

TURUN YLIOPISTON JULKAISUJA
ANNALES UNIVERSITATIS TURKUENSIS

SARJA - SER. AII OSA - TOM. 239

BIOLOGICA - GEOGRAPHICA - GEOLOGICA

**ROLE OF NUTRIENTS IN REGULATION OF
THE PHYTOPLANKTON COMMUNITY
IN THE ARCHIPELAGO SEA,
NORTHERN BALTIC SEA**

by

Annika Lagus

TURUN YLIOPISTO
UNIVERSITY OF TURKU
Turku 2009

From the Section of Ecology
Department of Biology
University of Turku
FIN-20014 Turku
Finland

Supervised by

Prof. Jouko Sarvala
Department of Biology
University of Turku
Finland

Dr. Pirjo Kuuppo
Neste Oil Corporation
Finland

Reviewed by

Prof. Jorma Kuparinen
Department of Biological and Environmental Sciences
University of Helsinki
Finland

Prof. Ulrich Sommer
Leibniz-Institute of Marine Sciences
Germany

Opponent

Prof. Anna-Stiina Heiskanen
Research Manager
Finnish Environment Institute
Finland

ISBN 978-951-29-3981-7 (PRINT)
ISBN 978-951-29-3982-4 (PDF)
ISSN 0082-6979
Painosalama Oy - Turku, Finland 2009

LIST OF ORIGINAL ARTICLES

This thesis is based on the following articles, which are referred to by the Roman numerals in the text:

- I. Lagus, A., Suomela, J., Weithoff, G., Heikkilä, K., Helminen, H. & Sipura, J. 2004. Species-specific differences in phytoplankton responses to N and P enrichments and the N:P ratio in the Archipelago Sea, northern Baltic Sea. *Journal of Plankton Research* 26: 779-798.
- II. Lagus, A., Suomela, J., Helminen, H., Lehtimäki, J. M., Sipura, J., Sivonen, K. & Suominen, L. 2007. Interaction effects of N:P ratios and frequency of nutrient supply on the plankton community in the northern Baltic Sea. *Marine Ecology Progress Series* 332: 77-92.
- III. Lagus, A., Silander, M. & Suomela, J. 2002. Influence of nutrient enrichments on cyanobacteria in the Archipelago Sea, northern Baltic. *Verhandlungen der Internationalen Vereinigung für Theoretische und Angewandte Limnologie* 28: 607-612.
- IV. Vuorio, K., Lagus, A., Lehtimäki, J. M., Suomela, J. & Helminen, H. 2005. Phytoplankton community responses to nutrient and iron enrichment under different nitrogen to phosphorus ratios in the northern Baltic Sea. *Journal of Experimental Marine Biology and Ecology* 322: 39-52.
- V. Suomela, J., Gran, V., Helminen, H., Lagus, A., Lehtoranta, J. & Sipura, J. 2005. Effects of sediment and nutrient enrichment on water quality in the Archipelago Sea, northern Baltic: An enclosure experiment in shallow water. *Estuarine, Coastal and Shelf Science* 65: 337-350.
- VI. Lagus, A., Suomela, J., Helminen, H. & Sipura, J. 2007. Impacts of nutrient enrichment and sediment on phytoplankton community structure in the northern Baltic Sea. *Hydrobiologia* 579: 351-368.

The original publications have been reprinted with the kind permission of Oxford University Press (Article I), Inter-Research Science Publisher (Article II), E. Schweizerbart'sche Verlagsbuchhandlung, Stuttgart, Germany, <http://www.schweizerbart.de> (Article III), Elsevier Science (Articles IV & V) and Springer Science and Business Media (Article VI)

CONTENTS

LIST OF ORIGINAL ARTICLES.....	3
CONTENTS.....	4
1. INTRODUCTION	5
1.1. Eutrophication and the Baltic Sea	5
1.2. Nutrient regulation of phytoplankton growth	7
1.3. Coastal food webs.....	9
1.4. Phytoplankton competition for limiting nutrients	11
1.5. Nutrient-phytoplankton-zooplankton interactions	13
1.6. Aim of the study	14
2. MATERIAL AND METHODS	15
2.1. Study Area	15
2.2. Mesocosm experiments	17
2.3. Plankton biomass	22
2.4. Primary production.....	22
2.5. Hepatotoxins.....	23
2.6. Nutrients and chlorophyll <i>a</i>	23
3. RESULTS AND DISCUSSION.....	24
3.1. Phytoplankton community	24
3.1.1. Nutrient limitation.....	24
3.1.2. Role of the N:P ratio.....	25
3.1.3. Frequency of nutrient supply	27
3.2. Diazotrophic cyanobacteria.....	28
3.2.1. Effects of nutrient enrichments and N:P ratio	28
3.2.2. Effects of nutrient supply frequency	30
3.2.3. Effects of Iron	31
3.2.4. Cyanobacterial hepatotoxins	32
3.3. The grazer community.....	32
3.3.1. Top-down effects of zooplankton.....	32
3.3.2. Bottom-up effects of nutrient enrichments on higher trophic levels.....	34
3.4. Role of the bottom sediment.....	36
3.4.1. Sediment as a source of nutrients	36
3.4.2. Effects of sediment on phytoplankton community structure	38
4. CONCLUSIONS	40
ACKNOWLEDGEMENTS	42
REFERENCES.....	44
ORIGINAL ARTICLES.....	57

1. INTRODUCTION

1.1. Eutrophication and the Baltic Sea

Increased nutrient loading due to human activity has caused eutrophication of coastal ecosystems throughout the world (Nixon 1995, Cloern 2001, Smith 2006). Eutrophication has been defined as “the enrichment of water by nutrients, especially nitrogen and/or phosphorus and organic matter, causing an increased growth of algae and higher forms of plant life to produce an unacceptable deviation in structure, function and stability of organisms present in the water and to the quality of water concerned, compared to reference conditions” (Andersen et al. 2006). The consequences of eutrophication include a possible shift in phytoplankton species composition (Wasmund & Uhlig 2003, Carstensen & Heiskanen 2007, Suikkanen et al. 2007), an increase in harmful algal blooms (Smayda 1990, Cloern 2001, Scavia & Bricker 2006), increased turbidity, oxygen deficiency in bottom waters (Rosenberg et al. 1990, Bishop et al. 2006, Kiirikki et al. 2006) and changes in fish (Baden et al. 1990, Rajasilta et al. 1999, Lappalainen et al. 2000) and benthos communities (Hansson & Rudstam 1990, Perus & Bonsdorff 2004, Perus et al. 2007).

In the Baltic Sea the total load of nitrogen (N) and phosphorus (P) have been estimated to have increased fourfold and eightfold respectively from the 1940s to the 1980s (Larsson et al. 1985). Enhanced nutrient inputs have increased primary production by 30 to 70 % and sedimentation by 70 to 190 % (Elmgren 1989). This has resulted in increased oxygen consumption in the sediments, leading to an increase in oxygen-deficient bottom areas (Jansson & Dahlberg 1999). The increase in anoxic bottom sediments in turn enhances the benthic release of P. Oxic bottom sediments function as a sink for P, which is bound to iron (III) hydroxides, but when the sediments turn anoxic P is released via reduction of the metal oxides (Krom & Berner 1981, Lehtoranta et al. 1997, Pitkänen et al. 2003, Blomqvist et al. 2004). This may lead to a vicious circle, whereby eutrophication increases the sedimentation rate leading to anoxic sediments, triggering the release of P, causing more nutrients to enter the system and further exacerbating the eutrophication problem (Tamminen & Andersen 2007, Vahtera et al. 2007a).

Although cyanobacterial blooms are a natural annual late summer phenomenon in the Baltic Sea (Bianchi et al. 2000), there are indications that they have increased during recent decades concomitantly with raised nutrient levels (Kahru et al. 1994, Finni et al. 2001, Kauppila & Lepistö 2001, Poutanen & Nikkilä 2001, Suikkanen et al. 2007). In open waters the blooms are dominated by the nitrogen-fixing species *Aphanizomenon* sp. and *Nodularia spumigena* Mertens ex Bornet and Flahault, while in coastal waters *Anabaena* spp. is also common (e.g. Sivonen et al. 2007). All three genera contain gas vesicles, making them buoyant; in calm weather they rise to the surface, where

they may form large aggregates (Walsby et al. 1995, Walsby et al. 1997, Ploug 2008). Cyanobacterial blooms are of particular concern because they are often toxic. In the Baltic Sea *Nodularia spumigena* produces the hepatotoxin nodularin (Sivonen et al. 1989), while *Anabaena* has recently been confirmed to produce microcystin, another hepatotoxin (Halinen et al. 2007). Baltic *Aphanizomenon* has not been found to be toxic (Sivonen et al. 1989, Repka et al. 2004), but freshwater species of both *Anabaena* and *Aphanizomenon* are capable of producing neurotoxins in addition to microcystins (Sivonen et al. 1990, Carmichael 1997, Willen & Mattson 1997). Toxin production by algae may be affected by nutrient availability (Granéli et al. 1998, Granéli & Flynn 2006, Lindehoff et al. 2009). Toxicity may increase under nutrient limitation due to cellular stress (Johansson & Granéli 1999). However, non-toxic algal blooms may also have negative effects due to their high biomass production. The blooms sometimes form an unpleasant scum on the water surface, reducing the recreational value of the water, and their decay may deplete water oxygen concentrations. Cyanobacterial blooms may moreover aggravate Baltic eutrophication by their nitrogen fixation (Savchuk & Wulff 1999, Rolff et al. 2007, Vahtera et al. 2007a). Recent studies suggest that diazotrophic cyanobacteria are responsible for one third to half of the total external nitrogen load in the Baltic proper (Larsson et al. 2001, Wasmund et al. 2001, Moisander et al. 2007, Rolff et al. 2007).

The high occurrence of N_2 -fixing cyanobacteria in the Baltic Sea has been suggested to be due to the low N:P ratio in the area (Niemi 1979, Stal et al. 2003). A low N:P ratio is assumed to favour the growth of diazotrophic cyanobacteria because of the competitive ability provided by N_2 fixation (Smith 1983, Granéli et al. 1990, Vrede et al. 2009). Mesocosm experiments in the Baltic, however, have yielded contradictory results as to the effects of the N:P ratio and P-enrichment on cyanobacterial growth (e.g. Wallström et al. 1992, Rydin et al. 2002, Kuuppo et al. 2003). Thus the effect on cyanobacteria of an increased nutrient load and of the N:P ratio in the Baltic Sea is still a debated subject. It is well known that cyanobacterial growth is affected by many other factors in addition to nutrient availability, including water temperature, salinity and water column stability (Kononen et al. 1996, Laamanen 1997, Wasmund 1997, Hyenstrand et al. 1998, Kahru et al. 2000, Larsson et al. 2001, Rydin et al. 2002, Kanoshina et al. 2003, Stal et al. 2003, Lips & Lips 2008). It has also been proposed that the availability of trace elements, especially iron, may be an important factor affecting the growth of Baltic cyanobacteria (Howarth & Marino 1998, Stal et al. 1999, Schubert et al. 2008). Iron is a component of the nitrogenase enzyme complex, the enzyme responsible for nitrogen fixing, and is thus essential for N_2 fixation (Fay 1992). It has been estimated that N_2 -fixing cyanobacteria require two orders of magnitude more iron than non-diazotrophic organisms (Raven 1988), and iron has been shown to limit the growth of N_2 -fixing cyanobacteria in some lakes (Elder & Horne 1977, Wurtsbaugh & Horne 1983, Hyenstrand et al. 2001).

Cyanobacteria have been the focus of interest in the Baltic Sea because of their increasingly frequent annual occurrence (Kahru et al. 2007); other algal blooms, which may also be harmful, have received less attention. Other potentially harmful species occur regularly in Baltic plankton (e.g. Leppänen et al. 1995, Lindholm & Öhman 1995, Hällfors 2004, Kuuppo et al. 2006), and mass occurrences of toxic dinoflagellates (Pertola et al. 2005, Hajdu et al. 2006, Kremp et al. 2009) and prymnesiophytes (Dahl et al. 1989, Lindholm & Virtanen 1992, Hajdu et al. 2008) are not unusual. Sometimes the blooms can have dramatic effects, as in 1988 in Skagerrak-Kattegat, where massive blooms of the toxic prymnesiophyte *Chrysochromulina polylepis* Manton & Parke caused mortality on all trophic levels, from phytoplankton to zooplankton, benthic macroalgae, fauna and fish (Dahl et al. 1989, Lindahl & Dahl 1990, Nielsen et al. 1990). Blooms of another prymnesiophyte, *Prymnesium parvum* Carter, have been associated with fish kills in Finland and Sweden (Lindholm & Virtanen 1992, Holmquist & Willén 1993, Lindholm et al. 1999). Nutrient availability and nutrient ratios may trigger the initiation of such blooms (Dahl et al. 2005, Hajdu et al. 2005). For example the abundance of *Chrysochromulina* species has been associated with high N:P ratios (Dahl et al. 2005) while blooms of the invasive, potentially toxic dinoflagellate *Prorocentrum minimum* (Pavillard) Schiller have been correlated with high nutrient concentrations (Hajdu et al. 2005, Pertola et al. 2005).

Knowledge of the responses of phytoplankton communities to changes in nutrient load and ratios is essential for making decisions in water management issues (Conley 2000, Olsen et al. 2001). It has been debated whether reductions in phosphorus, nitrogen or both are needed to deal with eutrophication in the Baltic Sea (e.g. Boesch et al. 2006). Some studies have indicated that in the short term a reduction in the N-load may increase the biomass of N₂-fixing cyanobacteria, due to their competitive advantage during N-limitation (Elmgren & Larsson 2001). It has even been suggested that any reduction in the N-load may be offset by increased N₂-fixation, making N reduction useless (Hellström 1996, Schindler et al. 2008).

1.2. Nutrient regulation of phytoplankton growth

Phytoplankton biomass accumulation is a function of growth rates and losses. Growth rate and productivity are often regulated by the availability of resources (bottom-up regulation), such as light (e.g. Huisman et al. 2004), temperature (e.g. Hagström et al. 2001) or nutrients (e.g. Hecky & Kilham 1988), while losses are due to grazing (top-down regulation) (e.g. Carpenter et al. 1985, Sterner 1989, Kagami et al. 2002), sedimentation out of the photic zone (e.g. Heiskanen 1998), and viral and fungal parasitism (e.g. Suttle et al. 1990, Bratbak et al. 1993, Brussaard 2004).

According to Liebig's law of the minimum, the yield of any organism is limited by the factor present in the lowest amount in relation to its requirements (de Baar 1994). In most systems phytoplankton production is limited by the availability of light or the supply

of N and/or P (Schindler 1978, Hecky & Kilham 1988, Downing 1997). The general paradigm is that N is the nutrient most often limiting production in marine waters (Fisher et al. 1992, Oviatt et al. 1995, Howarth & Marino 2006), as well as in estuaries and coastal marine systems, while freshwater phytoplankton tends to be P-limited (Schindler 1974, Hecky & Kilham 1988, Smith 2003). However, this paradigm has been the subject of controversial debate (e.g. Hecky & Kilham 1988, Tyrrell 1999, Schindler et al. 2008). It is indeed obvious that nutrient limitation patterns vary both spatially and seasonally; moreover, co-limitation by both nitrogen and phosphorus is common in both freshwaters and marine waters (Elser et al. 1990, Kivi et al. 1993, Maberly et al. 2002, Howarth & Marino 2006, Smith 2006, Elser et al. 2007).

Diatoms and some chrysophytes may additionally be limited by the availability of silica (Si), since they need Si in large amounts for their frustules (Egge & Aksnes 1992, Nelson & Dortch 1996). In eutrophicated waters the high supply of N and P often increases diatom growth and sedimentation, which in turn enhances Si accumulation in the sediments (Conley et al. 1993). This may lead to reduced Si concentrations and Si limitation in the water (Papush & Danielsson 2006), which will favour the growth of flagellates rather than diatoms (Smayda 1990, Wasmund & Uhlig 2003, Conley et al. 2008) and may also affect the diatom species composition (Olli et al. 2008). Ultimately, this shift in phytoplankton composition may cause major changes in the entire food web and may also lead to harmful algal blooms (Smayda 1990, Conley et al. 1993, Conley et al. 2008).

In some situations phytoplankton growth may also be limited by the availability of certain trace elements; oceanic phytoplankton, for instance, has been shown to be limited by the availability of iron (Kolber et al. 1994, Coale et al. 1996, Hopkinson et al. 2007).

Phytoplankton on average requires C, N and P in an approximate molar ratio of 106:16:1, the Redfield ratio (Redfield 1958). Deviations from this optimal ratio can be used to infer nutrient limitation of phytoplankton growth. However, species differ in their P and N requirements and the kinetics of nutrient uptake, and may thus have different optimal N:P ratios (Rhee & Gotham 1980, Hecky & Kilham 1988, Quigg et al. 2003, Klausmeier et al. 2004). In laboratory cultures, optimal molar N:P ratios measured for different phytoplankton species lie in the range between 7 and 84 (Rhee 1978, Healey & Hendzel 1979, Rhee & Gotham 1980, Smith 1982). The species-specific optimal ratios may vary depending on different factors, e.g. growth rate (Goldman et al. 1979, Terry et al. 1985, Elrifi & Turpin 1985, Turpin 1986), temperature (Tilman et al. 1986) light conditions (Healey 1985, Goldman 1986) or CO₂ availability (Burkhardt & Riebesell 1997).

In addition to ambient nutrient concentrations, the availability of nutrients for phytoplankton is affected by the regeneration rate of nutrients in the food web (e.g. Dugdale & Goering 1967, Andersen et al. 1991, Gaul et al. 1999). When primary

production is fuelled by recycled nutrients in the food web, it is referred to as regenerated production; production based on the external input of nutrients – i.e. from land and deep water, atmospheric fallout, allochthonous supply, and nitrogen fixation – is termed new production (Dugdale & Goering 1967, Eppley & Peterson 1979). Both the rate of nutrient cycling and the fate of new nutrient inputs in the system depend on the structure and function of the whole food web (Heiskanen et al. 1996, Verity & Smetacek 1996). Knowledge of the food web structure and of the mechanisms structuring community composition is thus of central importance in understanding the impact on these systems of environmental changes such as eutrophication.

1.3. Coastal food webs

Food webs are divided into trophic levels, in which the first level, i.e. the base of the food web, is formed by primary producers (Fig. 1). In the pelagic food web, primary producers consist of picoplankton (0.2-2 μm), nanophytoplankton (2-20 μm) and large microphytoplankton (20-200 μm). Picoplankton consists of both prokaryotes (unicellular cyanobacteria) and eukaryotes (Stockner & Antia 1986). Nanophytoplankton is usually dominated by flagellates, while diatoms, dinoflagellates and filamentous cyanobacteria are the most common microphytoplankton. Large phytoplankton may be preyed upon

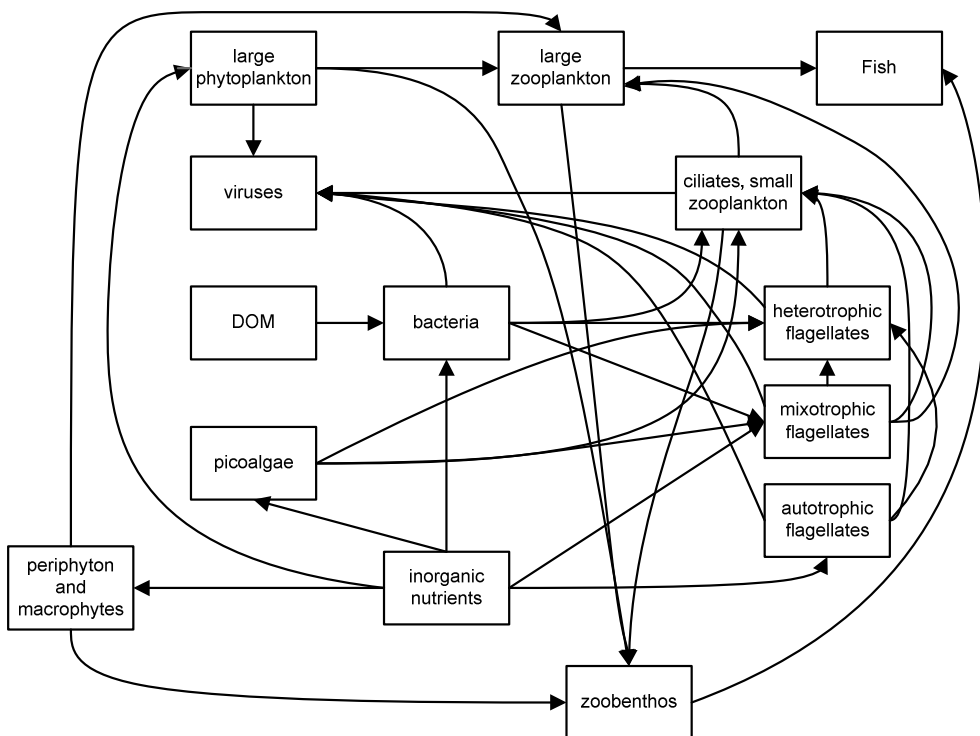


Figure 1. Simplified schematic illustration of the major pathways of flow of energy and nutrients in the coastal food web.

by herbivorous zooplankton, which again serves as food for carnivorous zooplankton; this in turn forms an important food for small fish and mysids. The flow of energy from phytoplankton via zooplankton to fish is known as the classic herbivorous food chain (Hairston et al. 1960, Carpenter et al. 1985, 1987).

Part of primary production is excreted or lost from the phytoplankton in the form of dissolved organic material (DOM) (Lignell 1990). DOM is also released due to incomplete ingestion and digestion by grazers, i.e. “sloppy feeding” (e.g. Lampert 1978, Strom et al. 1997, Titelman et al. 2008), and by excretion and leakage from their fecal pellets (e.g. Jumars et al. 1989, Urban-Rich 1999) as well as due to viral-induced cell lysis (Fuhrmann 1999, Riemann et al. 2009). This DOM is utilized by heterotrophic bacteria, which together with photosynthetic picoplankton form the basis of the microbial food web (Azam et al. 1983, Sherr & Sherr 1988, Titelman et al. 2008). The dominant grazers on bacteria and autotrophic picoplankton are heterotrophic flagellates (Kuuppo-Leinikki 1990, Kuuppo-Leinikki et al. 1994, Gasol et al. 2002), which in turn are grazed by ciliates and other protozoa and small zooplankton (Azam et al. 1983, Bernard & Rassoulzadegan 1990). Part of this ingested material is passed up the food chain to larger zooplankton, reconnecting the microbial food web with the classic food chain; part is regenerated into the water column and re-utilised by primary producers. Nutrient regeneration is of central importance in the microbial food web, but is difficult to measure since regenerated nutrients are so rapidly taken up by other cells.

Omnivory, i.e. the ability of organisms to obtain food from more than one trophic level, and mixotrophy, their ability to gain nutrition through a combination of autotrophy and heterotrophy, are common in pelagic food webs, and further add to the complexity of the food web structure. Viruses are considered as part of the planktonic food web and may play an important role in regulating phytoplankton (Suttle et al. 1990, Bratbak et al. 1993, Brussaard 2004), bacteria (Fuhrmann 1999, Tuomi & Kuuppo 1999, Riemann et al. 2009) and protists (Garza & Suttle 1995).

Energy transfer through the microbial food web is less efficient than through the classic food chain because of the increased average number of trophic links (Fenchel 1988, Pomeroy & Wiebe 1988, Berglund et al. 2007), but is considered highly significant for total energy throughput in the system (Pavés & González 2008). The importance of the microbial food web differs both seasonally and between different systems. The classic or herbivorous food chain has been considered more important in nutrient-rich waters, while the microbial food web is predominant in nutrient-constrained environments where productivity is based on nutrients regenerated within the system (Legendre & Rassoulzadegan 1995). The opposite, however, may also be true: high nutrient availability can stimulate the growth of either predation-resistant inedible algae or fast-growing small opportunistic primary producers which are not accessible to larger zooplankton, leading to a dominance of the microbial food web and reduced energy transfer to higher trophic levels (e.g. Andersson et al. 2006).

In shallow coastal and estuarine ecosystems the pelagic food web is closely coupled to the benthic food web (Fig. 1). The importance of bottom sediment in fluxes of nutrients and organic matter between the two habitats, and the role of sediment as a nutrient sink and source, are well known (reviewed by Graf 1992). In addition to nutrient fluxes, however, the pelagic and benthic systems are connected through several biological interactions between benthic and pelagic organisms, including grazing and competition for the same resources.

The base of the benthic food web is formed by periphyton, an assemblage of algae, bacteria, heterotrophic microbes and detritus which covers almost all substrates (Liess & Hillebrand 2004). Periphyton is grazed upon by invertebrate grazers, which in turn may be grazed by predatory macroinvertebrates (Hillebrand et al. 2000, Liess & Hillebrand 2004). The latter serve as food for fish, which may also feed directly on invertebrate grazers and periphyton (e.g. Mittelbach et al. 1992, Brönmark 1994). Periphyton may also be grazed by pelagic zooplankton, while benthic invertebrates may be important grazers on phyto- and zooplankton and may also compete with zooplankton for the phytoplankton food resource (e.g. Horsted et al. 1988, Sullivan et al. 1991, Prins et al. 1995, Noren et al. 1999). Moreover, the zoobenthos may affect the pelagic community by altering the nutrient fluxes near the sediment-water interface, either directly through nutrient excretion or indirectly by promoting nutrient release from the sediment through their bioturbation (Aller 1982, Kristensen & Hansen 1999, Karlson et al. 2007). In shallow waters, where much of the sediment surface is within the euphotic zone, benthic microalgae and macrophytes may be important primary producers and compete for nutrients with phytoplankton (Sand-Jensen & Borum 1991, McGlathery et al. 2001, Mulderij et al. 2007).

Benthic and pelagic systems are also coupled in that many marine organisms have both benthic and planktonic life stages (Marcus & Boero 1998, McQuoid & Godhe, 2004): many species of benthic macrofauna living in coastal systems have planktonic larvae, while many planktic organisms have benthic resting stages. Migration from the sediment surface via either recruitment or growth can play a significant role in plankton dynamics and bloom formation (Hansson 1996, Kremp 2001, McQuoid & Godhe 2004).

1.4. Phytoplankton competition for limiting nutrients

Competition for limiting nutrients is seen as an important factor in the determination of phytoplankton community composition (Tilman et al. 1982, Sommer 1989, Grover 1997). Competition occurs when two or more organisms have a demand for the same limited environmental resource. It may take the form either of direct interference by competing species against each other, for example through aggressive behavior or the release of chemical compounds (interference competition), or of indirect negative influence by one species on another, by consuming or controlling access to a common limited resource (exploitation or resource competition).

The ability of phytoplankton to compete for nutrients is largely determined by their physiological properties, including nutrient transport kinetics, half-saturation constants for growth (K_s), maximal growth rate and storage capacity (Tilman 1977, Tilman et al. 1982, Sommer 1989, Flynn 2002). The half-saturation constant for growth (K_s) is the concentration of the limiting nutrient at which the growth rate is one half of its maximum. With sufficient information about the uptake and growth kinetic parameters of different algae, their competitive abilities can be determined in relation to resource availability. However, since the growth parameters measured are influenced by environmental conditions and vary widely among studies, the extrapolation of growth parameters from one algal population to another may be unreliable (Guillard et al. 1973).

Sommer (1985) divided algae into three categories according to their ability to utilize nutrients; affinity, velocity and storage specialists. Affinity specialists have low requirements for nutrients and are efficient users of low nutrient concentrations. Velocity specialists have high uptake and growth rates and are able to utilize temporary high nutrient enrichment for rapid growth, thus offsetting the possible decline under lower nutrient concentrations. Storage specialists are able to use temporarily high nutrient concentrations to build-up an intracellular storage pool; they usually have relatively high uptake rates but only moderate maximum growth rates. A fluctuating nutrient supply should favour both velocity specialists, which are capable of rapid growth after nutrient pulses, and storage specialists, which are capable of luxury consumption, while a low and continuous nutrient supply should select for affinity specialists (Sommer 1985, Grover 1991).

The nutrient kinetics of phytoplankton are strongly related to size (Stolte & Riegman 1996). Small algal species, with a high cellular surface to volume ratio, appear to have the highest affinity for nutrients (Stolte & Riegman 1996), and are supposed to be favoured by continuous, stringent nutrient limitation (Malone 1980, Banse 1982, Probyn et al. 1990). Large species, on the other hand, are believed to benefit from a pulsed nutrient supply because of their higher uptake and storage potential (Turpin & Harrison 1979, Stolte & Riegman 1996).

Other nutritional strategies available to phytoplankton, such as nitrogen fixation and mixotrophy, seem to be especially advantageous in nutrient-limited conditions. Heterocystous cyanobacteria, which are able to fix atmospheric dinitrogen to supplement their N requirements, are thought to be primarily limited by the availability of P and thus favoured by a low N:P ratio (Smith 1983, Rydin et al. 2002, Stal et al. 2003). Mixotrophs may be favoured by nutrient limitation, because of their ability to utilize particulate food as a source of mineral nutrients (Nygaard & Tobiesen 1993, Isaksson 1998, Stibor & Sommer 2003). However, the need of mixotrophs to invest in both a photosynthetic apparatus and mechanisms for uptake and assimilation of organic substances is thought to be energetically costly, resulting for example in a lower growth rate compared to phototrophic or heterotrophic specialists (Rothhaupt 1996). Mixotrophs are therefore

thought to be inferior competitors in comparison with specialist phototrophs for light or specialist phagotrophs for prey.

For some algae, special life history patterns may function as a survival strategy under nutrient competition. The formation of resting spores, for example, may be an adaptation to survive nutrient depletion (Smetacek 1985).

The ability of phytoplankton to compete for nutrients is further influenced by cell motility (Ross & Sharples 2007). Under nutrient limitation, flagellates will derive an advantage from their swimming ability, enabling them to migrate vertically to exploit nutrient gradients (Smayda & Reynolds 2001). Many planktonic cyanobacteria, on the other hand, possess gas vesicles, allowing them to control their buoyancy and vertical position in the water column (Utkilen et al. 1985, Walsby et al. 1995, Walsby et al. 1997, Porat et al. 2001).

Phytoplankton nutrient competition may also be indirectly affected by interference competition by means of allelopathy (Granéli & Hansen 2006, Granéli et al. 2008). Allelopathy is the production of chemical compounds which inhibit the growth of competing organisms, thus indirectly preventing them from consuming common resources (Legrand et al. 2003, Suikkanen et al. 2005). Allelopathy is known among several different algal groups, including cyanobacteria, diatoms, dinoflagellates, prymnesiophytes, raphidophytes and chlorophytes (Granéli et al. 2008, Suikkanen 2008). For example the Baltic filamentous cyanobacteria *Anabaena*, *Aphanizomenon* and *Nodularia* inhibit the growth of cryptophytes (Suikkanen et al. 2004, Suikkanen et al. 2005), while the prymnesiophytes *Prymnesium parvum* and *Chrysochromulina polylepis* inhibit the growth of some diatoms, cryptophytes and dinoflagellates (Schmidt & Hansen 2001, Granéli & Johansson, 2003, Fistarol et al. 2005). The production of allelochemicals has been shown to increase in response to abiotic stress such as nutrient limitation (Granéli & Johansson 2003, Fistarol et al. 2005, Granéli & Hansen 2006, Granéli et al. 2008).

The outcome of nutrient competition is further affected by a number of other factors. These include continuously changing environmental conditions, such as temperature (Tilman et al. 1986) or light conditions (Sommer 1994); interactions with other species and with the abiotic environment; sedimentation, grazing, disease, and chaotic dynamics (Huisman & Weissing 1999, Cloern & Dufford 2005, Benincà et al. 2008). Furthermore, if a resource is so abundant that it does not limit phytoplankton, no competitive interactions will naturally occur. This could be the case if phytoplankton populations are kept at low densities by other factors, such as grazing or abiotic disturbance.

1.5. Nutrient-phytoplankton-zooplankton interactions

Zooplankton may affect phytoplankton community structure either directly, by selective grazing (Sterner 1989, Kivi et al. 1996, Sommer et al. 2001, Kagami et al. 2002), or indirectly, through nutrient regeneration (Elser et al. 1988, Sterner 1989, Kagami et al. 2002).

From freshwater studies it is well known that the effect of nutrient supply on phytoplankton biomass and species composition can be strongly modified by the top-down control exerted by the grazing community (e.g. Reynolds 1984, Sterner 1989, Carpenter et al. 1995, Cottingham & Schindler 2000, Cottingham et al. 2004). Cottingham et al. (2004), for instance, showed that large zooplankton grazers such as *Daphnia* spp. may reduce the effect of nutrient pulses on the phytoplankton community. In other studies, nutrient enrichment in combination with high zooplankton grazing pressure, led to the dominance of large grazing-resistant cells (e.g. Lynch & Shapiro 1981, Horsted et al. 1988, Mazumder et al. 1988). The role of top-down effects in shaping marine phytoplankton communities is less well known (e.g. Horsted et al. 1988, Riemann et al. 1988, Granéli et al. 1993, Gismervik et al. 2002).

Just as zooplankton can regulate the phytoplankton community, phytoplankton, as food, can have a major impact on its predators. Changes in phytoplankton abundance, species composition, chemical composition and palatability due to nutrient enrichment may affect zooplankton growth and reproduction (e.g. Sterner & Hessen 1994, Van Nieuwerburgh et al. 2004, Jones & Flynn 2005, Klein Breteler et al. 2005), which in turn may further affect higher trophic levels of the food web and alter the entire ecosystem (Smith 2006). The efficiency of energy transfer from phytoplankton to consumers and ultimate production at upper trophic levels vary with algal species composition. While some algae synthesize biochemicals that are essential dietary components for animal consumers, others produce toxins which inhibit animal growth or reproduction (Wolfe et al. 1997, Lindehoff et al. 2009).

1.6. Aim of the study

The aim of the present study was to examine the response of phytoplankton biomass and community composition to changes in external nutrient supply and the role of sediment in nutrient and phytoplankton dynamics in the Archipelago Sea, northern Baltic Sea. The main questions were as follows:

1. What is the role of the N:P ratio in structuring phytoplankton community composition? (Article I)
2. How does the frequency of nutrient pulses influence plankton community structure? (Article II)
3. Is the growth of N₂-fixing cyanobacteria favoured by nutrient enrichment, specifically by a nutrient supply with a low N:P ratio (Articles II - IV), and is it limited by the availability of Fe? (Articles III, IV)
4. What is the role of sediment in nutrient release (Article V) and in structuring the phytoplankton community (Article VI) in shallow coastal areas?

2. MATERIAL AND METHODS

2.1. Study Area

The Baltic Sea is a non-tidal brackish sea located in northern Europe with an area of about 412 000 km². The sea has a restricted connection to the North Sea through the Danish straits and the residence time of the water is long, about 30 years (Stigebrandt & Wulff 1987). The salinity of the surface waters ranges from around 20 psu in the Danish straits to 1–2 psu in the northernmost and easternmost parts of the sea. The sea is characterized by a strong seasonality: maximum summer water temperatures reach around + 20°C, while in winter part of the sea is covered by ice. The Baltic Sea has low species diversity, partly because of the young age of the sea (about 7 500 years) and partly due to the brackish water and the harsh climate. Organisms include limnic, marine and brackish water species.

The Archipelago Sea is located in the northern part of the Baltic Sea, between the Baltic Proper and the Bothnian Sea. The sea area is approximately 8,000 km² and includes a mosaic of about 22 000 islands and more than 14 000 km of shoreline (Granö et al. 1999). The sea is shallow: the mean depth is 23 m, but the coastal waters are usually less than 10 m deep. The high abundance of islands and the many narrow and shallow passages make the water exchange through the Archipelago Sea relatively slow. Thus the sea area acts as a filter between the coastline and the open sea, as well as between the northern Baltic proper and the Bothnian Sea (Jumppanen & Mattila 1994, Bonsdorff et al. 1997a, b). Surface salinity ranges from 4 to 7 psu from the inner archipelago towards the open sea.

Like other parts of the Baltic Sea, the Archipelago Sea is severely affected by eutrophication (Jumppanen & Mattila 1994, Bonsdorff et al. 1997a, b, Rönnerberg & Bonsdorff 2004). Signs of eutrophication were detected in the inner archipelago areas already in the 1960s (Jumppanen & Mattila 1994), while the outer areas became affected in the 1980s (Jumppanen & Mattila 1994). In the 1970s and 1980s the water quality improved close to urban areas because of more effective phosphorus removal from sewage waters (Suomela & Sydänoja 2006). During the 1990s, however, nutrient concentrations and the abundance of plankton algae continued to increase and the Secchi depth decreased in many parts of the middle and outer archipelago (Suomela 2001).

During the 2000s the phosphorus concentration has stopped rising or has even dropped slightly in many parts of the Archipelago Sea, but is still high (Suomela & Sydänoja 2006). The concentration of chlorophyll *a*, representing phytoplankton biomass, has continued to rise in large parts of the sea. The increase in nutrient concentrations and phytoplankton biomass has been suggested to be due to an increase in internal nutrient loading resulting from sediment P release (Suomela & Sydänoja 2006), since oxygen

deficiency and anoxic bottom sediments are common in the sea area (Virtasalo et al. 2005).

Annual succession of phytoplankton in the Archipelago Sea

The annual phytoplankton succession in the Archipelago Sea follows the general pattern for the northern Baltic Sea (Fig. 2). Low light intensity limits production during winter. The spring bloom begins in March-April after the melting of the ice, when the amount of light increases. The spring bloom is dominated by chain-forming diatoms such as *Achnanthes taeniata* Grunow, *Chaetoceros wighamii* Brightwell, *Chaetoceros* spp., *Skeletonema costatum* (Greville) Cleve, *Thalassiosira baltica* (Grunow) Ostenfeld and *Thalassiosira Levanderi* Van Goor and the dinoflagellates *Peridiniella catenata* (Levander) Balech and *Protoperidinium granii* (Ostenfeld) Balech, *Protoperidinium bipes* (Paulsen) Balech and *Gymnodinium* spp. In the northern Baltic proper the spring bloom has been estimated to be responsible for up to 60 % of annual planktonic primary production (Kuparinen 1984, Kuosa & Kivi 1989). A large part (40-70 %) of production during the spring bloom is lost from the planktonic food web due to high sedimentation rates (Lignell et al. 1993, Heiskanen & Leppänen 1995). The spring bloom ends when inorganic nutrients are depleted from the water column, in early June.

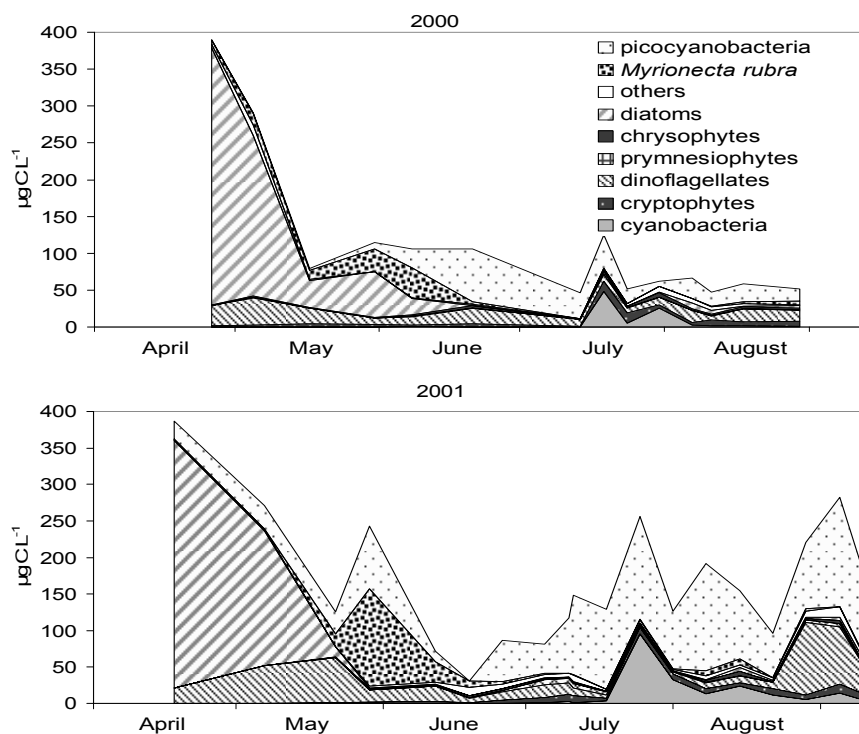


Figure 2. Seasonal succession of main phytoplankton groups at the study site in the Archipelago Sea during 2000 and 2001. Data from Suomela et al. (unpublished).

The spring bloom is often accompanied by a biomass peak of the autotrophic ciliate *Myrionecta rubra* Lohmann (Fig. 2), followed by a summer phytoplankton minimum, when inorganic N or P, or both, are almost completely depleted in the photic zone and autotrophic production is mainly based on regenerated nutrients. During this time picocyanobacteria may make up 25 - 80 % of the total autotrophic biomass (Fig. 2). The rest of the autotrophic biomass consists of a diverse phytoplankton community, dominated by small flagellates such as the cryptophytes *Plagioselmis prolonga* Butcher, *Teleaulax acuta* (Butcher) Hill, *Teleaulax amphioxeia*, (Conrad) Hill and *Katalepharis* spp, chrysophytes (*Pseudopedinella tricostata* (Rouchijajnen) Thomsen, *Pseudopedinella* spp., and *Uroglena* sp.), the prymnesiophytes *Chrysochromulina* spp., the prasinophytes *Pyramimonas* spp. and unidentified small flagellates. However, some larger dinoflagellates, especially *Dinophysis acuminata* Claparède & Lachmann, also contribute to the summer biomass.

In July-August there is often another peak in the phytoplankton biomass due to blooms of the nitrogen-fixing cyanobacteria *Aphanizomenon* sp., *Anabaena* spp., and *Nodularia spumigena*. In late summer, when water temperatures start to decline, blooms of dinoflagellates such as *Heterocapsa triquetra* (Ehrenberg) Stein and *Prorocentrum minimum* (Pavillard) Schiller may form (Fig. 2).

2.2. Mesocosm experiments

A mesocosm can be defined as a model ecosystem, such as an enclosed water-body, large tank, natural or artificial pond, which can be replicated and in which specific environmental factors can be manipulated and their effects monitored. During the last decade mesocosm experiments have successfully been used to study the response of plankton communities to different environmental changes, such as light, temperature, pH, mesozooplankton or nutrients. Mesocosms are intermediate between controlled laboratory experiments and field studies. Although they cannot be controlled to the same extent as laboratory experiments, they represent more natural conditions. The realism of a mesocosm, however, may be reduced by enclosure artifacts, factors in the experimental system that differ from the natural ecosystem: these include periphyton growth on mesocosm walls, changes in water turbulence in the enclosure, shifts in material exchange rates, and distortions in the mixing and light regimes (Brockmann 1990, Schindler 1998, Petersen et al. 1997, 1999). Moreover, experimental conditions can favour or disfavour different species present in the natural community, and the absence or uneven distribution of larger and less abundant species in a mesocosm can disrupt the function of the natural food web.

In this study, mesocosm experiments were conducted in a small, shallow bay (depth < 5 m) close to the island of Seili (60° 15'N, 21° 58'E) in the central part of the Archipelago Sea (Fig. 3). Two different types of mesocosms were used, 300-400 liter bags and large 30–40 m³ enclosures, of which some included the bottom sediment. The experiments

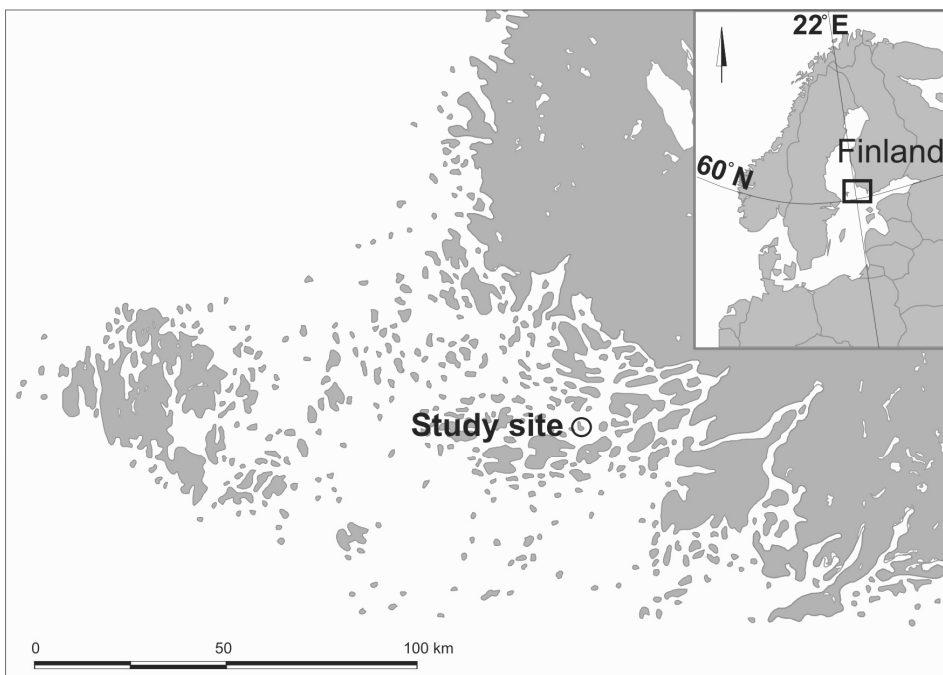


Figure 3. Location of the study site in the Archipelago Sea, northern Baltic Sea.

were based on factorial designs; treatments included the addition of N as NH_4Cl and P as KH_2PO_4 . Some of the experiments also dealt with the effects of iron (Fe). The individual experiments are summarised in Table 1 and are briefly described below. More detailed information on the experiments can be found in the respective articles.

Experiments with small enclosures (Articles I, III & IV)

The 300-400 liter transparent enclosures were made of 0.15 mm thick polyethylene and were about 1.5 m deep. The enclosures were mounted on three floating wooden racks, which were anchored in the sea in a row in an E-W direction (Fig. 4). The enclosures were protected from bird faeces with a plastic roof, but the exchange of gases between air and the sea was not prevented. The enclosures were filled with surface water from the study site on the evening prior to the start of the experiments.

The first experiment JUN99 was performed in the beginning of summer, after termination of the phytoplankton spring bloom (Article I). The focus of the experiment was to study the effect on the phytoplankton community composition of the N:P ratio versus the absolute nutrient concentration. The design of the experiment was such that the phytoplankton community in the different treatments would be potentially either N-limited, P-limited or supplied with N and P in an optimal ratio, according to the Redfield ratio. To be able to distinguish the N:P ratio effect from the direct resource effect, the three N:P mass ratios – 2.7 (N-deficient), 18 (P-deficient) and 6.9 (close to Redfield-ratio) – were supplied in two different concentrations (Low and High). In

Table 1. Experimental setup in the different experiments. All experiments except for JUL99 were based on a factorial design.

Experiment	JUN99	PULS01	JUL99	AUG01	SED01
Article	I	II	III	IV	V, VI
Focus of experiment	Effects of N:P ratio versus absolute nutrient levels	Interaction effects of N:P ratio and frequency of nutrient supply	Effects of N, P and Fe on especially cyanobacteria	Effects of Fe, EDTA and the N:P ratio on especially cyanobacteria	Effects of sediment vs. external nutrient enrichment
Mesocosms	300 liters	30-40 m ³	300 liters	400 liters	30-40 m ³
Experimental design	3 N:P ratios (N-deficient, Redfield, P-deficient) x 2 nutrient levels (Low, High) + zooplankton removal + control	2 N:P ratios (N-deficient, Redfield) x 2 nutrient addition frequencies (Daily, Weekly)	Control, only P, P and Fe + EDTA, N and P in 2 ratios (N-deficient, P-deficient)	1) Control and 2 N:P ratios (N-deficient, Redfield) x addition of Fe 2) addition of Fe x addition of EDTA	Control and Nutrient enrichment (Redfield) x sediment bottomed vs. plastic-bottomed enclosures
Number of replicates	3	3	2	3	3
Number of mesocosms	24	12	10	24	12
Experimental time	7 - 18 Jun 1999 11 days	8 Aug - 6 Sep 2001 29 days	22 Jul - 2 Aug 1999 11 days	7 - 27 Aug 2001 20 days	12 Jul - 2 Aug 2001 21 days
NH ₄ additions µg l ⁻¹ d ⁻¹	3.0; 7.6; 20	1.7; 12	9; 40	1.7; 12	5
PO ₄ additions µg l ⁻¹ d ⁻¹	0.42; 1.1; 2.9	1.7	3	1.7	0.7
DIN:DIP mass ratio of additions	2.7; 6.9; 18	1; 7	3; 13.3	1; 7	7

**Figure 4.** Small 300-400 liter enclosures. Photo: Janne Suomela.

addition, there was a control treatment with no nutrient addition and a zooplankton removal treatment, which was used to estimate the effect of zooplankton grazing on the phytoplankton community. The zooplankton removal treatment was supplied with the same amounts of nutrients as in the high Redfield nutrient enrichment, but the water was filtered through a 100 µm net during the filling of the enclosures. The enclosures were sampled for analysis of nutrient and chlorophyll concentrations and picocyanobacteria at intervals of two to three days. Phytoplankton was analysed three times during the experiment; zooplankton was analysed at the start and end of the experiment.

The two other experiments, JUL99 and AUG01, were performed in late summer, and focused on cyanobacterial responses to nutrient enrichments (Articles III & IV). Since the concentration of N₂-fixing cyanobacteria at the start of the experiments was low, an inoculum of cyanobacteria was added to the enclosures. In the JUL99 experiment the inoculum was water collected from a surface bloom dominated by *Anabaena lemmermannii* and *Aphanizomenon* sp. from a nearby area, while in AUG01 the cyanobacteria were collected from a bloom in the Gulf of Finland dominated by *Nodularia spumigena* and *Aphanizomenon* sp.

The JUL99 experiment was conducted over eleven days in July 1999 (Article III). Treatments included addition of P alone, P together with Fe and ethylenediaminetetraacetic acid (EDTA), P and N in a N-deficient ratio, P and N in a P-deficient ratio, and a control treatment without nutrient addition. The organic chelator EDTA was added in order to increase the bioavailability of Fe. In the course of the experiment, water nutrient and chlorophyll *a* concentrations and phytoplankton biomass were monitored.

In the AUG01 experiment, which lasted twenty days in August 2001, the treatments were based on two factorial designs (Article IV). In design 1, a control treatment without any additions of N and P and two nutrient enrichments with additions of N and P either at the optimal Redfield mass ratio 7:1 or at the N-deficient ratio 1:1 were crossed with the addition of Fe. In design 2, N and P were added at the N-deficient ratio 1:1 in all four treatments and the treatment factors were the addition of Fe and EDTA according to a two-way design. Water samples for measurements of primary productivity and concentrations of nutrients and chlorophyll *a* were taken at intervals of two to three days. Phytoplankton community structure and water hepatotoxin concentration were analysed three times during the experiment.

Experiments with large mesocosms (Articles II, V & VI)

Twelve 30 to 40 m³ cylindrical enclosures made of double-layered transparent polyethylene were placed in a small bay, where the euphotic zone reaches the bottom (Fig. 5). The surface sediment at the study site is characterized as an oxic transportation bottom with a low content of organic matter. The mean nutrient concentrations in the upper 0-3 cm of the sediment have been analysed as 285 µmol total N g⁻¹ DW (dry weight), 26 µmol total P g⁻¹ DW and 569 µmol total C g⁻¹ DW and the loss of ignition



Figure 5. Large 30–40 m³ experimental enclosures. Photo: Janne Suomela.

as 3.7 % DW (Gran, unpubl.). The enclosures contained the whole water column, from surface to bottom. The enclosures were of two types: with natural sediment as a bottom, or with a plastic bottom with no contact with the sediment. The enclosures were 3.6 m in diameter, with a water depth varying from 3.1 to 3.9 m. The upper edges extended about 1 m above sea level, to prevent the entrance of waves. During filling of the enclosures a nylon net of 1 mm mesh size was stretched over the upper edge to prevent the accidental entrance of fish and large mysids. In the sediment-bottomed enclosures mysids and fish were removed after filling with a 1-mm mesh seine net.

The effect of nutrient supply frequency under different N:P ratios was studied in PULS01, a four-week experiment in late summer 2001 (Article II). The experimental design was a 2 x 2 factorial, with the interval between nutrient additions and the N:P ratio of the enrichment as treatment factors. Nutrients (N and P) were added either once a day or once a week and in either an N-deficient (N-def) or an optimal Redfield ratio (Redf). Nutrient doses were seven times higher in the weekly than in the daily enrichments, so that integrated over the whole experimental period the enclosures which received nutrients in the same N:P ratio also received the same total amounts of N and P. The enclosures were sampled for analysis of nutrient and chlorophyll *a* concentrations at intervals of two to three days. The phytoplankton community and ambient hepatotoxin concentrations were analysed at the beginning, middle and end of the experiment. The zooplankton community was examined once a week.

The role of sediment in water quality and in phytoplankton dynamics was studied in SED01, a three-week experiment in July–August 2001 (Articles V & VI). The aim was to compare the effects of bottom sediment with those of a known external nutrient addition, and to determine if the effects of nutrient enrichment differ in the presence or absence

of natural sediment. The enclosures included or excluded the natural bottom sediment, and half of them were enriched with nitrogen and phosphorus. The experiment was a 2 x 2 factorial design, with presence or absence of sediment and nutrient enrichment as treatment factors. Prior to the start of the experiment, fish and mysids were removed with a 1-mm mesh seine net to minimize differences among the enclosures in densities of large predators. In addition, 60–80 individuals (2 ind m^{-3} , mean length 13.8 mm) of *Neomysis integer* Leach were placed in each enclosure, to prevent abrupt increases in mesozooplankton densities. Water samples were taken for analysis of chlorophyll *a* and nutrients concentrations, picocyanobacteria and primary productivity at intervals of three or four days. Phytoplankton and zooplankton community structure and sediment pore water nutrient concentrations were analysed once a week.

2.3. Plankton biomass

Phytoplankton samples were preserved in acid Lugol's solution and analysed with an inverted light microscope (Nikon Eclipse), using the Utermöhl technique (Utermöhl 1958), and identified to species level whenever possible. A small drop of detergent was added to the sedimentation chamber to improve the settling of gas-vacuolate cyanobacteria. At least 100 units of each of the dominant species were counted, yielding a precision of $\pm 20\%$ within 95% confidence limits if the algae were randomly distributed (Lund et al. 1958). Phytoplankton cell biovolumes were obtained using appropriate volume formula according to Edler (1979). Carbon biomass was calculated from the biovolume by estimating a carbon content of $0.22 \text{ pg C } \mu\text{m}^{-3}$ for picoplankton (Li 1986), $0.13 \text{ pg C } \mu\text{m}^{-3}$ for thecate dinoflagellates, and $0.11 \text{ pg C } \mu\text{m}^{-3}$ for all other phytoplankton cells (Mullin et al. 1966, HELCOM 1988). Autotrophic picoplankton samples were preserved with ice-cold 2% glutaraldehyde. Subsamples were filtered on black-stained Nuclepore filters (pore size $0.2 \mu\text{m}$). The filters were stored at -24°C and counted later with a Leica Dialux epifluorescence microscope using Leica M2 filter set with green excitation (BP 546/14). Mesozooplankton samples (30 L) were concentrated on a $25 \mu\text{m}$ mesh net and preserved in 70% ethanol. Zooplankton were identified and enumerated with an inverted microscope and the biomasses were calculated according to average species-specific biomass values or carbon biomass values (Hernroth 1985, Pellikka & Viljamaa 1998).

2.4. Primary production

Primary production was measured using the ^{14}C method (Steemann Nielsen 1952). Duplicate light and one dark incubation bottle were used per sample. The bottles (100 ml) were incubated with $4 \mu\text{Ci NaH}^{14}\text{CO}_3$ (International Agency for ^{14}C Determination, Hørsholm, Denmark) in a light- and temperature-controlled incubator (at an irradiance of $120 \mu\text{mols}^{-1}\text{m}^{-2}$ and a temperature of 20°C) for 4 h. The incubation was terminated by adding 0.5 ml 37% formaldehyde to the bottles and filtering the water through

membrane filters (Sartorius pore size 0.45 μ m). The filters were rinsed with prefiltered (Whatman GF/F) seawater, dried in a fume cupboard and transferred to scintillation vials. 20 ml of scintillation cocktail was added to the vials and the radioactivity of the samples was measured with a liquid scintillation counter (Rackbeta, LKB Wallac Finland), using the external standard channel ratio method. The total carbon dioxide concentration of the water was derived from measurements of pH, alkalinity, salinity and temperature according to HELCOM (1988). Water pH and conductivity were measured with a Multiline P4 meter with a SenTix 97/T probe (WTW, Germany). Alkalinity was measured by acid titration.

2.5. Hepatotoxins

Water samples for hepatotoxin (microcystin + nodularin) analyses were stored frozen until analysis. The samples (5 ml) were thawed at room temperature, sonicated in an ultrasonic bath (Sonorex Super 10P, Bandelin) for 60 minutes, filtered through syringe filters (Whatman Puradisck, nominal pore size 0.2 μ m), and kept in a refrigerator overnight. The next day the samples, microcystin-LR standards (0.1, 0.4 and 1.6 ppb) and negative controls were prepared and run in duplicate with an enzyme-linked immunosorbent assay (ELISA, EnviroGard Microcystins Plate Kit, Strategic Diagnostics Inc.). Hepatotoxins in the samples were measured with a spectrophotometer (Labsystems I EMS Reader MF) and analysed with Windows-based microplate software Genesis II (Labsystems and Life Sciences International Ltd.).

2.6. Nutrients and chlorophyll *a*

Nutrients were analysed from unfiltered samples within five to eight hours after sampling. Total P was analysed by digesting with $K_2S_2O_8$ in acidic conditions and measured spectrophotometrically as ammonium molybdate blue complex (SFS 3026, 1986). Phosphate-P (PO_4 -P) was analysed as total P but without the digestion phase (SFS 3025, 1986). Total N was measured by digesting the sample with $K_2S_2O_8$ to nitrate, which was further reduced to nitrite and measured in an FIA-ion analyser application according to the EPA 353.2 method (U.S. EPA, 1983). Nitrate-N (as a sum of (NO_2+NO_3) -N) was analysed as total N, but without digestion (U.S. EPA, 1983). Ammonium-N (NH_4 -N) was measured spectrophotometrically with the indophenol blue method (SFS 3032, 1976). Unfiltered silica (SiO_2) was analysed with a Bran & Luebbe AutoAnalyser according to ISO/DIS 16264 (2002) standard for soluble silicate. Chlorophyll *a* samples were filtered through Whatman GF/F-filters. The filters were air-dried, stored frozen, then extracted in ethanol and measured spectrophotometrically (SFS 5772, 1993).

3. RESULTS AND DISCUSSION

3.1. Phytoplankton community

3.1.1. Nutrient limitation

Nutrient enrichment increased primary production (Articles IV, VI) and phytoplankton biomass (Articles I, II, III, IV, VI), indicating nutrient limitation. This is in accordance with results from several other studies in coastal waters (e.g. Granéli et al. 1990, Lignell et al. 2003, Smith 2006, Tamminen & Andersen 2007). At the beginning of all experiments the ratio of inorganic N to P (DIN:DIP) in water ranged from 0.7 to 2.8 (by mass), suggesting potential N-limitation of the phytoplankton community (according to Forsberg et al. 1978). As expected from the low N:P ratio in water, total phytoplankton biomass responded most strongly to the addition of N (Fig. 6, Articles I, II, III, IV). This agrees with the results from laboratory enrichment experiments performed throughout the growth season, in which the Archipelago Sea was most often N-limited (Tamminen & Andersen 2007). According to the ambient N:P ratios, the Archipelago Sea has been shifting during the 1990s from a co-limitation of N and P towards a prevalence of N-limitation (Kirkkala et al. 1998), which is characteristic of eutrophicated coastal waters (Tamminen & Andersen 2007). It has been suggested that P-limitation prevails when the phytoplankton community is dominated by diazotrophic cyanobacteria which are able to utilize molecular N₂ (Granéli et al. 1990, Lignell et al. 2003). In the present study, however, phytoplankton biomass responded most strongly to the addition of N

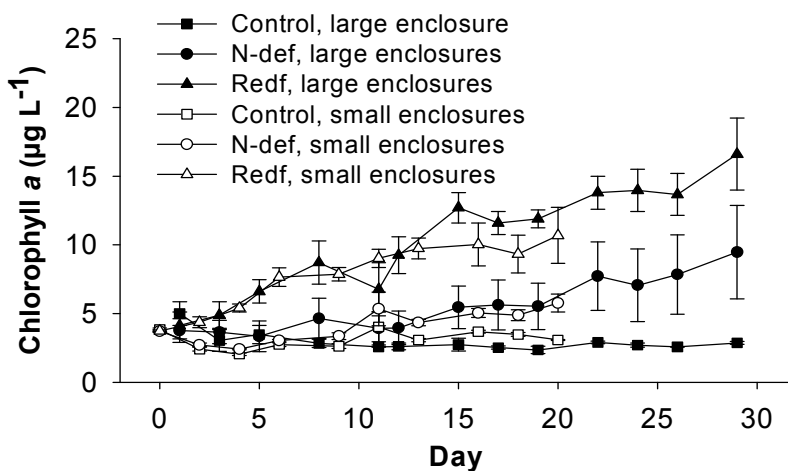


Figure 6. Time course of the concentration of chlorophyll *a* in the different treatments in the PULS01 experiment with large enclosures and the AUG01 experiment with small enclosures, carried out at the same time in July 2001. N-def = N-deficient nutrient enrichment; Redf = Redfield nutrient enrichment. Figure redrawn and modified from articles II & IV.

also when N₂-fixing cyanobacteria made up the major part of the biomass (Articles II, III, IV). The results are in line with those of Tamminen and Andersen (2007), and show that the growth of N₂-fixing cyanobacteria also depends on other factors besides the availability of P.

The phytoplankton groups most frequently stimulated by nutrient enrichments were picoplankton, chroococcalean and oscillatorian cyanobacteria, dinoflagellates, chrysophytes, diatoms and chlorophytes (Articles I, II, III, IV, VI). The same groups have also previously been stimulated by nutrient additions in mesocosm experiments in the Baltic Sea (Kononen et al. 1993, Heiskanen et al. 1996, Moisander et al. 2003, Pilkaityte & Razinkovas 2007, Kangro et al. 2007). The effect of nutrient enrichments on N₂-fixing cyanobacteria varied both between genera and among experiments, and will be dealt with in detail in section 3.2.

In SED01 experiment the external nutrient enrichment was primarily transferred to picosized cyanobacteria, the biomass of which increased four- to fivefold due to the enrichment (Article VI). Of the other phytoplankton groups only chlorophytes were clearly stimulated by nutrient enrichments. The reason why other phytoplankton responded less clearly to external nutrient enrichment in this experiment than in the others could be that the enrichment was lower than in the other experiments. Due to their high surface-to-volume ratio, picocyanobacteria are more efficient than larger algae in nutrient uptake at low nutrient concentrations.

The biomass of picocyanobacteria increased due to nutrient enrichment in the other experiments as well (Articles II & IV), except for the early summer experiment JUN99 (Article I). The increase in picocyanobacteria due to enrichment contradicts the theory that picoplankton, due to their small size and large surface-to-volume ratios, are seldom nutrient limited (Fogg 1986, Raven 1986, Suttle & Harrison 1986, Kuosa 1991, Agawin et al. 2000). Other studies too, however, have shown picocyanobacteria to be stimulated by nutrient enrichment (Vaulot et al. 1996, Stal et al. 1999, Kuuppo et al. 2003, Sipura et al. 2005)

3.1.2. Role of the N:P ratio

While total phytoplankton biomass correlated most highly with the addition of N, individual phytoplankton groups varied in their response to the nutrient enrichments. A low N:P ratio favoured the growth of the N₂-fixing cyanobacteria *Anabaena* spp., although the total biomass of N₂-fixing cyanobacteria was not affected by the N:P ratio of the enrichments (see section 3.2.1., Articles II, III & IV). A high N:P ratio increased the biomasses of dinoflagellates, diatoms and especially two mixotrophic algae, the chrysophyte *Uroglena* sp. and the prymnesiophyte *Chrysochromulina* spp. (Articles I & III).

Uroglena sp. made up 30-40 % of the total phytoplankton biomass in the two P-deficient enrichments at the end of the JUN99 experiment (Fig. 7, Article I). In

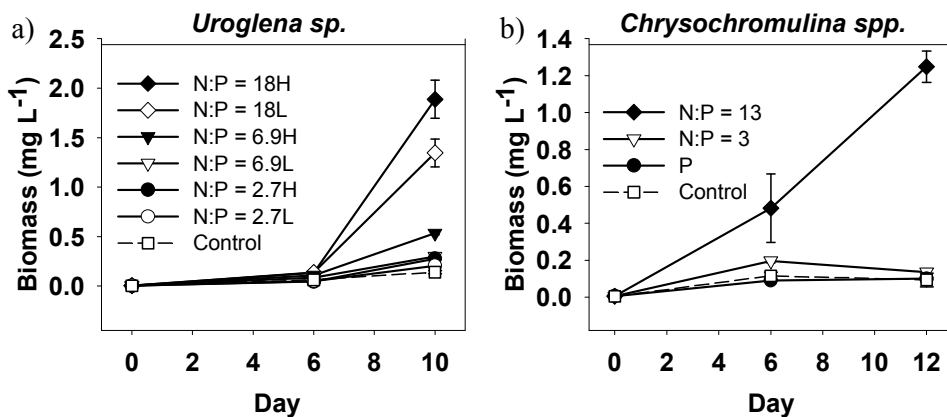


Figure 7. Growth of the mixotrophic flagellates a) *Uroglena sp.* and b) *Chrysochromulina spp.* in the different N:P supply mass ratios in a) JUN99 and b) JUL99 experiments. H = high nutrient concentration; L = low nutrient concentration. Figure 7a redrawn from article I.

the AUG99 experiment, on the other hand, *Chrysochromulina spp.* bloomed in the P-deficient enrichment with a high addition of ammonium, in which it made up of 40 % of the final total phytoplankton biomass (Fig. 7, Article III). The success of the mixotrophic flagellates in the P-deficient treatments may be due to their ability to obtain P through bacterivory at low dissolved P concentrations (Urabe et al. 1999, Stibor & Sommer 2003). Compared to flagellates, bacteria have a higher affinity for phosphate at low concentrations (Currie & Kalff 1984, Bratbak & Thingstad 1985, Güde 1985), and are also better competitors for nutrients due to their higher surface-to-volume ratio (Sieburth & Davis 1982, Fenchel 1986). Since both the C:P and N:P ratios are generally lower in bacteria than in phytoplankton (Fagerbakke et al. 1996), algae that are able to feed on P-rich bacteria may have a competitive advantage under P-limitation (Jansson et al. 1996).

Mixotrophy has been thought to be a competitively advantageous strategy under certain poor nutrient conditions; high abundances of mixotrophs are usually recorded in humic lakes with low nutrient concentrations and low light conditions (Jones 2000). The role of mixotrophs in brackish and marine environments is poorly known, but they may play an especially important role in transferring phosphorus to higher trophic levels during P limitation.

The results of the present study suggest that along with absolute nutrient concentrations, the N:P ratio is an important factor affecting phytoplankton community structure (Articles I, II, III & IV). While a low N:P ratio may favour the growth of some N_2 -fixing cyanobacteria such as *Anabaena*, an increase in the water N:P ratio may increase the abundances of mixotrophic algae, some of which might also be harmful. An indication of this occurred in 1988, when the bloom of the toxic *Chrysochromulina polylepis* occurred along the Scandinavian coast at a time when the N:P ratio of the water was high (Dahl et al. 1989).

3.1.3. Frequency of nutrient supply

The effect of the frequency of nutrient supply under different N:P ratios was studied in a four-week experiment (Article II). Nutrient enrichment included N and P, added either in a N-deficient (N-def) or in a Redfield (Redf) ratio, at either daily or one-week intervals.

The frequency of nutrient supply affected the phytoplankton community structure in addition to the absolute nutrient supply (Article II). The effect of nutrient addition frequency varied with time and between nutrient ratios. In the N-def treatments the phytoplankton biomass was higher in the daily than in the weekly enrichment, while in the Redf-enrichment the phytoplankton biomass increased more in the weekly than in the daily enrichment. In the N-def treatments, the higher biomass in the daily than the weekly enrichment was mainly due to a higher growth of N₂-fixing cyanobacteria and centric diatoms. The responses of N₂-fixing cyanobacteria differed among genera and will be discussed in section 3.2.2.

In the Redf-treatments the difference in phytoplankton biomass between addition frequencies seemed to be due mainly to the high growth of chlorophytes (dominated by *Dictyosphaerium subsolitarium* Van Goor and *Kirchneriella* sp.) towards the end of the experiment in the weekly enrichment. The biomass of dinoflagellates was also higher in the weekly enrichment at the middle of the experiment, but declined toward the end. The daily Redf-enrichment stimulated the growth particularly of chrysophytes. The biomasses of small centric diatoms and picoplankton were higher in the daily than in the weekly enrichment in the middle of the experiment but declined toward the end, possibly due to Si-limitation of the diatoms and high grazing pressure on the picoplankton (Article II).

The present results agree in part with an enclosure study conducted in Norwegian marine waters, in which nutrients given in two pulses increased phytoplankton biomass more than when they were given continuously (Svensen et al. 2002). Svensen et al. (2002) suggested that the higher biomass in the pulsed treatments was due to a larger temporal mismatch between the growth of phytoplankton and of their zooplankton grazers. In their experiment the pulsed nutrient supply resulted in a spring bloom-like system, with a high sedimentation rate. This was not the case in the PULS01 experiment, where the nutrient enrichments also affected the zooplankton community, the biomass of which increased 3- to 4-fold during the study (see section 3.3.2., Article II).

It has been suggested that pulsed nutrient supply should be advantageous for both velocity specialists, which have high uptake and growth rates, and storage specialists, which are able to take up nutrients in excess of what is required for growth (Sommer 1985, Grover 1991). The chlorococcalean chlorophytes, which in this experiment benefited from weekly nutrient pulses, have very high rates of cell division (Sommer & Kilham 1985) and can therefore be categorized as velocity specialists. They are known for their rapid growth responses to nutrient enrichment (Article IV, Kononen et al. 1993, Moisander et al. 2003) and have also previously been found to take advantage of nutrient pulses (Sommer 1985, Padisák & Tóth 1991, Jensen et al. 1994). On the other hand,

the biomasses of cyanobacteria and chrysophytes were higher in the daily than in the weekly enrichments. The results are only partly in accordance with Sommer (1985), who in a laboratory experiment with freshwater algae found that a pulsed P addition contributed to the advantage of chlorophytes but also to the cyanobacterial storage specialist *Aphanizomenon flos-aquae*.

The reason that storage specialists, such as large dinoflagellates (Dortch et al. 1984, Collos et al. 2004), were not favoured by the pulsed nutrient supply in the present study may be that the ability of phytoplankton to store N depends on the type of nitrogen source (Stolte et al. 1994, Stolte & Riegman 1996). NH_4^+ , which was used in this experiment, is a positive-charged or neutral (NH_3) molecule that may not be a suitable storage product, because it can easily diffuse across biological membranes (Stolte et al. 1994). NO_2^- is a negatively charged ion that does not diffuse so easily and can therefore be stored in higher concentrations in intracellular pools. Moreover, NH_4^+ is most preferred by pico- and nanophytoplankton, whereas larger phytoplankton are more dependent on NO_2^- (Stolte & Riegman 1996). In the present experiment the larger phytoplankton may also have been actively grazed by copepods, which increased in the weekly enrichments (see section 3.3.2, Article II).

3.2. Diazotrophic cyanobacteria

3.2.1. Effects of nutrient enrichments and N:P ratio

The biomass of N_2 -fixing cyanobacteria was dominated by *Aphanizomenon* sp, which in most experiments grew equally well in all treatments, independently of N and P enrichments (Articles II, III & VI). The biomass of *Aphanizomenon* also increased in the control treatments without nutrient enrichment (Articles III & VI), with the exception of the AUG01 experiment, where it declined 3-fold in the control (Article IV). Growth of *Anabaena* spp. was most stimulated by an N-deficient enrichment (Articles II, III & IV) or by the addition of P alone (Article III). A nutrient enrichment with a Redfield ratio, however, also increased the biomass of *Anabaena* compared to treatments without nutrient enrichments (Articles III, IV & VI).

The results for *Nodularia spumigena* are less clear, probably because in most of the experiments the species was not very abundant. *Nodularia* often dominates cyanobacterial blooms in open waters, but is less common in coastal waters. The biomass of *Nodularia* increased in all treatments during the experiments except for the control treatment in JUN99 (Articles II, III & IV). In both the JUL99 and the AUG01 experiments the *Nodularia* biomass was highest in the N-deficient enrichments, although in AUG01 the response was not statistically significant (Articles III & IV). In PULS01 there was a bloom of the species both in one enclosure with a N-deficient enrichment and in one with a Redfield enrichment, resulting in no effect of the N:P ratio of the enrichments (Article II). Thus the hypothesis that N_2 -fixing cyanobacteria are favoured in N-limited

conditions if enough P is available applied clearly only for *Anabaena* spp. Although *Nodularia* likewise seemed to be favoured by P-enrichment and a low N:P ratio, it also may grow well when N and P are supplied in a Redfield ratio (Articles II, III & IV).

The reason why *Aphanizomenon* showed no response to nutrient enrichments may be due to the ability of the genus to grow on stored phosphate (Uehlinger 1981, Sommer 1985, Larsson et al. 2001). *Aphanizomenon* is thought to be able to form late summer blooms in the Baltic Sea on the basis of intracellular P stores from the early summer (Larsson et al. 2001, Walve 2002, Walve & Larsson 2007). It is thus likely that already at the beginning of the experiments *Aphanizomenon* had enough stored P for growth during the experimental periods. The increase of *Aphanizomenon* biomass in the control treatments, without nutrient enrichment, was probably due to both P storage and N₂ fixation. Unlike *Aphanizomenon*, both *Nodularia* and *Anabaena* seem not to have early summer seed populations (Laamanen & Kuosa 2005) and may therefore be unable to form the same large nutrient reserves for later growth. However, *Nodularia* has been shown to have a higher affinity than *Aphanizomenon* for organic phosphorus and to grow better on an organic phosphorus source (Degerholm et al. 2006, Vahtera et al. 2007b), which has been suggested to give it a competitive advantage over *Aphanizomenon* later in the summer (Vahtera et al. 2007b). Lake isolates of *Anabaena* spp. have also been found to have a higher affinity for P than *Aphanizomenon* (De Nobel et al. 1997a).

The results of the present study are generally in accordance with the results of enrichment experiments in other parts of the Baltic Sea, in which the biomass of filamentous, N₂-fixing cyanobacteria dominated by *Aphanizomenon* and/or *Nodularia* was not affected by N and P additions (Kononen et al. 1993, Stal et al. 1999, Kuuppo et al. 2003), whereas *Anabaena* was occasionally stimulated by P additions (Moisander et al. 2003, Pilkaityte & Razinkovas 2007). In a mesocosm study by Kangro et al. (2007), on the other hand, both *Anabaena* and *Nodularia* were stimulated by P enrichments. Moreover, Rydin et al. (2002) found that P enrichments resulted in a cyanobacterial bloom dominated by *Aphanizomenon* sp. and *Anabaena* sp., whereas a Redfield nutrient enrichment resulted in the dominance of other algae than N₂-fixing cyanobacteria. In a short-term enrichment experiment in the eutrophic Curonian lagoon, in contrast, growth of *Aphanizomenon* was stimulated only by the combined addition of both P and N (Pilkaityte & Razinkovas 2007).

These discrepancies between the results in different studies may be due to many different factors, including type of experimental system, experiment duration, initial intracellular nutrient contents of the cyanobacteria, different nutrient regeneration, and/or different grazing pressure in the systems due to different food web structure. In addition there may be strain-specific differences in cyanobacterial responses to environmental factors. Strain-specific variation is commonly overlooked in experiments, but for example Wulff et al. (2007) found that the effects of UV-B radiation on *Nodularia spumigena* differed among Baltic strains.

Although nutrient enrichment had no effect on *Aphanizomenon* growth, a low N:P ratio or the addition of P alone increased the frequency of heterocysts in both *Anabaena* and *Aphanizomenon* compared to a control treatment and nutrient enrichment with a Redfield or high N:P ratio (Articles II & III). The result for *Aphanizomenon* corresponds to other studies in which the nitrogen fixation rate and nitrogenase activity were stimulated by P enrichment, but the growth of N₂-fixing cyanobacteria was not affected (Stal et al. 1999, Moisander et al. 2003). The reason may be that N₂-fixation is an energetically costly process, which in laboratory experiments has been observed to reduce growth in diazotrophic cyanobacteria (De Nobel et al. 1997b).

3.2.2. Effects of nutrient supply frequency

Large filamentous cyanobacteria have been thought to benefit from a pulsed nutrient supply because of their capability to store P (Sommer 1985, Suttle et al. 1987, Larsson et al. 2001, Walve 2002). Accordingly, mass occurrences of N₂-fixing cyanobacteria in the Baltic Sea have sometimes been recorded after previous nutrient pulses originating from the upwelling of nutrient-rich bottom water (Kononen & Nömmann 1992, Grönlund et al. 1996, Kononen et al. 1996). Thus the higher growth of N₂-fixing cyanobacteria found in the present study in daily than in weekly enrichments (see section 3.1.3.) was unexpected (Article II). However, there were again differences in the responses of the different genera. Of the N₂-fixing genera, the biomass of *Anabaena* and *Nodularia* was higher in daily than in weekly enrichments, while *Aphanizomenon* was unaffected by enrichment frequency (Article II). *Anabaena* grew clearly best in the N-def daily enrichment, whereas the positive effect of the daily enrichment on *Nodularia* was mainly due to a bloom of the species in two enclosures receiving nutrients daily but in different N:P ratios. The bloom formation of *Nodularia* in only two of the six enclosures with a daily enrichment shows that the initiation of cyanobacterial blooms is more complex than merely a matter of nutrient availability.

The concentration of inorganic phosphate in water was high in both the daily and the weekly N-deficient treatments (mean 0.18 and 0.27 μM respectively) and increased during the study (Article II). This indicates that cyanobacteria were not limited by the availability of P in these treatments, but the better cyanobacterial growth in the daily enrichment may have been due to the ability of cyanobacteria to compete for ammonium. This is supported by the fact that the cyanobacteria had fewer heterocysts in the daily than the weekly enrichment, indicating a lower N₂-fixing rate (Lehtimäki et al. 1997). Due to the energy required for the mechanism of N₂-fixation, it is more advantageous for algae to grow on inorganic N than to fix molecular N (Howarth et al. 1988, De Nobel et al. 1997b). In laboratory experiments the maximum growth rate of N₂-fixing *Aphanizomenon flos-aquae* cells was 67 % that of cells grown on ammonia (De Nobel et al. 1997b), whereas *Anabaena flos-aquae* (L.) de Brebisson reached 80 and 71% respectively of the values reported for growth on NH₄ (Rhee & Lederman 1983, Layzell

et al. 1985). The present study shows that when there is enough P available but inorganic N is in short supply, *Anabaena* seems to be favoured by a low regular supply of N (Article II). The same phenomenon was observed in the JUL99 experiment (Article III), where the biomass growth of *Nodularia* was higher in the treatment with P and some N than in the treatment with P alone or with P and excess N; this indicates that under N-limitation, when there is enough P available, N₂-fixing cyanobacteria may be able to compete for N.

Based on the results of this experiment, it seems that from a water quality management point of view pulsed discharges of nutrients may be less harmful than a regular nutrient supply, as the weekly nutrient enrichments resulted in a plankton community with fewer N₂-fixing cyanobacteria. The results are not in line with those from field studies in open waters, where blooms of N₂-fixing cyanobacteria have been initiated after nutrient pulses following the upwelling of nutrient-rich bottom water (Kononen & Nömmann 1992, Grönlund et al. 1996, Kononen et al. 1996, Vahtera et al. 2005). The cyanobacterial genus that has frequently been observed to be stimulated by upwelling, however, is *Aphanizomenon* sp., (Kononen & Nömmann 1992, Grönlund et al. 1996, Kononen et al. 1996, Lips & Lips 2008), whereas in this study the daily enrichment favoured *Anabaena* and *Nodularia*. Moreover, upwellings involve many other processes besides just nutrient supply, as the surface water and the whole plankton community within it is displaced by cold, nutrient-rich bottom water (Laanemets et al. 2009). The results of the present study are more closely comparable to pulsed nutrient supply following runoff from land, which is more relevant for the study area, whereas upwellings are more an outer archipelago phenomenon. However, due to the many ways in which a mesocosm may differ from natural systems, further work is needed before any definite conclusions can be drawn as to the role of nutrient supply frequency on the plankton community. This study, for example, did not include any top grazers, which are likely to be important regulators of zooplankton. Moreover, the results of mesocosm experiments are highly dependent on the inoculum plankton community, which may vary significantly not only seasonally but also diurnally (e.g. Article VI).

3.2.3. Effects of Iron

The addition of Fe together with the organic chelator EDTA increased the biomass of *Anabaena* spp. (Articles III & IV), while the addition of Fe or EDTA alone had no effect (Article IV). *Nodularia* was unaffected by Fe and EDTA enrichments, while the effects on *Aphanizomenon* sp. varied between experiments (Articles III & IV). In the AUG01 experiment *Aphanizomenon* was positively affected by both Fe and EDTA, but in the JUL99 experiment the enrichments had no effect. The discrepancy may be due to different initial conditions as well as to the different duration of the experiments. In the 11-day JUL99 experiment (Article III) the availability of Fe may not yet have started to limit *Aphanizomenon* growth, in contrast to the 20-day AUG01 experiment (Article IV).

The positive effect of EDTA was probably due to its improvement of the bioavailability of Fe or other trace elements necessary for cyanobacterial growth (Løvstad & Krogstad 2001). It is also possible that cyanobacteria were able to utilize the carbon (C) or N in EDTA, since they may be able to grow on dissolved organic N (Panosso & Granéli 2000, Berman 2001).

The results of this study agree with a recent Baltic mesocosm experiment, in which *Anabaena cf. inaequalis* was stimulated by the addition of iron together with EDTA and by land-derived organic matter (DOM), while *Nodularia spumigena* was stimulated by the addition of DOM alone (Stolte et al. 2006). In contrast, both the growth and nitrogenase activity of *Nodularia spumigena* have previously been stimulated by Fe enrichment (Stal et al. 1999, Paczuska & Kosakowska 2003). On the other hand, Moisander et al. (2003) found in short-term bioassay experiments that Fe enrichment had no effect on N₂-fixation or on the growth of heterocystous cyanobacteria, whereas EDTA increased the N₂-fixation rates. In a recent study by Schubert et al. (2008), the addition of Fe stimulated the photosynthesis of *Nodularia* in two out of four short-term experiments. They suggested that the stimulating effects of iron were linked to physiological photoprotection mechanisms, since the enzyme Fe-superoxide dismutase, which protects the algae from the damaging effects of high photon irradiances, contains iron (Canini et al. 1998, Schubert et al. 2008). The contradictory results of Fe enrichments on Baltic N₂-fixing cyanobacteria in different studies may thus be due to different light climates (Schubert et al. 2008). As noted earlier, however (see section 3.2.1.), there may also be other factors accounting for these discrepant results.

3.2.4. Cyanobacterial hepatotoxins

In this study cyanobacterial hepatotoxin concentration was not affected by nutrient enrichments (II, IV). The ambient hepatotoxin concentration increased during the experiments in line with the increased biomass of potentially toxic cyanobacteria. Previous results on the effect of nutrients on the nodularin production of *Nodularia* spp. have been contradictory. In some studies more nodularin was produced in conditions promoting growth (Lehtimäki et al. 1994, Lehtimäki et al. 1997) or during phosphate limitation (Granéli et al. 1998, Stolte et al. 2002), whereas in others nodularin production was unaffected by nutrient concentrations (Repka et al. 2001, Jonasson et al. 2008).

3.3. The grazer community

3.3.1. Top-down effects of zooplankton

In this study phytoplankton biomass seemed overall to be more affected by nutrient availability than by grazer control: the phytoplankton biomass responded to nutrient enrichments in the same way independently of the different initial zooplankton communities in the experiments (Articles I & VI). One exception to this was observed at

the end of the SED01 experiment, where the cladoceran *Bosmina longispina maritima* was abundant in four enclosures which had been filled one day later than the other enclosures (Article VI). In those enclosures the cladoceran reached very high densities (up to 0.3×10^6 ind m^{-3}) during the later part of the experiment. Due to the intensive grazing of *Bosmina* the phytoplankton biomass declined to lower levels than at the start of the experiment, independently of nutrient enrichments. The effect of *Bosmina* was thus comparable to freshwater *Daphnia* spp., which is known to be able to prevent an increase in phytoplankton biomass following nutrient enrichments in lakes (Cottingham et al. 2004). The high density of *Bosmina* in the mesocosms may have been an enclosure effect; such high densities are seldom recorded in nature, where the population of the cladoceran is probably efficiently controlled by predation by fish and mysids (Pellikka & Viljamaa 1998). However, high densities (up to 0.5×10^6 ind m^{-3}) of *Bosmina* have been recorded sporadically in the eutrophic inner archipelago waters of the Baltic Sea (Pellikka & Viljamaa 1998) and the cladoceran may thus locally be an important regulator of the phytoplankton community. The results from the SED01 experiment also show the importance of the initial plankton community for the outcome of experimental results (Article VI).

In the JUN99 experiment the effect of large zooplankton on the plankton community was studied by sieving the water through a 100 μm net in one treatment at the start of the experiment (Article I). This prefiltering successfully removed copepods, cladocerans and the large rotifers *Synchaeta baltica*, but did not affect the smaller rotifers *Synchaeta* spp. The biomass of *Synchaeta* spp. increased in the prefiltered enclosures during the experiment, resulting in a higher total zooplankton biomass at the end of the experiment than in the treatment without filtration. This increase of *Synchaeta* spp. may have been due both to decreased predation by larger zooplankton and to reduced competition for food. Prefiltering had no effect on the total phytoplankton biomass, in accordance with the study of Kivi et al. (1993) in the northern Baltic, where 100 μm prefiltration in summer experiments resulted in high growth of protozooplankton, but did not affect total phytoplankton biomass. In the present study, however, prefiltration was shown to result in a change in phytoplankton species composition, increasing the biomass of *Dinobryon faiculiferum* Willén, small *Myrionecta rubra*, *Skeletonema costatum* (Grev.) Cleve, pennate diatoms and *Chrysochromulina* spp., but depressing *Nitzschia* spp. and *Pseudopedinella* spp. (Article I). Decreased grazing by copepods and cladocerans was probably the reason for the increases in the prefiltered treatment, whereas the decreases may have been due to both increased grazing by *Synchaeta* spp. and increased competition among the phytoplankton species.

The results of this study do not permit precise quantification of the role of top-down regulation by zooplankton in the phytoplankton community; in accordance with other studies, however, zooplankton was shown to play an important role in shaping the

plankton community structure in the northern Baltic Sea (Article, I, Kivi et al. 1993, Kivi et al. 1996).

3.3.2. Bottom-up effects of nutrient enrichments on higher trophic levels

The effects of nutrient enrichments on the zooplankton community differed among the experiments. In JUN99 the total zooplankton biomass increased in the different treatments in line with the total phytoplankton biomass, and like the phytoplankton biomass was positively related to the N dose of the treatments (Article I). This increase was due to the growth of rotifers, which dominated the zooplankton biomass; copepods were not affected by the nutrient treatments, and cladocerans were most affected by the P dose of the enrichment (Article I). In SED01 there were no statistically significant differences among the treatments in zooplankton biomass, although the biomass of rotifers was highest in the nutrient enrichment treatments (Article IV). In PULS01 the total zooplankton biomass and the biomass of copepods increased most in the weekly Redfield enrichments, whereas rotifers became dominant in the daily Redfield enrichment (Article II).

The differences among treatments in zooplankton species composition may have been due to a change in the taxonomic composition of the phytoplankton community and/or to a change in phytoplankton chemical composition (Articles I & IV). Since zooplankton species differ in their demand for and elemental composition of C, N and P (Andersen & Hessen 1991, Sterner & Hessen 1994, Elser & Urabe 1999, Elser et al. 2003) the community structure may be directly affected by food quality in terms of the N and P content of the prey (Andersen & Hessen 1991, Sterner et al. 1993, Lürling & Donk 1997). In freshwater systems the cladoceran *Daphnia* has a high P content and a low N:P ratio and thus is usually P-limited (Andersen & Hessen 1991, Urabe et al. 1997), while copepods generally have a lower P content and higher N:P ratios and therefore more often face N limitation. In rotifers both P and N limitation have been documented (Rothhaupt, 1995, Jensen & Verschoor 2004, Jensen et al. 2006).

In the Baltic Sea, no clear differences have been observed between zooplankton species in their C:N:P stoichiometry (Walve & Larsson 1999, Pertola et al. 2002). However, Walve and Larsson (1999) reported a lower content of N in the cladocerans *Bosmina longispina maritima* and *Evadne nordmannii* than in the copepod *Acartia* sp. Moreover, in Norwegian marine waters the cladocerans *Evadne* sp. and *Podon* sp. displayed low C:P ratios and a high P content, corresponding to freshwater cladocerans (Gismervik 1997). Accordingly, the positive response to the P dose of the cladocerans (dominated by *Bosmina longispina maritima* and *Podon intermedius*) in the JUN99 experiment may have been due to P-limitation, whereas rotifers may have been N-limited (Article I).

The lack of a clear effect of nutrient enrichments on the zooplankton community in the SED01 experiment may be due to the fact that nutrient enrichment in this experiment was primarily transferred to picoplanktonic algae. Small picoplankton are not directly

accessible to most large zooplankton (Hansen et al. 1994, Vargas & Gonzalez 2004, Finlay & Roff 2004); they probably entered the microbial food web, resulting in a less efficient energy transfer to higher trophic levels. It is also possible that the zooplankton in this experiment was controlled by predation by mysids, which in this experiment were added to the enclosures as top predators.

The bottom-up effect of nutrient enrichments on the zooplankton community was most striking in the PULS01 experiment, where a daily nutrient dose in a Redfield ratio led to a greater proportion of rotifers; when nutrients were added in a weekly high dose, calanoids became dominant (Article II). In contrast to these results, nutrient addition frequencies had no effect on mesozooplankton in mesocosm experiments in Norwegian marine waters (Svensen et al. 2002). While the phytoplankton biomass in that study too was higher in treatments with a lower nutrient addition frequency, the higher production resulted only in a higher sedimentation rate (Svensen et al. 2002). The results of the present study, however, are consistent with microcosm experiments conducted in two Texan estuaries, where a pulsed inflow of nutrient-rich river water every third day resulted in a higher biomass of copepods as well as of total zooplankton than a continuous flow (Buyukates & Roelke 2005, Miller et al. 2008). This also generally agrees with a modeling study, in which higher zooplankton biomass was predicted when nutrient inflow was pulsed (Roelke 2000). The better performance of zooplankton during a pulsed nutrient supply in these studies was due to better food quality in terms of algal content of N and P. A pulsed nutrient supply usually results in elevated uptake rates by phytoplankton; if the uptake rate exceeds the growth rate, this will lead to higher intracellular nutrient concentrations (Droop 1974, Goldman & Gilbert 1982, Sommer 1989, Roelke 2000). According to this theory, however, zooplankton grazing in pulsed inflows should also reduce phytoplankton biomass (Roelke 2000, Buyukates & Roelke 2005); this was not the case either in the present study or in one of the microcosm experiments (Article II, Miller et al. 2008).

The difference in zooplankton species composition among treatments in the PULS01 experiment may also have been due to a change in the taxonomic composition of the phytoplankton community (Article II). In the daily enrichment there was an increase of filamentous cyanobacteria, which are considered unpalatable and little grazed in the Baltic (Sellner et al. 1994), and are therefore unlikely to directly support much consumer production. On the other hand, the small chrysophyte flagellates which increased in the daily Redfield enrichment were probably good food for rotifers, which increased in the same treatment. It is also possible that the weekly enrichment favored the growth of larger algae, which were so rapidly grazed by copepods that changes in phytoplankton community structure were not detectable in the phytoplankton results. This was indicated by the fact that the biomass of dinoflagellates in the Redfield weekly enrichment was high in the middle of the experiment, but decreased towards the end (see section 3.1.3., Article II).

Our findings indicate that pulsed inflows may favour the dominance of the classic grazing food chain, enhancing energy transfer up the food web by stimulating the growth of larger zooplankton which are the preferred food of fish (Article II). Daily low enrichment, in contrast, may lead to dominance of the microbial food web, stimulating the growth of small rotifers and protozoa. However, our experimental enclosures did not explicitly include predators on zooplankton or many other components of the natural system, and the results thus cannot be scaled up to the ecosystem level. It is possible that under natural conditions the zooplankton community is often so strongly controlled by predators (Rudstam et al. 1994) or by other factors, such as hydrography (e.g. Viitasalo et al. 1995), that the role of food remains low. It has been suggested that in marine systems the linkages between nutrient load and the upper trophic levels are weak due to the complexity within trophic levels and the advection of nutrients and organisms from open marine systems (Micheli 1999).

3.4. Role of the bottom sediment

3.4.1. Sediment as a source of nutrients

The role of sediment in water quality and in plankton dynamics was studied in a three-week mesocosm experiment in July-August 2001 (Articles VI & V). The enclosures included or excluded the natural bottom sediment, and half of them were enriched with nitrogen and phosphorus.

Both nutrient addition and the presence of the sediment significantly increased the concentrations of total N and total P (Fig. 8). The increase was highest in the sediment-bottomed enclosures with nutrient enrichment, where the concentrations of total N and P increased from mean initial values of 25.7 and 0.68 μM to 32.2 and 1.2 μM respectively. In the sediment-bottomed enclosures without nutrient enrichment the concentrations of total N and P increased as much as in the plastic-bottomed enclosures with nutrient enrichment, while the concentrations decreased in the plastic bottomed enclosures without nutrient enrichment. The concentration of Si was 6.7-8.3 μM at the beginning of the experiment and increased 2.5 to 3-fold in the sediment-bottomed enclosures, but decreased to 2.8 and 5.6 μM in the plastic-bottomed enclosures with and without nutrient enrichments respectively (Fig. 8). By calculating the difference in nutrient concentrations between the plastic- and sediment-bottomed enclosures at the end of the experiment, the average net flux of nutrients from the sediment for the whole three-week period was calculated as 23 $\mu\text{mol m}^{-2} \text{h}^{-1}$ N, 2.6 $\mu\text{mol m}^{-2} \text{h}^{-1}$ P and 98 $\mu\text{mol m}^{-2} \text{h}^{-1}$ Si (Article V). The N flux was within the range of results from laboratory measurements of sediment cores from deeper areas of the Baltic Sea, but the P flux was clearly lower (Koop et al. 1990, Conley et al. 1997, Pitkänen et al. 2001). The Si flux was at the same level or higher than results from measurements in the Dutch Wadden Sea, North Sea and northern Baltic Sea, in which the flux rates were based on calculations or on measurements conducted in

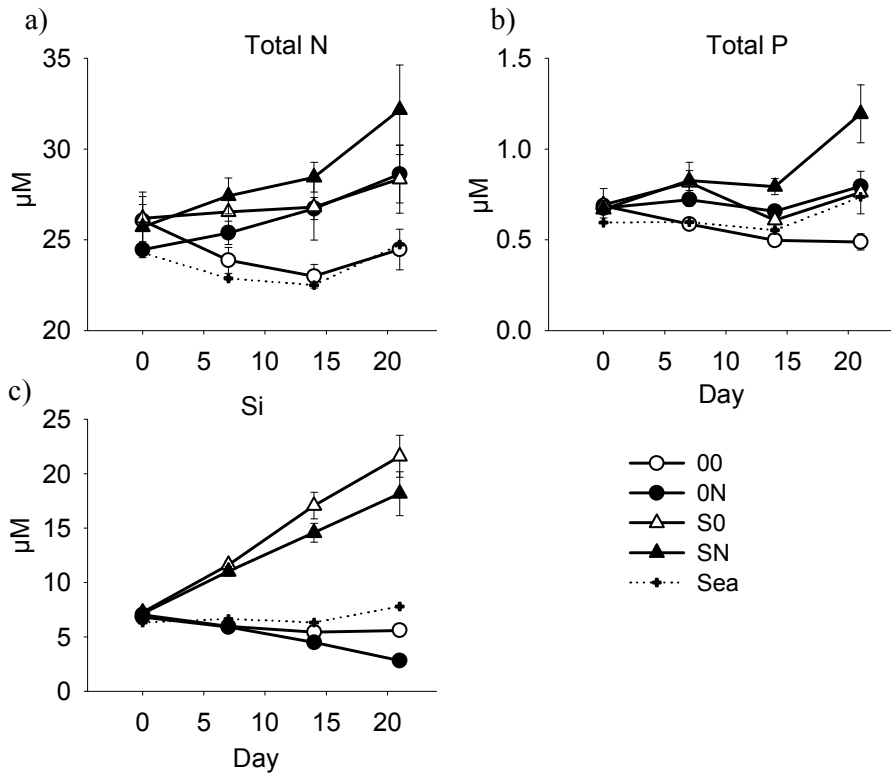


Figure 8. Concentrations (means \pm SE) of a) total N, b) total P, and c) Si in the different treatments and in the surrounding sea in the SED01 experiment. 00 = no sediment, no nutrients; 0N = no sediment, nutrients; S0 = sediment, no nutrients; SN = sediment, nutrients. Figure redrawn from article V.

chambers in situ (Van Bennekom et al. 1974, Rutgers van der Loeff et al. 1984, Conley et al. 1997).

The concentration of NH_4^+ in the sediment pore water declined considerably during the experiment and indicated high fluxes from the sediment to the overlying water. Recruitment of plankton organisms from resting stages in the sediment may also have contributed to the transport of nutrients to the water column (Salonen et al. 1984, Petterson et al. 1993, Schallenberg & Burns 2004).

These results agree with other studies, in which significant benthic fluxes have been measured in shallow marine waters (Rozan et al. 2002, Sundbäck et al. 2003). Smetacek et al. (1982) found significant nutrient release from the sediment to the water column in Kiel Bight, and Riemann et al. (1988) found in enclosure experiments off the Danish coast that summertime chlorophyll *a* concentrations were higher in sediment-bottomed enclosures than in controls without sediment. The results indicate that sediment may have a crucial effect on nutrient dynamics and may contribute to eutrophication in shallow coastal areas, even when the content of organic matter of the sediment is low.

3.4.2. Effects of sediment on phytoplankton community structure

Primary production and phytoplankton biomass increased with increasing total nutrient concentrations in the water (Figs. 8 & 9, Article VI). Although the presence of sediment and external nutrient enrichment resulted in an almost identical increase in primary production, the phytoplankton species composition differed between the treatments. The external nutrient enrichment resulted in a drastic increase in picoplanktonic cyanobacteria, dominated by the cyanobacteria *Synechococcus* spp., whereas the presence of sediment stimulated the growth of small flagellated algae, including cryptophytes, chrysophytes and prasinophytes, and decreased the biomass of N₂-fixing cyanobacteria (Fig. 9). In addition to picocyanobacteria, small chlorococcalean algae also benefited from external nutrient enrichment.

The negative effect of the presence of sediment on N₂-fixing cyanobacteria was due to *Anabaena* spp., which grew better in the plastic-bottomed than in the sediment-bottomed enclosures (Article VI). This finding is similar to the results of a freshwater experiment, in which exposure to sediment reduced the biovolume of cyanobacteria (Beklioglu & Moss 1996). The reason for this negative effect of sediment exposure on cyanobacterial growth is unclear (Article VI, Beklioglu & Moss 1996). Since the

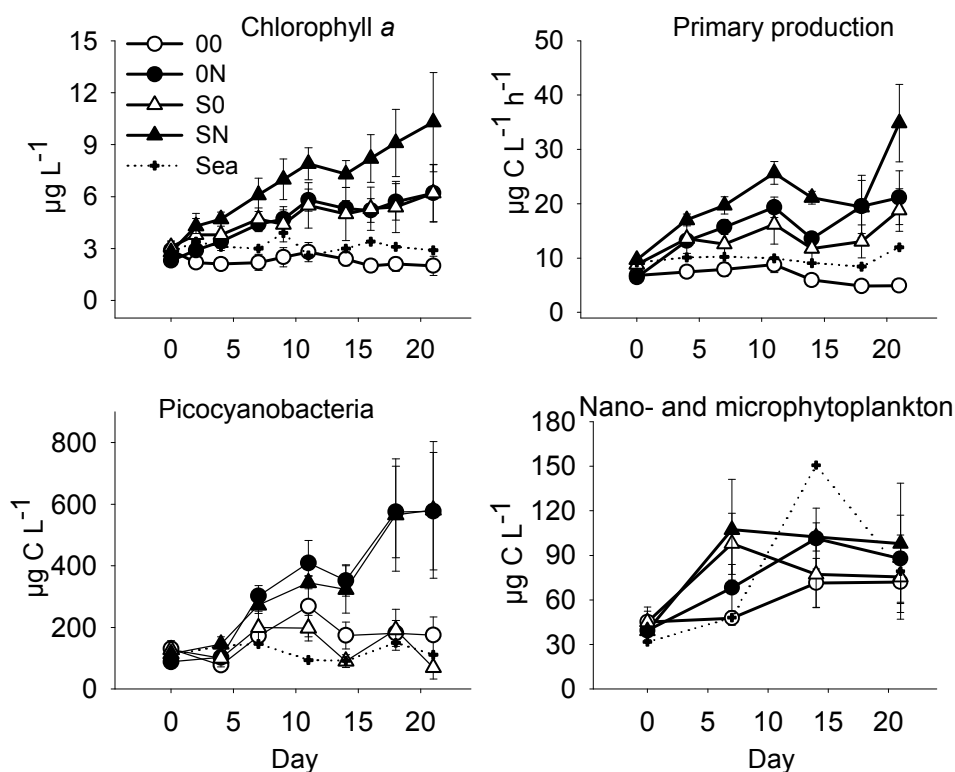


Figure 9. Chlorophyll *a* concentration, rate of primary production, biomasses of picocyanobacteria and nano- and microphytoplankton during the SED01 experiment in different treatments (means \pm SE) and in the surrounding sea. 00= no sediment, no nutrients, 0N= no sediment, nutrients, S0 = sediment, no nutrients, SN = sediment, nutrients. Figure redrawn from article VI.

zooplankton community did not differ among the treatments and the macrobenthos was dominated by deposit feeders, the grazing community did not seem responsible for the effect (Article VI).

In previous studies the effects of sediment on phytoplankton community structure have been variable (Riemann et al. 1988, Sullivan et al. 1991, Beklioglu & Moss 1996, Schallenberg & Burns 2004). Bottom sediment has been found to stimulate primary production due to nutrient fluxes from the sediment or recruitment or resuspension of phytoplankton (Beklioglu & Moss 1996, Schallenberg & Burns, 2004). On the other hand, phytoplankton biomass may decrease due to predation by benthic suspension feeders (Riemann et al. 1988, Sullivan et al. 1991) or to increased grazing pressure by zooplankton due to the hatching of zooplankton resting eggs and the revival of dormant organisms from the sediment (Ortega-Mayagoitia et al. 2002).

The positive effect of the sediment on small flagellated algae in the present experiment was probably due to their ability to utilize nutrients close to the bottom sediment because of their capacity for short-term vertical migration in the water column. Vertical migrations have been documented in dinoflagellates, cryptophytes and chrysophytes (Arvola 1984, Salonen et al. 1984, Sandgren 1988, Roenneberg & Deng 1997, Olli & Seppälä 2001); of these groups, dinoflagellate biomass was unaffected by the presence of sediment in this study. It is also possible that some algal cells were recruited from resting spores in the sediment. Recruitment from sediment has been observed among various algal groups, including cyanobacteria (Pettersson et al. 1993, Olli et al. 2005), dinoflagellates (Hansson 1996, Kremp 2001, McQuoid 2005) cryptophytes (Salonen et al. 1984, Hansson 1996), chrysophytes (Sandgren 1983), diatoms (McQuoid & Godhe 2004, McQuoid 2005), and euglenophytes (Olli et al. 1996).

The present study showed that the effects of sediment on the structure of the plankton community are not related to nutrient fluxes alone but include more complex interactions among the systems, which at present are not fully understood.

4. CONCLUSIONS

Increased nutrient loading favours the development of photosynthetic biomass (Articles I, II, III, IV & VI). The Archipelago Sea proved in this study to be primarily N-limited during the summer growth period (Articles I, II, III & IV). The results of this study show that in addition to the absolute nutrient concentration, the nutrient supply ratio is an important factor structuring the phytoplankton community (Articles I & III). While certain N_2 -fixing cyanobacteria may be favoured by a low N:P ratio, an increase in the water N:P ratio may favour the growth of some mixotrophic species, such as *Uroglena* and *Chrysochromulina*, which are able to gain P through bacterivory (Articles I & III).

In addition, this work showed that the frequency of the nutrient supply may influence the outcome of nutrient enrichments in aquatic ecosystems (Article II). The effects of the nutrient ratio and the frequency of nutrient supply were not independent of each other, but had a combined impact as well. Weekly nutrient enrichment resulted in a plankton community with fewer cyanobacteria, more chlorophytes and larger zooplankton species than daily enrichments. If these findings can be verified in future studies, they may have important implications regarding the management of nutrient inputs from point sources to aquatic environments.

In this study the total biomass of N_2 -fixing cyanobacteria was not affected by the N:P ratio of the nutrient enrichments, but there were differences in responses among the dominant genera (Articles II, III, IV & VI). The dominating genus *Aphanizomenon* showed no clear response to the nutrient enrichments, probably because the algae in the experiments were growing on stored P and fixing N_2 . *Anabaena*, on the other hand, was favoured by additions of P alone or a N-deficient nutrient enrichment, fitting the general paradigm that a low N:P ratio favours diazotrophic cyanobacteria. However, under N limitation, and when the concentration of P is sufficient, N_2 -fixing cyanobacteria may also benefit from a regular moderate supply of nitrogen. The results also indicate that iron and its bioavailability may play an important role in regulating the growth of cyanobacteria in the Archipelago Sea (Articles III & IV). Furthermore, when conditions are favourable, the initiation of cyanobacterial blooms is probably triggered by other factors than nutrient availability (Article II).

The present study showed that bottom sediment plays a considerable role in nutrient dynamics in coastal, oxygenated waters, even when the content of organic matter in the sediment is low (Article V). The role of sediment is not restricted to nutrient and material fluxes but also includes more complex biological interactions between benthic and pelagic organisms (Article VI). The close coupling between the benthic and pelagic habitats underlines the importance of including both of these in studies of plankton food webs in shallow waters.

The only way to combat the effects of eutrophication and reduce the intensity of cyanobacterial blooms is the management of both N and P discharges. This study underlines in particular the importance of N reduction in the Archipelago Sea. Although initially a reduction in N load may lead to a local increase in some N₂-fixing cyanobacteria, especially in the potentially toxic *Anabaena* spp., a decrease in N input would reduce the overall production and sedimentation rate. A lower export of O₂-consuming organic material to the bottom water, on the other hand, would be likely to reduce the amount of anoxic bottom sediments, which are one important source of P for the water column, and would also decrease the resuspension of nutrients from oxygenated shallow bottoms. Due to internal nutrient loading, however, the effects of a reduction in external nutrient load will probably not be seen directly, but may take time.

ACKNOWLEDGEMENTS

This thesis is based on research conducted at the Southwest Finland Regional Environment Centre as part of two projects: “Experimental analysis of eutrophication mechanisms in the Archipelago Sea, SW Finland”, financed by the Maj and Tor Nessling Foundation, and “ROLEX: Role of nutrients in regulating algal dynamics in the Archipelago Sea, northern Baltic: an experimental analysis”, financed by the Academy of Finland. I owe my deepest gratitude to Pasi Laihonen and Harri Helminen, who gave me the opportunity to participate in these projects.

I have not words enough to thank Janne Suomela, with whom I have worked all these years. Janne has supervised me throughout this work, although not officially, and has participated in every experiment and article. His technical and practical knowledge with building of the enclosures as well as his help with experiment planning and results analysis were invaluable. I am indebted to Professor Jouko Sarvala and Docent Pirjo Kuuppo for being my official supervisors during this thesis and for their support, encouragements and always positive attitude to my work. I am especially thankful for their constructive criticism on an earlier version of the thesis summary. I would also like to thank the co-authors – Vesa Gran, Kirsi Heikkilä, Harri Helminen, Jaana Lehtimäki, Jouni Lehtoranta, Maija Silander, Jaana Sipura, Kaarina Sivonen, Lassi Suominen, Kristiina Vuorio and Guntram Weithoff- for their contribution to the articles. I gratefully acknowledge Professors Jorma Kuparinen and Ulrich Sommer for reviewing this thesis and Ellen Valle for revising the language.

My studies in Baltic Sea ecology started at the Åbo Akademi University, and I thank everyone at the Department of Biology, Division of Environmental and Marine Biology for that pleasant study period. I am particularly grateful to Tore Lindholm, who supervised my M.Sc. work, introduced me to the world of plankton, and shared with me some of his broad knowledge of aquatic ecology as well as general biology. Without the meticulousness he taught me in carrying out basic methods in aquatic research, this thesis would not be what it is.

I am grateful to all the friendly laboratory technicians at the former laboratory of the Southwest Finland Regional Environment Centre, who were always ready to help in any way necessary. In particular I would like to thank Helmi Kotilainen for answering many questions on water chemistry, and for her excellent cooperation and flexibility in the analysis of our chemical samples during the whole project. I enjoyed my time at Inkilänkatu and appreciated the peaceful working conditions there. The only problem was that somehow the computer systems seemed always to be updated, and the computer connections therefore shut down in the afternoon or early evening before an important deadline. In spite of that, I never learned not to leave important deadlines to the last

minute, but I did become a great believer in Murphy's law, which indeed has ruled throughout this thesis.

I would like to thank Ilppo Vuorinen, who let us conduct our experiments at the Archipelago Research Station at Seili. Thanks are due to the whole staff at Seili for all their help with the practical arrangements, and for their help with the enclosures. I also thank all the project workers and students who participated in the project and shared the long days at Seili: Kajsa Appelgren, Vesa Gran, Sini Hautakangas, Kirsi Heikkilä, Malin Lönnroth, Maija Mikkola, Tuuli Mäkinen, Annukka Näyhä, Mikko Paajanen, Renata Pilkaityte, Hanna Rosenlund, Jaana Sipura, Kati Suomalainen, Lassi Suominen and Tapio Suominen. I was very lucky to have such great co-workers! Special thanks go to Maija, Kirsi and Kati, who were there sharing all the work and trouble from the very beginning, in the summer of 1999. I'm amazed that after the hard work of that first summer you were willing to come back for another two!

Later, I was warmly welcomed by the staff at the Section of Ecology at University of Turku, where I was offered a work space. I am especially grateful to Kristiina Vuorio for her help with phytoplankton identification, for co-authorship and for friendship.

I am thankful to all my financial supporters: the Maj and Tor Nessling Foundation, the Ella and Georg Ehrnrooth Foundation, the Turku University Foundation, the Finnish Foundation for Nature Conservation and the Jenny and Antti Wihuri Foundation.

Finally, I would like to thank my family and friends. Marko is acknowledged for all his support and for trying to make my working conditions as good as possible independently of circumstances, and for keeping my computer working. Moreover, I am especially grateful to my sister Marit, who has always been ready to help in every way. Many thanks also go to Amanda for just sometimes letting mommy work on the computer, as well as (somewhat less) for her valiant efforts to help with the typing of the thesis summary. Last but not least, I am thankful to my always faithful dog Jelda, whom I lost during this project, as well as to my other two dogs, Ronja and Mendy. At the hardest times they kept my life going outside the world of science and kept my working days down to a reasonable length. I still feel bad about the long, long working days they had to share with me at Seili.

REFERENCES

- Agawin, N.S.R., Duarte, C.M. & Agusti, S. 2000. Nutrient and temperature control of the contribution of picoplankton to phytoplankton biomass and production. *Limnology and Oceanography* 45: 591–600.
- Aller, R.C. 1982. The effects of macrobenthos on chemical properties of marine sediments and overlying water. In McCall, P.L. & Tevesz, M.J.S. (eds.), *Animal Sediment Relations*. Plenum Press, New York, pp. 53–102.
- Andersen, T. & Hessen, D.O. 1991. Carbon, nitrogen and phosphorus content of freshwater zooplankton. *Limnology and Oceanography* 36: 807–814.
- Andersen, T., Schartau, A.K.L. & Paasche, E. 1991. Quantifying external and internal nitrogen and phosphorus, as well as nitrogen and phosphorus supplied through remineralization, in coastal marine plankton by means of a dilution technique. *Marine Ecology Progress Series* 69: 67–80.
- Andersen, J.H., Schlüter, L. & Ærtebjerg, G. 2006. Coastal eutrophication: recent developments in definitions and implications for monitoring strategies. *Journal of Plankton Research* 28: 621–628.
- Andersson, A., Samuelsson, K., Haecky, P. & Albertsson, J. 2006. Changes in the pelagic microbial food web due to artificial eutrophication. *Aquatic Ecology* 40: 299–313.
- Arvola, L. 1984. Diel variation in primary production and the vertical distribution of phytoplankton in a polyhumic lake. *Archiv für Hydrobiologie* 101: 503–519.
- Azam, F., Fenchel, T., Gray, J.G., Meyer-Reil, L.A. & Thingstad, F. 1983. The ecological role of water-column microbes in the sea. *Marine Ecology Progress Series* 10: 257–263.
- Baden, S.P., Loo, L.O., Pihl, L. & Rosenberg, R. 1990. Effects of eutrophication on benthic communities including fish: Swedish west coast. *Ambio* 19: 113–122.
- Banse, K. 1982. Cell volumes, maximal growth rates of algae and ciliates, and the role of ciliates in the marine pelagial. *Limnology and Oceanography* 27: 1059–1071.
- Beklioglu, M. & Moss, B. 1996. Mesocosm experiments on the interaction of sediment influence, fish predation and aquatic plants on the structure of phytoplankton and zooplankton communities. *Freshwater Biology* 36: 315–325.
- Benincà, E., Huisman, J., Heerkloss, R., Jöhnk, K.D., Branco, P., van Nes, E.H., Scheffer, M. & Ellner, S.P. 2008. Chaos in a long-term experiment with a plankton community. *Nature* 451: 822–825.
- Berglund J., Müren, U., Båmstedt, U. & Andersson, A. 2007. Efficiency of a phytoplankton-based and a bacterial-based food web in a pelagic marine system. *Limnology and Oceanography* 52: 121–131.
- Berman, T. 2001. The role of DON and the effect of N:P ratios on occurrence of cyanobacterial blooms: implications from the outgrowth of *Aphanizomenon* in Lake Kinneret. *Limnology and Oceanography* 46: 443–447.
- Bernard, C. & Rassoulzadegan, F. 1990. Bacteria or microflagellates as unicellular a major food source for marine ciliates: Possible implications for the microzooplankton. *Marine Ecology Progress Series* 64: 147–155.
- Bianchi, T.S., Engelhaupt, E., Westman, P., Andrén, T., Rolff, C. & Elmgren, R. 2000. Cyanobacterial blooms in the Baltic Sea: natural or human-induced? *Limnology and Oceanography* 45: 716–726.
- Bishop, M.J., Powers, S.P., Porter, H.J. & Peterson, C.H. 2006. Benthic biological effects of seasonal hypoxia in a eutrophic estuary predate rapid coastal development. *Estuarine, Coastal and Shelf Science* 70: 415–422.
- Blomqvist, S., Gunnars, A. & Elmgren, R. 2004. Why the limiting nutrient differs between temperate coastal seas and freshwater lakes: a matter of salt. *Limnology and Oceanography* 49: 2236–2241.
- Boesch, D., Hecky, R., O'Melia, C., Schindler, D. & Seitzinger, S. 2006. Eutrophication of Swedish Seas. Report No. 5509, Naturvårdsverket, Stockholm.
- Bonsdorff, E., Blomqvist, E.M., Mattila, J. & Norkko, A. 1997a. Coastal eutrophication—causes, consequences and perspectives. *Estuarine, Coastal and Shelf Science* 44: 63–72.
- Bonsdorff, E., Blomqvist, E.M., Mattila, J. & Norkko, A. 1997b. Long-term changes and coastal eutrophication. Examples from the Åland Islands and the Archipelago Sea, northern Baltic Sea. *Oceanologica Acta* 20: 319–329.
- Bratbak, G. & Thingstad, T.F. 1985. Phytoplankton-bacteria interactions: Analysis of a model system with both competition and commensalisms. *Marine Ecology Progress Series* 25: 23–30.
- Bratbak, G., Egge, J.K. & Heldal, M. 1993. Viral mortality of the marine alga *Emiliania huxleyi*, (Haptophyceae) and termination of algal blooms. *Marine Ecology Progress Series* 93: 39–48.
- Brockmann, U. 1990. Pelagic mesocosms: II. Process studies, In Lalli, C.M (ed.), *Enclosed experimental marine ecosystems: A review and recommendations*. Springer-Verlag, pp. 81–108.
- Brönmark, C. 1994. Effects of tench and perch on interactions in a freshwater, benthic food chain. *Ecology* 75: 1818–1828.
- Brussaard, C.P. 2004. Viral control of phytoplankton populations—a review. *The Journal Eukaryotic Microbiology* 51: 125–138.
- Burkhardt, S. & Riebesell, U. 1997. CO₂ availability affects elemental composition (C:N:P) of the marine diatom *Skeletonema costatum*. *Marine Ecology Progress Series* 155: 67–76.
- Buyukates, Y. & Roelke, D.L. 2005. Influence of pulsed inflows and nutrient loading on zooplankton and phytoplankton community structure and biomass in microcosm experiments using estuarine assemblages. *Hydrobiologia* 548: 233–249.
- Canini, A., Albertano, P. & Caiola, M.G. 1998. Localization of Fe-containing superoxide dismutase in cyanobacteria from the Baltic Sea: depth and light dependency. *New Phytologist* 139: 247–254.

- Carmichael, W.W. 1997. The cyanotoxins. In Callow, J. (ed.), *Advances in Botanical Research* 27: 211-256, Academic Press, London.
- Carpenter, S.R., Kitchell, J.F. & Hodgson, J.R. 1985. Cascading trophic interactions and lake productivity; Fish predation and herbivory can regulate lake ecosystems. *BioScience* 35: 634-639.
- Carpenter, S.R., Kitchell, J.F., Hodgson, J.R., Cochran, P.A., Elser, J.J., Elser, M.M., Lodge, D.M., Kretchmer, D., He, X. & von Ende, C.N. 1987. Regulation of lake primary productivity by food web structure. *Ecology* 68: 1863-1876.
- Carpenter, S.R., Christensen, D.L., Cole, J.J., Cottingham, K.L., He, X., Hodgson, J.R., Kitchell, J.F., Knight, S.E., Pace, M.L., Post, D.M., Schindler, D.E. & Voichick, N. 1995. Biological control of eutrophication in lakes. *Environmental Science and Technology* 29: 784-786.
- Carstensen, J. & Heiskanen, A.-S. 2007. Phytoplankton species-specific responses to nutrient status in the Baltic Sea. *Marine Ecology Progress Series* 336: 29-42.
- Cloern, J.E. 2001. Our evolving conceptual model of the coastal eutrophication problem. *Marine Ecology Progress Series* 210: 223-253.
- Cloern, J.E. & Dufford, R. 2005. Phytoplankton community ecology: principles applied in the San Francisco Bay. *Marine Ecology Progress Series* 285: 11-28.
- Coale, K.H., Johnson, K.S., Fitzwater, S.E., Gordon, R.M., Tanner, S., Chavez, F.P., Ferioli, L., Sakamoto, C., Rogers, P., Millero, F., Steinberg, P., Nightingale, P., Copper, D., Cochlan, W.P., Landry, M.R., Constantinou, J., Rollwagen, G., Trasvina, A. & Kudela, R. 1996. A massive phytoplankton bloom induced by an ecosystem-scale iron fertilization experiment in the equatorial Pacific Ocean. *Nature* 383: 495-501.
- Collos, Y., Gagne, C., Laabir, M., Vaquer, A., Cecchi, P. & Souchu, P. 2004. Nitrogenous nutrition of *Alexandrium catenella* (Dinophyceae) in cultures and in Thau lagoon, southern France. *Journal of Phycology* 40: 96-103.
- Conley, D.J. 2000. Biogeochemical nutrient cycles and nutrient management strategies. *Hydrobiologia* 410: 87-96.
- Conley, D.J., Humborg, C., Smedberg, E., Rahm, L., Papush, L., Danielsson, Å., Clarke, A., Pastuszak, M., Aigars, J., Ciuffa, D. & Mörth, C.-M. 2008. Past, present and future state of the biogeochemical Si cycle in the Baltic Sea. *Journal of Marine Systems* 73: 338-346.
- Conley, D.J., Schelske, C.L. & Stoermer, E.F. 1993. Modification of the biogeochemical cycle of silica with eutrophication. *Marine Ecology Progress Series* 101: 179-192.
- Conley, D.J., Stockenberg, A., Carman, R., Johnstone, R.W., Rahm, L. & Wulff, F. 1997. Sediment-water nutrient fluxes in the Gulf of Finland, Baltic Sea. *Estuarine, Coastal and Shelf Science* 45: 591-598.
- Cottingham, K.L. & Schindler, D.E. 2000. Effects of grazer community structure on phytoplankton response to nutrient pulses. *Ecology* 81: 183-200.
- Cottingham, K.L., Glaholt, S. & Brown, A.C. 2004. Zooplankton community structure affects how phytoplankton respond to nutrient pulses. *Ecology* 85: 158-171.
- Currie, D.J. & Kalf, J. 1984. A comparison of the abilities of freshwater algae and bacteria to acquire and retain phosphorus. *Limnology and Oceanography* 29: 298-310.
- Dahl, E., Bagøien, E., Edvardsen, B. & Stenseth, N.C. 2005. The dynamics of *Chrysochromulina* species in the Skagerrak in relation to environmental conditions. *Journal of Sea Research* 4: 15-24.
- Dahl, E., Lindahl, O., Paasche, E. & Thronsdén, J. 1989. The *Chrysochromulina polylepsis* bloom in Scandinavian waters during spring 1988. In Cosper, E.M., Bricelj, V.M. & Carpenter, E.J. (eds.), *Novel Phytoplankton Blooms*, Springer Verlag. pp. 383-405.
- de Baar, H.J.W. 1994. von Liebig's law of the minimum and plankton ecology (1899-1991). *Progress in Oceanography* 33: 347-386.
- Degerholm, J., Gundersen, K., Bergman, B. & Söderbäck, E. 2006. Phosphorus-limited growth dynamics in two Baltic Sea cyanobacteria: *Nodularia* sp. and *Aphanizomenon* sp. *FEMS Microbiology Ecology* 58: 323-332.
- De Nobel, W.T., Huisman, J., Snoep, J.L. & Mur, L.R. 1997a. Competition for phosphorus between the nitrogen-fixing cyanobacteria *Anabaena* and *Aphanizomenon*. *FEMS Microbiology Ecology* 24: 259-267.
- De Nobel, W.T., Snoep, J.L., Westerhoff, H.V. & Mur, L.R. 1997b. Interaction of nitrogen fixation and phosphorus limitation in *Aphanizomenon flos-aquae* (Cyanophyceae). *Journal of Phycology* 33: 794-799.
- Dortch, Q., Clayton, Jr, J.R., Thoresen, S.S. & Ahmed, S.I. 1984. Species differences in accumulation of nitrogen pools in phytoplankton. *Marine Biology* 81: 237-250.
- Downing, J.A. 1997. Marine nitrogen:phosphorus stoichiometry and the global N:P cycle. *Biogeochemistry* 37: 237-252.
- Droop, M.R. 1974. Nutrient status of algal cells in continuous culture. *Journal of the Marine Biological Association of the United Kingdom* 54: 825-855.
- Dugdale, R.C. & Goering, J.J. 1967. Uptake of new and regenerated forms of nitrogen in primary productivity. *Limnology and Oceanography* 12: 196-206.
- EGGE, J.K. & AKSNES, D.L. 1992. Silicate as regulating nutrient in phytoplankton competition. *Marine Ecology Progress Series* 83: 281-289.
- Elder, L. (ed.) 1979. Recommendations for marine biological studies in the Baltic Sea. Phytoplankton and chlorophyll. The Baltic Marine Biologists, publication No. 5, 38 pp.
- Elder, J.F. & Horne, A.J. 1977. Biostimulatory capacity of dissolved iron for cyanophycean blooms in a nitrogen-free reservoir. *Chemosphere* 9: 525-530.
- Elmgren, R. 1989. Man's impact on the ecosystem of the Baltic Sea: energy flows today and at the turn of the century. *Ambio* 18: 326-332.
- Elmgren, R. & Larsson, U. 2001. Eutrophication in the Baltic Sea area: integrated coastal management issues. In von Bodungen, B., Turner, R.K. (eds.), *Science and integrated coastal management*. Dahlem University Press, Berlin, pp. 15-35.
- Elrifí, I.R. & Turpin, D.H. 1985. Steady-state luxury consumption and the concept of optimum nutrient ratios: a study with phosphate and nitrate limited

- Selenastrum minutum* (Chlorophyta). *Journal of Phycology* 21: 592–602.
- Elser, J.J., Bracken, M.E.S., Cleland, E.E., Gruner, D.S., Harpole, W.S., Hillebrand, H., Ngai, J.T., Seabloom, E.W., Shurin, J.B. & Smith, J.E. 2007. Global analysis of nitrogen and phosphorus limitation of primary producers in freshwater, marine, and terrestrial ecosystems. *Ecology Letters* 10: 1135–1142.
- Elser, J.J., Elser, M.M., MacKay, N.A. & Carpenter S.R. 1988. Zooplankton-mediated transitions between N and P limited algal growth. *Limnology and Oceanography* 33: 1–14.
- Elser, J.J., Marzolf, E.R. & Goldman, C.R. 1990. Phosphorus and nitrogen limitation of phytoplankton growth in the freshwaters of North America: a review and critique of experimental enrichment. *Canadian Journal of Fisheries and Aquatic Sciences* 47: 1468–1477.
- Elser, J.J. & Urabe, J. 1999. The stoichiometry of consumer-driven nutrient recycling: theory, observations, and consequences. *Ecology* 80: 745–751.
- Elser, J.J., Acharya, K., Kyle, M., Cotner, J., Makino, W., Markow, T., Watts, T., Hobbie, S., Fagan, W., Schade, J., Hood, J. & Sterner, R.W. 2003. Growth rate-stoichiometry couplings in diverse biota. *Ecology Letters* 6: 936–943.
- Eppley, R. W. & Peterson, B. J. 1979. Particulate organic matter flux and planktonic new production in the deep ocean. *Nature* 282: 677–680.
- Fagerbakke, K.M., Heldal, M. & Norland, S. 1996. Content of carbon, nitrogen, oxygen, sulfur and phosphorus in native aquatic and cultured bacteria. *Aquatic Microbial Ecology* 10: 15–27.
- Fay, P. 1992. Oxygen relations of nitrogen fixation in cyanobacteria. *Microbiological Reviews* 56: 340–373.
- Fenchel, T. 1986. The ecology of heterotrophic microflagellates. In Marshall, K.C. (ed.), *Advances in Microbial Ecology Plenum*, New York, pp. 57–98.
- Fenchel, T. 1988. Marine plankton food chains. *Annual Review of Ecology, Evolution, & Systematics* 19: 19–38.
- Finni, T., Kononen, K., Olsonen, R. & Wallström, K. 2001. The history of cyanobacterial blooms in the Baltic Sea. *Ambio* 30: 172–178.
- Finlay, K. & Roff, J.C. 2004. Radiotracer determination of the diet of calanoid copepod nauplii and copepodites in a temperate estuary. *ICES Journal of Marine Science* 61: 552–562.
- Fisher, T.R., Peele, E.R., Ammerman, J.W. & Harding, L.W. Jr. 1992. Nutrient limitation of phytoplankton in Chesapeake Bay. *Marine Ecology Progress Series* 82: 51–63.
- Fistarol, G.O., Legrand, C. & Granéli, E. 2005. Allelopathic effect on a nutrient-limited phytoplankton species. *Aquatic Microbial Ecology* 41: 153–161.
- Flynn, K.J. 2002. How critical is the critical N:P ratio? *Journal of Phycology* 38: 961–970.
- Fogg, G.E. 1986. Picoplankton. *Proceedings of the Royal Society of London* 228: 1–30.
- Forsberg, C., Ryding, S.O., Claesson, A. & Forsberg, Å. 1978. Water chemical analyses and/or algal assay? Sewage effluent and polluted lake water studies. *Mitteilungen Internationale Vereinigung für Theoretische und Angewandte Limnologie* 21: 352–363.
- Fuhrmann, J.A. 1999. Marine viruses and their biogeochemical ecological effects. *Nature* 399: 541–548.
- Garza, D.R. & Suttle, C.A. 1995. Large double-stranded DNA viruses which cause the lysis of marine heterotrophic nanoflagellates (*Bodo* sp.) occur in natural marine virus communities. *Aquatic Microbial Ecology* 9: 203–210.
- Gasol, J., Comerma, M., Garcia, J.-C., Armengol, J., Casamayor, E., Kojacká, P. & Šimek, K. 2002. A transplant experiment to identify the factors controlling bacterial abundance, activity, production, and community composition in a eutrophic canyon-shaped reservoir. *Limnology and Oceanography* 47: 62–77.
- Gaul, W., Antia, A.N., Koeve, W. 1999. Microzooplankton grazing and nitrogen supply of phytoplankton growth in the temperate and subtropical Atlantic. *Marine Ecology Progress Series* 189: 93–104.
- Gismervik, I. 1997. Stoichiometry of some marine planktonic crustaceans. *Journal of Plankton Research* 19: 279–285.
- Gismervik, I., Olsen, Y. & Vadstein, O. 2002. Micro- and mesozooplankton response to enhanced nutrient input - a mesocosm study. *Hydrobiologia* 484: 75–87.
- Goldman, J.C. 1986. On phytoplankton growth rates and particulate C:N:P ratios at low light. *Limnology and Oceanography* 31: 1358–1363.
- Goldman, J.C. & Glibert, P.M. 1982. Comparative rapid ammonia uptake by four species of marine phytoplankton. *Limnology and Oceanography* 27: 814–827.
- Goldman, J.C., McCarthy, J.J. & Peavey, D.G. 1979. Growth rate influence on the chemical composition of phytoplankton in oceanic waters. *Nature* 279: 210–215.
- Graf, G. 1992. Benthic-pelagic coupling: A benthic view. *Oceanography and Marine Biology, An Annual Review* 30: 149–190.
- Granéli, E. & Flynn, K. 2006. Chemical and physical factors influencing toxin content. In Granéli E. & Turner, J. (eds.), *Ecology of Harmful Algae, Series: Ecological Studies Vol. 189*, Springer Verlag, Heidelberg, pp. 229–241.
- Granéli, E. & Hansen, P.J. 2006. Allelopathy in harmful algae: a mechanism to compete for resources? In Granéli, E. & Turner, J. (eds.), *Ecology of Harmful Algae, Series: Ecological Studies Vol. 189*, Springer Verlag, Heidelberg, pp. 189–201.
- Granéli, E. & Johansson, N. 2003. Increase in the production of allelopathic substances by *Prymnesium parvum* cells grown under N- or P-deficient conditions. *Harmful Algae* 2: 135–145.
- Granéli, E., Johansson, N. & Panosso, R., 1998. Cellular toxin contents in relation to nutrient conditions for different groups of phycotoxins. In Reguera, B., Blanco, J., Fernández, M.L. & Wyatt, T. (eds.), *Harmful Algae. Xunta de Galicia and Intergovernmental Oceanographic Commission of UNESCO, Paris*, pp. 321–324.
- Granéli, E., Olsson, P., Carlsson, P., Graneli, W. & Nylander, C. 1993. Weak "top-down" control of

- dinoflagellate growth in the coastal Skagerrak. *Journal of Plankton Research* 15: 213-237.
- Granéli, E., Wallström, K., Larsson, U., Granéli, W. & Elmgren, R. 1990. Nutrient limitation of primary production in the Baltic Sea area. *Ambio* 19: 142-151.
- Granéli, E., Weberg, M. & Salomon, P.S. 2008. Harmful algal blooms of allelopathic microalgal species: The role of eutrophication. *Harmful Algae* 8: 94-102.
- Granö, O., Roto, M. & Laurila, L. 1999. Environment and land use in the shore zone of the coast of Finland. *Publications Instituti Geographici Universitatis Turkuensis* 160: 1-76.
- Grover, J.P. 1991. Resource competition in a variable environment: phytoplankton growing according to the variable internal-stores model. *American Naturalist* 138: 811-835.
- Grover, J.P. 1997. *Resource Competition*. Chapman and Hall, London, UK, 342 pp.
- Grönlund, L., Kononen, K., Lahdes, E. & Mäkelä, K. 1996. Community development and modes of phosphorus utilization in a late summer ecosystem in the central Gulf of Finland, the Baltic Sea. *Hydrobiologia* 331: 97-108.
- Güde, H. 1985. Influence of phagotrophic processes on the regeneration of nutrients in two-stage continuous culture systems. *Microbial Ecology* 11: 193-204.
- Guillard, R.R.L., Kilham, P. & Jackson, T.A. 1973. Kinetics of silicon-limited growth in the marine diatom *Thalassiosira pseudonana* Hasle and Heimdal (= *Cyclotella nana* Hustedt). *Journal of Phycology* 9: 233-237.
- Hagström, Å., Azam, F., Kuparinen, J. & Zweifel, U.-L. 2001. Pelagic plankton growth and resource limitations in the Baltic Sea. In Wulff, F., Larsson, P. & Rahm, L. (eds.), *A System Analysis of the Baltic Sea*. Ecological Studies, vol. 148, pp. 177-210.
- Hairton, N.G., Smith, F.E. & Slobodkin, L.B. 1960. Community structure, population control, and competition. *American Naturalist* 94: 421-425.
- Hajdu, S., Hällfors, S., Gromisz, S., Skjevik, A.-T., Busch, S., Kownacka, J., Jurgensone, I., Olenina, I., Huseby, S., Andersson, A., Wasmund, N., Jaanus, A., Hällfors, G., Rintala, J.-M., Majaneva, M. & Blomster, J. 2008. Unusual phytoplankton event during winter-spring 2007-2008. HELCOM Indicator Fact Sheets 2008. Online (August 28, 2008) http://www.helcom.fi/environment2/ifs/en_GB/cover/.
- Hajdu, S., Olenina, I., Wasmund, N., Edler, L. & Witek, B. 2006. Unusual phytoplankton events in 2005. HELCOM Indicator Fact Sheets 2006. Online (August 17, 2006) http://www.helcom.fi/environment2/ifs/en_GB/cover/.
- Hajdu, S., Pertola, S. & Kuosa, H. 2005. *Prorocentrum minimum* (Dinophyceae) in the Baltic Sea: morphology, occurrence- a review. *Harmful Algae* 4: 471-480.
- Halinen, K., Jokela, J., Fewer, D.P., Wahsten, M. & Sivonen, K. 2007. Direct evidence for production of microcystins by *Anabaena* strains from the Baltic Sea. *Applied and Environmental Microbiology* 73: 6543-6550.
- Hansen, B., Bjørnsen, P.K. & Hansen, P.J. 1994. The size ratio between planktonic predators and their prey. *Limnology and Oceanography* 39: 395-403.
- Hansson, L.-A. 1996. Algal recruitment from lake sediments in relation to grazing, sinking, and dominance patterns in the phytoplankton community. *Limnology and Oceanography* 41: 1312-1323.
- Hansson, S. & Rudstam, L.G. 1990. Eutrophication and Baltic fish communities. *Ambio* 19: 123-125.
- Healey, F.P. 1985. Interacting effects of light and nutrient limitation on the growth rate of *Synechococcus linearis* (Cyanophyceae). *Journal of Phycology* 21: 134-146.
- Healey, F.P. & Hendzel, L.L. 1979. Indicators of phosphorus and nitrogen deficiency in five algae in culture. *Journal of the Fisheries Research Board of Canada* 36: 1364-1369.
- Hecky, R.E. & Kilham, P. 1988. Nutrient limitation of phytoplankton in freshwater and marine environments: A review of recent evidence on the effects of enrichment. *Limnology and Oceanography* 33: 796-822.
- Heiskanen, A.-S. 1998. Factors governing sedimentation and pelagic nutrient cycles in the northern Baltic Sea. PhD Thesis, Helsinki University, Helsinki, 80 pp.
- Heiskanen, A.-S. & Leppänen, J.M. 1995. Estimation of export production in the coastal Baltic Sea: effects of resuspension and microbial decomposition on sedimentation measurements. *Hydrobiologia* 316: 211-224.
- Heiskanen, A.-S., Tamminen, T., & Gundersen, K. 1996. The impact of planktonic food web structure on nutrient retention and loss from a late summer pelagic system in the coastal northern Baltic sea. *Marine Ecology Progress Series* 145: 195-208.
- HELCOM, 1988. Guidelines for the Baltic Monitoring Programme for the third stage, Part D. Biological determinands. *Baltic Sea Environment Proceedings* 27 D: 2-16.
- Hellström, T. 1996. An empirical study of nitrogen dynamics in lakes. *Water Environmental Research* 68: 55-65.
- Hernroth, L. 1985. Recommendations on Methods for Marine Biological Studies in the Baltic Sea. *Mesozooplankton Biomass Assessment*. The Baltic Marine Biologists Publication 10: 1-32.
- Hillebrand, H., Worm, B. & Lotze, H.K. 2000. Marine microbenthic community structure regulated by nitrogen loading and herbivore pressure. *Marine Ecology Progress Series* 204: 27-38.
- Holmquist, E. & Willén, T. 1993. Fiskdöd orsakad av *Prymnesium parvum* (in Swedish, with English abstract). *Vatten* 49: 110-115.
- Hopkinson, B.M., Mitchell, B.G., Reynolds, R.A., Wang, H., Selph, K.E., Measures, C.I., Hewes, C.D., Holm-Hansen, O. & Barbeau, K.A. 2007. Iron limitation across chlorophyll gradients in the southern Drake Passage: Phytoplankton responses to iron addition and photosynthetic indicators of iron stress. *Limnology and Oceanography* 52: 2540-2554.
- Horsted, S.J., Nielsen, T.G., Riemann, B., Pock-Steen, J. & Bjørnsen, P.K. 1988. Regulation of zooplankton by suspension-feeding bivalves and fish in estuarine enclosures. *Marine Ecology Progress Series* 48: 217-224.
- Howarth, R.W. & Marino, R. 1998. A mechanistic approach to understanding why so many estuaries and brackish waters are nitrogen limited, In *Effects of*

- nitrogen in the aquatic environment, KVA Report 1998: 1, Kungliga Vetenskapsakademien (Royal Swedish Academy of Sciences), Stockholm, pp. 117–136.
- Howarth, R.W. & Marino, R. 2006. Nitrogen as the limiting nutrient for eutrophication in coastal marine ecosystems: Evolving views over three decades. *Limnology and Oceanography* 51: 364–376.
- Howarth, R.W., Marino, R. & Cole, J.J. 1988. Nitrogen fixation in freshwater, estuarine, and marine ecosystems. 2. Biogeochemical controls. *Limnology and Oceanography* 33: 688–701.
- Huisman, J., Sharples, J., Stroom, J., Visser, P.M., Kardinaal, W.E.A., Vesphagen, J.M.H. & Sommeijer, B., 2004. Changes in turbulent mixing shift competition for light between plankton species. *Ecology* 85: 2960–2970.
- Huisman, J. & Weissing, F.J. 1999. Biodiversity of plankton by species oscillations and chaos. *Nature* 402: 407–410.
- Hyenstrand, P., Blomqvist, P. & Pettersson, A. 1998. Factors determining cyanobacterial success in aquatic systems: A literature review. *Archiv für Hydrobiologie Special Issues: Advances in Limnology* 51: 41–61.
- Hyenstrand, P., Rydin, E., Gunnerhed, M., Linder, J. & Blomqvist, P. 2001. Response of the cyanobacterium *Gloeotrichia echinulata* to iron and boron additions—an experiment from Lake Erken. *Freshwater Biology* 46: 735–741.
- Hällfors, G. 2004. Checklist of Baltic Sea phytoplankton species (including some heterotrophic protistan groups). *Baltic Sea Environment Proceedings No. 95*, Helsinki Commission, Baltic Marine Environment Protection Commission, 210 pp.
- Isaksson, A. 1998. Phagotrophic phytoflagellates in lakes – a literature review. *Archiv für Hydrobiologie Special Issues: Advances in Limnology* 51: 63–90.
- ISO/DIS 16264, 2002. Water quality—determination of soluble silicates by flow analysis (FIA and CFA) and photometric detection.
- Jansson, B. & Dahlberg, K. 1999. The environmental status of the Baltic Sea in the 1940s, today and in the future. *Ambio* 28: 312–319.
- Jansson, M., Blomqvist, P., Jonsson, A. & Bergström, A.-K. 1996. Nutrient limitation of bacterioplankton, autotrophic and mixotrophic phytoplankton, and heterotrophic nanoflagellates in Lake Örräsket. *Limnology and Oceanography* 41: 1552–1559.
- Jensen, T.C., Anderson, T.R., Daufresne, M. & Hessen, D.O. 2006. Does excess carbon affect respiration of the rotifer *Brachionus calyciflorus* Pallas? *Freshwater Biology* 51: 2320–2333.
- Jensen, J.P., Jeppesen, E., Orlík, K. & Kristensen, P. 1994. Impact of nutrients and physical factors on the shift from cyanobacterial to chlorococcal green algal dominance in shallow Danish lakes. *Canadian Journal of Fisheries and Aquatic Sciences* 51: 1692–1699.
- Jensen, T.C. & Verschoor A.M. 2004. Effects of food quality on life history of the rotifer *Brachionus calyciflorus* Pallas. *Freshwater Biology* 49: 1138–1151.
- Johansson, N. & Granéli, E. 1999. Influence of different nutrient conditions on cell density, chemical composition and toxicity of *Prymnesium parvum* (Haptophyta) in semicontinuous cultures. *Journal of Experimental Marine Biology and Ecology* 239: 243–258.
- Jonasson, S., Vintila, S., Sivonen, K. & El-Shehawy, R. 2008. Expression of the nodularin synthetase genes in the Baltic Sea bloom-former cyanobacterium *Nodularia spumigena* strain AV1. *FEMS Microbiology Ecology* 65: 31–39.
- Jones, R.H. & Flynn, K.J. 2005. Nutritional status and diet composition affect the value of diatoms as copepod prey. *Science* 307: 1457–1459.
- Jones, R.I. 2000. Mixotrophy in planktonic protists: an overview. *Freshwater Biology* 45: 219–226.
- Jumars, P.A., Penry, D.L., Baross, J.A., Perry, M.J. & Frost, B.W. 1989. Closing the microbial loop—dissolved carbon pathway to heterotrophic bacteria from incomplete ingestion, digestion and absorption in animals. *Deep-Sea Research* 36: 483–495.
- Jumppanen, K. & Mattila, J. 1994. Saaristomeren tilan kehitys ja siihen vaikuttavat tekijät. *Lounais-Suomen Vesiensuojeluyhdistyksen Julkaisuja* 82: 1–206.
- Kahru, M., Horstmann, U. & Rud, O. 1994. Satellite detection of increased cyanobacteria blooms in the Baltic Sea: natural fluctuation or ecosystem change? *Ambio* 23: 469–472.
- Kahru, M., Leppänen, J.-M., Rud, O. & Savchuk, P. 2000. Cyanobacteria blooms in the Gulf of Finland triggered by saltwater inflow into the Baltic Sea. *Marine Ecology Progress Series* 207: 13–18.
- Kahru, M., Savchuk, O.P. & Elmgren, R. 2007. Satellite measurements of cyanobacterial bloom frequency in the Baltic Sea: interannual and spatial variability. *Marine Ecology Progress Series* 343: 15–23.
- Kagami, M., Yoshida, T., Gurung, T.B. & Urabe, J. 2002. Direct and indirect effects of zooplankton on algal composition in situ grazing experiments. *Oecologia* 133: 356–363.
- Kangro, K., Olli, K., Tamminen, T. & Lignell, R. 2007. Species-specific responses of a cyanobacteria-dominated phytoplankton community to artificial nutrient limitation: a Baltic Sea coastal mesocosm study. *Marine Ecology Progress Series* 336: 15–27.
- Kanoshina, I., Lips, U. & Leppänen, J.-M. 2003. The influence of weather conditions (temperature and wind) on cyanobacterial bloom development in the Gulf of Finland (Baltic Sea). *Harmful Algae* 2: 29–41.
- Karlson, K., Bonsdorff, E. & Rosenberg, R. 2007. The impact of benthic macrofauna for nutrient fluxes from Baltic Sea sediments. *Ambio* 36: 161–167.
- Kaupilla, P. & Lepistö, L. 2001. Changes in phytoplankton. In Kaupilla, P. & Bäck, S. (eds.), *The State of Finnish Coastal Waters in the 1990s. The Finnish Environment* 472, pp. 61–70.
- Kiirikki, M., Lehtoranta, J., Inkala, A., Pitkänen, H., Hietanen, S., Hall, P.O.J., Tengberg, A., Koponen, J. & Sarkkula, J. 2006. A simple sediment process description suitable for 3D-ecosystem modelling – Development and testing in the Gulf of Finland. *Journal of Marine Systems* 61: 55–66.
- Kirkkala, T., Helminen, H. & Erkkilä, A. 1998. Variability of nutrient limitation in the Archipelago Sea, SW Finland. *Hydrobiologia* 363: 117–126.
- Kivi, K., Kaitala, S., Kuosa, H., Kuparinen, J., Leskinen, E., Lignell, R., Marcussen, B. & Tamminen, T. 1993.

- Nutrient limitation and grazing control of the Baltic plankton community during annual succession. *Limnology and Oceanography* 38: 893–905.
- Kivi, K., Kuosa, H. & Tanskanen, S. 1996. An experimental study on the role of crustacean and microprotozoan grazers in the planktonic food web. *Marine Ecology Progress Series* 136: 59–68.
- Klausmeier, C.A., Litchman, E., Daufresne, T. & Levin, S.A. 2004. Optimal nitrogen-to-phosphorus stoichiometry of phytoplankton. *Nature* 429: 171–174.
- Klein Breteler, W.C.M., Schogt, N. & Rampen, S. 2005. Effect of diatom nutrient limitation on copepod development: role of essential lipids. *Marine Ecology Progress Series* 291: 125–133.
- Kolber, Z.S., Barber, R.T., Coale, K.H., Fitzwater, S.E., Greene, R.M., Johnson, K.S., Lindley, S. & Falkowski, P.G. 1994. Iron limitation of phytoplankton photosynthesis in the Equatorial Pacific Ocean. *Nature* 371: 145–149.
- Kononen, K., Kuparinen, J., Mäkelä, K., Laanemets, J., Pavelson, J. & Nömmann, S. 1996. Initiation of cyanobacterial blooms in a frontal region at the entrance to the Gulf of Finland, Baltic Sea. *Limnology and Oceanography* 41: 98–112.
- Kononen, K., Lahdes, E.O. & Grönlund, L. 1993. Physiological and community responses of summer plankton to nutrient manipulation in the Gulf of Finland (Baltic Sea) with special reference to phosphorus. *Sarsia* 78: 243–253.
- Kononen, K. & Nömmann, S. 1992. Spatio-temporal dynamics of the cyanobacterial bloom in the Gulf of Finland, Baltic Sea. In Carpenter, E.J., Capone, D. & Rueter, J. (eds.), *Marine pelagic cyanobacteria: Trichodesmium and other diazotrophs*. Kluwer, Dordrecht, pp. 95–114.
- Koop, K., Boynton, W.R., Wulff, F. & Carman, R. 1990. Sediment-water oxygen and nutrient exchanges along a depth gradient in the Baltic Sea. *Marine Ecology Progress Series* 63: 65–77.
- Kremp, A. 2001. Effects of cyst resuspension on germination and seeding of two bloom-forming dinoflagellates in the Baltic Sea. *Marine Ecology Progress Series* 216: 57–66.
- Kremp, A., Lindholm, T., Dreßler, N., Erler, K., Gerdt, G., Eirtovaara, S. & Leskinen, E. 2009. Bloom forming *Alexandrium ostensefeldii* (Dinophyceae) in shallow waters of the Åland Archipelago, Northern Baltic Sea. *Harmful Algae* 8: 318–328.
- Kristensen, K. & Hansen, K. 1999. Transport of carbon dioxide and ammonium in bioturbated (*Nereis diversicolor*) coastal, marine sediments. *Biogeochemistry* 45: 147–168.
- Krom, M.D. & Berner, R.A. 1981. The diagenesis of phosphorus in a nearshore marine sediment. *Geochimica et Cosmochimica Acta* 45: 207–216.
- Kuosa, H. 1991. Picoplanktonic algae in the northern Baltic Sea: seasonal dynamics and flagellate grazing. *Marine Ecology Progress Series* 73: 269–276.
- Kuosa, H. & Kivi, K. 1989. Bacteria and heterotrophic flagellates in the pelagic carbon cycle in the northern Baltic Sea. *Marine Ecology Progress Series* 53: 93–100.
- Kuparinen, J. 1984. Annual and seasonal fluctuation of primary productivity and overall respiration in a pelagic community off Tvärminne, SW coast of Finland. *Ophelia*, Supplement 3: 111–122.
- Kuuppo, P., Samuelsson, K., Lignell, R., Seppälä, J., Tamminen, T. & Andersson, A. 2003. Fate of increased production in late summer plankton communities due to nutrient enrichment of the Baltic Proper. *Aquatic Microbial Ecology* 32: 47–60.
- Kuuppo, P., Uronen, P., Petermann, A., Tamminen, T. & Granéli, E. 2006. Pectenotoxin-2 and dinophysistoxin-1 in suspended and sedimenting organic matter in the Baltic Sea. *Limnology and Oceanography* 51: 2300–2307.
- Kuuppo-Leinikki, P. 1990. Protozoan grazing on planktonic bacteria and its impact on bacterial production. *Marine Ecology Progress Series* 63: 227–238.
- Kuuppo-Leinikki, P., Autio, R., Hällfors, S., Kuosa, H., Kuparinen, J. & Pajuniemi, R. 1994. Trophic interactions and carbon flow between picoplankton and protozoa in pelagic enclosures manipulated with nutrients and a top predator. *Marine Ecology Progress Series* 107: 89–102.
- Laamanen, M. 1997. Environmental factors affecting the occurrence of different morphological forms of cyanoprokaryotes in the northern Baltic Sea. *Journal of Plankton Research* 19: 1385–1403.
- Laamanen, M. & Kuosa, H. 2005. Annual variability of biomass and heterocysts of the N_2 -fixing cyanobacterium *Aphanizomenon flos-aquae* in the Baltic Sea with reference to *Anabaena* spp. and *Nodularia spumigena*. *Boreal Environment Research* 10: 19–30.
- Laanemets, J., Zhurbas, V., Elken, J. & Vahtera, E. 2009. Dependence of upwelling-mediated nutrient transport on wind forcing, bottom topography and stratification in the Gulf of Finland: Model experiments. *Boreal Environment Research* 14: 213–225.
- Lampert, W. 1978. Release of dissolved organic carbon by grazing zooplankton. *Limnology and Oceanography* 23: 831–834.
- Lappalainen, A., Shurukhin, A., Alekseev, G. & Rinne, J. 2000. Coastal fish communities along the northern coast of the Gulf of Finland, Baltic Sea: responses to salinity and eutrophication. *International Review of Hydrobiology* 85: 687–696.
- Larsson, U., Elmgren, R. & Wulff, F. 1985. Eutrophication and the Baltic Sea: Causes and consequences. *Ambio* 14: 10–14.
- Larsson, U., Hajdu, S., Walve, J. & Elmgren, R. 2001. Baltic Sea nitrogen fixation estimated from the summer increase in upper mixed layer total nitrogen. *Limnology and Oceanography* 46: 811–820.
- Layzell, D.B., Turpin, D.H. & Elrif, I.R. 1985. Effects of nitrogen source on the steady state growth and nitrogen assimilation of phosphorus-limited *Anabaena flos-aquae*. *Plant Physiology* 78: 739–745.
- Legendre, L. & Rassoulzadegan, F. 1995. Plankton and nutrient dynamics in marine waters. *Ophelia* 41: 153–172.
- Legrand, C., Rengefors, K., Fistarol, G.O., Granéli, E. 2003. Allelopathy in phytoplankton - biochemical, ecological and evolutionary aspects. *Phycologia* 42: 406–419.

- Lehtimäki, J., Moisander, P., Sivonen, K. & Kononen, K. 1997. Growth, nitrogen fixation, and nodularin production by two Baltic Sea cyanobacteria. *Applied and Environmental Microbiology* 63: 1647–1656.
- Lehtimäki, J., Sivonen, K., Luukkainen, R. & Niemelä, S.I. 1994. The effects of incubation time, temperature, light, salinity, and phosphorus on growth and hepatotoxin production by *Nodularia* strains. *Archiv für Hydrobiologie* 130: 269–282.
- Lehtoranta, J., Pitkänen, H. & Sandman, O. 1997. Sediment accumulation of nutrients (N, P) in the eastern Gulf of Finland (Baltic Sea). *Water, Air, and Soil Pollution* 99: 477–486.
- Leppänen, J.M., Rantajarvi, E., Hällfors, S., Kruskopf, M. & Laine, V. 1995. Unattended monitoring of potentially toxic phytoplankton species in the Baltic Sea in 1993. *Journal of Plankton Research* 17: 891–902.
- Li, W.K.W. 1986. Experimental approaches to field measurements: methods and interpretation. *Canadian Bulletin of Fisheries and Aquatic Sciences* 214: 251–286.
- Liess, A. & Hillebrand, H. 2004. Invited review: Direct and indirect effects in herbivore periphyton interactions. *Archiv für Hydrobiologie* 159: 433–453.
- Lignell, R. 1990. Excretion of organic carbon by phytoplankton: Its relation to algal biomass, primary productivity and bacterial secondary productivity in the Baltic Sea. *Marine Ecology Progress Series* 68: 85–99.
- Lignell, R., Heiskanen, A.-S., Kuosa, H., Gundersen, K., Kuuppo-Leinikki, P., Pajuniemi, R. & Uitto, A. 1993. Fate of a phytoplankton spring bloom: sedimentation and carbon flow in the planktonic food web in the northern Baltic. *Marine Ecology Progress Series* 94: 239–252.
- Lignell, R., Seppälä, J., Kuuppo, P., Tamminen, T., Andersen, T. & Gismervik, I. 2003. Beyond bulk properties: responses of coastal summer plankton communities to nutrient enrichment in the northern Baltic Sea. *Limnology and Oceanography* 48: 189–209.
- Lindahl, O. & Dahl, E. 1990. On the development of the *Chrysochromulina polylepsis* bloom in the Skagerrak in May–June 1988. In Granéli, E., Sundström, B., Edler, L. & Anderson, D.M (eds.), *Toxic Marine Phytoplankton*. Elsevier, pp. 189–194.
- Lindehoff, E., Granéli, E. & Granéli, W. 2009. Effect of tertiary sewage effluent additions on *Prymnesium parvum* cell toxicity and stable isotope ratios. *Harmful Algae* 8: 247–253.
- Lindholm, T. & Virtanen, S. 1992. A bloom of *Prymnesium parvum* Carter in a small coastal inlet in Dragsfjärd, Southwestern Finland. *Environmental Toxicology and Water Quality* 7: 165–170.
- Lindholm, T. & Öhman, P. 1995. Occurrence of bloom-forming and potentially harmful phytoplankton in the Åland archipelago in the summer of 1993. *Memoranda Societatis Pro Fauna et Flora Fennica* 71: 10–18.
- Lindholm, T., Öhman, P., Kurki-Helasma, K., Kincaid, B. & Meriluoto, J. 1999. Toxic algae and fish mortality in a brackish-water lake in Åland, SW Finland. *Hydrobiologia* 397: 109–120.
- Lips, I. & Lips, U. 2008. Abiotic factors influencing cyanobacterial bloom development in the Gulf of Finland (Baltic Sea). *Hydrobiologia* 614: 133–140.
- Lund, J.W., Kipling, C. & Le Cren, E.D. 1958. The inverted microscope method for estimating algal numbers and statistical basis of estimations by counting. *Hydrobiologia* 11: 143–170.
- Lürling, M. & Donk, E. 1997. Life history consequences for *Daphnia pulex* feeding on nutrient-limited phytoplankton. *Freshwater Biology* 38: 693–709.
- Lynch, M. & Shapiro, J. 1981. Predation, enrichment, and phytoplankton community structure. *Limnology and Oceanography* 26: 86–102.
- Løvstad, Ø. & Krogstad, T. 2001. Effects of EDTA, FeEDTA and soils on the phosphorus bioavailability for diatom and bluegreen algal growth in oligotrophic waters studied by transplant biotest. *Hydrobiologia* 450: 71–81.
- Maberly, S.C., King, L., Dent, M.M., Jones, R.I. & Gibson, C.E. 2002. Nutrient limitation of phytoplankton and periphyton growth in upland lakes. *Freshwater Biology* 47: 2136–2152.
- Malone, T.C. 1980. Algal size. In Morris, I. (ed.), *The physiological ecology of phytoplankton*, Blackwell Scientific Publications, Oxford, pp. 433–463.
- Marcus, N.H. & Boero, F. 1998. Minireview: The importance of benthic-pelagic coupling and the forgotten role of life cycles in coastal aquatic systems. *Limnology and Oceanography* 43: 763–768.
- Mazumder, A., McQueen, D.J., Taylor, W.D. & Lean, D.R.S. 1988. Effects of fertilization and planktivorous fish (yellow perch) predation on size distribution of particulate phosphorus and assimilated phosphate: Large enclosure experiments. *Limnology and Oceanography* 33: 421–430.
- McGlathery, K.J., Anderson, I.C. & Tyler, A.C. 2001. Magnitude and variability of benthic and pelagic metabolism in a temperate coastal lagoon. *Marine Ecology Progress Series* 216: 1–15.
- McQuoid, M.R. 2005. Influence of salinity on seasonal germination of resting stages and composition of microplankton on the Swedish west coast. *Marine Ecology Progress Series* 289: 151–163.
- McQuoid, M.R. & Godhe, A. 2004. Recruitment of coastal planktonic diatoms from benthic versus pelagic cells: Variations in bloom development and species composition. *Limnology and Oceanography* 49: 1123–1133.
- Micheli, F. 1999. Eutrophication, fisheries, and consumer-resource dynamics in marine pelagic ecosystems. *Science* 285: 1396–1398.
- Miller, C.J., Roelke, D.L., Davis, S.E., Li, H.-P. & Gable, G. 2008. The role of inflow magnitude and frequency on plankton communities from the Guadalupe Estuary, Texas, USA: Findings from microcosm experiments. *Estuarine, Coastal, and Shelf Science* 80: 67–73.
- Mittelbach, G.G., Osenberg, C.W. & Wainwright, P.C. 1992. Variation in resource abundance affects diet and feeding morphology in the pumpkinseed sunfish (*Lepomis gibbosus*). *Oecologia* 90: 8–13.
- Moisander, P.H., Paerl, H.W., Dyble, J. & Sivonen, K. 2007. Phosphorus limitation and diel control of nitrogen-fixing cyanobacteria in the Baltic Sea. *Marine Ecology Progress Series* 345: 41–50.
- Moisander, P.H., Steppe, T.F., Hall, N.S., Kuparinen, J. & Paerl, H.W. 2003. Variability in nitrogen and

- phosphorus limitation for Baltic Sea phytoplankton during nitrogen-fixing cyanobacterial blooms. *Marine Ecology Progress Series* 262: 81–95.
- Mulderij, G., Van Nes, E.H. & Van Donk, E. 2007. Macrophyte-phytoplankton interactions: The relative importance of allelopathy versus other factors. *Ecological Modelling* 204: 85–92.
- Mullin, M.M., Sloan, P.R. & Eppley, R.W. 1966. Relationship between carbon content, cell volume, and area in phytoplankton. *Limnology and Oceanography* 11: 307–311.
- Nelson, D.M. & Dortch, Q. 1996. Silicic acid depletion and silicon limitation in the plume of the Mississippi River: evidence from kinetic studies in spring and summer. *Marine Ecology Progress Series* 136: 163–178.
- Nielsen, T.G., Kiørboe, T.H. & Bjørnsen, P.K. 1990. Effects of a *Chrysochromulina polylepis* subsurface bloom on the planktonic community. *Marine Ecology Progress Series* 62: 21–35.
- Niemi, Å. 1979. Blue-green algal blooms and N:P ratio in the Baltic Sea. *Acta Botanica Fennica* 110: 57–61.
- Nixon, S.W. 1995. Coastal marine eutrophication: a definition, social causes, and future concerns. *Ophelia* 41: 199–219.
- Noren, F., Haamer, J. & Lindahl, O. 1999. Changes in the plankton community passing a *Mytilus edulis* mussel bed. *Marine Ecology Progress Series* 191: 187–194.
- Nygaard, K. & Tobiesen, A. 1993. Bacterivory in algae: a survival strategy during nutrient limitation. *Limnology and Oceanography* 38: 273–279.
- Olli, K., Clarke, A., Danielsson, Å., Aigars, J., Conley, D.J. & Tamminen, T. 2008. Diatom stratigraphy and long term dissolved silicate concentration in the Baltic Sea. *Journal of Marine Systems* 73: 284–299.
- Olli, K., Heiskanen, A.-S. & Seppälä, J. 1996. Development and fate of *Eutreptiella gymnastica* bloom in nutrient-enriched enclosures in the coastal Baltic Sea. *Journal of Plankton Research* 18: 1587–1604.
- Olli, K., Kangro, K. & Kabel, M. 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.
- Olli, K. & Seppälä, J. 2001. Vertical niche separation of phytoplankton: large-scale mesocosm experiments. *Marine Ecology Progress Series* 217: 219–233.
- Olsen, Y., Reinertsen, H., Vadstein, O., Andersen, T., Gismervick, I., Duarte, C., Agusti, S., Stibor, H., Sommer, U., Lignell, R., Tamminen, T., Lancelot, C., Rousseau, V., Hoell, E. & Sanderud, K.A. 2001. Comparative analysis of food webs based on flow networks: effects of nutrient supply on structure and function of coastal plankton communities. *Continental Shelf Research* 21: 2043–2053.
- Ortega-Mayagoitia, E., Rojo, C. & Rodrigo, M.A. 2002. Factors masking the trophic cascade in shallow eutrophic wetlands: Evidence from a microcosm study. *Archiv für Hydrobiologie* 155: 43–63.
- Oviatt, C., Doering, P., Nowicki, B., Reed, L., Cole, J. & Frihtsen, J. 1995. An ecosystem-level experiment on nutrient limitation in temperate coastal marine environments. *Marine Ecology Progress Series* 116: 171–179.
- Paczuska, L. & Kosakowska, A. 2003. Is iron a limiting factor of *Nodularia spumigena* blooms? *Oceanologia*, 45: 679–692.
- Padisák, J. & Tóth, L.G. 1991. Some aspects of the ecology of the subdominant green algae in a large nutrient limited shallow lake (Balaton, Hungary). *Archiv für Protistenkunde* 139: 225–242.
- Panosso, R. & Granéli, E. 2000. Effects of dissolved organic matter on the growth of *Nodularia spumigena* (Cyanophyceae) cultivated under N or P deficiency. *Marine Biology* 136: 331–336.
- Papush, L. & Danielsson, Å. 2006. Silicon in the marine environment: dissolved silica trends in the Baltic Sea. *Estuarine, Coastal and Shelf Science* 67: 53–66.
- Pavés, H.J. & González, H.E. 2008. Carbon fluxes within the pelagic food web in the coastal area off Antofagasta (23°S), Chile: The significance of the microbial versus classical food webs. *Ecological Modelling* 212: 218–232.
- Pellikka, K. & Viljamaa, H. 1998. Zooplankton in the Helsinki sea area 1969–1996. Publ. No. 12/1998 City of Helsinki Environment Centre, Helsinki, 48 pp. (in Finnish with English summary).
- Pertola, S., Koski, M. & Viitasalo, M. 2002. Stoichiometry of mesozooplankton in N- and P-limited areas of the Baltic Sea. *Marine Biology* 140: 425–434.
- Pertola, S., Kuosa, H. & Olsonen, R. 2005. Is the invasion of *Prorocentrum minimum* (Dinophyceae) related to the nitrogen enrichment of the Baltic Sea? *Harmful Algae* 4: 481–492.
- Perus, J. & Bonsdorff, E. 2004. Long-term changes in macrozoobenthos in the Åland archipelago, northern Baltic Sea. *Journal of Sea Research* 52: 45–56.
- Perus, J., Bonsdorff, E., Bäck, S., Lax, H.G., Villnäs, A. & Westberg, V. 2007. Zoobenthos as indicators of ecological status in coastal brackish waters: a comparative study from the Baltic Sea. *Ambio* 36: 250–256.
- Petersen, J.E., Chen, C.-C. & Kemp, W.M. 1997. Scaling aquatic production: Experiments under nutrient and light limited conditions. *Ecology* 78: 2326–2338.
- Petersen, J.E., Cornwell, J.C. & Kemp, W.M. 1999. Implicit scaling in the design of experimental aquatic ecosystems. *Oikos* 85: 3–18.
- Petterson, K., Herlitz, E. & Istvánovics, V. 1993. The role of *Gloeotrichia echinulata* in the transfer of phosphorus from sediments to water in Lake Erken. *Hydrobiologia* 253: 123–129.
- Pilkaityte, R. & Razinkovas, A. 2007. Seasonal changes in phytoplankton composition and nutrient limitation in a shallow Baltic lagoon. *Boreal Environment Research* 12: 551–559.
- Pitkänen, H., Lehtoranta, J., Peltonen, H., Laine, A., Kotta, J., Kotta, I., Moskalenko, P., Mäkinen, A., Kangas, P., Perttilä, M. & Kiirikki, M. 2003. Benthic release of phosphorus and its relation to environmental conditions in the estuarial Gulf of Finland, Baltic Sea, in the early 2000s. *Proceedings of the Estonian Academy of Sciences* 52: 173–192.
- Pitkänen, H., Lehtoranta, J. & Räike, A. 2001. Internal nutrient fluxes counteract decreases in external load:

- the case of the estuarial eastern Gulf of Finland, Baltic Sea. *Ambio* 30: 195-201.
- Ploug, H. 2008. Cyanobacterial surface blooms formed by *Aphanizomenon* sp. and *Nodularia spumigena* in the Baltic Sea: Small-scale fluxes, pH, and oxygen microenvironments. *Limnology and Oceanography* 53: 914-921.
- Pomeroy, L.R. & Wiebe, W.J. 1988. Energetics of microbial food webs. *Hydrobiologia*, 159: 7-18.
- Poutanen, E.-L. & Nikkilä, K. 2001. Carotenoid pigments as tracers of cyanobacterial blooms in recent and post-glacial sediments of the Baltic Sea. *Ambio* 15: 4-5.
- Porat, R., Teltsch, B., Perelman, A. & Dubinsky, Z. 2001. Diel buoyancy changes by the cyanobacterium *Aphanizomenon ovalisporum* from a shallow reservoir. *Journal of Plankton Research* 23: 753-763.
- Prins, T.C., Escaravage, V., Smaal, A.C. & Peeters, J.C.H. 1995. Nutrient cycling and phytoplankton dynamics in relation to mussel grazing in a mesocosm experiment. *Ophelia* 41: 289-315.
- Probyn, T.A., Waldron, H.N. & James, A.G. 1990. Size-fractionated measurements of nitrogen uptake in aged upwelled waters: Implications for pelagic food webs. *Limnology and Oceanography* 35: 202-210.
- Quigg, A., Finkel, Z.V., Irwin, A.J., Reinfelder, J.R., Rosenthal, Y., Ho, T.-Y., Schofield, O., Rosenthal, F.M.M. & Falkowski, P.G. 2003. The evolutionary inheritance of elemental stoichiometry in marine phytoplankton. *Nature* 425: 291-294.
- Rajasilta, M., Mankki, J., Ranta-aho, K. & Vuorinen, I. 1999. Littoral fish communities in the Archipelago Sea, SW Finland: a preliminary study of changes during the past 20 years. *Hydrobiologia* 135: 253-260.
- Raven, J.A. 1986. Physiological consequences of extremely small size for autotrophic organisms in the sea. In Platt, T. & Li, W.K.W. (eds.), *Photosynthetic picoplankton*. Canadian Bulletin of Fisheries and Aquatic Sciences 214: 1-70.
- Raven, J.A. 1988. The iron and molybdenum use efficiencies of plant growth with different energy, carbon and nitrogen sources. *New Phytologist* 109: 279-287.
- Redfield, A.C. 1958. The biological control of chemical factors in the environment. *American Scientist* 46: 205-221.
- Repka, S., Mentonen, J., Vaitomaa, J., Saari, L. & Sivonen, K. 2001. Effects of nutrients on growth and nodularin production of *Nodularia* strain GB8b. *Microbial Ecology* 42: 606-613.
- Repka, S., Meyerhöfer, M., von Bröckel, K. & Sivonen, K. 2004. Associations of cyanobacterial toxin, nodularin, with environmental factors and zooplankton in the Baltic Sea. *Microbial Ecology* 47: 350-358.
- Reynolds, C.S. 1984. *The Ecology of Freshwater Phytoplankton*. Cambridge University Press, Cambridge, 384 pp.
- Rhee, G.-Y. 1978. Effects of N:P atomic ratios and nitrate limitation on algal growth, cell composition, and nitrate uptake. *Limnology and Oceanography* 23: 10-25.
- Rhee, G.-Y. & Gotham, I.J. 1980. Optimum N:P ratios and coexistence of planktonic algae. *Journal of Phycology* 16: 486-489.
- Rhee, G.-Y. & Lederman, T.C. 1983. Effects of nitrogen sources on P-limited growth of *Anabaena flos-aquae*. *Journal of Phycology* 19: 179-185.
- Riemann, B., Nielsen, T.G., Horsted, S.J., Bjørnsen, P.K. & Pock-Steen, J. 1988. Regulation of phytoplankton biomass in estuarine enclosures. *Marine Ecology Progress Series* 48: 205-215.
- Riemann, L., Holmfeldt, K. & Titelman, J. 2009. Importance of viral lysis and dissolved DNA for bacterioplankton activity in a P-limited estuary, northern Baltic Sea. *Microbial Ecology* 57: 286-294.
- Roelke, D.L. 2000. Copepod food-quality threshold as a mechanism influencing phytoplankton succession and accumulation of biomass, and secondary productivity: a modeling study with management implications. *Ecological Modelling* 134: 245-274.
- Roenneberg, T. & Deng, T.-S. 1997. Photobiology of the *Gonyaulax* circadian system. I. Different phase response curves for red and blue light. *Planta* 202: 494-501.
- Rolff, C., Almesjö, L. & Elmgren, R. 2007. Nitrogen fixation and abundance of the diazotrophic cyanobacterium *Aphanizomenon* sp. in the Baltic Proper. *Marine Ecology Progress Series* 332: 107-118.
- Rosenberg, R., Elmgren, R., Fleischer, S., Johnsson, P., Persson, G. & Dahlin, H. 1990. Marine eutrophication studies in Sweden. *Ambio* 19: 102-108.
- Ross, O.N. & Sharples, J. 2007. Phytoplankton motility and the competition for nutrients in the thermocline. *Marine Ecology Progress Series* 347: 21-38.
- Rothhaupt, K.O. 1995. Algal nutrient limitation affects rotifer growth rate but not ingestion rate. *Limnology and Oceanography* 40: 1201-1208.
- Rothhaupt, K.O. 1996. Laboratory experiments with a mixotrophic chrysophyte and obligately phagotrophic and phototrophic competitors. *Ecology* 77: 716-724.
- Rozan, T.F., Taillefert, M., Trouwborst, R.E., Glazer, B.T., Shufen, M., Herszage, J., Valdes, L.M., Price, K.S. & Luther, G.W. 2002. Iron-sulphur-phosphorus cycling in the sediments of a shallow coastal bay: implications for sediment nutrient release and benthic macroalgal blooms. *Limnology and Oceanography* 47: 1346-1354.
- Rudstam, L.G., Aneer, G. & Hildén, M. 1994. Top-down control in the pelagic Baltic ecosystem. *Dana* 10: 105-129.
- Rutgers van der Loeff, M.M., Anderson, L.G., Hall, P.O.J., Iverfeldt, Å., Josefson, A.B., Sundby, B. & Westerlund, S.F.G. 1984. The asphyxiation technique: an approach to distinguishing between molecular diffusion and biologically mediated transport at the sediment-water interface. *Limnology and Oceanography* 29: 675-686.
- Rydin, E., Hyenstrand, P., Gunnerhed, M. & Bomqvist, P. 2002. Nutrient limitation of cyanobacterial blooms: an enclosure experiment from the coastal zone of the NW Baltic proper. *Marine Ecology Progress Series* 239: 31-36.
- Rönneberg, C. & Bonsdorff, E. 2004. Baltic Sea eutrophication: area-specific ecological consequences. *Hydrobiologia* 514: 227-241.
- Salonen, K., Jones, R. I. & Arvola, L. 1984. Hypolimnetic phosphorus retrieval by diel vertical migrations of lake phytoplankton. *Freshwater Biology* 14: 431-438.

- Sandgren, C.D. 1988. The ecology of chrysophyte flagellates: their growth and perennation strategies as freshwater phytoplankton. In Sandgren, C.D. (ed.), Growth and reproductive strategies of freshwater phytoplankton. Cambridge University Press, Cambridge, pp. 9-104.
- Sandgren, C.D. 1983. Survival strategies of chrysophycean flagellates: Reproduction and the formation of resistant resting cysts. In Fryxell, G.A. (ed.) Survival strategies of the algae. Cambridge University Press, Cambridge, pp. 23-48.
- Sand-Jensen, K. & Borum, J. 1991. Interactions among phytoplankton, periphyton, and macrophytes in temperate freshwaters and estuaries. *Aquatic Botany* 41: 137-175.
- Savchuk, O. & Wulff, F. 1999. Modelling regional and large-scale response of the Baltic Sea ecosystem to nutrient load reductions. *Hydrobiologia* 393: 35-43.
- Scavia, D. & Bricker, S.B. 2006. Coastal eutrophication assessment in the United States. *Biogeochemistry* 76: 187-208.
- Schallenberg, M. & Burns, C.W. 2004. Effects of sediment resuspension on phytoplankton production: Teasing apart the influences of light, nutrients, and algal entrainment. *Freshwater Biology* 49: 143-159.
- Schindler, D.W. 1974. Eutrophication and recovery in experimental lakes: Implications for lake management. *Science* 184: 897-899.
- Schindler, D.W. 1978. Factors regulating phytoplankton production and standing crop in the world's freshwaters. *Limnology and Oceanography* 23: 478-486.
- Schindler, D.W. 1998. Replication versus realism: The need for ecosystem-scale experiments. *Ecosystems* 1: 323-334.
- Schindler, D.W., Hecky, R.E., Findlay, D.L., Stainton, M.P., Parker, B.R., Paterson, M.J., Beaty, K.G., Lyng, M. & Kasian, S.E.M. 2008. Eutrophication of lakes cannot be controlled by reducing nitrogen input: Results of a 37-year whole-ecosystem experiment. *Proceedings of the National Academy of Sciences of the United States of America* 105: 11254-11258.
- Schmidt, L.E. & Hansen, P.J. 2001. Allelopathy in the prymnesiophyte *Chrysochromulina polylepis*: effect of cell concentration, growth phase and pH. *Marine Ecology Progress Series* 216: 67-81.
- Schubert, B., Dahlke, S. & Schoor, A. 2008. Effects of short-term manipulations in iron nutrition of *Nodularia spumigena* from near-coast blooms (southern Baltic Sea). *Journal of Marine Systems* 74: 97-107.
- Sellner, K.G., Olson, M.M. & Kononen, K. 1994. Copepod grazing in a summer cyanobacteria bloom in the Gulf of Finland. *Hydrobiologia*, 292/293: 249-254.
- SFS 3025, 1986. Determination of Phosphorus in Water. Finnish Standards Association SFS, Helsinki, Finland.
- SFS 3026, 1986. Determination of Phosphate in Water. Finnish Standards Association SFS, Helsinki, Finland.
- SFS 3032, 1976. Determination of Ammonia in Water. Finnish Standards Association SFS, Helsinki, Finland.
- SFS 5772, 1993. Determination of Chlorophyll a in Water. Extraction with Ethanol. Finnish Standards Association SFS, Helsinki, Finland.
- Sherr, E.B. & Sherr, B.F. 1988. Role of microbes in pelagic food webs: a revised concept. *Limnology and Oceanography* 33: 1225-1227.
- Sieburth, J.McN. & Davis, P.G. 1982. The role of heterotrophic nanoplankton in the grazing and nurturing of planktonic bacteria in the Sargasso and Caribbean seas. *Annales de l'Institut Oceanographique* 58: 285-296.
- Sipura, J., Haukka, K., Helminen, H., Lagus, A., Suomela J. & Sivonen, K. 2005. Effect of nutrient enrichment on bacterioplankton biomass and community composition in mesocosms in the Archipelago Sea, northern Baltic. *Journal of Plankton Research* 27: 1261-1272.
- Sivonen, K., Halinen, K., Sihvonen, L.M., Koskenniemi, K., Sinkko, H., Rantasärkkä, K., Moisaner, P.H. & Lyra C. 2007. Bacterial diversity and function in the Baltic Sea with an emphasis on cyanobacteria. *Ambio* 36: 180-185
- Sivonen, K., Kononen, K., Carmichael, W.W., Dahlem, A.M., Rinehart, K., Kiviranta, J. & Niemelä, S.I. 1989. Occurrence of the hepatotoxic cyanobacterium *Nodularia spumigena* in the Baltic Sea and the structure of the toxin. *Applied and Environmental Microbiology* 55: 1990-1995.
- Sivonen, K., Niemelä, S.I., Niemi, R.M., Lepistö, L., Luoma, T.H. & Räsänen, L.A. 1990. Toxic cyanobacteria (blue-green algae) in Finnish fresh and coastal waters. *Hydrobiologia* 190: 267-275.
- Smayda, T.J. 1990. Novel and nuisance phytoplankton blooms in the sea: Evidence for a global epidemic. In Granéli, E., Sundström, B., Edler, L. & Anderson, D.M. (eds.), Toxic marine phytoplankton. Elsevier Science Publishing Co, New York, pp. 29-40.
- Smayda, T.J. & Reynolds, C.S. 2001. Community assembly in marine phytoplankton: application of recent models to harmful dinoflagellate blooms. *Journal of Plankton Research* 23: 447-461.
- Smetacek, V. 1985. Role of sinking in diatom life-history cycles: ecological, evolutionary and geological significance. *Marine Biology* 84: 239-251.
- Smetacek, V., von Bodungen, B., Knoppers, B., Pollehne, F. & Zeitzschel, B. 1982. The plankton tower. IV. Interactions between water column and sediment in enclosure experiments in Kiel Bight. In: Grice, G.D. & Reeve, M.R. (eds.), Marine Mesocosms Biological and Chemical Research in Experimental Ecosystems. Springer-Verlag, Berlin, pp. 205-216.
- Smith, V.H. 1982. The nitrogen and phosphorus dependence of algal biomass in lakes: An empirical and theoretical analysis. *Limnology and Oceanography* 27: 1101-1112.
- Smith, V.H. 1983. Low nitrogen to phosphorus ratios favor dominance by blue-green algae in lake phytoplankton. *Science* 221: 669-671.
- Smith, V.H. 2003. Eutrophication of freshwater and coastal marine ecosystems: a global problem. *Environmental Science and Pollution Research* 10:126-139.
- Smith, V.H. 2006. Responses of estuarine and coastal marine phytoplankton to nitrogen and phosphorus enrichment. *Limnology and Oceanography* 51: 377-384.
- Sommer, U. 1985. Comparison between steady state and nonsteady state competition: experiments with natural

- phytoplankton. *Limnology and Oceanography* 30: 335–346.
- Sommer, U. 1989. The role of competition for resources in phytoplankton succession. In: Sommer, U. (ed.), *Plankton Ecology: Succession in Plankton Communities*. Springer, Berlin, pp. 57–107.
- Sommer, U. 1994. The impact of light intensity and daylength on silicate and nitrate competition among marine phytoplankton. *Limnology and Oceanography* 39: 1680–1688.
- Sommer, U. & Kilham, S.S. 1985. Phytoplankton natural community composition experiments: A reinterpretation. *Limnology and Oceanography* 30: 436–440.
- Sommer, U., Sommer, F., Santer, B., Jamieson, C., Boersma, M., Becker, C. & Hansen, T. 2001. Complementary impact of copepods and cladocerans on phytoplankton. *Ecology Letters* 4: 545–550.
- Stal, L.J., Albertano, P., Bergman, B., von Bröckel, K., Gallon, J.R., Hayes, P.K., Sivonen, K. & Walsby, A.E. 2003. BASIC: Baltic Sea cyanobacteria. An investigation of the structure and dynamics of water blooms of cyanobacteria in the Baltic Sea—responses to a changing environment. *Continental Shelf Research* 23: 1695–1714.
- Stal, L.J., Staal, M. & Villbrandt, M., 1999. Nutrient control of cyanobacterial blooms in the Baltic Sea. *Aquatic Microbial Ecology* 18: 165–173.
- Stemann Nielsen, E. 1952. The use of radioactive carbon (14C) for measuring organic production in the sea. *Journal du Conseil Permanent international pour l'Exploration de la Mer* 18: 117–140.
- Sterner, R.W. 1989. The role of grazers in phytoplankton succession. In Sommer, U. (ed.), *Plankton ecology: Succession in plankton communities*. Springer, pp. 107–170.
- Sterner, R.W., Hagemeyer, D.D., Smith, W.L. & Smith, R.F. 1993. Phytoplankton nutrient limitation and food quality for *Daphnia*. *Limnology and Oceanography* 38: 871–875.
- Sterner, R.W. & Hessen, D.O. 1994. Algal nutrient limitation and the nutrition of aquatic herbivores. *Annual Review of Ecology, Evolution and Systematics* 25: 1–29.
- Stibor, H. & Sommer, U. 2003. Mixotrophy of a photosynthetic flagellate viewed from an optimal foraging perspective. *Protist* 154: 91–98.
- Stigebrandt, A. & Wulff, F. 1987. A model for the dynamics of nutrients and oxygen in the Baltic Proper. *Journal of Marine Research* 45: 729–759.
- Stockner, J.G. & Antia, N.J. 1986. Algal picoplankton from marine and freshwater ecosystems: A multidisciplinary perspective. *Canadian Journal of Fisheries and Aquatic Sciences* 43: 2472–2503.
- Stolte, W., Balode, M., Carlsson, P., Grzebyk, D., Janson, S., Lips, I., Panosso, R., Ward, C.J. & Granéli, E. 2006. Stimulation of nitrogen-fixing cyanobacteria in a Baltic Sea plankton community by land-derived organic matter or iron addition. *Marine Ecology Progress Series* 327: 71–82.
- Stolte, W., Karlsson, C., Carlsson, P. & Granéli, E. 2002. Modeling the increase of nodularin content in Baltic Sea *Nodularia spumigena* during stationary phase in phosphorus-limited batch cultures. *FEMS Microbiology Ecology* 41: 211–220.
- Stolte, W., McCollin, T., Noordeloos, A.A.M. & Riegman, R. 1994. Effect of nitrogen on the size distribution within marine phytoplankton populations. *Journal of Experimental Marine Biology and Ecology* 184: 83–97.
- Stolte, W. & Riegman, R. 1996. A model approach for size selective competition of marine phytoplankton for fluctuating nitrate and ammonium. *Journal of Phycology* 32: 732–740.
- Strom, S.L., Benner, R., Ziegler, S. & Dagg, M.J. 1997. Planktonic grazers are a potentially important source of marine dissolved organic carbon. *Limnology and Oceanography* 42: 1364–1374.
- Suikkanen, S. 2008. Allelopathic effects of filamentous cyanobacteria on phytoplankton in the Baltic Sea. Finnish Institute of Marine Research - Contributions No. 15. 41 pp.
- Suikkanen, S., Fistarol, G.O. & Granéli, E. 2004. Allelopathic effects of the Baltic cyanobacteria *Nodularia spumigena*, *Aphanizomenon flos-aquae* and *Anabaena lemmermannii* on algal monocultures. *Journal of Experimental Marine Biology and Ecology* 308: 85–101.
- Suikkanen, S., Fistarol, G.O. & Granéli, E. 2005. Effects of cyanobacterial allelochemicals on a natural plankton community. *Marine Ecology Progress Series* 287: 1–9.
- Suikkanen, S., Laamanen, M. & Huttunen, M. 2007. Long-term changes in summer phytoplankton communities of the open northern Baltic Sea. *Estuarine, Coastal and Shelf Science* 71: 580–592.
- Sullivan, B.K., Doering, P.H., Oviatt, C.A., Keller, A.A. & Frithsen, J.B. 1991. Interactions with the benthos alter pelagic food web structure in coastal waters. *Canadian Journal of Fisheries and Aquatic Sciences* 48: 2276–2284.
- Sundbäck, K., Miles, A., Hulth, S., Pihl, L., Engström, P., Selander, E. & Svenson, A. 2003. Importance of benthic nutrient regeneration during initiation of macroalgal blooms in shallow bays. *Marine Ecology Progress Series* 246: 115–126.
- Suomela, J. 2001. Saaristomeren tila vuosituhannen vaihteessa. Lounais-Suomen ympäristökeskuksen moniste 20/2001. 99 pp.
- Suomela, J. & Sydänoja, A. 2006. Saaristomeren tila 2005. Skärgårdshavets tillstånd 2005. Katsauslehti, tammikuu 2006, Lounais-Suomen ympäristökeskus. 8 pp.
- Suttle, C.A., Chan, A.M., & Cottrell, M.T. 1990. Infection of phytoplankton by viruses and reduction of primary production. *Nature* 347: 467–9.
- Suttle, C.A. & Harrison, P.J. 1986. Phosphate uptake rates of phytoplankton assemblages grown at different dilution rates in semi-continuous culture. *Canadian Journal of Fisheries and Aquatic Science* 43: 1474–1481.
- Suttle, C.A., Stockner, J.G. & Harrison, P.J. 1987. Effects of nutrient pulses on community structure and cell size of a freshwater phytoplankton assemblage in culture. *Canadian Journal of Fisheries and Aquatic Science* 44: 1768–1774.
- Svensen, C., Nejstgaard, J.C., Egge, J.K. & Wassmann, P. 2002. Pulsing versus constant supply of nutrients (N,

- P and Si): effect on phytoplankton, mesozooplankton and vertical flux of biogenic matter. *Scientia Marina* 66: 189–203.
- Tamminen, T. & Andersen, T. 2007. Seasonal phytoplankton nutrient limitation patterns as revealed by bioassays over Baltic Sea gradients of salinity and eutrophication. *Marine Ecology Progress Series* 340: 121–138.
- Terry, K.L., Laws, E.A. & Burns, D.J. 1985. The critical ratio concept: Growth rate variation in the N:P requirement ratio of phytoplankton. *Journal of Phycology* 21: 323–329.
- Tilman, D. 1977. Resource competition between planktonic algae: an experimental and theoretical approach. *Ecology* 58: 338–348.
- Tilman, D., Kiesling, R.L., Sterner, R., Kilham, S.S. & Johnson, F.A. 1986. Green, bluegreen and diatom algae: taxonomic differences in competitive ability for phosphorus, silicon, and nitrogen. *Archiv für Hydrobiologie* 106: 473–485.
- Tilman, D., Kilham, S.S. & Kilham, P. 1982. Phytoplankton community ecology: the role of limiting nutrients. *Annual Review of Ecology and Systematics* 13: 349–372.
- Titelman, J., Riemann, L., Holmfeldt, K. & Nilsen, T. 2008. Copepod feeding stimulates bacterioplankton in a low phosphorus system. *Aquatic Biology* 2: 131–141.
- Turpin, D.H. 1986. Growth rate dependent optimum ratios in *Selenastrum minutum* (Chlorophyta): implications for competition, coexistence and stability in phytoplankton communities. *Journal of Phycology* 22: 94–102.
- Turpin, D.H. & Harrison, P.J. 1979. Limiting nutrient patchiness and its role in phytoplankton ecology. *Journal of Experimental Marine Biology and Ecology* 39: 151–166.
- Tuomi, P. & Kuoppo, P. 1999. Viral lysis and grazing loss of bacteria in nutrient- and carbon-manipulated brackish water enclosures. *Journal of Plankton Research* 21: 923–937.
- Tyrrell, T. 1999. The relative influences of nitrogen and phosphorus on oceanic primary production. *Nature* 400: 525–531.
- Uehlinger, U. 1981. Experimental studies on the autecology of *Aphanizomenon flos-aquae* (Experimentelle Untersuchungen zur Autökologie von *Aphanizomenon flos-aquae*). *Archiv für Hydrobiologie Suppl.* 60 (Algalogical Studies 28): 260–288 (in German).
- Urabe, J., Clasen, J. & Sterner, R.W. 1997. Phosphorus-limitation of *Daphnia* growth: is it real? *Limnology and Oceanography* 42: 1436–1443.
- Urabe, J., Gurung, T.B. & Yoshida, T. 1999. Effects of phosphorus supply on phagotrophy by the mixotrophic alga *Uroglena americana* (Chrysophyceae). *Aquatic Microbial Ecology* 18: 77–83.
- Urban-Rich, J. 1999. Release of dissolved organic carbon from copepod fecal pellets in the Greenland Sea. *Journal of Experimental Marine Biology and Ecology* 232: 107–124.
- U.S. EPA. 1983. Methods for Chemical Analysis of Water and Wastes, EPA 600/4-79-020, Method 353.2. Environmental Protection Agency, Environmental Monitoring and Support Laboratory, Cincinnati, Ohio.
- Utermöhl, H. 1958. Zur Vervollkommnung der quantitativen Phytoplankton-Methodik. *Mitteilungen Internationale Vereinigung Theoretische und Angewandte Limnologie* 9: 1–38.
- Utkilen, H.C., Oliver, R.L. & Walsby, A.E. 1985. Buoyancy regulation in a red *Oscillatoria* unable to collapse gas vacuoles by turgor pressure. *Archiv für Hydrobiologie* 102: 319–329.
- Vahtera, E., Conley, D.J., Gustafsson, B.G., Kuosa, H., Pitkänen, H., Savchuk, O.P., Tamminen, T., Viitasalo, M., Voss, M., Wasmund, N. & Wulff, F. 2007a. Internal ecosystem feedbacks enhance nitrogen-fixing cyanobacteria blooms and complicate management in the Baltic Sea. *Ambio* 36: 186–194.
- Vahtera, E., Laamanen, M. & Rintala, J.-M. 2007b. Use of different phosphorus sources by the bloomforming cyanobacteria *Aphanizomenon flos-aquae* and *Nodularia spumigena*. *Aquatic Microbial Ecology* 46: 225–237.
- Vahtera, E., Laanemets, J., Pavelson, J., Huttunen, M. & Kononen, K. 2005. The effect of upwelling on the pelagic environment and bloom-forming cyanobacteria in the western Gulf of Finland, Baltic Sea. *Journal of Marine Systems* 58: 67–82.
- Van Bennekom, A.J., Krijgsman-van Hartingsveld, E., van der Veer, G.C.M. & van Voorst, H.F.J. 1974. The seasonal cycles of reactive silicate and suspended diatoms in the Dutch Wadden Sea. *Netherlands Journal of Sea Research* 8: 174–207.
- Van Nieuwerburgh, L., Wänstrand, I. & Snoeijis, P. 2004. Growth and C:N:P ratios in copepods grazing on N- or Si-limited phytoplankton blooms. *Hydrobiologia* 514: 57–72.
- Vargas, C.A. & Gonzalez, H.E. 2004. Plankton community structure and carbon cycling in coastal upwelling system. I. Bacteria, microprotozoans and phytoplankton in the diet of copepods and appendicularians. *Aquatic Microbial Ecology* 34: 151–164.
- Vaulot, D., LeBot, N., Marie, D. & Fukai, E. 1996. Effect of phosphorus on the *Synechococcus* cell cycle in surface Mediterranean waters during summer. *Applied and Environmental Microbiology* 62: 2527–2533.
- Verity, P.G. & Smetacek, V. 1996. Organism life cycles, predation, and the structure of marine pelagic ecosystems. *Marine Ecology Progress Series* 130: 277–293.
- Viitasalo, M., Vuorinen, I. & Saesmaa, S. 1995. Mesozooplankton dynamics in the northern Baltic Sea: implications of variations in hydrography and climate. *Journal of Plankton Research* 17: 1857–1878.
- Virtasalo, J.J., Kohonen, T., Vuorinen, I. & Huttula, T. 2005. Sea bottom anoxia in the Archipelago Sea, northern Baltic Sea - implications for phosphorus remineralization at the sediment surface. *Marine Geology* 224: 103–122.
- Vrede, T., Ballantyne, A., Mille-Lindblom, C., Algesten, G., Gudas, C., Lindahl, S. & Brunberg, A.K. 2009. Effects of N:P loading ratios on phytoplankton community composition, primary production and N fixation in a eutrophic lake. *Freshwater Biology* 54: 331–344.
- Wallström, K., Johansson, S. & Larsson, U. 1992. Effects of nutrient enrichment on planktonic blue-green algae

- in the Baltic Sea. *Acta Phytogeographica Suecica* 78: 25–31.
- Walsby, A.E., Hayes, P.K. & Boje, R. 1995. The gas vesicles, buoyancy and vertical distribution of cyanobacteria in the Baltic Sea. *European Journal of Phycology* 30: 87–94.
- Walsby, A.E., Hayes, P.K., Boje, R. & Stal, L.J. 1997. The selective advantage of buoyancy provided by gas vesicles for planktonic cyanobacteria in the Baltic Sea. *New Phytologist* 136: 407–417.
- Walve, J. 2002. Nutrient limitation and elemental ratios in Baltic Sea plankton. PhD thesis, Stockholm University, Stockholm, 49pp.
- Walve, J. & Larsson, U. 1999. Carbon, nitrogen and phosphorus stoichiometry of crustacean zooplankton in the Baltic Sea: implications for nutrient recycling. *Journal of Plankton Research* 21: 2309–2321.
- Walve, J. & Larsson, U. 2007. Blooms of Baltic Sea *Aphanizomenon* sp. (Cyanobacteria) collapse after internal phosphorus depletion. *Aquatic Microbial Ecology* 49: 57–69.
- Wasmund, N. 1997. Occurrence of cyanobacterial blooms in the Baltic Sea in relation to environmental conditions. *Internationale Revue der gesamten Hydrobiologie* 82: 169–184.
- Wasmund, N. & Uhlig, S. 2003. Phytoplankton trends in the Baltic Sea. *ICES Journal of Marine Science* 60: 177–186.
- Wasmund, N., Voss, M. & Lochte, K. 2001. Evidence of nitrogen fixation by non-heterocystous cyanobacteria in the Baltic Sea and re-calculation of a budget of nitrogen fixation. *Marine Ecology Progress Series* 214: 1–14.
- Willén, T. & Mattsson, R. 1997. Water-blooming and toxin-producing cyanobacteria. in Swedish fresh and brackish waters, 1981–1995. *Hydrobiologia* 353: 181–192.
- Wolfe, G.V., Steinke, M. & Kirst, G.O. 1997. Grazing-activated chemical defence in a unicellular marine alga. *Nature* 387: 895–897.
- Wulff, A., Mohlin, M. & Sundbäck, K. 2007. Intraspecific variation in the response of the cyanobacterium *Nodularia spumigena* to moderate UV-B radiation. *Harmful Algae* 6: 388–399.
- Wurtsbaugh, W.A. & Horne, A.J. 1983. Iron in eutrophic Clear Lake, California: its importance for algal nitrogen fixation and growth. *Canadian Journal of Fisheries and Aquatic Science* 40: 1419–1429.