodularia* (grey bars), *Anabaena* (white bars) and average water temperature during the bloom period (black circles).

6.4. Water stratification

Temperature is an important factor also for another reason: thermal stratification stabilizes the water column and decreases the mixing depth, thereby increasing the light irradiance available for the cyanobacterial community (Stal *et al.*, 2003). Increased access to light may significantly increase the daily production rates in cyanobacterial blooms (Walsby *et al.*, 1997). Also the uptake of phosphorus is an active process which depends on light and increases with temperature (review of Rapala, 1998). Water column stability allows cyanobacteria to make use of buoyancy regulation to maintain an optimal depth, enhancing their competitive advantage over sinking phytoplankton. In turbulent conditions buoyancy regulation cannot compete with vertical entrainment caused by turbulent mixing (Walsby *et al.*, 1995).

So, the strong vertical stratification favours the accumulation of cyanobacteria at depths optimal for growth. It has been shown earlier by Kahru *et al.* (1986) that cyanobacteria lost their dominant position in the frontal upwelling

areas and that other phytoplankton species were favoured in these more mixed waters. The strong stratification that is favourable for cyanobacterial bloom development can be suggested as a major reason for the heaviest bloom in the Gulf of Finland in 1997 (I). Relatively intensive upwelling events were observed in late May and June in 1997 (Fig. 2d in paper II). In the beginning of July the cyanobacterial filaments were distributed in the upper 10 m layer. Later, when the thermocline raised remarkably high (the upper mixed layer was occasionally only 1 m), dense cyanobacterial accumulations formed at the water surface. The increased stratification, surface temperature and irradiance can have positive feedback on the cyanobacteria by further enhancing their buoyancy and trapping them at the top of the water column.

Cyanobacterial blooms decline when the wind speed rises above a certain limit. Galat and Verdin (1989) noticed the disappearance of a *Nodularia* bloom, related to a reduction of the share of living cells in the trichomes, when wind speed exceeded 5 m s^{-1} . Kahru *et al.* (1993) and Wasmund (1997) have found cyanobacterial bloom development and surface accumulations in the Baltic Sea only at wind speeds lower than 6 m s^{-1} . One explanation for cyanobacterial bloom decline during mixing events is obviously connected with reduced light supply for the downward transported algae. As the fixation of N_2 is energetically expensive the organism must have access to sufficient light. Mixing also destroys the aggregates of cyanobacteria. *Aphanizomenon*, which forms densely packed colonies, is less influenced with the turbulent condition than *Nodularia*, which colonies are far less densely packed and may hence have a greater impact of turbulence on aggregates compared with *Aphanizomenon* (Stal *et al.*, 2003). Moisander *et al.* (2002) with their laboratory experiments and Stal *et al.* (2003) with field observations have both shown that a stable water column is one of the main factors favouring *Nodularia* over *Aphanizomenon* and mixing events may almost wipe *Nodularia* out.

6.5. Occurrence of blooms *versus* environmental factors

For 1997–2004 the weekly data of cyanobacterial biomasses and water temperature at 4–5 m depth along the transect between Tallinn and Helsinki, together with eP values measured at the station in the middle of the Gulf of Finland and PAR data from the region are analysed to determine the main factors which could influence the cyanobacterial growth in the Gulf of Finland. The analysis is conducted by using similarity-dissimilarity/distance estimates and consequent CLUSTER, RELATE, SIMPER and multivariate BIO-ENV analysis (Clarke and Warwick, 2001).

Collected phytoplankton data reveal the changes in species composition and biomass of three main bloom forming species during bloom periods in years 1997–2004. The integrated biomass of *Aphanizomenon*, *Nodularia* and *Ana-*

baena over the bloom periods in 1997–2004 is shown in Fig. 7. The most intensive bloom was observed in 2002, mainly due to a very high biomass of *Aphanizomenon*. High biomass of cyanobacteria was recorded in 1997, 1999 and 2001 but they were low in 1998, 2000 and 2003. Cluster analysis of measured biomasses supported our definition of bloom (1997, 1999, 2001 and 2002) and non-bloom (1998, 2000, 2003 and 2004) years (Fig. 8). Low biomass was also recorded in our data collected between Tallinn and Helsinki in 2004, although satellite images indicate that at the same time cyanobacterial blooms were present in many regions of the Gulf of Finland (T. Kutser, personal communication). Even though there were no big cyanobacterial blooms in the Gulf of Finland in years 1998, 2000 and 2003 there was still high biomass of *Aphanizomenon* filaments in the upper water column. The four low biomass years were characterised by very low biomass of *Nodularia* and *Anabaena* (Fig. 7). Also the SIMPER (species contribution to similarity) test for species composition shows that the dissimilarity between years (15.5%) is contributed with 100% by dynamics of *Nodularia* and *Anabaena* biomass.

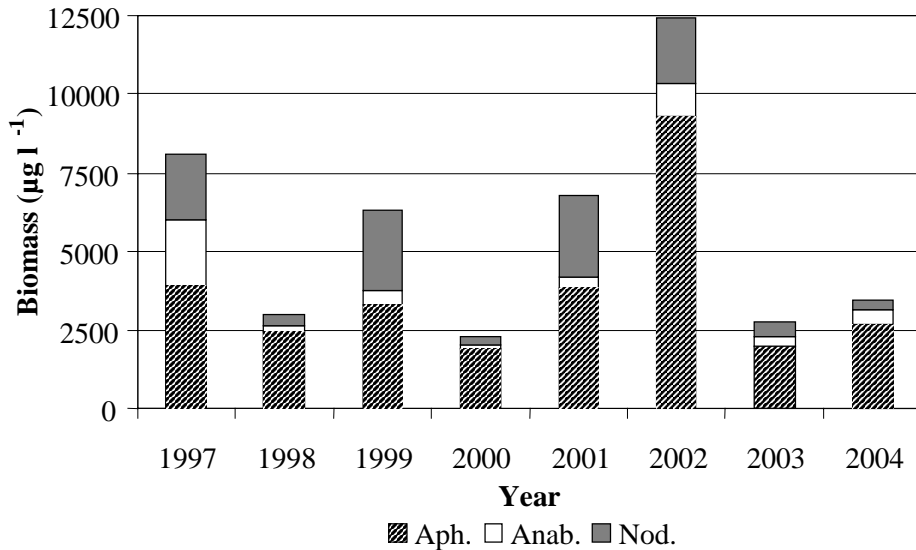


Figure 7. The integrated biomass of *Aphanizomenon*, *Nodularia* and *Anabaena* over the bloom period in 1997–2004 along the transect between Tallinn and Helsinki.

Statistical analysis which links cyanobacterial biomass data to multivariate environmental variables (BIO-ENV — Bray-Curtis dissimilarity of community data (transformed by square root) was linked to the Euclidian distance for environmental variables by weighted Spearman correlation) showed that the single abiotic variable which best grouped with the biotic variables was PAR

($\rho_w = 0.71$; a standard Spearman rank correlation at $p < 0.01$) and the best two-variable combination also involved PAR together with the upwelling intensity index ($\rho_w = 0.70$, $p < 0.004$). By similarity percentage analysis (SIMPER, Clarke and Warwick, 2001), when the occurrence of a bloom determines the groups (bloom/non bloom year with dissimilarities 8.8%), the difference between two groups is explained with 96% by PAR and upwelling intensity index variations. The variation of these two environmental parameters can explain 46% ($p < 0.004$) of the dynamics in cyanobacterial bloom intensities.

Different species were also analysed separately and it was found that for *Aphanizomenon* the highest correlation from BIO-ENV analysis came from the combination of PAR and upwelling intensity index ($\rho_w = 0.76$, $p < 0.005$) and for *Nodularia* the combination of water temperature and PAR gave the highest value ($\rho_w = 0.62$, $p < 0.007$). The single abiotic variable which best grouped with the *Aphanizomenon* was upwelling index ($\rho_w = 0.63$, $p < 0.03$) and with *Nodularia* it was PAR ($\rho_w = 0.61$, $p < 0.02$). These analyses provide strong support to the different autecological needs for high biomass development of these two main bloom forming species and this also helps to understand the occurrence/non-occurrence of certain species in different years. Inter-annual biomass variation of *Anabaena* is similar to that in *Nodularia* i.e. correlating highest with PAR (BIOENV, $\rho_w = 0.49$, $p < 0.005$) but it does not significantly correlate with the water temperature. The results show that blooms of *Aphanizomenon* are initiated rather by pre-bloom upwelling of phosphorus-rich deeper waters whereas growth stimulation of *Nodularia* is mostly related to the increased irradiation or/and increased water temperature. It is very difficult to provide any conclusions regarding *Anabaena* biomass fluctuation from the data collected along the transect between Tallinn and Helsinki.

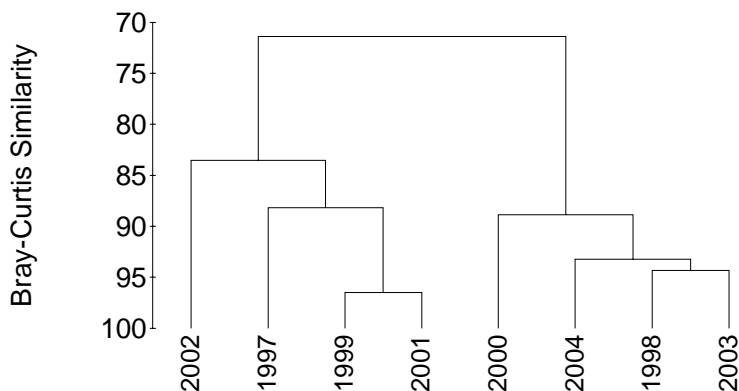


Figure 8. Dendrogram for hierarchical clustering of the 8 years data of *Aphanizomenon*, *Nodularia* and *Anabaena*, using Bray-Curtis similarities calculated on $\sqrt{}$ -transformed biomass data.

7. MESO-SCALE PHYSICAL PROCESSES CONTROLLING THE DEVELOPMENT AND DISTRIBUTION OF BLOOMS IN THE GULF OF FINLAND

Cyanobacterial and algal blooms in general are often extremely 'patchy', both temporally and spatially. The spatial distribution of plankton blooms is usually connected to the physical variability of the water body (Kononen and Leppänen, 1997). Patterns of patchiness in the sea are variable and continually shaped by the water movement, which either transports cyanobacterial or other phytoplankton cells from one place to another or creates conditions for growth enhancement.

In the areas of inclined isopycnal surfaces, vertical movements of water masses and the associated nutrient fluxes from the deeper layers to the upper water layer via different physical processes can occur. These fluxes can increase primary production and under certain conditions can initiate algal blooms (Franks, 1992). Examples of enhanced production related to an upwelling event (e.g. Talpsepp *et al.*, 1994; **I**), to an anticyclonic eddy (e.g. Nelson *et al.*, 1989; **IV**) and to frontal dynamics in combination with the wind induced mixing (e.g. Kononen *et al.*, 1996) have been described.

7.1. Upwelling

Upwelling areas have been usually considered as places for phytoplankton growth enhancement (e.g. Talpsepp *et al.*, 1994; Richardson, 1997). Upwelled waters are typically rich in nutrients. Thus, higher biomass values and even phytoplankton blooms are expected in these areas.

In 1997 and 1999, when the intensive cyanobacterial blooms occurred in the Gulf of Finland, extensive upwelling events were also observed. The biomass of cyanobacteria was low in the upwelling areas in both cases (Fig. 9, see also Fig. 7 in paper **I**). As upwelled waters come from lower layers, their temperature is much lower than in the replaced surface waters. During both years — 1997 and 1999 — water temperature in the upwelling areas was 4–9°C lower (mainly below 16°C) than in the surface layer. The cyanobacteria, as it was discussed above, have rather high temperature optima. Thus, if the temperature conditions are not favourable then even high nutrient concentrations in the upwelling areas cannot facilitate the cyanobacterial growth. Also, influence of the vertical mixing processes should be considered as cyanobacteria are favoured if the water is stratified. It has been shown earlier by Kahru *et al.* (1984) that cyanobacteria lost their dominant position in the frontal upwelling areas and that other phytoplankton species were favoured in these more mixed waters.

Similar upwelling situations related to the meso-scale eddy and the salinity front are discussed later (chapters 7.2 and 7.3).

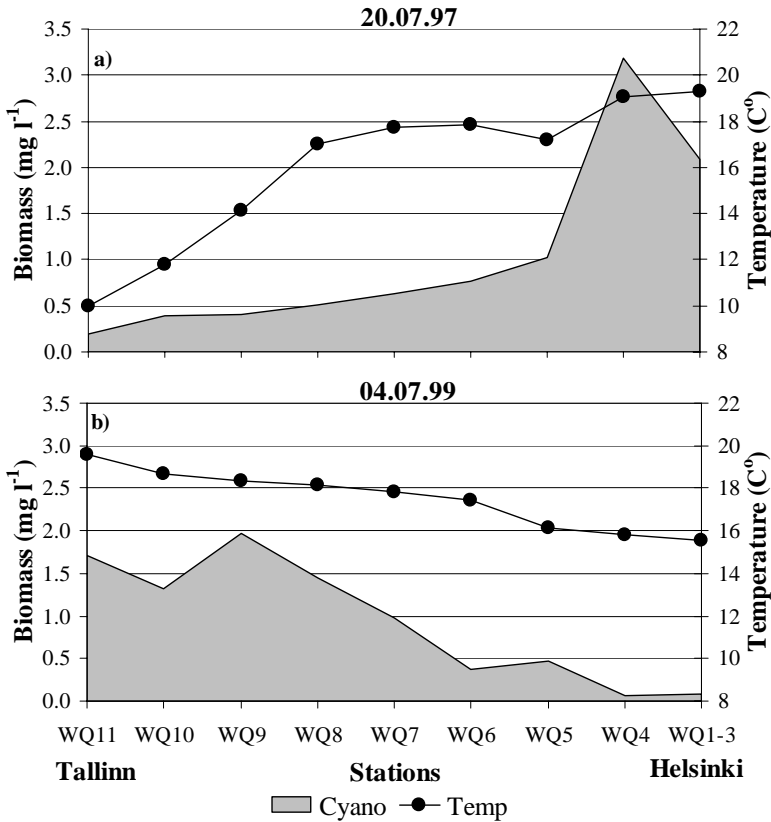


Figure 9. Distribution of cyanobacterial biomass (grey area) and temperature (black circles) along the ferry route on 20 July 1997 and 4 July 1999.

The different distribution of observed cyanobacterial blooms in 1997 and 1999 across the Gulf (Fig. 3 in paper I) can be related to the observed upwelling events at the same period. Cyanobacterial blooms were more intensive near the coasts where the surface water was transported to by the wind-induced currents and less intensive near the coasts where the upwelling events occurred.

7.2. Meso-scale eddy

Mechanisms for vertical nutrient transport related to meso-scale eddies (McGilliguddy and Robinson, 1997; Oschlies, 2002; Martin and Pondaven, 2003; McGilliguddy *et al.*, 2003) including also sub-surface anticyclonic eddies (Martin and Richards, 2001) have been discussed in recent papers. Due to the varying wind forcing and complicated bottom topography, meso-scale physical phenomena — eddies and current jets — can often be observed in the Gulf of Finland.

It has been discovered that anticyclonic eddies from the Gulf Stream can develop phytoplankton biomass maximums at the edges as well in the centres of the rings. Nelson *et al.* (1989) found that slow upwelling in the interior of the ring altered the vertical distributions of both nutrients and density in a manner that greatly facilitated the wind-driven mixing of nutrients upward into a nutrient-depleted surface layer. Comparison of density profiles showed that the pycnocline was both less intense and closer to the sea surface near the centre of the ring than in the adjacent waters.

Highest primary production values in the surface layer were also measured inside the anticyclonic eddy (Fig. 10; stations A1–A4 and C are shown in Fig. 1) discovered after the relaxation of downwelling at the entrance area to the Gulf of Finland during a multidisciplinary study in 1996 (**IV**). The nutricline depth was estimated to vary from 20 to 40 m, and higher variability was found inside the eddy than outside. However, the estimated characteristics of vertical turbulent mixing (considering existing stratification) showed that the wind seems to be too weak ($2\text{--}8\text{ m s}^{-1}$) to transfer the nutrients into the upper mixed layer from the nutricline, even inside the eddy. For a sub-surface anticyclonic eddy, which had similar structure to the eddy mapped in the Gulf of Finland in the frames of this study, the ageostrophic circulation has been suggested as the main mechanism for the vertical transport of nutrients (Martin and Richards, 2001). A rough estimate of daily vertical movements due to the ageostrophic motions along inclined isopycnal surfaces (taking characteristic scales for horizontal velocity equal to 10 cm s^{-1} , and inclination as 15 m per 7–8 km) was obtained equal to 17 m (**IV**).

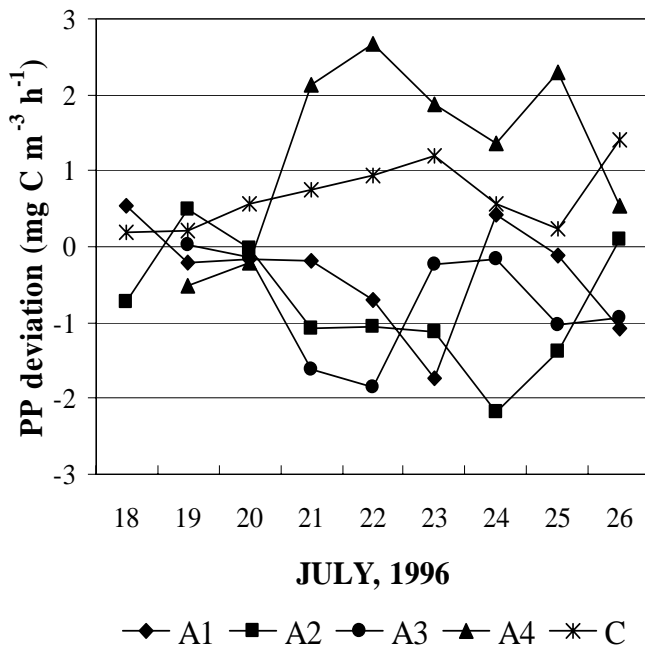


Figure 10. Primary productivity deviations from mean at the sampling stations on 18–26 July 1996 (station A4 was inside the eddy on 21–26 July).

Phytoplankton communities isolated in the rings undergo their own evolution (La Fèvre, 1986). During the observations in 1996 (IV, V), the phytoplankton community structure changed in the whole study area after the eddy formation, except in the water mass trapped inside the anticyclonic eddy. During the first period of the study dinoflagellate *Heterocapsa triquetra* dominated, during the second period (after eddy formation) *Aphanizomenon* prevailed in the study area. Only inside the observed eddy did *H. triquetra* continue to dominate during the whole study time. In addition, several small flagellate species (*Hemiselmis virescens* Droop, *Plagioselmis prolunga* Butcher, *Teleaulax amphioxeia* (Conrad) Hill, *Pyramimonas* spp., *Heterocapsa rotundata* (Lohmann) Fott, *Chrysochromulina* spp.) were more abundant (even increasing in numbers) inside the eddy than outside. Very high and significant correlation ($r^2 = 0.92$, $p < 0.005$; IV) between salinity and primary production deviations may support the hypothesis that inside the eddy the increase in biomass was due to the upward nutrient fluxes (even if these were small) and outside the eddy the changes in biomass were mainly caused by the horizontal advection (V). Vertical ageostrophic motions associated with a meso-scale eddy and occasional events of mixing against a background of low DIN and DIP concentrations seem to be favourable for different groups of phytoplankton.

7.3. Salinity front

Hydrophysical processes influence phytoplankton production by controlling the availability of light and nutrients. It is especially in regions where different water masses make contact that new combinations of light and nutrient availability are created. This is why biomass accumulations (as a result of production or concentration) are often encountered in association with fronts where stratified and mixed waters meet (Richardson and Pedersen, 1998). Fronts are regions of strong horizontal density gradients. The strong horizontal pressure gradients generated at the front are often balanced by the Coriolis force, leading to strong along-front currents. When these two forces are not exactly balanced, vertical circulation can be generated at the front. These vertical motions have a potential to bring deep, nutrient-rich waters into the well-lit surface waters, and stimulate phytoplankton growth. Strong residual circulation parallel to the front and complex cross-frontal exchanges through the eddy motion exist. Transport is therefore a major characteristic of fronts, which largely contributes to their unique biological characteristics (La Fèvre, 1986).

The entrance area to the Gulf of Finland is characterised by marked hydrodynamic activity. Several studies (e.g. Pavelson *et al.*, 1997) have revealed the existence of a quasi-permanent salinity front in the area. Also Kononen and Nömmann (1992) found several quasi-stationary frontal systems inside the Gulf of Finland. Numerous studies in the Gulf of Finland have shown higher biomass and production values at the frontal areas (e.g. Kononen *et al.*, 1996; Kononen and Nömmann, 1992; Kahru *et al.*, 1984).

During the multidisciplinary study at the entrance to the Gulf of Finland in July 1997 (stations B1–B4 in Fig. 1), the salinity front between the fresher coastal waters and saltier open Gulf waters crossed the sampling transect. The front observed in the northern part of the transect during the first days of the study, migrated southward in the middle, and back to the initial position at the end of the observations (Fig. 11). The higher chlorophyll *a* and primary productivity values were observed in the vicinity of the salinity front (Fig. 12). No clear pattern was detected in cyanobacterial spatial distribution as the bloom was in its last phase during the field measurements and most of the cyanobacteria had accumulated at the surface.

The results obtained during studies of Kononen *et al.* (1996) in a frontal region at the entrance to the Gulf of Finland demonstrate that *Nodularia* and *Aphanizomenon* benefited from the wind induced vertical mixing and corresponding nutrient pulses in a different way. Nutrient pulses were followed by enhancement of *Aphanizomenon* biomass. Later the calm weather and solar heating decreased the upper mixed layer initiating the bloom of *Nodularia*. This study revealed the mechanism of co-blooming, but confirmed that the scales of the bloom are different for the two species (Kononen, 2001).

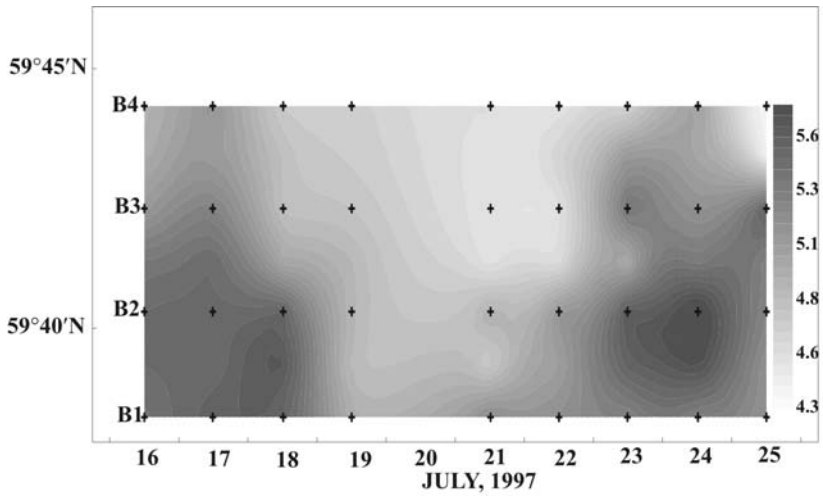


Figure 11. Temporal variation of salinity in the surface layer (5 m) at the sampling transect (stations B1–B4) on 16–25 July 1997.

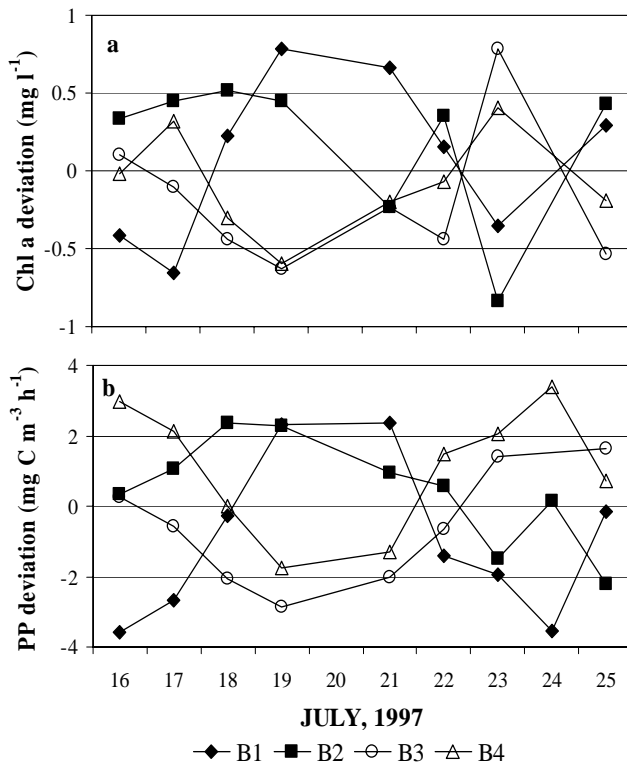


Figure 12. Chlorophyll *a* (a) and primary production (b) deviations from mean at the sampling stations on 16–25 July 1997.

8. FUTURE PERSPECTIVES

The possible factors that influence the cyanobacterial mass occurrence in the Baltic Sea including the Gulf of Finland are: surplus of phosphorus (related to pre-bloom upwelling events and in some extent to winter time eP); light conditions; and water temperature (which also influences water column stability). Finni *et al.* (2001) found that the increased intensity of cyanobacterial blooms in the Baltic Sea from the late 1960s coincided with an increased anthropogenic nutrient load. However, they also noticed that the intensive blooms in 1969 and 1970s were enhanced by warm summers. In addition, the latter period (1969–1975) was characterized by longer sunshine duration and higher photosynthetically active radiation in June–August (Russak and Kallis, 2003; Fig. 4 in paper II).

The nutrient balance of the Gulf of Finland is governed by inputs from the catchment areas, exchange between the Gulf and the Baltic Proper, as well as exchange between sea bed sediments and the water column. The total input of both phosphorus and nitrogen from the catchment has continuously decreased over the last one and a half decade (Pitkänen *et al.*, 2003). Thus, catchment loads into the Gulf of Finland do not support, in a straightforward way, the growth of N₂-fixing cyanobacteria and cannot alone explain the observed decrease in inorganic N:P ratio. It follows that the changes in cyanobacterial communities should be related to the internal loading or inputs from the Baltic Proper.

Good correlations found between cyanobacterial biomass and PAR or water temperature suggest that meteorological parameters are triggering the blooms. But if necessary meteorological conditions are fulfilled then the intensity of blooms can be related to the available DIP concentration in the water body. In this respect the seasonal convective mixing and the vertical transport of nutrients via different hydrodynamical processes in summer is very important. The outcome of the bloom is very dependent of the DIN:DIP ratio in the lower layers. As seen from the measured inorganic nutrient values in the bottom layer in the Gulf of Finland the DIP values have increased during the last decade (see Fig. 5 in paper II). Future climate scenarios (Jaagus, 1998) predict that the probability of relatively cold summers in the near future is very low hence the future meteorological conditions will be favourable for cyanobacterial blooms. In this case the available DIP is the most important factor and it is dependent to a large extent upon the internal load.

The well known realistic way to achieve lower internal loading is to reduce further the external loading. The response of the system to reduced river loads can be delayed by a subsequent release of nutrients stored in the sediments, as it is in the Baltic. The importance of internal loading can be influenced by reducing the production of organic matter which takes place mainly during and just after the spring bloom (Heiskanen, 1998). The produced organic matter will

settle to the bottom using oxygen during the decomposition process, leading to poor oxygen conditions, or in the worst case, to anoxia in the near bottom layer. An indication that less primary production in spring will lead to a lower internal load in the Gulf of Finland can be found by comparing spring bloom intensities in one year with eP values the following year. Correlation between the spring bloom index in the Gulf of Finland (Fleming and Kaitala, 2005) and next winter eP was found as high as $r^2 = 0.73$ ($p < 0.007$; **II**).

Cyanobacteria have been present in the Baltic Sea throughout its history. Because populations of cyanobacteria are a natural feature of the Baltic Sea, measures aimed at restoring the Baltic Sea environment to a more nutrient-poor state will not automatically result in an elimination of such blooms but make them less intense than now. Neumann *et al.* (2005) have shown with their model that the overall effect of a nutrient load reduction for the Baltic Sea ecosystem is a reduced biomass with diatoms and flagellates the main phytoplankton groups during the spring bloom. Consequently we can reduce cyanobacterial blooms by reducing both nitrogen and phosphorus load. The same results are also given by Pitkänen *et al.* (2003) but in this study, for the first time, different interactions and correlations are statistically calculated using relatively long-time and high frequency field measurements. The response of the system is non-linear and effects can have considerable spatial differences as was described by several authors (Johansson and Wallström, 2001; Wallström, 1991). Measures to reduce eutrophication might be seen as high priority in contributing to the reduced health risks due to cyanobacterial toxins in recreational waters (Codd, 2000). The results of reduced nutrient loading could be seen in the Gulf of Finland only after several decades.

9. CONCLUDING REMARKS

In the following summary, the main findings of the studies in this thesis are presented.

- 1) Ship-of-opportunity measurements have high temporal and spatial coverage and are thus an effective method for studying cyanobacterial blooms.
- 2) According to the cyanobacterial biomass values the bloom years (1997, 1999, 2001 and 2002) and non-bloom years (1998, 2000, 2003 and 2004) can be distinguished during this study period.
- 3) Analysis of ship-of-opportunity data along the ferry route Tallinn-Helsinki from years 1997–2004 as well as weather service and marine monitoring data have demonstrated that the difference between bloom and non-bloom years is explained with 96% by PAR and upwelling intensity index variations. The variation of these two environmental parameters can explain with 46% likelihood the dynamics in cyanobacterial bloom intensities.
- 4) The outcome of the *Nodularia* bloom is highly dependent on the weather conditions like PAR and water temperature.
- 5) The intensity of *Aphanizomenon* blooms is largely determined by the surplus of phosphorus related mainly to the pre-bloom upwelling events.
- 6) Pre-bloom upwelling events influence cyanobacterial bloom development by transporting nutrients from the lower layers to the upper layer. Upwelling events during the bloom period determine the spatial distribution of cyanobacterial blooms in the Gulf by wind-forced advection.
- 7) In the sea areas where coastal upwelling is not so important in bringing nutrients from the lower layers to the upper layer the upwelling of water along inclined isopycnals related to meso-scale eddies and fronts can be important.
- 8) The measures which, in the long term, could reduce the cyanobacterial blooms in the Gulf of Finland must be directed toward the overall abatement of primary production and related accumulation of organic matter (containing mobile phosphorus) in the sediment.

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SUMMARY IN ESTONIAN

Tsüanobakterite massvohamise esinemist kontrollivad abiootilised tegurid Soome lahes

Avalikkuse tähelepanu teravnemine rannikumere keskkonnaseisundi halvemise suhtes on tinginud ka suurenenud vajaduse Läänemere tsüanobakterite massvohamiste intensiivistumise teaduslikuks hindamiseks. Need massvohamised on iga-aastased nähtused, kuid nende ulatus, kestus, intensiivsus ja liigiline koosseis varieeruvad aasta-aastalt. Massvohamiste esinemist seostatakse traditsiooniliselt madala lämmastik:fosfori suhtega, mis on omakorda tingitud hapnikuvaese või anoksilise põhjalähedase veekihi suurest fosforiühendite sisaldusest. Viimasel kümnendil on tsüanobakterite massvohamised esinenud Soome lahes igal aastal. Nendes massvohamistes on domineerivateks liikideks *Aphanizomenon* sp., *Nodularia spumigena* ja vähemal määral *Anabaena* spp. Kõik need liigid on võimelised koosluses massiliselt koos esinema, kuid nende massvohamise mastaabid on erinevad.

Regulaarseid, suure sagedusega tsüanobakterite massvohamise uuringuid Soome lahe pinnalähedases veekihis on teostatud piki Tallinn-Helsingi laevaliini 1997. aastast alates. Need uuringud on aidanud välja tuua mitmeid olulisi aspekte erinevate tsüanobakteri liikide massvohamise dünaamikas peale 1996. aastat Soome lahes väljakujunenud madala lämmastik:fosfori suhte tingimustes. Tsüanobakterite massvohamise moodustumine toimub juuni lõpus-juuli alguses. Üldiselt kontrollib massvohamiste kujunemist veetemperatuur, kuid veesamba vertikaalne kihistumine tundub olevat peamiseks teguriks, mis määrab massvohamise intensiivsuse liigilisel tasemel. Tugev vertikaalne kihistumine soodustab *N. spumigena* niitude kogunemist kasvaks optimaalsele sügavusele. Segunemine võib selle liigi biomassi muuta olematuks, samal ajal kui mõõdukas segunemine võib soodustada *Aphanizomenon* sp. kasvu.

Kaheksa aasta biomassi andmete analüüs koos erinevate meteoroloogiliste ning mereseire andmetega on näidanud, et tsüanobakterite massvohamiste erinevused aatate lõikes on 96% ulatuses seletatavad fotosünteesiliselt aktiivse kiirguse ja massvohamiste eelsete süvaveekergete intensiivsuse aastatevahelise varieerumisega. Nende kahe keskkonnaparameetri muutlikkus võib 46% tõenäosusega määrata tsüanobakterite massvohamise intensiivsuse. Liigi *Aphanizomenon* sp. massvohamise intensiivsus on suures osas määratud peamiselt massvohamise eelsete süvaveekergetega ülemisse kihti transporditud täiendava (liigse) fosforikoguse poolt. Merealadel, kus rannikulähedased süvaveekerked on väiksema tähtsusega, on olulised meso-mastaapsete pöörise ja frontaaltsoonidega seotud süvaveekerked. *N. spumigena* massvohamise intensiivsus on suures osas sõltuvuses valitsevatest meteoroloogilistest tingimustest nagu fotosünteesiliselt aktiivne kiirgus ja veetemperatuur. Täiendava fosforivooga otsese

seose puudumine lubab arvata, et see liik võib kasvada kasutades peamiselt suve jooksul ülemises veekihi taasringlusse suunatud fosforivarusid.

Massvohamiste ajal esinevad süvavee kerked ei soodusta tsüanobakterite kasvu, sest neid iseloomustab intensiivne vertikaalne segunemine ning madal veetemperatuur. Massvohamise aegsed süvavee kerked määravad tsüanobakterite ruumilise jaotuse Soome lahes nendega kaasneva, tuulest tingitud pinnalähedase veekihi liikumisega.

Meetmed, mis võiksid pika-ajalises perspektiivis vähendada tsüanobakterite massvohamiste intensiivsust Soome lahes, peaksid olema suunatud üldisele primaarproduksiooni ning sellega seotud orgaanilise materjali settimise vähendamisele.

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PUBLICATIONS

CURRICULUM VITAE

General

Name	Inga Lips (maiden name Kanoshina)
Date and place of birth	27 June 1974 in Tabivere, Estonia
Citizenship	Estonian
Marital status	Married
Address	Kaluri 15–3, 11712 Tallinn
Phone	372 6718972
E-mail	inga@sea.ee
Position	Estonian Marine Institute, University of Tartu, researcher

Education

1989–1992	Pärnu L. Koidula Secondary School
1993–1997	University of Tartu, <i>baccalaureus scientiarum</i> in hydrobiology in 1997
1998–2000	University of Tartu, <i>magister scientiarum</i> in hydrobiology in 2000
2000–2005	University of Tartu, doctoral course in hydrobiology

Foreign languages

English, Russian

Professional experience

2001–until now	Estonian Marine Institute, University of Tartu, researcher
1998–2000	Estonian Marine Institute, assistant
1997–1998	Estonian Marine Institute, engineer
1996–1997	Estonian Marine Institute, technician
1995–1996	Estonian Marine Institute, laboratory worker

Scientific work

Scientific work on hydrodynamic and meteorological control of phytoplankton bloom development in the Baltic Sea

List of publications

1. Jaanus, A., Hajdu, S., Andersson, A., Kaitala, S., Kaljurand, K., Ledaine, I., **Lips, I.** & Olenina, I. 2005. Distribution patterns of the red tide dinoflagellate *Scrippsiella hangoei* in the Baltic Sea. (accepted by *Hydrobiologia*)
2. Laanemets, J., Lilover, M.-J., Raudsepp, U., Autio, R., Nyman, E., **Lips, I.** & Lips, U. 2005. A fuzzy logic model to describe the cyanobacteria *Nodularia spumigena* bloom in the Gulf of Finland, Baltic Sea. (accepted by *Hydrobiologia*)
3. **Lips, I.**, Lips, U., Kononen, K. & Jaanus, A. 2005. The effect of hydrodynamics on the phytoplankton primary production and species composition at the entrance to the Gulf of Finland (Baltic Sea) in July 1996. (accepted by *Proc. Est. Acad. Sci.*)
4. Kotta, J., Simm, M., Kotta, I., **Kanoshina, I.**, Kallaste, K. & Raid, T. 2004. Factors controlling the long-term changes of the eutrophicated ecosystem of Pärnu Bay, the Gulf of Riga. *Hydrobiologia*, 514: 259–268.
5. **Kanoshina, I.**, Lips, U. & Leppänen, J.-M. 2003. The influence of weather conditions (temperature and wind) on cyanobacterial bloom development in the Gulf of Finland (Baltic Sea). *Harmful Algae*, 2: 29–41.
6. Kononen, K., M. Huttunen, **I. Kanoshina**, J. Laanemets, P. Moisander & J. Pavelson. 1999. Spatial and temporal variability of a dinoflagellate-cyanobacterium community under a complex hydrodynamical influence: a case study at the entrance to the Gulf of Finland. *Mar. Ecol. Prog. Ser.*, 186: 43–57.

Grants

- 2001 Research project: “The sensitivity of the Narva Bay ecosystem to possible changes in N:P ratio”, granted by the Centre of Environmental Investments in Estonia.

CURRICULUM VITAE

Üldinfo

Nimi	Inga Lips (neiupõlve nimi Kanošina)
Sünniaeg ja koht	27. juuni 1974.a. Tabivere, Eesti
Kodakondsus	eesti
Perekonnaseis	abielus
Aadress	Kaluri 15–3, 11712 Tallinn
Telefon	372 6718972
E-post	inga@sea.ee
Praegune töökoht, amet	Eesti Mereinstituut, Tartu Ülikool, teadur

Haridus

1989–1992	Pärnu L. Koidula nim. II Keskkool
1993–1997	Tartu Ülikool, <i>baccalaureus scientiarum</i> hüdrobioloogias 1997.a.
1998–2000	Tartu Ülikool, <i>magister scientiarum</i> hüdrobioloogias 2000.a.
2000–2005	Tartu Ülikool, doktorantuur hüdrobioloogias

Keelteoskus

Inglise keel, vene keel.

Teenistuskäik

2001–praeguseni	TÜ Eesti Mereinstituut — teadur
1998–2000	Eesti Mereinstituut — assistent
1997–1998	Eesti Mereinstituut — insener
1996–1997	Eesti Mereinstituut — tehnik
1995–1996	Eesti Mereinstituut — laborant

Peamised uurimisvaldkonnad

Hüdrofüüsikaliste ja meteoroloogiliste tegurite mõju fütoplanktoni mass-
vohamiste arenemisele Läänemeres.

Publikatsioonide loetelu

1. Jaanus, A., Hajdu, S., Andersson, A., Kaitala, S., Kaljurand, K., Ledaine, I., **Lips, I.** & Olenina, I. 2005. Distribution patterns of the red tide dinoflagellate *Scrippsiella hangoei* in the Baltic Sea. (accepted by *Hydrobiologia*)
2. Laanemets, J., Lilover, M.-J., Raudsepp, U., Autio, R., Nyman, E., **Lips, I.** & Lips, U. 2005. A fuzzy logic model to describe the cyanobacteria *Nodularia spumigena* bloom in the Gulf of Finland, Baltic Sea. (accepted by *Hydrobiologia*)
3. **Lips, I.**, Lips, U., Kononen, K. & Jaanus, A. 2005. The effect of hydrodynamics on the phytoplankton primary production and species composition at the entrance to the Gulf of Finland (Baltic Sea) in July 1996. (accepted by *Proc. Est. Acad. Sci.*)
4. Kotta, J., Simm, M., Kotta, I., **Kanoshina, I.**, Kallaste, K. & Raid, T. 2004. Factors controlling the long-term changes of the eutrophicated ecosystem of Pärnu Bay, the Gulf of Riga. *Hydrobiologia*, 514: 259–268.
5. **Kanoshina, I.**, Lips, U. & Leppänen, J.-M. 2003. The influence of weather conditions (temperature and wind) on cyanobacterial bloom development in the Gulf of Finland (Baltic Sea). *Harmful Algae*, 2: 29–41.
6. Kononen, K., M. Huttunen, **I. Kanoshina**, J. Laanemets, P. Moisander & J. Pavelson. 1999. Spatial and temporal variability of a dinoflagellate-cyanobacterium community under a complex hydrodynamical influence: a case study at the entrance to the Gulf of Finland. *Mar. Ecol. Prog. Ser.*, 186: 43–57.

Uurimistoetused

- 2001 Keskkonnainvesteeringute Keskuse rakenduslik projekt: “Narva lahe ökosüsteemi tundlikkus lämmastik-fosfori suhte võimalikele muutustele”.