DISSERTATIONES BIOLOGICAE UNIVERSITATIS TARTUENSIS

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KERSTI KANGRO

The response of phytoplankton community to the changes in nutrient loading

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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 numbers

I. Kangro, K., Olli, K, Tamminen, T. & R. Lignell 2007. Species-specific responses of a cyanobacteria-dominated phytoplankton community to artificial nutrient limitation in the Baltic Sea. Marine Ecology Progress Series 336: 15–27

II. Olli, K., Kangro, K. & M. Kabel 2005. Akinete production of *Anabaena lemmermannii* and *A. cylindrica* (Cyanophyceae) in natural populations of N- and P- limited coastal mesocosms. Journal of Phycology 41: 1094–1098

III. Kangro, K. & K. Olli 2005. The effect of nutrient limitation on *Dinobryon balticum* (Chrysophyceae): a mesocosm study. Nova Hedwigia, Beiheft 128: 197–210

IV. Kangro, K., Laugaste, R., Nõges, P. & I. Ott 2005. Long-term changes and seasonal development of phytoplankton in a strongly stratified, hypertrophic lake. Hydrobiologia 547 (1): 91–103

Author contributions:

I. Author was responsible for sample collection, phytoplankton determination and counting, for the data analysis and preparing the manuscript. K. Olli supervised the work, T. Tamminen and R. Lignell added valuable comments.

II. Author was responsible for phytoplankton microscopy and preparation of sediment samples for chlorophyll a, POC, PON and POP analyses. M. Kabel counted the spores and K. Olli was responsible for the manuscript.

III. Author was responsible for phytoplankton microscopy, for the data analyses and paper writing. K. Olli supervised the work.

IV. Author was responsible for the sample collection and phytoplankton microscopy since year 1999, for the data analyses and paper writing. P. Nõges and R. Laugaste were responsible for earlier phytoplankton data and I. Ott helped in writing.

1. INTRODUCTION

Autotrophic phytoplankton is the key component in aquatic food chains, converting carbon dioxide, water and minerals into carbohydrates, proteins and fats, forming thus the base of energy and carbon source for other organisms. Phytoplankton itself needs macro- (C, N, P, Si) and micronutrients (Fe, Mn, Cu, Zn, B, Mo, V, Co) for growth. Without sufficient amount of nutrients phytoplankton cells cannot grow and multiply. Lack of phytoplankton leads to lower amount of zooplankton and through reduced food availability to poor conditions of fish stocks. Nutrients are the basis for all life in aquatic environment, and thus the manipulation of nutrient amounts can be used to control the primary production.

The idea of nutrients controlling the functioning of the water body is not new, it goes back to the Swedish limnologist E. Naumann (Naumann, 1929), who stated the need of phytoplankton for N and P and their central role in the water body. Limiting nutrients have received considerable attention since then and even today the key issue is mechanistic understanding what limits the primary productivity and energy flow to higher trophic levels (Grimm et al., 2003). A common goal for aquatic ecosystems management is to reduce the phytoplankton productivity and biomass accumulations, whereas the identification of the limiting nutrient is important for cost-efficient management. The main attention has for a long time been focused on macronutrients, but with developing techniques also more and more studies reveal the importance of micronutrients (Brand et al., 1983; Morel et al., 1994; Shaked et al., 2006).

The Liebig's Law of the Minimum was at first developed for agricultural plants. The law of minimum, states that the element, which is in shortest supply relative to the needs of the plants limits its biomass yield. The concept is central to the nutrient paradigm in lakes because it insists that very few factors (usually only one factor, often a plant nutrient such as nitrogen or phosphorus) will actually limit the plant growth.

Every water body is different with its various species and physical-chemical background. Rapid shifts in species composition of phytoplankton communities as a response to changing environmental conditions are common in aquatic systems (Brook, 1965; Cottingham, 1999; Biggs & Smith, 2002). The rapid response of phytoplankton communities stems from the shorter generation time and high turnover rate of the species. By this feature the aquatic ecosystem differs from terrestrial one, since shifts in terrestrial communities take usually a long time (Grimm et al., 2003). One of the dominant structuring forces of communities and ecosystems is resource availability (Goddard & Bradford, 2003). Increased nutrient loading is one of the major factors, which may change the community composition (Herbert et al., 1999; Smith et al., 1999), which in turn cause changes in the food web structure and functioning (Rejmánková & Komárková, 2005). Small changes usually remain unnoticed, but problems become apparent, when massive algal development e.g. algal bloom occurs or changes in community composition occur in a way, which makes the damage to ecosystem visible. This is not a problem in one site or in some water bodies, cases of both algal and cyanobacterial blooms have become more frequent in most inland and coastal waters all around the world (Jones et al., 1994; Kahru & Brown, 1997b; Revenga et al., 2000; Smayda, 2000; Albay et al., 2005; Xu et al., 2008).

Phytoplankton blooms are fundamental features of coastal ecosystems and lakes, but processes that select for blooms of certain species are still not well understood (Carter et al., 2005). A combination of physical, chemical and biological factors governs the development of phytoplankton blooms. Usually the increase in blooms abundance and development is connected to increase in nutrient loading, but in some locations algal and cyanobacterial blooms have been a recurrent feature in pristine conditions. For example, in the Baltic Sea blooms of cyanobacteria have been occurring since ca 7000 B.P. (McGowan et al., 1999; Bianchi et al., 2000).

An anthropogenic nutrient input through agricultural and municipal sources has been behind the deterioration of water quality in many water bodies (Søndergaard et al., 2000; Gulati & Donk, 2002; Justic et al., 2005), making the nutrient reductions one of the critical issues in water management. The control of nutrient flow from land to the water body has been a continuous issue in many countries. Although a great deal is known about algal blooms, many factors controlling the population dynamics of algae are still poorly understood (Graneli et al., 1999). Our knowledge about factors influencing phytoplankton community composition needs broadening by a species-specific approach. The response of phytoplankton species to nutrient availability has received therefore much attention. In recent years several new techniques for analysing phytoplankton have been developed (flow cytometry, pigment analyses, molecular probes), each with their own benefits and restrictions. However, if one is interested in the detailed species composition, traditional microscopy is still widely used (Rutten et al., 2005).

2. OVERVIEW OF THE LITERATURE

2.1. Eutrophication

Eutrophication is a natural process of water body's ageing, which usually takes decades or centuries. Human activities have accelerated nutrient cycling and enhanced the input of nutrients (Galloway et al., 1995; Vitousek et al., 1997). While natural eutrophication proceeds at a rate related to inputs from the natural watershed, human influence and increased nutrient input from the modified and cultivated watershed make the eutrophication process considerably faster.

Eutrophication has been reported from a wide variety of coastal and estuarine systems (Officer et al., 1984; Nixon, 1995; Cloern, 2001; Justic et al., 2005) and in numerous lakes all over the world (WHO, 1997; Revenga et al., 2000). The extent of symptoms has increased especially during the 20th century together with extensive use of fertilizers (Cooper & Brush, 1991; Hickel et al., 1993; Howarth et al., 1996). Fertilization of the coastal waters and lakes has become a serious environmental problem, due to the degradation of ecosystem and food chains.

For a long time the solution for managing the pollution in industrialized countries was dilution, and waste was simply dumped to the nearest water body (Hinrichsen, 1998). Nowadays this trend is continuing in developing countries with the majority of waste water discharged into surface waters without any treatment (Carty, 1991). This affects the water quality of freshwater and coastal areas, causing symptoms of eutrophication. In developed countries there are regulations and laws for wastewater treatment, but in developing countries this field also is under development. In 1965 USA National Academy of Sciences appointed a planning committee on eutrophication, which organised first symposium on eutrophication (Report... 1965). Since then, it has been a focus of research for many scientists.

Main consequences of eutrophication include:

- Phytoplankton massive development e.g. algal blooms due to imbalance between production and consumption → unstable pH → stress conditions for fishes (Cloern, 2001).
- Increase in blooms frequency and intensity.
- Decreased recreational and economic value of water and beaches due to algal blooms → closure of beaches, restrictions to swimming activities, problems with drinking water purification.
- Presence of harmful taxa and toxin production → problems for fauna and aquacultures (Smayda, 2002b).
- Fluctuations in oxygen content → problems for fishes and benthic fauna.
- Higher rate of accumulation of organic matter → excessive oxygen consumption in bottom sediments → anoxic conditions, H_2S and NH_4 accumulation in the bottom water (HELCOM, 1993).

- Changes in the food web caused by monodomination, where dominance of one or a few species leads to detrimental effect on biodiversity (Stal et al., 2003).
- Changes in the phytoplankton community in lakes: declining abundance of desmids, chrysophytes and cryptophytes at first, then decline of some chlorophytes and diatoms together with increasing amount and importance of cyanobacteria and euglenophytes (Watson et al., 1997; Trifonova, 1998; Watson et al., 2001). In addition to cyanobacterial blooms also Chlorococcales may form blooms in case of heavy load of easily degradable organic material (Ott & Laugaste, 1998).
- Accelerated transfer of organic matter to bacterial production.
- Overgrowth of macrophytes by filamentous green algae (Fletcher, 1996; Beusekom et al., 2005).
- Deterioration in light climate → reduction and disappearance of macrophyte beds → less refuges for zooplankton and fish larvae (Munkes, 2005).

Increasing human population causes changes around their settlements. Apart from enhanced nutrient inputs, increasing population size has caused changes in land use and loss of wetlands (Dahl, 1990), which decreases natural pre-processing of the water entering the water body. Land-use impacts on wetlands may cause changes in plant communities, altered hydrologic regimes and nutrient cycles, or increased nutrient and chemical pollutant inflows (Galatowitsch et al., 2000). Large-scale structural changes affected the ability of ecosystems to process nutrients. For example, draining of wetlands has greatly reduced denitrification (Billen & Garnier, 1997). Wetlands, meadows, marshland and forests are transformed into farmland, which disrupts natural water cycle. Higher nutrient loadings from extensively used agricultural area accelerate eutrophication processes in lakes and coastal waters.

There are several factors, which have an influence on the response of a lake to the increased nutrient loading:

1) Lake depth and volume: shallow lakes with small volume are more susceptible to eutrophication (Scheffer, 1998).
2) Water hardness: lakes with hard water are less affected, since P is bound to Ca^{2+} and sediments out of the water column.
3) Residence time, which strongly mediates the availability and rate of use of nutrients by phytoplankton and higher plants (Paerl, 2005). Lakes with shorter residence time have lower possibility for bloom development (Ferreira et al., 2005).
4) Land use of the catchment area. Nutrient amounts coming to the water body differ in case of forested catchment and catchment with intensive agriculture and farming.

Catchment areas differ by their origin. There is a difference between naturally fertile watershed, where lakes are naturally eutrophic, and nutrient-poor watershed, where natural lakes are oligotrophic. Norway is a good example of naturally nutrient-poor watersheds, but even there the situation has changed during the last century. Trophic status of the runoff water in inland is turning more and more eutrophic due to agricultural practices and human settlements together with an increase in cyanobacterial species number and abundance (Skulberg, 2005). Naturally eutrophic lakes are often characterised by diverse community and high productivity both in auto- and heterotrophic levels. There are even some examples of naturally hypereutrophic lakes in the world (Eilers et al., 2001), with shallow morphometry, deep organic-rich sediments, and phosphorus-enriched soils in the watershed. Generally lakes are not naturally hypertrophic, but driven into those conditions.

2.2. Limiting nutrients in lakes and in the Baltic Sea

Bottom-up control – the availability of nutrients is one of the dominant structuring forces of communities (Elser et al., 2000). Among the nutrients that are in short supply, bioavailable nitrate (NH_4^+, NO_3^-, urea), iron (bioavailable Fe), phosphate (PO_4^{3-}), and dissolved silicon [$Si(OH)_4$] are most often found in a concentration below the requirements for phytoplankton growth (Barsanti & Gualtieri, 2006).

There are 3 three main sources of mineral nutrients to support algal growth (Lignell et al., 2003):

- an external free mineral nutrient pool,
- intracellular stores of algae,
- nutrients recycled via mineralization by zooplankton.

As the extracellular pool decreases, phytoplankton starts to use intracellular storage, the growth is restricted only after all intracellular stores have been mobilised (Fisher et al., 1995).

2.2.1. Phosphorus and nitrogen

Control of lacustrine phytoplankton biomass by phosphorus (P) is the one of the oldest paradigms in limnology (Sawyer, 1947; Vollenweider, 1968; Vollenweider, 1975), but even nowadays P is still cited as the dominant limiting nutrient in lakes (Wetzel, 2001; Cooke et al., 2005; Dodson, 2005).

Phosphorus may enter the water body mainly through the inflows and from the sediments, and it is removed from the water column by sedimentation and through the outflow. Processes, which affect the availability of P:

- Inflow of P
- Release of bioavailable P from particulate P (complexes with Fe and Ca, organic matter)

- Release of bioavailable P from sediments due to anoxic conditions
- Recycling of phosphorus in the water column

Phytoplankton is using mainly dissolved form of phosphorus, but limited use of organic P is also possible (Bentzen & Taylor, 1991). Phytoplankton is not the only component of the food web taking P from water. Bacteria (when not carbon limited) compete with phytoplankton for macro- and micronutrients (Aota & Nakajima, 2001). Bacteria are more efficient competitors for P compared to phytoplankton due to their smaller size and efficient use of alkaline phosphatases (Currie & Kalff, 1984; Thingstad et al., 1998). In contrast Løvdal et al. (2008) found that bacteria had no advantage over phytoplankton in P assimilation.

Nitrogen (N) has many chemical forms – it occurs in the gas, liquid (dissolved in water), and solid phases (Niemi, 1979; Barsanti & Gualtieri, 2006). Important inorganic species include nitrate (NO_3^-), nitrite (NO_2^-), nitric acid (HNO_3), ammonium (NH_4^+), ammonia (NH_3), gaseous N_2, nitrous oxide (N_2O), nitric oxide (NO), and nitrogen dioxide (NO_2). Most of the organic N species are biomolecules, such as proteins, peptides, enzymes, and nucleic acids.

Due to the large number of different forms nitrogen cycle in the water column is more complex compared to phosphorus cycling. In addition to the inputs and outputs described for phosphorus, nitrogen can enter and leave a water body in the form of free nitrogen gas (N_2) through atmospheric exchange. This makes the reduction of nitrogen more complicated compared to phosphorus, since cyanobacteria with N_2-fixing abilities may bring new bioavailable nitrogen into the water body. Most of the transformations with N in the water body are mediated by different bacteria, whereas assimilation and N_2-fixation are important in algal perspective.

Generally eukaryotic phytoplankton uses inorganic forms of nitrogen (Barsanti & Gualtieri, 2006), but in case of N limitation the use dissolved organic nitrogen forms (free amino acids, amids) is possible (Ietswaart et al., 1994; Palenik & Henson, 1997). Heterotrophic bacteria acquire N from organic compounds more efficiently than phytoplankton (Løvdal et al., 2008) and may supply phytoplankton growth via transformation of organic N forms to ammonium or urea (Stepanauskas et al., 2000).

Bioavailable nitrogen originates from a variety of human activities and ultimately arrive to the waterbody (Pawlak et al., 2009):

- emissions to the atmosphere, mainly through various combustion activities. Once in the atmosphere, nitrogen compounds deposit either directly onto the sea surface or onto land and water bodies in the catchment area,
- discharges from point sources located along the coast or originating in the catchment area and transported via rivers, and
- losses from diffuse sources, mainly agriculture and scattered dwellings, along the coastline or in the catchment area.

According to Pawlak et al. (2009) about 75% of the nitrogen and at least 95% of the phosphorus enters the Baltic Sea via rivers or as direct discharges. The major anthropogenic source of waterborne nitrogen is the diffuse input – up to 71% of the total N load. Agriculture contributed about 80% of the reported total diffuse load. The largest loads of phosphorus originated from point sources (56%), with municipalities as the main source, constituting 90% of total point source discharges in 2000 (Pawlak et al., 2009).

Processes, which affect the availability of N are:

- riverine inflow of inorganic and organic forms of N
- nitrogen fixation
- denitrification
- mineralisation in the water column and sediments
- atmospheric wet and dry deposition

In the coastal waters of the Baltic Sea the amount of inorganic nutrients increased between 1950s and 1980s (Wulff et al., 1990; Conley, 2000; Grimvall et al., 2000; Munkes, 2005) by factors of at least 8 (for P) and 5 (for N) (Larsson et al., 1985). However, Grimvall et al. (2000) claim that even these values are underestimations. During the period 1970–1993 approximately 1 360 kt of N and 595 kt of P was annually discharged into the Baltic Sea through riverine load, coastal point sources, atmospheric deposition and N_2- fixation (Stålnacke, 1996). According to Suikkanen et al. (2007) summer temperature and winter DIN concentration were the most important factors determining the long-term (24 years) changes in the phytoplankton community structure in the open northern Baltic Sea.

Nitrogen concentration in rivers depends largely on the processes in the catchment area. Lowered use of organic and inorganic fertilisers (Iital et al., 2010) has resulted in a remarkable decrease in the maximum concentrations of nitrogen in Estonian rivers in the early 1990s (Loigu & Vassiljev, 1997). During last 2 decades the concentration of phosphorus has declined also in all areas except in the Gulf of Finland (Pawlak et al., 2009). The increasing spring bloom biomass in the Gulf of Finland until 1990s indicated ongoing eutrophication. Since the 1990s the decreased availability of N has lowered the magnitude of spring blooms, while leaving increasing amounts of unused P (Raateoja et al., 2005), which promotes cyanobacterial production in summer. Despite decreased nutrient loading from the surrounding countries, inorganic P levels increase due to internal loading from sediments (Pitkänen et al., 2001). The spreading of anoxia in deep water enhances benthic P release, which might exceed anthropogenic load even seven-fold (Lehtoranta et al., 1997; Pitkänen et al., 2003).

Atmospheric load in eutrophication has been underestimated for a long time. Atmospheric sources of phosphorus are either unimportant or not known, but input of nitrogen can be significant in some areas (Frohn & Hertel, 2004). Increased deposition of inorganic N over large areas of Europe and North America has caused an elevated availability of inorganic N in unproductive lakes, leading to higher phytoplankton biomass (Bergström & Jansson, 2006). The atmospheric deposition of nitrogen to the sea comprises about one quarter of the total nitrogen load to the Baltic Sea; it originates from emissions both inside and outside the Baltic catchment area, with shipping being the most important and increasing source (Pawlak et al., 2009). For example, in the Kattegat the atmospheric input of N can be up to 40% of the total input for the summer period (Ærteberg et al., 2003) and in the southern North Sea the atmospheric contribution is ~34% of the total input (Spokes & Jickells, 2005). Still, atmospheric transport and deposition processes are highly episodic, related to emission patterns and meteorological conditions (Prospero et al., 1996).

Freshwater and marine waters have different patterns of nutrient cycling, leading to differences in relative importance of N and P as limiting nutrients (Cloern, 2001). It was a rule for a thumb for long time that phytoplankton in lakes is limited by P (Schindler, 1977) and phytoplankton in the sea is limited mainly by N (Niemi, 1979; Barsanti & Gualtieri, 2006). In temperate estuaries the pattern is more complicated, with seasonally varying freshwater inflow the limitation may switch between N and P, and also co-limitation is possible. In estuaries N is limiting the production during summertime and P in spring due to higher freshwater influence (Conley, 2000; Cloern, 2001).

Nutrient limitation might change in time according to balance of incoming nutrients. For example, nutrient limitation assays undertaken by the U.S. Environmental Protection Agency during the 1970's suggested that roughly 72% of U.S. lakes were P limited, while 16% were N limited, whereas newer data from eighties suggested nearly equal incidence of P and N limitation (47 versus 40%) (Elser et al., 1990).

2.2.2. Other nutrients

Iron (Fe) is needed for chlorophyll synthesis and nitrogen metabolism in phytoplankton cells. The nitrate and nitrite reductase have both high iron content, whereas the energy for nitrate reduction comes from Fe-dependent photosynthetic redox reactions (Hoffmann et al., 2007; Gnanadesikan & Marinov, 2008). Therefore iron is vital for phytoplankton cells and iron-limitation can inhibit phytoplankton growth. Most of the iron in aerobic environments occurs in the virtually insoluble ferric (Fe^{3+}) state. Bioavailable ferrous ion (Fe^{2+}) exists under anoxic conditions, being found in anoxic layers of coastal marine sediments and water (Arquitt & Johnstone, 2004). In aerobic conditions bioavailable iron forms complexes with humic or fulvic acids originating from land (Arquitt & Johnstone, 2004), which complicates the algal uptake.

Due to complex formation, the concentration of bioavailable iron in the sea is generally very low (Stal et al., 1999) and algae need high-affinity acquisition mechanisms for the Fe uptake. The result of iron limitation is a decrease in chlorophyll a (Chl *a*) and soluble protein content, as well as reduced growth (Davey & Geider, 2001; Lewandowska & Kosakowska, 2004). According to Pempkowiak et al. (2000) the concentration of dissolved iron in the Baltic Proper surface water may reach 1 μg l^{-1} (18 nM), which is quite high, but still, cyanobacteria are occasionally found to be limited by Fe (Stal et al., 1999). Iron is found to be an important factor constraining primary production in oligotrophic clearwater lakes, for example, in 30% of 659 Scandinavian lakes Fe had strongest enhancing effect compared to N and P (Vrede & Tranvik, 2006).

Silicon (Si) comes mainly from weathering of silicate-containing minerals and is supplied mainly by rivers (Papush & Danielsson, 2006). The main consumers are diatoms, due to their siliceous cell-wall. Diatoms convert dissolved Si to biogenic Si or opal, which has a low dissolution rate and thus easily accumulates in sediments (Muylaert et al., 2009). Since the amount of Si is not increasing in eutrophication process together with N and P, it alters the nutrient ratio and causes changes in the phytoplankton community structure and succession. Limited diatom growth has an important impact on the trophic structure and the cycles of nutrients in marine environments (Officer & Ryther, 1980; Conley et al., 1993; Ragueneau et al., 2006), since diatoms are the preferred food for many grazers in the upper trophic layers (Danielsson et al., 2008).

In the Baltic Sea the concentrations of dissolved silicon (DSi) have had decreasing trends during the time period 1970–2000 (Rahm et al., 1995), at a rate of -0.05 – -1.2 μmol Si l^{-1} y^{-1} (Papush & Danielsson, 2006). The reason behind this may be both, reduced riverine input (Humborg et al., 2000) and increasing eutrophication (Papush & Danielsson, 2006). DSi concentration coming via riverine transport is strongly influenced by river damming (Conley, 2000) – runoff normalized DSi yield of the regulated watershed was only half the DSi yield of the unperturbed watershed (Humborg et al., 2006). Lack of DSi has been found to limit the diatom blooms in spring (Conley, 2000), leaving unused N and P for the summer consumption. This may happen especially in the Gulf of Riga and in the Gulf of Finland, which may become silica limited in near future (Danielsson et al., 2008). However, during the last decade declining trends appear to have leveled off with the slope of the decrease in DSi for the period 1990–2001 being less than for 1970–2001 (Conley et al., 2008). The present day DSi load to the Baltic Sea is 855 kt y^{-1}, whereas 1074 kt y^{-1} of biogenic silica is accumulating in the sediments (Conley et al., 2008). The recycling of silica is much slower than both nitrogen and phosphorus, which means that phosphorus can be used many times more during its “life cycle” compared to silicon (Conley et al., 1988).

Microelements: There is always a possibility that even though macronutrients are not limiting, low availability of bioactive trace metals may directly limit physiological processes of phytoplankton (McKay et al., 2001). For example, Mo limitation inhibits the N_2-fixing in cyanobacteria (Paerl et al., 1987). Cyanobacteria and other phytoplankton may accumulate biologically important microelements (B, Mo, Se, Co and Zn) (Sunda & Huntsman, 1995; Sedykh et al., 2005), whereas intracellular storage delays nutrient limitation of the growth rate (Fisher et al., 1995).

Elevated level of micronutrients, brought by high freshwater run-off, can promote harmful algal blooms. This was an hypothesised reason behind the bloom of *Chrysochromulina polylepis* Manton & Parke in Skagerrak in 1988

(Dahl et al., 2005), since *Chrysochromulina* spp. need rather high levels of micronutrients such as cobalt (Granéli & Risinger, 1994) and selenium (Dahl et al., 1989). On the other hand, elevated concentration of trace metals like copper, zinc, lead, nickel and cobalt may be toxic to phytoplankton (Hollibaugh et al., 1980; Chakraborty et al., 2010).

2.2.3. The effect of nutrient reduction

Due to the increased frequency and intensity of harmful algal blooms the knowledge about phytoplankton responses to nutrient additions is a key issue in the management of water bodies. In lakes it is easier to implement various restoration methods, e.g. sediment removal, aeration, use of chemicals and biomanipulation methods, but in larger lakes similarly to coastal areas the reduction of discharge is the only reliable way to reduce nutrient inputs. Point-source pollutants are discharges of industrial waters and municipal waste water (Meyer-Reil & Köster, 2000). Point sources are easier to control or eliminate with more efficient water purification techniques (Kauppila & Bäck, 2002). However, in modern societies the majority of nutrients come from diffuse sources, reduction of which is much more complicated. Non-point pollution originates from agricultural run-off, groundwater transport and atmospheric inputs by dry or wet deposition (Meyer-Reil & Köster, 2000). For example, in Danish lakes the relative P loading from diffuse sources is on average 57% and N loading from diffuse sources about 72% of the total input (Jensen et al., 2004).

In recent decades increased eutrophication has led to extensive investments world-wide to reduce the nutrient inputs to the lakes and coastal areas. For example in Germany extensive measures were implemented:

- usage of phosphate-free detergents,
- regulations for atmospheric sources,
- reduction of intensive livestock farming,
- drastic decrease in fertilizers use,
- installation of new wastewater-purification systems,
- usage of better nutrient removal techniques,

which has greatly reduced nutrient loads to the southern part of the Baltic Sea (Meyer-Reil & Köster, 2000). Measures taken to reduce the P loading in the western European rivers were very successful: within one decade (1980–1990) the riverine P-discharge to the Wadden Sea decreased to the pre-increase level (Kuipers & van Noort, 2008). Due to efficient nutrient removal during last 20 years the amount of incoming P to the Greifswalder Bodden, which is the largest bay on the southern coast, has decreased significantly (Munkes, 2005). Decrease in external P loading has been larger (up to 70% of the P loads from pre-reduction period) than in case of nitrogen (40%) (Munkes, 2005). Despite the reductions only slight improvement in water quality of both Wadden Sea and Greifswalder Bodden are evident (Munkes, 2005; Kuipers & van Noort, 2008). In the Wadden Sea the reduction in primary production was evident only after 10 years from the beginning of P removal, most likely due to the benthic release compensating the external reduction (Kuipers & van Noort, 2008). In lakes it is easier to reduce incoming nutrients. However, Søndergaard (2007) reports that the reduction measures usually did not led to desired effects of water quality improvement (increase in transparency and decrease in Chl *a* concentration) in most Danish lakes. Reason for poor improval may lay in internal loading e.g. release of phosphorus from sediments in anaerobic conditions (Phillips et al., 1994; Kauppila & Bäck, 2002) or inadequate nutrient reductions (Søndergaard, 2007). Since zooplankton grazing is an important way of reducing the algal mass, the decoupling between grazers and phytoplankton may be also a reason behind non-improval, for example in the case, when filamentous cyanobacteria dominate in the community (Blindow et al., 2000; DeMott et al., 2001) or planktivorous fish remove the grazers (Van Donk et al., 1994).

Duarte et al. (2009) analysed published cases of success and failure in terms of reducing Chl *a* concentration followed by a long term nutrient reduction in coastal systems. They described 4 scenarios of oligotrophication and concluded that a direct linear response to nutrient reduction is an oversimplification and happens seldom if at all in real life.

2.3. Nutrient ratios

Tilman was the first to underline the significance of not only actual concentrations, but also resources ratios (Sommer, 1993). He claimed that species competition near competitive equilibrium should be determined by the ratios of limiting resources, whereas even a few resources can generate a wide range of resource ratios (Tilman, 1977). Tilman's theory was based on a mechanistic approach to predict competitive success as a function of the limiting resources (Grace, 1991). Ratios together with a plausible amount of environmental heterogeneity can be behind the structure of phytoplankton communities (Thompson, 1987).

For many years, oceanographers have considered the Redfield ratio (C:N:P = 106:16:1 by atoms) a cornerstone concept to illustrate phytoplankton need for nutrients. A serious deviation from that ratio can indicate the limiting nutrient. However, Redfield N:P ratio of 16 is not a universal biochemical optimum, but represents an average ratio for the whole phytoplankton community (Klausmeier et al., 2004; Lagus et al., 2004), whereas more than two-fold deviations from that ratio have been found (Bertilsson et al., 2003; Heldal et al., 2003; Klausmeier et al., 2004).

In reality the ratio of macronutrients is species-specific and depends on many factors. Species differ in their kinetics of nutrient uptake, assimilation and storage capacities and may have different nutrient requirements as well as different cellular composition of N and P (Hecky & Kilham, 1988; Quigg et al., 2003). For example, cyanobacteria with N-fixing abilities preferably develop in conditions, where N:P ratio tends to be lower than Redfield ratio (Finni et al., 2001; Stal et al., 2003), whereas N:P ratio in their cells is higher compared to non-N fixing species (Klausmeier et al., 2004). Also growth rate, light conditions, CO_2 availability and ambient nutrient concentrations may cause a variation in species-specific nutrient ratios (Lagus et al., 2004).

There are several ways to describe, which nutrient is limiting phytoplankton production:

1) Dissolved mineral nutrient concentrations in water (Smith, 1984; Kirkkala et al., 1998). The concentration will give some indication whether the nutrient is limiting (Barsanti & Gualtieri, 2006). For example when the concentration of P is more than few µg l^{-1}, it is not considered as limiting. In routine monitoring in Odense Fjord potentially limiting concentrations sensu Fisher et al. (1992) are used, i.e. for dissolved inorganic nitrogen (DIN) < 2 µmol l^{-1}, dissolved inorganic phosphorus (DIP) < 0.2 µmol l^{-1} and DSi < 2 µmol l^{-1}. Nutrient concentration may be low also in the case when supply rate is high, since the turnover rate of bioavailable nutrients is high and low levels of dissolved inorganic nutrients can be found even in highly productive waters (Dodds, 2003). Tanaka et al. (2006) suggest that PO_4 < 1 nmol-P l^{-1} seems to indicate P limitation of osmotrophs in different aquatic systems. Unfortunately, no reliable methods are currently available for direct and precise measurement of the bioavailable PO_4 pool, since conventional DIP measurements by molybdenum blue reaction tend to overestimate true PO_4 pool (Thingstad et al., 1993; Hudson et al., 2000; Tanaka et al., 2003).
2) DIN:DIP ratio
   According to an extensive overview (Anonymous, 2000) DIN:DIP is a good predictor to nutrient limitation in both coastal and estuarine systems. Nutrient ratios, DSi:DIN, DSi:DIP and DIN:DIP, are often used to determine which nutrient may limit the primary production, focusing often to departures from Redfield ratio (Danielsson et al., 2008). However, Dodds (2003) claims that N is not limiting only in case, when DIN levels are much higher than the DIP (e.g., 100:1) and P is not limiting, when DIN:DIP < 1.
3) Total nitrogen to total phosphorus ratio (TN:TP) is quite widely used, in earlier works as well as recently (Schindler, 1977; Smith, 1983; Teubner & Dokulil, 2002; Tõnno & Nõges, 2003; Elser et al., 2009; Bergström, 2010; Guan et al., 2010). According to Guildford and Hecky (2000), TN:TP ratio < 20 generally indicates nitrogen limitation and TN:TP > 50 phosphorus limitation. In the Baltic Sea DIN:DIP ratio can be low (suggesting to N limitation), while TN:TP ratio is high (suggesting to P limitation). Despite the high TN:TP ratio phytoplankton in the Baltic Sea can still be N limited (Moisander et al., 2003). This suggest that TN:TP ratio is not suitable for predicting the limiting nutrient in the Baltic Sea, where diazotrophic cyanobacteria form a substantial fraction of the phytoplankton community.

4) DIN:TP
Several authors (Morris & Lewis, 1988; Lafrancois et al., 2003; Bergström, 2010) argue that DIN:TP ratio describes phytoplankton nutrient limitation better than the usage of TN:TP ratio, since it represents best the nutrient supply for phytoplankton growth. Phytoplankton can use P derived from organic P forms justifying the use of TP (Wetzel, 2001; Lewis & Wurtsbaugh, 2008). Concomitantly, significant amount of TN consist of refractory DON compounds, even in oligotrophic lakes, which makes TN a poor predictor of bioavailable N (Lewis & Wurtsbaugh, 2008). According to Sickman (2001), phytoplankton is N-limited, when DIN:TP ratio is below 0.5 and P-limited, when the ratio is above 4. According to Bergström (2010) phytoplankton shifted from N to P limitation when DIN:TP mass ratios increase from 1.5 to 3.4.
5) Particulate organic nitrogen to particulate organic phosphorus ratio (PON: POP) shows the internal stores of N and P, and is often used both, in lakes and marine waters (Flemer et al., 1998; Guildford & Hecky, 2000). According to these authors, the ratio below 11 indicates N limitation and above 22 P limitation. The use of PON:POP must be used with caution, since it also includes N and P in detritus and zooplankton, not only in algal cells (Lignell et al., 2003).
6) Nutrient limitation assays give the most accurate answer, which nutrient is limiting the production, but are also most laborious to perform. The phytoplankton response to the nutrient addition is under continuous observation; addition of the limiting nutrient causes an increase in abundance or biomass. These responses include short-term ^{14}C uptake, N and P uptake rates, phosphatase assays and changes in biomass indicators such as chlorophyll a and particulate carbon (Holmboe et al., 1999; Andersen et al., 2007).
7) Alkaline phosphatase activity can be used as a convenient molecular indicator of P deficiency, since phytoplankton and bacteria use phosphatases to get P from organic matter, the enzymatic activity increases in case of P limitation (Cembella et al., 1984; Hoppe, 2003; Tanaka et al., 2006).

According to Lignell et al. (2003) concentrations and ratios of essential elements neither permit precise identification of the limiting nutrient nor allow quantification of the flow of nutrients through the plankton food web, since algae can grow in nutrient concentrations below detection limit. Indices based on dissolved nutrient ratios are inconclusive if more than one nutrient is below chemical detection limits at the same time, which is often the case throughout the productive season (Lignell, 2003) and the calculation of ratios becomes exceedingly inaccurate. The usage of ratios is often a simplification. Factors such as release of particle bound phosphorus, sediment phosphorus releases and phytoplankton recycling can make the simplistic use of the ratio inappropriate.

2.4. Cyanobacteria as bloom-formers

Cyanobacterial blooms have attracted scientific interest since the 19th century (Eichwald, 1847; Geitler, 1925; Huber-Pestalozzi, 1938; Kullus, 1964; Finni et al., 2001; Huisman et al., 2005). Massive development of cyanobacteria create problems mainly in lakes and water reservoirs, affecting water quality by biomass accumulation, by generating visible surface scum and by producing toxic compounds (Reynolds, 1987; Chorus, 2001; Codd et al., 2005; Znachor et al., 2006). Surface scum usually forms during warm and calm weather, being unsightly, odiferous and sometimes toxic (Reynolds, 1984). Problems with cyanobacterial blooms are widespread, with occurrence all over the world (Dow & Swoboda, 2000), being far more common in lakes than in marine waters. The Baltic Sea is an exception, with blooms of cyanobacteria occurring every summer. Blooms of cyanobacteria are an increasing nuisance in the open Baltic (Kahru et al., 1994; Finni et al., 2001). Visible cyanobacterial blooms are unevenly distributed in the Baltic Sea. The blooms are lacking in the Bothnian Bay, in the Kattegat and the Kiel Bight, but are frequent and massive in the Gulf of Finland (Lips & Lips, 2008), the Gulf of Riga (Seppälä & Balode, 1999) and the Baltic Proper (Finni et al., 2001). The collection of representative water samples for cyanobacterial abundance is a difficult task due to the patchy nature of the blooms (Kutser, 2004; Simis et al., 2007). Remote sensing techniques allow more accurate overview of the blooms extent and density (Kahru & Brown, 1997a; Lavender & Groom, 2001; Kutser, 2004; Gower et al., 2008).

Blooms develop as a combination of growth, accumulation and physical advection exceeding loss processes such as lysis, sinking and predation (Irigoien et al., 2005). It has been suggested that cyanobacterial blooms are caused by a complex interaction of elevated P concentrations, sunlight, warm temperature, turbidity, pH, conductivity, carbon availability and suitable hydrological conditions (Apeldoorn et al., 2007). The intensity of these blooms is related to low DIN:DIP ratio, high temperature of the surface waters, and low wind mixing (Mazur & Plinski, 2003; Lips & Lips, 2008). Since blooms of cyanobacteria are natural phenomena in the Baltic Sea, the reduction of nutrients will not eliminate blooms, but can at best reduce their intensity (Bianchi et al., 2000). The general consensus is that reductions of both, nitrogen and phosphorus external loads is essential to reduce cyanobacterial blooms (Kangro et al., 2007; Vahtera et al., 2007).

Blooms end due to nutrient limitation, light limitation by self-shading, viruses or weather-caused turbulent mixing, which may break up the filaments (Moisander et al., 2002a). The organic matter formed during the blooms is largely cycled through bacteria and a bacteria-dependent microbial food-web in the mixed surface water (Heiskanen & Kononen, 1994; Sellner, 1997), unused biomass settles to the bottom, providing a food source for benthic feeders (Heiskanen & Olli, 1996).

2.4.1. Main bloom-forming species in lakes and in the Baltic Sea

The main bloom-forming species in the Baltic Sea are toxic *Nodularia spumigena* Mertens, potentially toxic *Anabaena* spp. and non-toxic strain of *Aphanizomenon* (Finni et al., 2001). According to Laamanen & Kuosa (2005) *Nodularia* is the only proven toxic cyanobacterial genus in the Baltic Sea, which makes up large part of the annual blooms. In less saline near-shore waters *Anabaena lemmermannii* P. Richter may form blooms (Sivonen et al., 2007) and the species is found to be toxic in lakes (Onodera et al., 1997). According to Sivonen et al. (2007) also other *Anabaena* species in the Baltic Sea may produce toxins. There is a variety of *Anabaena* species, for example in Vistula lagoon *Anabaena flos-aquae* Brebisson, *Anabaena spiroides* Klebahn, *Anabaena lemmermannii*, *Anabaena mendotae* Trelease, *Anabaena* cf. *circinalis* Rabenhorst, *Anabaena crassa* (Lemm.) Kom.-Legn. et Cronb. form a significant component in blue-green algal blooms during the summer seasons (Rybicka, 2005).

In lakes cyanobacteria often dominate during summer period. An estimated 40 genera of freshwater cyanobacteria are known to form toxic blooms, the most common genera are *Anabaena*, *Aphanizomenon*, *Cylindrospermopsis*, *Lyngb*ya, *Nodularia*, *Microcystis*, *Nostoc* and *Oscillatoria* (*Planktothrix*) (Carmichael, 2001; Mazur & Plinski, 2003). *Anabaena*, *Microcystis*, *Aphanizomenon* and *Gloeotrichia* form blooms in eutrophic lakes (Ott & Kõiv, 1999; Wilson et al., 2005). *Planktothrix agardhii* (Gomont) Anagn. & Komarek may form dense blooms in hypertrophic lakes through the year (Laugaste, 1990). Toxic blooms get more attention than non-toxic, but with the development of biochemical and chromatographical methods toxins are discovered in wider and wider range of species.

Despite the fact that growth rates of bloom-forming cyanobacteria are relatively low, a variety of properties provide an ability of bloom-forming taxa to outcompete other phytoplankton species (Paerl & Millie, 1996). Buoyancy regulation together with plasticity in photopigments allows cyanobacteria to inhabit deeper parts of the water column as well as water layers near the surface. Cyanobacteria with gas vesicles can migrate vertically and store P-reserves in deeper water layers (Oliver & Ganf, 2002). By concentrating to the water surface, cyanobacteria ensure light availability to themselves and suppression of other competitive species by shading.

2.4.2. Factors favouring cyanobacterial domination

- **Nutrients**

In general, low nitrogen and high phosphorus concentration in summer, and as an outcome, a low N:P ratio have been suggested as the principal factor of the domination of diazotrophic cyanobacteria in the Baltic Sea (Niemi, 1979; Smith, 1983; Reynolds, 1987; Pitkänen & Tamminen, 1995). During recent decades, the winter pool of DIP has increased in the Baltic Sea, while DIN concentration on average show a decreasing trend (Lips et al., 2002), leading towards favourable conditions for cyanobacterial bloom development. The decrease in DIN:DIP ratio favour development of N_2-fixing cyanobacteria. P availability is found to be an important factor for cyanobacterial bloom development. The dominating filamentous cyanobacteria in the Baltic Sea use a variety of P sources: intracellular storage accumulated during spring, remineralisation of P in the upper mixed layer, and utilisation of new P input through turbulent mixing and upwelling (Kononen et al., 1996; Larsson et al., 2001; Lignell et al., 2003). Phosphorous release from bottom sediments during anoxic conditions is one of the major factors favouring cyanobacterial development in the Baltic Sea (Ziller & Conley, 2010). Physical transport of released phosphorus to surface layers would enhance N_2-fixation by diazotrophic cyanobacteria (Fig. 1).

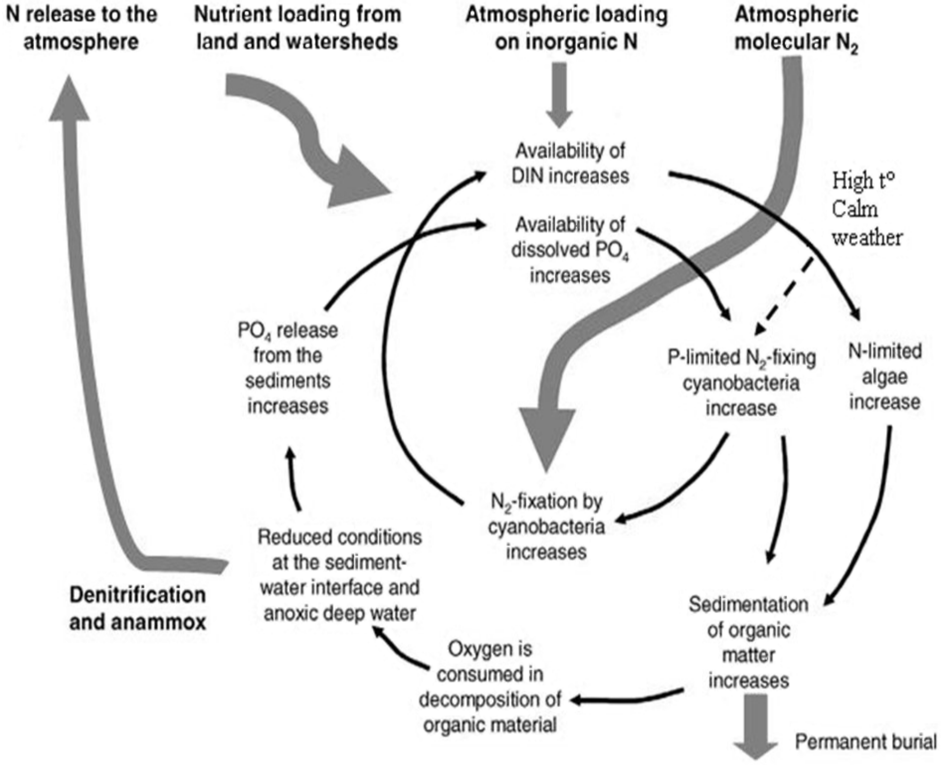

Figure 1. Main feedback processes that inhibit the recovery from eutrophication and favour cyanobacterial blooms in the Baltic Sea. Grey arrows denote material flows. Thin arrows denote causal relationships and successive events. Dotted line denotes enhancing factors of cyanobacterial blooms. With modifications from Vahtera et al. (2007).

Low N:P ratio favours only nitrogen-fixers, other cyanobacteria still need external DIN sources for growth. Nitrogen limitation may be especially detrimental to non-nitrogen fixing bloom-forming species (Oliver & Ganf, 2002). Nitrogen addition promoted the growth of *Microcystis*, while the biomass of *Anabaena* sp. and *Aphanizomenon* sp. was successfully reduced by the treatment (Stockner & Shortreed, 1988). According to a mesocosm study performed by Levine & Schindler (1999) several non-heterocysteous taxa increased in relative abundance along N:P gradient.

Fe availability is one of the factors limiting the development of cyanobacterial blooms in the Baltic Sea (Balode et al., 1998; Hyenstrand et al., 1999; Stal et al., 1999). Fe is required for the main enzyme in nitrogen fixing process – nitrogenase and for ferredoxin, which acts as an electron donor to nitrogenase (Stal et al., 2003). Lack of Fe limits the growth and nitrogen fixation of cyanobacteria (Stal et al., 1999; Vuorio et al., 2005).

- **Temperature**

Cyanobacterial blooms occur most frequently during warm seasons, i.e. summer-fall, with ambient temperature playing a key regulatory role (Jacoby et al., 2000; Jöhnk et al., 2008; Paerl & Huisman, 2008). Bloom development is often associated with elevated water temperature, increased light levels (Stal et al., 2003; Lips & Lips, 2008) and stabilization of the water column (Laamanen & Kuosa, 2005). Intensive biomass growth of *Aphanizomenon* sp. occurs at temperatures > 10ºC, with temperature optimum between 16–22ºC (Lehtimäki et al., 1997). Although Kanoshina et al. (2003) suggest that other factors like P availability are more important for *Aphanizomenon* sp. than temperature, the integrated biomass of *Aphanizomenon* sp. in the Baltic Sea was lower during colder summers (Lips & Lips, 2008).

Temperature conditions are found to be the main factor for determining the intensity of *Nodularia spumigena* blooms (Kanoshina et al., 2003). Lips & Lips (2008) found the biomass of *N. spumigena* to be more strongly correlated to temperature than the biomass of other bloom-forming cyanobacteria. The temperature optimum for *N. spumigena* is at higher temperatures (25–28ºC), the critical temperature for bloom development is >16ºC (Wasmund, 1997; Kanoshina et al., 2003). Dependence of higher temperature is one of the factors behind shorter bloom duration periods of *N. spumigena* compared to *Aphanizomenon* sp. (Vahtera et al., 2005; Vahtera et al., 2007).

- **Irradiance**

Light has received less attention as a selective factor of phytoplankton community, probably because the changing vertical light gradient makes light a rather complex factor when compared with the nutrient competition (Bhutiani et al., 2009). Nevertheless, light is often mentioned as one of most important external drivers of phytoplankton development (Scharfe et al., 2009). Availability of light for phytoplankton growth in a lake is determined by water transparency, mixing depth and incident light intensity. Thus light may be the main limiting factor in shallow lakes and estuaries, where wind constantly mixes sedimented material and the incoming river adds particulate matter (Scheffer, 1998). Thus the limitation of the algal growth by light is dependent on the particulate matter concentrations and on self-shading (Schroeder, 1997). Accessory pigments phycoerythrin and phycocyanin give cyanobacteria an opportunity to harvest light in wavelengths, where other phytoplankton cannot.

Some researchers (Stal et al., 2003) denote that light is a major factor determining the formation of a cyanobacterial bloom, since without sufficient amount of light cyanobacteria are not able to support nitrogen fixation (Klausmeier et al., 2004). The main bloom-formers in the Baltic Sea, *Aphanizomenon* sp. and *Nodularia spumigena* are positioned differently in the water column: *Aphanizomenon* is frequently found relatively evenly distributed in the mixed surface layer, but the actual bloom peak is around 10 m depth, whereas *N. spumigena* appears to depend on a relatively stagnant water column and accumulates in the high irradiance, warm upper 5 m surface layer, in order to reach bloom densities (Kononen et al., 1996; Vahtera et al., 2005). This can be explained by lower demand for light of *Aphanizomenon* sp. compared to *N. spumigena* (Lehtimäki et al., 1997). The optimal range of light intensity for the growth of *A. flos-aquae* and *N. spumigena* is 25–45 and 105–155 µmol photons $m^{-2} s^{-1}$, respectively (Kanoshina et al., 2003).

- **Water column stability**

Blooms can take place, when the mixing depth does not exceed the critical depth, where the respiration exceeds the primary production of cyanobacterial community (Huisman et al., 1999). In lakes the mixing process is important for bringing nutrients out of the sediments and physical transport of phytoplankton cells. High turbulence in the surface mixed layer inhibits the growth of heterocysteous cyanobacteria (Paerl, 2002), causing filament breaking and inhibition of N_2-fixation (Moisander et al., 2002a).

Wind action effectively disrupts cyanobacterial bloom. According to Webster & Hutchinson (1994) wind speed > 2–3 m s^{-1} is required to mix phytoplankton floating cells from the lake surface to non-stratified water column, but during calm conditions intense surface concentrations appear rapidly (Oliver & Ganf, 2002). Wind speed of 1 m s^{-1} generates a surface current of 2.5 cm s^{-1}, and surface accumulations are rapidly transported horizontally, which causes surface biomass accumulations at the downwind side of a lake (Oliver & Ganf, 2002).

Upwelling in the Baltic Sea also affects cyanobacterial development: prebloom upwelling event enhances the bloom (due to rise of nutrient-rich water), whereas upwelling during the bloom inhibits the growth of cyanobacteria due to colder water temperature and mixing processes (Kanoshina et al., 2003). The cyanobacterial biomass increase as a response to nutrient loading from upwelling event is not instant, but may take weeks due to the relatively slow growth rate (Vahtera et al., 2007).

- **Salinity**

Salinity is affecting the development and distribution of cyanobacteria, being an effective barrier to freshwater nuisance species (Paerl, 2002). Freshwater species are transported into the Baltic Sea via rivers, but only a few of them are capable of bloom formation in the brackish water. There has been considerable taxonomic confusion around the Baltic Sea strain of *Aphanizomenon*. Various species of *Anabaena* and *Aphanizomenon* inhabit the lakes around the Baltic Sea. Laamanen & Kuosa (2005) suggested the *Aphanizomenon* in the Baltic Sea being *flos-aquae*, whereas Barker et al. (2000) and Janson & Graneli (2002) pointed to genetical differences between *A. flos-aquae* from lakes and *Aphanizomenon* sp. from the Baltic and consider them as different species. Various identities are used in the literature: *Aphanizomenon* sp. (Larsson et al., 2001), *A.* ''*baltica*'' (Engel et al., 2002) or *A. flos-aquae* (Suikkanen et al., 2006; Suikkanen et al., 2010).

Both *Aphanizomenon* and *Nodularia* form blooms in salinities up to 11.5 in the Baltic Sea (Wasmund, 1997). Generally *Aphanizomenon* sp. prefers lower salinity (0–5 psu) and inshore regions of the archipelagos (Niemistö et al., 1989), but high growth rate is found also at salinities 5–10 psu (Lehtimäki et al., 1997). *N. spumigena* is found to grow well in salinities between 4–20 psu in culture conditions, with 8 psu as an optimum (Moisander et al., 2002b; Musial & Plinski, 2003). Growth rate, nitrogenase activity and CO_2 fixation appeared to be higher at 6–20 psu, but various strains may act differently (Moisander et al., 2002b). High salinity is found to inhibit nitrogen fixation – via the inhibition of nitrogenase by high concentrations of SO_4^{2-} (Stal et al., 2003). Stal et al. (1999) found significant decrease in nitrogenase activity of *N. spumigena* at salinity 9 psu. However, *Nodularia* has the ability to acclimate to salt stress over short- (24 h) and long-term (several days to weeks) exposures (Moisander et al., 2002b). The Baltic Sea *Nodularia* strains are more stenohaline than the strains isolated from Australian waters, which grew well in a range of 0–35 psu (Blackburn et al., 1996; Musial & Plinski, 2003).

There are salinity-tolerant strains of *Anabaena*, but generally the growth rate is higher in freshwater (Moisander et al., 2002b). However, estuarine *Anabaena aphanizomenoides* Forti maintained high growth rates in a saline range of 0–10 psu, with a tolerance between 0–20 psu (Moisander et al., 2002b). Faithfull & Burns (2006) found that salinity did not affect the germination of *Anabaena flos-aquae* akinetes, but filament development was significantly lower at 6 psu compared to lower salinities.

- **Zooplankton effects**

Weak control by zooplankton is one of the prerequisites of phytoplankton bloom. Filamentous or otherwise unpalatable forms have an advantage and are more likely to form blooms. Large cells can effectively avoid grazing, but their growth rates are generally lower compared to smaller cells (Irigoien et al., 2005).

Since filamentous cyanobacteria have relatively low growth rates, zooplankton grazing pressure on competitive species favours bloom development. Copepods avoid feeding on filaments and thus the grazing pressure on cyanobacteria is generally lower than to other phytoplankton group (Sellner et al., 1996; Engström et al., 2000). Potentially toxic filamentous cyanobacteria *Planktothrix*, *Anabaena*, *Aphanizomenon* and *Nodularia* are found to be grazed at least in lakes by zooplankton (Epp, 1996; Schmidt et al., 2002; Oberhaus et al., 2007). However, cyanobacteria may negatively affect crustacean communities (Reinikainen et al., 1994; Ghadouani et al., 2003; Chen et al., 2005), lowering their fecundity and reproductive success (Koski et al., 1999) and many examples of the toxic effects of cyanobacteria on zooplankton exist (Weithoff & Walz, 1995; Thostrup & Christoffersen, 1999; Rohrlack et al., 2005).

The main copepod species in the Baltic Sea *Acartia bifilosa* and *Eurytemora affinis* have low clearance rates on filamentous cyanobacteria (Sellner et al., 1994; Sellner et al., 1996), suggesting that copepod herbivory is not an important mechanism for bloom termination (Sellner, 1997). Hairston et al. (1999) suggest that populations of zooplankton that co-occur with dense cyanobacterial populations may be better adapted to digest cyanobacteria than unexposed zooplankton. Generally cyanobacteria present obstacles to feeding, growth and survival of the grazer population (de Bernardi & Giussani, 1990). Although copepods may consume either portions of filaments or entire cyanobacterial filaments (Schaffner et al., 1994), they prefer other food sources, if available (Work & Havens, 2003).

The role of zooplankton in the control of cyanobacterial blooms and the transfer of cyanotoxins to higher trophic levels are of great importance for the management of water resources. E.g. *Daphnia* may transfer cyanobacterial toxins up the food chain (Oberhaus et al., 2007).

2.4.3. Cyanobacteria as nitrogen-fixers

Cyanobacteria are unique among algae for their ability to fix atmospheric nitrogen. In the Baltic Sea large heterocysteous filamentous cyanobacteria are the main nitrogen fixing organisms (Stal & Walsby, 2000). The amount of fixed nitrogen may exceed atmospheric deposition (Larsson et al., 2001), and be equal the riverine input (Huber, 1986; Wasmund et al., 2001). Thus nitrogen fixation is an important pathway of bringing new nitrogen to the system. The average annual estimate of nitrogen fixation in the Baltic Proper was 190 kt N in 1997–2005 (Håkanson & Bryhn, 2008). The estimate varies between years, and during years of low cyanobacterial abundance e.g. 1985 and 1988 (Kahru et al., 1994) the contribution may have been much lower. The variation between years may be up to a factor of 20 (Håkanson & Bryhn, 2008). According to Larsson et al.

(2001) total N fixation in the Baltic Proper is 180–430 kt N per year. This amount of fixed nitrogen was sufficient to sustain 30–90% of the pelagic community net production during summertime (Larsson et al., 2001). However, N_2 fixation is energetically expensive, requiring 16 molecules of ATP per each fixed N_2 molecule (Stal et al., 2003), thus cyanobacteria use first ammonium and nitrate, if available, and only then start to fix atmospheric nitrogen (Ferber et al., 2004).

Cyanobacteria may release part of the fixed nitrogen as ammonium or amino acids, which promote the growth of bacteria and N-limited phytoplankton (Bianchi et al., 2000; Ohlendieck et al., 2000; Gallon et al., 2002). Approximately 10 to 20% of the fixed nitrogen is directly transferred from diazotrophic cyanobacteria to other consumers (Stal & Walsby, 1998). Decaying blooms support the growth of bacteria and heterotrophic food chain (Engström-Öst et al., 2002) and increase the N:P ratio in water column (Heiskanen & Tallberg, 1999).

Filamentous diazotrophic cyanobacteria are not the only nitrogen-fixers. Unicellular small-celled cyanobacteria are also found to be capable of nitrogen fixation in rates, which are equal or larger than the contribution by filamentous diazotrophs to oligotrophic ocean environment (Montoya et al., 2004).

2.4.4. Akinetes as a specific feature of lifecycle

Cyanobacteria from orders Nostocales and Stigonematales form akinetes, which are thick-walled cells specialized for survival of unsuitable environmental conditions (Thiel & Wolk, 1983). Cyanobacterial akinetes develop from vegetative cells and contain large amounts of cyanophycin polypeptide and cyanophycean starch, but no polyphosphate (Van den Hoek et al., 1995). Akinetes are generally larger than vegetative cells, they are more resistant, with a thickened cell wall and a multilayered extracellular envelope, which ensures resistance to desiccation and temperature fluctuations (Adams & Duggan, 1999). The formation of akinetes may be triggered by low light levels (shelf-shading), desiccation or abrupt changes in temperature (Fisher & Wolk, 1976; Nichols et al., 1980). Lack of P (Wolk, 1965; van Dok & Hart, 1996) and N (Rao et al., 1987) induces akinete formation. Akinete formation occur towards the end or after the cessation of exponential growth phase (Nichols & Adams, 1982), decreased cell division is the proximal cue for the start of akinete production (Adams & Duggan, 1999). Akinetes show reduced level of metabolic activity (Thiel & Wolk, 1983) and processes like N-fixing and protein synthesis are generally at undetectably low level (Adams & Duggan, 1999).

Akinetes accumulate in the sediment and germinate in suitable conditions, providing a source of inoculum that starts the seasonal blooms (Padisák, 2003; Moore et al., 2004). Higher light availability, longer day-length, presence of dissolved oxygen in the sediments and especially increasing temperature trigger germination (Adams & Duggan, 1999). Phosphorus availability is necessary, whereas nitrogen seems to be less important (Dok & Hart, 1996; van Dok & Hart, 1997). Excellent review by Agrawal (2009) gives an overview of known factors, which may affect algal spore germination.

Most of the studies on akinete formation and germination are done in culture conditions. Quantitative studies on akinete production in natural population are almost lacking (however, see Karlsson (2003), Karlsson-Elfgren et al. (2003; 2005) and Suikkanen et al. (2010)).

3. GOALS

The aim of the study was to investigate both short and long-time changes in phytoplankton biomass and community composition caused by the changes in nutrient loadings. The main objective of this thesis is to describe the effect of nutrient addition and selective nutrient limitation on the natural phytoplankton community enclosed into mesocosms (**I**, **II**, **III**).

Second objective was to study, how N or P limitation affects akinete production of two *Anabaena* species (**II**).

Third: to show that dynamic of some phytoplankton species cannot be explained solely by bottom-up regulation (**I**, **III**)

Fourth: to show the changes in the phytoplankton community composition and in lake's ecological status due to nutrient addition based on a long-term study in a small stratified lake (**IV**).

4. MATERIAL AND METHODS

4.1. Study sites

The Baltic Sea is the largest brackish water body in the world, with a total area of 415 000 km^2, a water volume of almost 22 000 km^3, and a coastline of about 22 000 km. It is surrounded by many large cities and regions with intensive agriculture and industry – the catchment area comprises 1.7 million km^2 with a population of more than 80 million inhabitants. The Baltic Sea is semi-enclosed, connected to the North Sea via the narrow Öresund and the Belts. The limited water exchange produces a gradient of salinity from 9 in the southern part of the Baltic proper to 1–2 psu in the northern Bothnian Bay. The bottom salinity may reach 20 psu at the bottom of Bornholm basin. A steep halocline at 50–70 m separates the deep water from the surface waters. During summers the surface layer warms up, leading to thermally stratified water column. Tidal activities are not pronounced; differences in water level of the coastal inlets result from wind-induced water movements. Eutrophication and associated hypoxia, defined as < 2 mg l^{-1} dissolved oxygen, are the main threats to the health of the Baltic Sea ecosystem (HELCOM, 2007).

I., **II**. The Gulf of Finland is one of the most heavily nutrient-loaded basins of the Baltic Sea. Its catchment area is approximately 421 000 km^2 (Estonia 35 000 km^2, Finland 110 000 km^2, Russia 276 000 km^2). The city of St. Petersburg with the adjacent region, Karelia, and Estonia are main contributors to the pollution of the Gulf. For example, about 25 percent of the phosphorus point-source load for the whole of the Baltic Sea is discharged into the Gulf of Finland (HELCOM, 1993). During summertime nitrogen is generally the limiting nutrient of the primary production in the Gulf of Finland (Kivi et al., 1993; Lignell et al., 2003). Four main periods of phytoplankton community can be distinguished: a low-biomass winter state, an extensive bloom in April-May dominated by dinoflagellates and diatoms, high abundance of nitrogen-fixing cyanobacteria during summertime and lower biomass autumn bloom of dinoflagellates or diatoms. Rotifers are common in early and late summer (Kivi, 1986), calanoid copepods, mainly *Acartia bifilosa* Giesbrecht and *Eurytemora affinis* (Poppe) and a cladoceran *Bosmina longispina maritima* (P.E. Muller) form a biomass peak in late summer (Viitasalo, 1992).

III. The catchment area of the Kattegat is 25 800 km^2, with 15 800 km^2 belonging to Denmark and about 10 000 km^2 located in the territory of Sweden. Odense Fjord (~60 km^2) is shallow (average depth of 2.25 m) mesohaline estuary located in the northern part of the island of Fyn (Fig. 1. in **III**). The catchment area of the fjord is large, approximately 1000 km^2 (about one third of the island of Fyn), most of which is agricultural land. The main freshwater source to the fjord is River Odense, the mouth of which is located in the innermost part of the fjord. The water in the fjord is a mixture of freshwater and salty water from Kattegat. The anthropogenic load of nutrients to the fjord is high; the main influence comes from agriculture. Due to establishment of a waste-water treatment plant P load to the estuary is reduced 6-7 fold since 1980s, whereas N load has being reduced by 15-30% (Anonymous, 2003).

IV. Lake Verevi is a sharply stratified, partly meromictic lake with steep gradients in nutrient concentrations and temperature in summertime. The spring turnover is often incomplete even in homothermal conditions. It is located in a small town Elva and acts as a popular recreational place in summertime. The historical phytoplankton records go back to 1920s, allowing us to follow the long-term changes in phytoplankton community composition. Due to overflow from sewage-ponds, which were located near-shore, the lake has suffered severe nutrient inputs.

The main limnological and morphometrical data about the lake are given in Table 1 and the bathymetric map is presented in Fig. 2.

Table 1. The general information about L. Verevi.

Morphometrical data	
Surface (ha)	12.6
Maximum depht (m)	11
Mean depth (m)	3.6
Drainage area (ha)	1.1
Times of water exchange per year	0.63
Water volume (10 ^{6} m^{-3})	453.6

Limnological data (year 2000)	**Epilimnion**		**Hypolimnion**	
	min	**max**	**min**	**max**
Transparency m	0.7	4.2		
Tot P µg l^{-1}	22	153	375	2900
Tot N µg l^{-1}	670	2450	4200	18620
Chl *a* µg l^{-1}	4	110	63	532
Si µg l^{-1}	8	100	688	10800

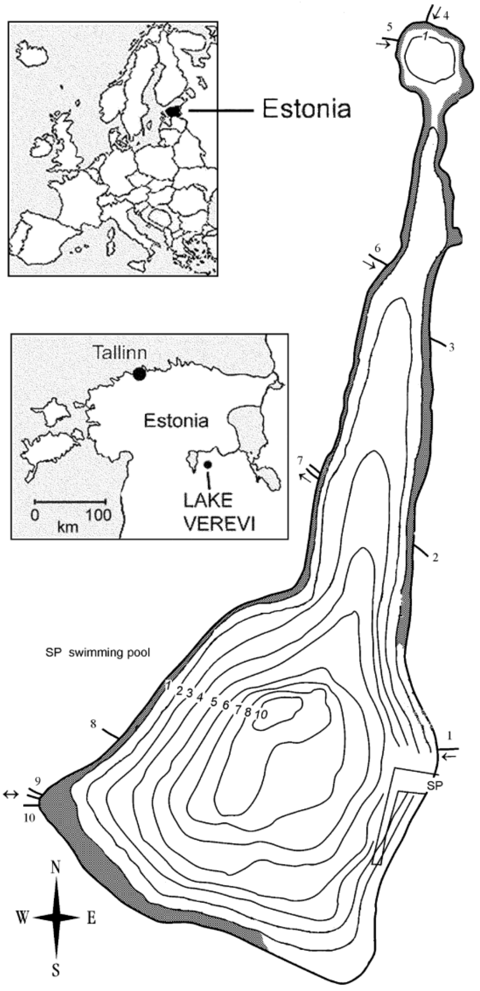

Figure 2. Location and map of Lake Verevi. Numbers indicate inlets, except 7, which is an outlet. Redrawn from Ott et al. (2005a).

4.2. Mesocosms and experimental design

Mesocosms have been used for a long time to study the effect of various manipulations on the plankton community (Harrisson et al., 1977; Lalli, 1990; DeYoe et al., 2000; Belzile et al., 2006; Longhi et al., 2006; Pilkaityte & Razinkovas, 2006). Mesocosm experiments have their intrinsic limitations: the elimination of advection, absence of some food-web components, changes in light and mixing regime and isolation from bottom-sediments (Jacquet et al., 2002). Although mesocosms are not a perfect representations of natural ecosystems (Egge & Heimdal, 1994), they are still valuable tools for understanding the changes in food-webs. Assessment of the phytoplankton biomass response to controlled experimental treatments is a first-step approach for determining the positive or negative impacts of the nutrient manipulations on phytoplankton productivity in the presence of grazers (Örnólfsdóttir et al., 2004).

The mesocosm experiments were carried out in 2003 from 1 to 22 July in a sheltered archipelago site near the Tvärminne Zooloogical Station (NW Gulf of Finland) (**I**, **II**) and from 28th April to 15th May in the Odense Fjord, Denmark (**III**). A natural water column was enclosed in nine floating transparent plastic bags (double-layered polyethylene interspersed with reinforcing glass-fiber threads). The mesocosms were first lowered to sub-surface depth, then filled with water by lifting the collar up. Mesocosms were fastened to wooden rafts and connected separately to a central buoy (distance ca. 30 m from each mesocosm) to ensure even light conditions. Plastic covers were used to protect against contamination by birds, but exchange of gases between air and sea was not prevented. The Tvärminne mesocosms had a total volume of 51 m^3 each, diameter 2.3 m., 12 m deep main cylindrical part and 2 m conical bottom part. In Odense the enclosures were smaller due to the shallow location: a total depth 3 m and a total volume 5 m^3.

Table 2. Experimental design in mesocosm experiments.
Additions: N – nitrogen, P – phosphorus, Si – silicon, C – organic carbon source. In Tvärminne experiment N = 1 μmol $L^{-1}d^{-1}$, P = 1/16 μmol $L^{-1}d^{-1}$, C = 13.3 μmol $L^{-1}d^{-1}$. In Odense experiment N = 0.8 μmol $L^{-1}d^{-1}$, P = 0.05 μmol $L^{-1}d^{-1}$, Si = 0.8 μmol $L^{-1}d^{-1}$, C = 18 μmol $L^{-1}d^{-1}$.

Mesocosm (Unit #)		**Odense**		**Tvärminne**	
		Days 1–3	Days 5–17	Days 1–5	Days 6–20
1	NP	N+P+Si	N+P+Si	N+P	N+P
2	N	N+P+Si	N+Si	N+P	N
3	P	N+P+Si	P+Si	N+P	P
4	5N	N+P+Si	5N+5Si	N+P	5N
5	5P	N+P+Si	5P+5Si	N+P	5P
6	5NC	N+P+Si+C	5N+5Si+C	N+P	5N+C
7	5PC	N+P+Si+C	5P+5Si+C	N+P	5P+C
8	NPC	N+P+Si+C	5N+5P+5Si+C	N+P	5N+5P+C
9	Control	N+P+Si	N+P	none	none

During the first days (the boosting period) the mesocosms were treated with mineral nutrients in Redfield ratio to induce a phytoplankton bloom and the elevated demand for nutrients. Thereafter a gradient of N or P limitation was induced over a 2 weeks period by cutting the supply of one macronutrient, while keeping or increasing the supply of the other (Table 2). Organic carbon source was added to enhance bacterial growth and promote mineral nutrient competition with algae, thus further increasing nutrient limitation.

4.3. Sampling and sample analysis

Discrete water column samples were taken at 1 m depth intervals with a 5 l volume cylindrical tube sampler and pooled thereafter into 1 composite sample. All sampling was done in the morning hours prior to the daily enrichments. From L. Verevi water samples were taken from the deepest point of the lake (Fig. 2). Aliquots for phytoplankton counts (250 ml, Lugol preserved) were analysed with inverted microscopes Leica DM IL (125–500x magnification) or Ceti (100–400x magnification) by using the Utermöhl (1958) technique. Before 1994 phytoplankton from L. Verevi was sedimented and counted from delineated glass-slide with microscope MBI-3, at magnifications 300x or 600x (**IV**).

The mean volume of each species was estimated in all samples by approximating the shape of species to the closest geometric form (Wetzel & Likens, 1991). The length of at least 50 cyanobacterial filaments on fixed width transects over the phytoplankton settling chamber was recorded for each species. *Nodularia*, *Aphanizomenon* and *Pseudanabaena* were treated as cylinders. For *Anabaena* spp. the mean cell number per unit filament length was calculated, and the cells were treated as spheres.

For phytoplankton community analysis the phytoplankton compound quotient (PCQ) was used (**IV**). This is one of the methods used in monitoring the status of Estonian lakes according to requirements of European Water Framework Directive (Ott, 2008). PCQ takes into account the number of different species in the lake.

Calculation of the PCQ (Ott & Laugaste, 1996):

$$\frac{\textit{Cyanophyta} + \textit{Chlorococcales} + \textit{Centrales} + \textit{Euglenophyceaea} + \textit{Cryptophyta} + 1}{\textit{Desmidiales} + \textit{Chrysophyceae} + 1}$$

PCQ scale:

oligotrophic and dystrophic lakes	< 2
mesotrophic	2–5
eutrophic	5–7
hypertrophic lakes	> 7

The amount of inorganic nutrients in Lake Verevi was analysed according to Grasshof (1983). Chlorophyll a concentration was measured according to HELCOM COMBINE guidelines (available at http://www.helcom.fi/groups/monas/CombineManual/AnnexesC/en_GB/annex4/) in Odense and Jespersen and Christoffersen (1987) in Tvärminne. Samples were collected on glass fiber filters (Advantec GF 75 filters, Toyo Roshi Kaisha, Japan or Whatman GF/F filters), extracted with 96% ethanol for 24 h in the dark at room temperature, and analyzed by spectrophotometer (Milton Roy Spectronic 1201 or Shimadzu RFPC 5001). Chl *a* concentration was calibrated with pure Chl *a* (Sigma).

Every second day 8 l of bottom water was pumped out of the mesocosms using a hand pump connected to the lower conical part of the enclosures with a plastic tube. The settled material was analysed for cyanobacterial akinetes (light microscopy) and particulate nutrients for nutrient mass balance. By relating the absolute abundance of akinetes in the bottom water to the sampling interval (2 days) and mesocosm surface area (4.14 m^2), we calculated the akinete flux rate to the bottom of the mesocosms (akinetes*m^{-2}*d^{-1}). By relating the latter to the planktonic population size on the previous day estimates the specific akinete production rate (akinetes*10^{-3} vegetative $cells^{-1}$*d^{-1}).

Cyanobacterial nitrogen fixation was estimated from the mass balance of inorganic and organic nitrogen species, considering the daily added nitrogen doses, nitrogen pumped out from the bottom water, and changes in the suspended pools.

5. RESULTS AND DISCUSSION

5.1. Nutrient effects on phytoplankton community in the mesocosms

5.1.1. The initial community composition and boosting effect

The outcome of mesocosm experiments is always highly dependent on the initial phytoplankton community composition. The initial phytoplankton community composition cannot be predetermined and remains a random variable in a mesoscale experiments.

The initial phytoplankton composition in the Tvärminne and Odense experiments was dominated by small flagellates, including chrysophytes (*Uroglena americana* Calkins) (**I**), chlorophytes (*Pyramimonas* spp.) (**I**), dinoflagellates (*Heterocapsa rotundata* (Lohmann) Hansen) (**I**, **III**) and cryptophytes (*Plagioselmis* sp.) (**I**, **III**). Diazotrophic and non-diazotrophic filamentous cyanobacteria were abundant in Tvärminne (**I**, **II**), with *Aphanizomenon* sp. being the most numerous. In the southern Baltic Sea filamentous cyanobacteria are rare in the plankton and these groups were not encountered in the Odense Fjord experiment.

A major difference between the two experiments was the presence of diatoms. In the northern Baltic Sea diatoms are abundant during the spring bloom period, but fail to form significant biomass in summer, irrespective of the Si availability (**I**, **II**; Kuosa et al., 1997; Wasmund & Uhlig, 2002; Danielsson et al., 2008). However, in the Odense Fjord diatoms are a major phytoplankton component in spring (**II**) and also throughout the summer (Riisgård et al., 2008; Kangro, unpubl. results). In Tvärminne diatoms were present only in negligible amounts (small-sized *Chaetoceros* species and *Cylindrotheca closterium* (Ehrenberg) Lewin and Reimann), in Odense the diatom flora was rich, with several *Chaetoceros* species dominating, mainly *C. constrictus*.

In both experiments the initial phytoplankton community was under strong grazing pressure. In Tvärminne, the initial mesozooplankton biomass exceeded the phototrophic biomass by a factor of 2.8 and in Odense by a factor of 1.8 (**I** and **III**). However, there were also major differences in the herbivore community between the two experiments. In Tvärminne the zooplankton community was dominated by small rotifers (*Synhaeta* spp., *Keratella* spp.), while the biomass of copepods increased gradually. In Odense the 90% of the mesozooplankton biomass was formed by larger species, copepods (mainly *Acartia bifilosa* and *Centropages hamatus*) and nauplii, while another important groups were small rotifers (*Synchaeta* spp.).

Despite the apparently strong grazing pressure, nutrient additions had a significant positive effect on the overall phytoplankton biomass in both experiments (**I**, **II**, **III**). In the Tvärminne experiment the phytoplankton biomass increased from initial 0.35 ± 0.05 to 1.2 ± 0.5 mg l^{-1}. In terms of chlorophyll, the initial increase was by a factor of 4–5 during the boosting period. In the Odense experiment the initial phytoplankton biomass (< 0.26 mg l^{-1}) increased by a factor of 6 and Chl concentration by a factor of 10 during the boosting period.

Although Chl *a* is often used as a proxy for the phytoplankton biomass (Ruddick et al., 2001; Gons et al., 2002), the dynamics of Chl *a* concentration and phytoplankton biomass do not always match. In our case Chl *a* indicated a higher phototrophic biomass in the 5N units compared to microscopy counts (**I**). This may partly be due to counting statistics and bio-volume conversion factors, but was more likely caused by higher cellular chlorophyll content, due to excess nitrogen availability. Increasing the amount of cellular Chl *a* is a more rapid response to nitrogen limitation than biomass increase (Latasa & Berdalet, 1994; Eriksen & Iversen, 1995; Henriksen et al., 2002).

It is almost impossible to predict, which of the phytoplankton species will benefit most from the changed conditions in the mesocosms and improved nutrient availability. Often small opportunistic flagellates with high growth potential cause the overall phytoplankton biomass increase (Olli et al., 1996; Olli & Seppälä, 2001; Smayda, 2002a).

In Tvärminne the most remarkable initial increase was caused by *Heterocapsa rotundata*, *Uroglena americana* and *Plagioselmis prolonga* Butcher; in Odense the biomass had an almost linear increase due to *Chaetoceros constrictus* Gran and *H. rotundata*. Consequently, although both systems were under strong herbivorous pressure, increasing the nutrient availability led to a mismatch between the primary production and zooplankton grazing.

5.1.2. Gulf of Finland – limitation effects in initially N-limited system

In the Tvärminne experiment the biomass increase of phytoplankton was highest in the mesocosms, where both N and P were added. However, when only one nutrient was added, mesocosms receiving N gained higher biomass than mesocosms with P (**I**). This agrees with the assumption that the Gulf of Finland is mainly N-limited in summer (Lignell et al., 2003; Tamminen & Andersen, 2007) and in line with other nutrient addition experiments from that area, where phytoplankton biomass responded more strongly to N than to P addition (Lagus et al., 2007a).

In the Tvärminne experiment we found clear separation of species specific responses along the N and P limitation gradient (Fig. 4 in **I**). The biomass response to nutrient limitation distinguished three groups of phytoplankton:

1) Nitrogen-limited – chlorophytes, non-heterocysteous cyanobacteria from the genus *Pseudanabaena* and colonial small-celled cyanobacteria
2) Phosphorus-limited – nitrogen-fixers *Anabaena* spp. (dominated by *A. lemmermannii*) and *Nodularia spumigena*

3) Indifferent species – heterotrophic and opportunistic flagellates; N_2- fixer *Aphanizomenon* sp., which was the dominant species during this experiment and increased almost equally in all mesocosms.

Many of the non-diazotrophic cyanobacteria clearly benefited from excess N addition. These include *Pseudanabaena limnetica* Lemmerm. and a variety of colonial picoplanktonic cyanobacteria (*Cyanodictyon* spp., *Aphanocapsa* sp., *Gomphosphaeria* sp., *Coelosphaerium* sp., *Snowella* sp.). The positive effect of nutrient addition to the biomass of pico-size cyanobacteria has been noticed in other experiments (Kuuppo et al., 2003; Lagus et al., 2007b).

Provided surplus N and P availability, common bloom-forming non-diazotrophic cyanobacteria *Microcystis* spp. and *Planktothrix agardhii* may proliferate in freshwater (**IV**). The presence of *P. agardhii* is not restricted to freshwater, it may thrive also in the Baltic Sea (HELCOM, 2003). Due to low salinity tolerance these species may dominate in the late-summer community near the freshwater inflows – for example Eastern Gulf of Finland and Curonian lagoon (Kauppila et al., 1995; Carstensen et al., 2007; Pilkaityte, 2007).

Restricting the external nitrogen supply resulted in lower phytoplankton total biomass, but more bloom-forming N_2-fixing cyanobacteria. This suggests that within the time scale of two weeks, the diazotrophic cyanobacteria compensated the lack of external nitrogen supply by N_2-fixation, effectively utilizing their competitive advantage over other phytoplankton species. Thus, lowering the external N:P supply ratio somewhat decreased the phytoplankton biomass, but shifted the community composition towards dominance of filamentous bloom-forming cyanobacteria. According to Sivonen et al. (2007) N_2-fixing cyanobacteria are commonly phosphate-limited in the Baltic Sea and from other studies (Rydin et al., 2002; Moisander et al., 2003) is also evident that *Anabaena* spp. and *N. spumigena* in the Baltic Sea generally benefit from P addition. This finding has implications on nutrient and eutrophication management of the Baltic Sea, because diazotrophic cyanobacteria gain competitive advantage as a response to nitrogen reduction and shift the phytoplankton community composition towards hazardous filamentous species, thus making the efforts of N reduction questionable (Schindler et al., 2008).

From the nitrogen mass balance in the mesocosms without N addition we could calculate an average nitrogen fixation rate of 3.3 to 7.4 mmol N m^{-2} d^{-1}, which was significantly less than the external nitrogen supply (21 mmol N m^{-2} d^{-1}), but still in the same order of magnitude.

We observed distinctly different biomass responses to nutrient enrichment within the group of filamentous diazotrophic cyanobacteria. *Anabaena lemmermannii* was favoured by P amendment, particularly when lack of external N addition kept non-diazotrophic competitors at a disadvantage. The same tendency could be observed with *Nodularia spumigena*, though the growth of this species was slow and tightly coupled to the increase of water temperature at the late phase of the experiment. However, the most abundant diazotrophic filamentous cyanobacterium, *Aphanizomenon* sp. revealed a biomass response apparently not related to differences in nutrient supply rates. The biomass of

Aphanizomenon sp. increased in all mesocosms, including the ones without P addition and the control mesocosm, which received no external nutrients throughout the experiment. Increase of *Aphanizomenon* sp. was on average 50-fold from the initial 0.03 to 0.05 mg l^{-1} (5 to 18% of the total phytoplankton biomass) to 0.9 to 2.5 mg l^{-1} (40 to 50% of the biomass, but 75% in the control unit). As the control mesocosm had a relatively low phytoplankton biomass, the proportion of *Aphanizomenon* sp. was the highest among all mesocosms by the end of the experiment. The growth of *Aphanizomenon* sp. was apparently more related to the increase in surface water temperature throughout the experimental period than to nutrient availability and perhaps the reduced turbulence in the mesocosms. The growth of *Aphanizomenon* sp. is enhanced by temperature > 16 ºC (Kononen, 1992; Plinski & Jozwiak, 1999), which corresponds to the water temperature at the beginning of the experiment. During the course of the experiment the surface temperature increased up to 22°C, which probably favoured the proliferation of filamentous cyanobacteria. The later appearance of *N. spumigena* in the experiment is in line with the gradual temperature increase, since *Nodularia* has higher temperature optimum (>20ºC) compared to *Aphanizomenon* sp. (Kononen, 1992; Plinski & Jozwiak, 1999).

Previous nutrient enrichments experiments in the Baltic Sea have revealed controversial evidence of *Aphanizomenon* sp. response to nutrient additions. High P concentrations and a low N:P ratio stimulated the growth of *Aphanizomenon* sp. in some studies (Granéli et al., 1990; Rydin et al., 2002), whereas in others, in accordance to our study, no effect of enrichments was found (Lagus et al., 2002; Vuorio et al., 2005; Lagus et al., 2007a). In contrast, in a short-term enrichment experiment in the eutrophic Curonian lagoon, growth of *Aphanizomenon* was stimulated by the combined addition of both P and N (Pilkaityte & Razinkovas, 2007). Different results from mesocosm experiments may be explained by the differences in experiment durations and setups, initial intracellular nutrient contents of the cyanobacteria and different nutrient regeneration during the experiments (Lagus, 2009).

The increase of phytoplankton biomass due to the proliferation of *Aphanizomenon* sp. changed the overall stoichiometry of particulate matter. In mesocosms without P addition the PON:POP ratio exceeded 30 from day 8 onwards, suggesting P-limitation. By the end of the experiment POC:POP ratio reached 300 and PON:POP ratio 50. In contrast, the stoichiometric ratios remained close to the Redfield ratio in mesocosms with no P addition, suggesting that bulk level N deficiency was alleviated by nitrogen fixation. We suggest that the biomass response of *Aphanizomenon* sp. was supported by the internal cellular phosphorus reserves. The unusual C:N:P stoichiometric flexibility of *Aphanizomenon* sp. enables the build-up of large standing stocks to be sustained in phosphorus-limited conditions (Lignell, 2003). Several authors (Larsson et al., 2001; Walve & Larsson, 2007) have denoted that *Aphanizomenon* sp. is able to form late-summer blooms supported by cellular P reserves from the early summer. The stoichiometric flexibility effectively uncouples *Aphanizomenon* sp. from eutrophication and nutrient management efforts. The species can use atmospheric nitrogen and increase it's biomass by an order of magnitude at the expense of cellular P reserves alone.

According to the field observations from the Gulf of Finland, the biomass of diazotrophic cyanobacteria *Aphanizomenon* sp., *Anabaena* spp., and *Nodularia* did not correlate well with nutrient concentrations (Jaanus et al., 2009). Jaanus et al. (2009) suggested that the dynamics and intensity of filamentous diazotrophic cyanobacterial blooms were mainly determined by hydrodynamic factors, not by nutrients. In our experiments the differences between mesocosms were caused primarily by nutrients, since temperature, light climate, hydrodynamic factors and zooplankton biomass and composition were similar in all bags.

5.1.3. Odense Fjord – limitation effect in initially P-limited system

Generally phytoplankton growth in the Danish coastal waters is nitrogen limited (Nielsen et al., 2002), but Odense Fjord is expected to be P limited at least during springtime (Ærteberg et al., 2003). Nutrient additions had a significant effect on the phytoplankton community, but in contrast to the Tvärminne experiment, mesocosms with P addition developed a higher biomass peaks compared to mesocosms with N addition. The higher biomass in mesocosms with P addition was mainly due to the response of diatoms (Fig. 3), which formed the majority (up to 97%) of the total phytoplankton biomass during the experiment.

Not all phytoplankton groups were more favoured by phosphorus. For example, the biomass of cryptophytes was higher in mesocosms receiving excess N (Fig. 4). Si addition caused changes in the diatom species composition. In the bags with lower Si concentration *Skeletonema costatum* (Grev.) Kleve and *Attheya septentrionalis* (Østrup) Crawford dominated, whereas in the bags with excess Si addition *Chaetoceros* spp. dominated.

This difference may reflect the silicification of particular species (Spilling et al., 2010), allowing less silicified species to build up higher biomass per unit Si available. Alternatively the observed pattern may reflect high Si uptake affinity of *S. costatum* and *A. septentrionalis.*

Chaetoceros and *Skeletonema* are both important spring bloom taxa in the southern Baltic Sea (Wasmund et al., 2008), but at low Si concentrations *S. costatum* is a better competitor than *Chaetoceros* (Paasche, 1973; Harrison et al., 1989).

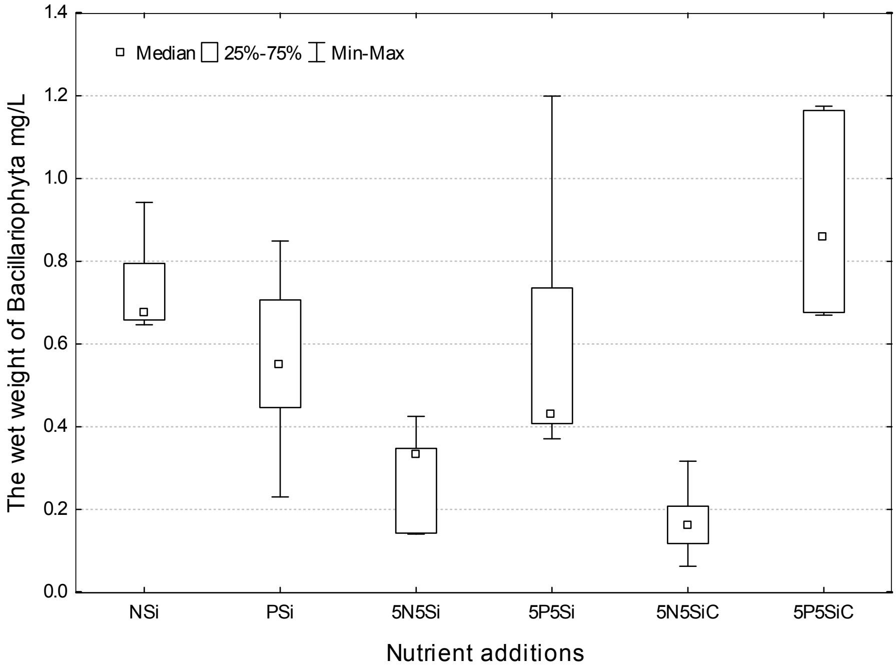

Figure 3. The wet weight of Bacillariophyta (mg l^{-1}) in bags with different nutrient additions from day 9-17 in the experiment in Odense Fjord.

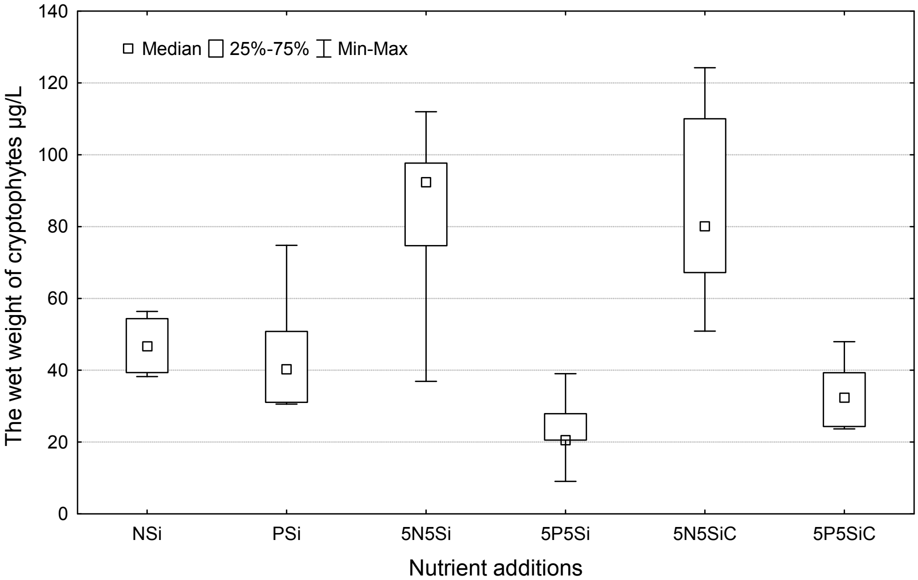

Figure 4. The wet weight of cryptophytes (µg l^{-1}) in bags with different nutrient additions from day 9-17 in the experiment in Odense Fjord.

In the Odense experiment we observed an increase and decline of a mixotrophic chrysophyte D*inobryon balticum* (Schütt) Lemmermann (**III**). Apparently mineral nutrient manipulations were not an important factor determining the biomass dynamics of *D. balticum* (**III**). We believe more important was the reduced competition from opportunistic fast-growing species. The biomass increase (experimental days 7–11) coincided with a rapid decline of *H. rotundata* and *C. constrictus*. Compared to other phytoplankton species *D. balticum* has a relatively low growth rate and competitive ability, making it a typical post-bloom species (Lee, 1989). The species of *Dinobryon* are capable of mixotrophic feeding (Jones, 2000; Unrein et al., 2010). The role of mixotrophs in brackish and marine environments is poorly known, but it is suggested that they may have an advantage in periods of nutrient (especially P) limitation due to ability to ingest P-rich bacteria (Lagus, 2009). During the peak of *D. balticum* the abundance of bacteria declined up to 10%, suggesting bacterivory. There were no differences in bacterial abundance between the mesocosms, but also *D. balticum* had a relatively equal abundance between the bags.

Both mesocosm experiments revealed species and even larger taxonomic groups, which were favoured by either P or N. Overall we observed N limitation in Tvärminne (**I**) and P limitation in Odense Fjord (**III**). However, important phytoplankton components did not directly respond to nutrient additions. Consequently there were other important factors, which influenced the phytoplankton community structure and composition.

5.2. The effect of nutrients on resting cyst formation

Phytoplankton resting stage formation is often induced by nutrient stress (Anderson et al., 1985) and as thus may indicate population level nutrient limitation. Physiological control of akinete formation and subsequent germination is important in understanding and predicting how natural populations of cyanobacteria respond to the changes in their environment (Suikkanen et al., 2010).

During the Tvärminne mesocosm experiment the biomass of *A. lemmermannii* increased in 3 weeks by a factor of 50 (**I**, **II**). The population increase of *A. lemmermannii* was higher in the phosphorus added mesocosms (by a factor of 2.4), while the production rate of akinetes was higher in nitrogen added units (by a factor of 2.5) (**I**, **II**). Input of freshly produced *A. lemmermannii* akinetes to the benthos was on average $15*10^6$ and $6*10^6$ cells m^{-2} d^{-1} in the N-and P-added mesocosms, respectively. The estimates of specific akinete production rate of *A. lemmermannii* in N- and P-added mesocosms revealed an even larger divergence (a factor of 5.5), being on average 2.4 and 0.4 akinetes $*10^3$ vegetative $cells^{-1}$ d^{-1}, respectively (**II**). The phosphorus addition effectively retarded akinete production of *A. lemmermannii*, suggesting that whenever phosphorus was added, *A. lemmermannii* invested very little resources to the akinete production.

We found that P-limitation favoured specific akinete production in *A. lemmermannii*, whereas according to Suikkanen et al. (2010) nutrient depletion in the surface water is not the only trigger for *Anabaena* spp. akinete production. In general, the cessation of cell division due to a combination of various factors led to increase in akinete production of *Anabaena* spp. (Suikkanen et al., 2010).

In contrast, another *Anabaena* species, *A. cylindrica* Lemmermann, had an indifferent akinete production pattern in both, N and P limited mesocosms. The abundance of *A. cylindrica* was lower throughout the experiment and the counting statistic of the cells and akinetes was relatively poor. However, we are confident that the akinete production of the two species responded differently to mineral nutrient limitation.

During the Odense experiment (**III**), the development of stomatocysts of *D. balticum* started at 9th experimental day, with maximum suspended concentration (110 cells ml^{-1}) observed in bag with 5P+5Si+C addition. Although nutrient limitation is considered one of the main factors for initiation of stomatocysts development (Firsova et al., 2008), we found vague, if any link between the population dynamics of *D. balticum* and nutrient manipulation. Thus it would be premature to associate the stomatocyst production with any type of nutrient limitation.

The timing of resting stage formation is an important parameter of phytoplankton bloom dynamics, i.e. when does the population invest energy and other resources into the formation of resting stages. A variety of strategies have been observed among phytoplankton species, where resting stages are produced during a short interval at the late phase of the exponential growth (Heiskanen, 1993), or at a relatively constant rate throughout the bloom (Ishikawa & Taniguchi, 1996). In *A. cylindrica* we observed peak akinete production rate ca. 1-week after the vegetative population peak. No such delay was obvious in case of *A. lemmermannii*, akinetes were produced at a relatively equal rate throughout the growth of the population (**II**). Regardless of the high akinete flux of *A. lemmermannii* to the benthos, it comprised only a minor fraction, approximately 0.12% (with a maximum of 0.6%) of the planktonic cell population. This is in line with earlier similar scale mesocosm experiments, where resting cyst production of a phototrophic euglenid *Eutreptiella gymnastica* (Olli et al., 1996) or temporary cysts of a dinoflagellate *Heterocapsa triquetra* (Olli, 2004) formed only a very low percentage of vegetative population size. Large-scale mesocosms provide a suitable experimental design to quantify benthic resting stage formation. As the systems are closed, we can achieve a good control on the population size of both, planktonic stages and sinking resting stages. This avoids the main uncertainty in field studies - the horizontal advection of water masses, but retains the environmental conditions close to natural.

For the main bloom-formers in the Baltic Sea, akinetes play the greatest role in the life cycle of *Anabaena* spp., which barely occur as planktonic vegetative filament outside the warm summer period (Suikkanen et al., 2010). The overwintering strategy of *Aphanizomenon* sp. is different – it maintains small population in the plankton, with filaments present year round, even under ice (Laamanen, 2002). *Aphanizomenon* sp. is able to form akinetes, but during routine monthly sampling akinetes may remain unnoticed (Palińska & Surosz, 2008). In the Tvärminne mesocosm experiment *Aphanizomenon* sp. was the most abundant cyanobacterial species and overall biomass dominant (**I**). Although the nutrient manipulations were designed to create a wide range of nutrient limitation scenarios in the mesocosms, we could not observe any akinete production of *Aphanizomenon* sp. Akinetes of *Aphanizomenon* sp. were not found in the bottom sediment water, neither was akinete differentiation observed in the planktonic population. In the Baltic Sea *Aphanizomenon* sp. is present in the water column year round (Niemi, 1973) and has been found in the sea ice (Laamanen, 1996). It has been suggested that akinetes probably do not play a role as *Aphanizomenon* sp. seed population in the Baltic Sea (Kononen, 2002), which is in line with our findings of no akinete accumulation in the mesocosm sediment water.

5.3. Long-term changes in the phytoplankton community due to nutrient pollution

According to chemical composition, the water in L. Verevi is currently stratified all the year round (Starast et al., 2007). Due to incomplete mixing nutrients will be trapped in the hypolimnion. Strong stratification leads to anoxic conditions in hypolimnion, lower pH and phosphorous leakage from sediments, which will be available for phytoplankters in case of mixing events take place (Ott et al., 2005b). Considering the total amounts of nutrients stored in the hypolimnion, the average potential concentrations in the whole water column could achieve 1885 mg m^{-3} of TN and 170 mg m^{-3} of TP, reflecting hypertrophic conditions (Nõges & Kangro, 2005).

Three stages in phytoplankton community of L. Verevi can be distinguished (**IV**):

a) Pristine state of the lake – pre-pollution phase – mesotrophic to moderately eutrophic, with diverse algal community. *Planktothrix agardhii* occurred first time in the lake in the fifties.
b) Heavy pollution from waste-water ponds during eighties – hypertrophic state characterised by the dominance and very high biomasses of *P. agardhii* (up to 174 g m^{-3}). Phytoplankton compound quotient (PCQ) increased to hypertrophic level (Fig. 5). Species composition changed from a diverse community to monospecific dominance of *P. agardhii.*
c) Post-pollution phase – large vertical variation in the phytoplankton composition. Epilimnion is in the clear-water state, with a transparency up to 2.5 m. Epilimnion is relatively nutrient-poor with low algal biomass. Sharp gradient of temperature and nutrients in late summer generate micronisches – picocyanobacteria dominate in the epilimnion, while the phytoplankton biomass peak, often dominated by *Ceratium hirundinella* (O.F. Müller)

Dujardin, is typically at 5 metres depth. The biomass maxima of various cryptophytes are at 6 metres. PCQ in the epilimnion indicates mesotrophy (Fig. 5), but PCQ in the meta- and hypolimnion shows hypertrophic conditions. Based only on epilimnetic values the improvement of the water quality and oligotrophication is evident. Even more, in 2005 and 2006 previous dominants and indicators of hypertrophic condition, *P. agardhii* and *Limnothrix redekei* (Van Goor) Meffert were not found in the phytoplankton (Ott, 2006). Changes in the phytoplankton community are now highly dependent of the mixing regime of the lake, primarily the occurrence of spring and autumn turnover.

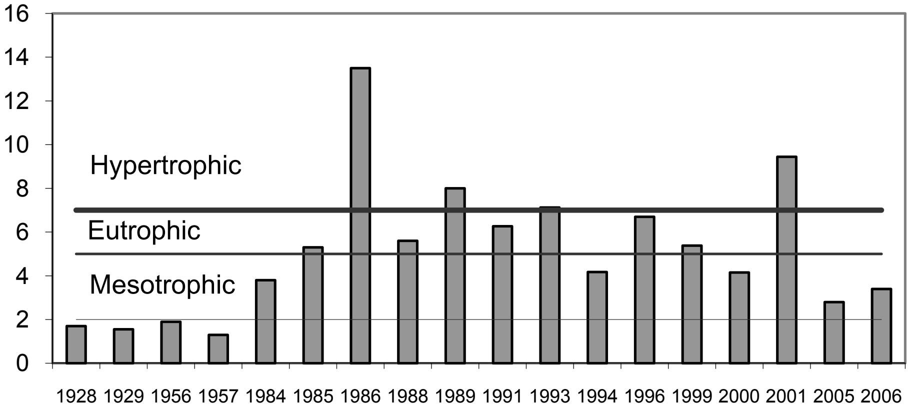

Figure 5. Phytoplankton Compound Quotient in the epilimnion of the Lake Verevi.

P. agardhii is considered as the most important bloom-forming species in temperate shallow lakes (Scheffer et al., 1997), being able to grow also in deeper, stratified lakes (Kangro & Nõges, 2003). *P. agardhii* possesses gas vacuoles and is able to move vertically in the water column. *P. agardhii* is considered to be characteristical to eutrophied lakes, but can also occur in the more eutrophied parts of the Baltic Sea (Graneli et al., 1998).

In the post-pollution phase species composition and dominants varied greatly both in seasonal and vertical scale. Diatoms (peak up to 18.6 g m^{-3}) and cryptophytes (14.8 g m^{-3}) dominated during spring. Cyanobacteria dominated in summer, with filamentous *Aphanizomenon klebahnii* (Elenk.) Pechar & Kalina and *P. agardhii* being abundant until 2002. Typical summertime diatoms with thinner frustules like *Acanthoceras zachariasii* (Brun) Simonsen and *Rhizosolenia longiseta* Zacharias and dinoflagellate *Ceratium hirundinella* were also present. During autumn small-celled colonial cyanobacteria were numerous. This kind of dynamics of phytoplankton biomass with the spring peak in April-May and the late summer peak in July-August is typical to Estonian eutrophic lakes (Kõiv & Kangro, 2005).

In stratified lakes the gradients of light, temperature, oxygen and inorganic substances combine and cause a variety of microhabitats (Davey & Heany, 1989; Reynolds, 1992; Nõges & Nõges, 1998). Sharp gradients generate more nisches than are available in shallow well-mixed water column (Wetzel, 2001), with epilimnion being relatively nutrient-poor, isolated from nutrient-rich hypolimnion. In the lake Verevi cryptophytes and euglenophytes inhabited preferably the nutrient rich meta- and hypolimnion. The presence of cryptophytes in metalimnion and the development of deep-water biomass maxima is reported from several stratified lakes (Gasol et al., 1993; Gervais, 1997). Biomass maxima of particular species may be in very thin layers, which are easy to miss with conventional sampling (Lindholm et al., 1985; Gervais et al., 2003). Cryptophytes are tolerant to low light intensities and low oxygen concentration in metalimnion (Gasol et al., 1993). Even more, metalimnetic populations of cryptophytes may tolerate sulphides, which irreversibly inhibits photosynthesis in most phytoplankton species (Gervais, 1998; Camacho et al., 2000).

SUMMARY

Blooms of autotrophic algae are increasingly frequent in coastal waters, and cause a need for countermeasures, strategies and plans for bloom management and mitigation (Sellner et al., 2003). Without knowledge, how different phytoplankton species respond to the increase or limitation of nutrients in natural environment, thoughtless actions may even harm the environment. Nutrient limitation is one of the major drivers of the phytoplankton community composition. The response of the planktonic community to increased nutrient availability can be studied by using large scale ecosystem enclosures (Grice & Reeve, 1982), where uncertainties caused by advective transport and patchiness can be minimized, while keeping other variables (temperature, light climate) similar to the surrounding environment.

Mesocosm experiments took place in 2003, in spring in Odense Fjord (Denmark) and in summer in Tvärminne Archipelago (SW coast of Finland). First, combined nutrient addition was used to enhance the phytoplankton growth. Thereafter additions diverged to create different levels of nutrient limitations. Mineral nutrient addition led to a rapid increase of chlorophyll and overall phytoplankton biomass (**I**, **III**). The response to specific nutrient additions was species-specific. Diazotrophic cyanobacteria were generally favored by P (**I**, **II**), since they can fix their own nitrogen. However, nitrogen fixation is energetically expensive and in the time scale of weeks only partly compensated the N demand of the phytoplankton community. Moderate, even excessive N additions lowered the competitive ability of some filamentous cyanobacteria (*Anabaena spp.*), but generally failed to prevent cyanobacterial bloom, when other conditions were favourable. Not all diazotrophic cyanobacteria respond similarly to nutrient limitation – the biomass of *Aphanizomenon* sp., which was the dominant species in the Tvärminne mesocosm experiment, increased independently of the nutrient additions (**I**).

Nutrient availability affects the production of the resting cells – P limitation induced the akinete production of *Anabaena lemmermannii* (**II**), while P addition effectively retarded akinete production. No apparent nutrient limitation pattern could be associated with the akinete production of *A. cylindrica* or stomatocysts production of *D. balticum* (**III**). Despite wide range of nutrient limitation patterns, *Aphanizomenon* sp. did not form akinetes during the 3 weeks period (**I**).

However, nutrients do not explain the whole dynamics of phytoplankton community. Many species depend on other factors like temperature, zooplankton grazing and reduced competition with other species that can be more important in shaping population dynamics than nutrients. Abundance of *Heterocapsa rotundata* and *Plagioselmis* sp. decreased despite the nutrient additions due to grazing (**I**, **III**), abundance of *Dinobryon balticum* increased probably due to reduced competition and mixotrophic feeding (**III**).

The intensity of vertical mixing is an important factor shaping the phytoplankton community composition and biomass distribution in stratified lakes

(**IV**). In stratified lakes thin vertical layers create small-scale micronisches, which may support large biomass of various species, and may easily be overlooked during routine sampling.

Due to the nutrient input from near-by sewage-ponds the trophic state of Lake Verevi changed from initial mesotrophic to hypertrophy during the eighties, and the filamentous cyanobacterium *Planktothrix agardhii* became a monodominant phytoplankton species. In the post-pollution phase partial meromixia prevents the mixing of nutrients from enriched sediments and hypolimnion to the upper water column, and the state of the lake has greatly improved. Water transparency has increased, the overall phytoplankton biomass has decreased, *P. agardhii* is no longer dominating and the community composition is diverse. However, this apparent improvement may be temporary, since nutrients are still present in the hypolimnion and in the sediments. Intensive water column mixing may provide the nutrients for phytoplankton blooms, even though the present condition in the epilimnion is reasonably good.

SUMMARY IN ESTONIAN

Toiteainete mõju fütoplanktoni koosluse dünaamikale

Toiteainete liigne lisandumine viib veekogude eutrofeerumisele, mille üheks sümptomiks on fütoplanktoni liigne hulk. Fütoplankton on toiduahela aluslüliks, fütoplanktoni hulk ja liigiline koosseis mõjutab kogu veekogu toiduvõrgustikku. Liigne fütoplanktoni biomass põhjustab hapnikuolude ja pH kõikumist, veekogude mudastumist ja stressitingimusi teistele veekogu asukatele. Iga-suvised veeõitsengud on järvedes ja Läänemere kalda-aladel järjest suuremaks probleemiks, mistõttu on tarvis leida meetodeid õitsengute vähendamiseks. Mikrovetikad reageerivad toiteainete tingimuste muutustele suhteliselt kiiresti nii muutustega liigilises koosseisus kui ka biomassis. Seetõttu on veekogu efektiivseks majandamiseks eelkõige vaja teadmisi erinevate vetikaliikide toiteainetele reageerimise kohta, sest erinevatel vetikaliikidel on erinevad nõudlused ja võimalused toiteainete omastamiseks.

Kõik vetikad vajavad oma elutegevuseks mineraalset lämmastikku ja fosforit (rusikareegli järgi Redfieldi suhtes 16:1), rauda ning mikroelemente. Ränivetikad vajavad ka lisaks ka räni. Enamus vetikaid vajab mineraalse lämmastiku allikat, osad niitjad ning mitmed üherakulised sinivetikad on aga võimelised õhulämmastikku siduma ning seeläbi lämmastikupuudusest jagu saama ning teisi konkurentsitingimustes edestama. Mitmed sinivetikad on võimelised mürke tootma ning põhjustama seeläbi lisaprobleeme vee kasutamisel. Seega, toiteainete vähendamine ilma laialdaste eelteadmisteta võib loodetud kasu asemel keskkonnale hoopiski kahju tuua.

Mesokosmieksperimendid võimaldavad uurida vetikakooslust nii, et toiteainete lisandumine on kontrollitud, kusjuures muud näitajad, nagu temperatuur ja valgusolude muutused on sarnased ümbritseva keskkonnaga. Mesokosmieksperimendid toimusid 2003 kevadel Odense Fjordis (Taani) ja suvel Tvärminne saarestikus (Soome). Esmalt lisati kõigisse mesokosmidesse liiaga toiteaineid, et soodustada vetikate kasvu, seejärel aga jätkati valikulise toiteainete lisamisega. Meie mesokosmieksperimentidest selgus, et mõlemad uuritud kooslused reageerisid lineaarse biomassitõusuga toiteainete liiaga lisamisele (**I**, **III**). Lisaks algselt arvukatele väiksetele viburlastele domineerisid Tvärminne koosluses sinivetikad, eriti niitjas sinivetikas *Aphanizomenon*, mis on üheks tüüpiliseks õitsenguid põhjustavaks liigiks Läänemeres. Teine, potentsiaalselt mürke tootev niitjas sinivetikas *Nodularia spumigena* muutus arvukamaks eksperimendi lõpu poole kooskõlas temperatuuri tõusuga. Kolmandaks biomassi dominandiks oli õitsenguid põhjustav perekond *Anabaena*, peamiselt *A. lemmermannii*.

Vastus toiteainete valikulisele lisamisele oli liigi-spetsiifiline, mitte kõik lämmastiku-fikseerimisvõimelised sinivetikad ei reageerinud ühtemoodi (**I**, **II**). Anorgaanilise lämmastiku puudus põhjustas üldiselt fütoplanktoni madalama biomassi, aga protsentuaalselt suurema lämmastiku-sidujate hulga. Fosfori-puudus vähendas osade lämmastiku-fikseerijate (*Anabaena* erinevad liigid ja *Nodularia*) konkurentsivõimet, aga sinivetikaõitsengut see ei välistanud, eeldusel, et teised tingimused olid soodsad. *Aphanizomenon* sp. kasutas efektiivselt raku-siseseid fosforireserve, ning kasvas hästi toiteainete lisamisest sõltumatult.

Akineetide e. puhkerakkude moodustamine on üks sinivetikate elutsükli oluline osa, mis aitab neil ebasoodsaid keskkonnatingimusi üle elada. Toite-ainete kättesaadavus mõjutas *Anabaena lemmermannii* akineetide moodus-tumist (**II**) – neid oli rohkem fosforipuuduse tingimustes. Fosfori lisamine tõkestas efektiivselt akineetide moodustumist. Toiteainete valikuline lisamine *Anabaena cylindrica* akineetide moodustumist ei mõjutanud ning hoolimata erinevatest limitatsioonitingimustest *Aphanizomenon* sp. 3 nädala vältel akineete ei moodustanud.

Keskmiselt soolase veega Odense fjordis reageeris enamus fütoplantoni liike positiivselt P lisamisele, samas mõjutas lisatava räni hulk ränivetikate liigilist koosseisu (**III**) – mõõduka ränisisaldusega kottides tõusid eksperimendi teisel poolel esile õhema räniskeletiga *Skeletonema costatum* ja *Attheya septentrionalis*.

Samas ei seletanud toiteainete hulga muutused kogu fütoplanktoni koosluse dünaamikat. Paljusid liike mõjutasid teised faktorid, näiteks temperatuur, zooplanktoni ärasööm ning liikide-vahelise konkurentsi vähenemine rohkem kui toiteained. Väikeste viburlaste (*Heterocapsa rotundata* ja *Plagioselmis* sp.) arvukus langes hoolimata toiteainete lisamisest zooplanktoni ärasöömise tõttu (**I, III**), *Dinobryon balticum'*i arvukus tõusis arvatavasti vähenenud konkurentsi ja miksotroofse toitumise tõttu (**III**).

Verevi järv on ilmekas näide fütoplanktoni koosluse muutusest ajas toiteainete liigse lisandumise tulemusena. Reoveetiikide ülevoolu tõttu suure hulga toiteaineid saanud kooslus muutus oluliselt – esialgsest mesotroofsest seisundist (veel 50ndatel) *Planktothrix agardhii* monodominantsiga hüpertroofseks järveks 80ndatel (**IV**). Tasapisi on järve seisund paranenud, kuna reoveetiikidega enam ühendust ei ole ja osalise meromiksia tõttu on toiteainete tulek toiteainerikastest setetest veesambasse takistatud. Järvele on iseloomulik teravate vertikaalsete niššide olemasolu, kus mõnesentimeetrises kihis võib olla väga suur ühe liigi/perekonna biomass. Praeguses faasis iseloomustab järve suhteliselt suur läbipaistvus, eutroofsele seisundile vastav vetikakooslus (*P. agardhii* praktiliselt puudub) ja vähenenud fütoplanktoni biomass. Samas võib öelda, et olukorra paranemine võib olla ajutine, kuna toiteained on settes ikkagi olemas ning segunemise korral püsib enesereostuse oht ja fütoplanktoni õitsengu võimalus endiselt.

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