DISSERTATIONES BIOLOGICAE UNIVERSITATIS TARTUENSIS
165

DISSERTATIONES BIOLOGICAE UNIVERSITATIS TARTUENSIS
165

LIISA METSAMAA

Model-based assessment to improve the use of remote sensing in recognition and quantitative mapping of cyanobacteria

TARTU UNIVERSITY
PRESS

Chair of Hydrobiology, Institute of Ecology and Earth Sciences, Faculty of Science and Technology, University of Tartu, Estonia

Dissertation is accepted for the commencement of the degree of *Doctor philosophiae* in hydrobiology on 13th of April 2009 by the Council of the Faculty of Science and Technology, University of Tartu.

Supervisor: Dr Tiit Kutser
University of Tartu
Faculty of Science and Technology
Estonian Marine Institute
Department of Remote Sensing and Marine Optics
Tallinn, Estonia

Opponent: Dr Stefan Simis
Finnish Environment Institute (SYKE)
Marine Centre
Helsinki, Finland

Commencement: on 19th of June 2009, at 13:15 in room 301, Vanemuise 46, Tartu.

ISSN 1024–6479
ISBN 978–9949–19–135–2 (trükis)
ISBN 978–9949–19–136–9 (PDF)

Tartu Ülikooli Kirjastus
www.tyk.ee
Tellimus nr 161

All we have to decide is
what to do with the time
that is given to us.

J. R. R. Tolkien

CONTENTS

LIST OF ACRONYMS AND SYMBOLS

ALI – Advanced Land Imager
AVHRR – Advanced Very High Resolution Radiometer
CDOM – Coloured dissolved organic matter
CZCS – Coastal Zone Color Scanner
Landsat – Series of Earth observing satellites
MERIS – Medium Resolution Imaging Spectrometer
MODIS – Moderate Resolution Imaging Spectroradiometer
NIR – Near-infrared

$a(\lambda)$ – Absorption coefficient
$a_{CDOM}(\lambda)$ – Absorption coefficient of coloured dissolved organic matter
$a^*_{Ph}(\lambda)$ – Specific absorption coefficient of phytoplankton
$a^*_{SM}(\lambda)$ – Specific absorption coefficient of suspended matter
a_w – Absorption coefficient of water
$b_b(\lambda)$ – Backscattering coefficient
$b^*_{b,Ph}$ – Specific backscattering coefficient of phytoplankton
$b^*_{b,SM}$ – Specific backscattering coefficient of suspended matter
b_{bw} – Backscattering coefficient of water
C_{Chl} – Concentration of chlorophyll *a*
C_{SM} – Concentration of suspended matter
$R(0+\lambda)$ – Reflectance just above the water surface
λ – Wavelength
μ_0 – Cosine of solar zenith angle

ORIGINAL PUBLICATIONS

The thesis contains the overview of the following papers, which are referred to in the text by Roman numerals. The papers are reprinted with the kind permission of the publishers.

I Metsamaa, L., Kutser, T. & Strömbeck, N. (2006). Recognising cyanobacterial blooms based on their optical signature a modelling study. *Boreal Environment Research.* 11: 493–506.

II Kutser, T., Metsamaa, L., Strömbeck, N. & Vahtmäe, E. (2006). Monitoring cyanobacterial blooms by satellite remote sensing. *Estuarine, Coastal and Shelf Science.* 67: 303–312.

III Kutser, T., Metsamaa, L., Vahtmäe, E. & Strömbeck, N. (2006). Suitability of MODIS 250 m resolution band data for quantitative mapping. *Proceedings of the Estonian Academy of Sciences. Biology. Ecology.* 55(4): 318–328.

IV Kutser, T., Metsamaa, L. & Dekker, A.G. (2008). Influence of the vertical distribution of cyanobacteria in the water column on the remote sensing signal. *Estuarine, Coastal and Shelf Science.* 78: 649–654.

V Kutser, T., Hiire, M., Metsamaa, L., Vahtmäe, E., Paavel, B. & Aps, R. (2009). Field measurements of spectral backscattering coefficient of the Baltic Sea and boreal lakes. *Boreal Environment Research.* 14: 305–312.

The contribution of the papers' authors was as follows:

Paper:	**I**	**II**	**III**	**IV**	**V**
Original idea:	LM, TK	TK, LM	TK	TK, LM	TK
Study design:	LM, TK	TK, LM	TK, LM	TK, LM, AD	TK
Data collection:	NS, LM	NS, LM, EV	NS, LM, EV	LM, TK	LM, EV, TK, BP, RA
Data analysis:	LM, NS	LM, EV, NS	TK, LM, EV, NS	LM, TK	MH, TK, LM, EV, BP
Manuscript preparation:	LM, TK, NS	LM, TK	TK, LM, EV	TK, LM, AD	TK, MH, RA

LM – Liisa Metsamaa
TK – Tiit Kutser
NS – Niklas Strömbeck
EV – Ele Vahtmäe
AD – Arnold G. Dekker
MH – Marian Hiire
BP – Birgot Paavel
RA – Robert Aps

1. INTRODUCTION

1.1. Cyanobacteria in aquatic ecosystems

Cyanobacteria are known to be one of the oldest living organisms on the planet. In respect to their build they are unicellular bacteria, which often form colonies or filaments. Biologically are cyanobacteria like plants because of getting their energy trough photosynthesis (Golubic and Soeng-Joo, 1999; Lotter, 2001).

Cyanobacteria are one of the main primary producers in the water's ecosystem. Phytoplanktons primary production forms the basis of marine food webs and which expresses the production of chemical energy in the organic compounds (Waterbury *et al.*, 1979; Ting *et al.*, 2002). The primary factors of production controlling and limiting in the water are the presence of light and nutrients and the temperature level of the water, which is inherent to each species of phytoplankton. The light penetrates the aquatic environment mainly vertically, and then the light is absorbed, scattered and re-emitted as fluorescence. The mentioned processes taking place during light the mentioned processes taking place during the light propagation in the water depend on the amount of material in the water (living organisms and their pigments, organic matter, suspended sediments, detritial matter etc.). The more material in the superface layers of the water, the smaller is the maximum light penetration depth (Kirk, 1994; Lillesand and Kiefer, 1999).

The most important nutrients of the phytoplankton include nitrogen and phosphorus. The more there are nutrients in the water, the more there are phytoplankton present. In certain high amount of distribution the condition is called formation of mass population i.e. the phytoplankton "bloom" (Fogg *et al.*, 1973; Sutcliffe & Jones, 1992) (Fig.1.). Some species of cyanobacteria, mostly filamentous cyanobacteria, also have a unique ability to fixate gaseous nitrogen from the air. This is an advantage over other phytoplankton species as they only need phosphate to be present in the aquatic environment. For instance, it has been noticed that as a result of wastewater treatment most of the nitrogen is separated from the water but a lot of phosphate remains, which again, with the right light and water temperature gives cyanobacteria better production conditions and a possibility to form blooms (Vahtera *et al*. 2007).

Figure 1. Example of the very dense cyanobacterial bloom (photo by F. Andrews 2005).

Cyanobacterial mass populations increasingly attract the attention of environmental agencies, water authorities, human and animal health organizations, since cyanobacteria present a range of issues related with water quality and treatment problems, and hazards to human and animal health (Ferguson *et al*., 1996). The main reason why these problems arise is that about 60–80 of 300 blooms forming species of phytoplankton can produce toxins (Smayda, 1997). There are various health issues associated with more than 60 identified toxins of cyanobacteria. The main problem-causing toxins include neurotoxins, hepatotoxins, cytototoxins, skin irritants and gastrointestinal toxins. Toxins get into the food chain because shellfish such as clams, mussels, oysters, or scallops filter phytoplankton from the water and as a consequence of this the algal toxins eventually accumulate in their organisms on such a high level that they might be harmful to humans or other consumers (Codd, 1998).

Some cyanobacterial blooms are not toxic but they may cause problems in other ways. It is well known that the decaying biomass of cyanobacterial bloom can cause oxygen depletion and widespread mortality of plants and animals in the affected area. Extensive blooms of cyanobacteria can also reduce light penetration to the bottom in very wide range of the water column, decreasing densities of submerged aquatic vegetation (Anderson, 2003). The incidence of dying blooms washing upon beaches during the peak of the summer holiday season has resulted in an economic loss (Subramaniam *et al*., 2000).

1.2. Detection of cyanobacterial blooms

Cyanobacterial blooms may be detected using a range of techniques in laboratories and in the field. Different water management authorities suggest water sampling in the regular monitoring stations and unattended flow-through systems on ships-of-opportunity.

Conventional sampling stations are located in one fixed location and monitoring results are extrapolated for surrounding areas. Measurements are taken only during the determined time period and scale. It has been shown (Rantajärvi *et al.*, 1998) that spatial and temporal frequencies of this type of conventional water-sampling programs may not be adequate to report changes in phytoplankton biomass, especially during bloom conditions when spatial and temporal variability in phytoplankton density is particularly high.

The autonomous flow-through systems on ships-of-opportunity map chlorophyll fluorescence along their routes. This means that the studied area is very narrow. These flow-through systems take water from a fixed depth. It is assumed that the top water layer is well mixed and that the concentration of chlorophyll is constant in the upper mixed layer. However, some cyanobacteria species have the ability to regulate their buoyancy and in calm weather tend to keep themselves close to the water surface, forming very dense accumulations just below the water surface (Walsby *et al.* 1995). These remain undetected by flow-through systems as the water intake is often below the layer where the cyanobacteria are. These bloom areas are also often spread out by the ferries that are collecting the samples. Moreover, fluorometers commonly used in the flow-through systems to measure chlorophyll *a*, do not provide precise information about the amount of cyanobacteria, which contain high level of phycobili-protein pigments (Lee *et al*., 1994; Simis *et al*., 2005; Seppälä *et al.*, 2007). This is so because most of the chlorophyll *a* in cyanobacteria is in non-fluorescing photosystem I (Bryant, 1986).

All of these problems suggest that new developments for monitoring methods are needed. Remote sensing could be one practical tool to support detection of cyanobacterial dynamics over extensive marine areas or large number of lakes. Research in remote sensing has been driven by the ongoing development of new sensors, with sufficient qualities for the monitoring of natural environment in the body of water (Richardson, 1996).

1.3. Passive optical remote sensing

Remote sensing is the science of obtaining information about an object, area or phenomenon through the analysis of data acquired by a sensor that is not in contact with the object, area or phenomenon. Usually this object is located on or in close proximity to the Earth's surface and the sensor is located on an aircraft or on a satellite platform (Lillesand and Kiefer, 1999).

Remote sensing instruments exploit electromagnetic radiation to study surface processes on Earth. Passive sensors use reflected sunlight or heat emitted by objects along the Earth's surface, while active sensors transmit laser beam or microwaves that are then reflected back to and recorded by the sensor. Many orbiting satellites currently map ocean properties such as colour, surface temperature, wind velocities, roughness of the ocean surface, and wave height. There are several advantages to using remote sensing techniques, such as accessing otherwise difficult locations and rapidly mapping large swaths of the Earth's surface (Capone and Subramaniam, 2005).

The characteristics of remote sensing sensors are described by their spatial, spectral, and radiometric resolution. The spatial resolution of the sensor describes the size of the ground area corresponding to one pixel in the image, e.g. 20x20 meters. The spectral resolution describes a sensor's ability to define fine wavelength intervals, i.e., the width of the spectral bands in the sensor. Usually, the number and the position of the bands are also mentioned in connection with the spectral resolution. Radiometric resolution describes how many grey-levels the measured signal is divided into. Older satellite sensors have 8-bit radiometric resolution (256 gray-levels) while more advanced sensors have up to 16-bit resolution (65 536 gray-levels) (Lillesand and Kiefer, 1999).

1.4. Remote sensing of cyanobacterial blooms

The use of airborne (Dekker *et al.* 1992; Jupp *et al.* 1994) and satellite remote sensing (Kahru 1993 and 1997; Kahru *et al.* 2000; Kutser 2004; Simis *et al*. 2005 and 2007; Reinart and Kutser 2006) has been recommended for providing more reliable information about the extent of the cyanobacterial blooms than the conventional monitoring programs can provide.

In calm weather conditions the aggregations of cyanobacterial cells accumulate just below the water surface or even form surface scum floating on the surface. Both are so distinct that the extent of the blooms (Fig.2.) can be mapped using almost any remote sensing instrument e.g. broadband sensors like the AVHRR (Kahru 1993; Håkanson and Moberg 1994), multispectral sensors such as the CZCS (Siegel *et al.* 1999) and the SeaWiFS (Joint and Groom 2000; Siegel and Gerth 2000). Even synthetic aperture radars have been utilised to map the extent of cyanobacterial blooms (Svejkovsky and Shandley, 2001) despite the fact that radar beam cannot penetrate water surface. Elevated sea surface temperature may indicate the presence of phytoplankton blooms (Kahru *et al*. 1993). However, the quantitative estimation of the phytoplankton concentration in turbid waters is still a challenge mainly because the standard chlorophyll retrieval algorithms, for the oceans, fail in coastal and inland waters (Vepsäläinen *et al*., 2005).

The standard products of chlorophyll produced by space agencies irregularly over- and underestimate measured chlorophyll values in turbid waters (Darecki and Stramski, 2004). Correlation between *in situ* and satellite chlorophyll is often very low. This can be explained by high absorption of light by CDOM at shorter wavelengths exploited in the standard chlorophyll retrieval algorithms. New approaches and new parameterizations for pigment algorithms are needed. Variability of the optical properties of water in different locations complicates the algorithm development even further (Darecki and Stramski, 2004). It may be that for different optically complex waters, regional or even seasonal remote sensing algorithms may be needed.

As already mentioned, many phytoplankton accessory pigments are taxonomically significant (Rowan, 1989). The presence and colour of the phycobilin pigments are typical features and main identification basis of cyanobacteria. All species of cyanobacteria contain phycobilin pigments in their cell structure. The pigments' colour depends on which area of the spectrum they absorb light. There are several phycobilin pigments but two of them, phycoerythrin and phycocyanin, are usually distinguished. Phycoerythrin absorbs light in the spectrum's green part (545 nm) and therefore has pink colour. Phycocyanin appears blue because it absorbs the orange light (615–620 nm) (cf. Viskari and Colyer, 2003).

Therefore, detection of specific accessory pigments in aquatic systems can reveal what type(s) of phytoplankton is (are) present there (Gieskes, 1991; Millie *et al*., 1993). The development of algorithms for retrieving phycocyanin from remote sensing data could lead to better detection of the cyanobacteria. It is shown that the presence of phycocyanin can be detected from spectral reflectance (Dekker *et al*., 1991; Jupp *et al*., 1994; Simis *et al*. 2005). The development of the necessary remote sensing algorithms needs to be connected to the available *in situ* data. The problem is that phycocyanin and phycoerythrin are not routinely measured from water samples, and can not be regularly compared with available ocean colour satellite data.

Comparing satellite and *in situ* data for developing and validating remote sensing algorithms and methods is complicated and may lead to several errors. A difference in spatial and temporal sampling frequency between ship-borne observations and satellite measurements is one of the main errors. For example, depending on the total time difference and wind speed, the bloom structures may be displaced a few kilometres away from their first sampling point for the time of satellite overpass.

The concentration of chlorophyll *a* in cyanobacterial blooms may vary by orders of magnitude within tens of meters (Kutser 2004). Consequently, it is difficult to get exact matchups (in space and time) of remote sensing and *in situ* data. The spatial resolution of satellite sensors is typically around 1000 m meaning that the satellite result is an average chlorophyll *a* concentration over this 1000x1000 m area where the actual variability in chlorophyll *a* is unknown.

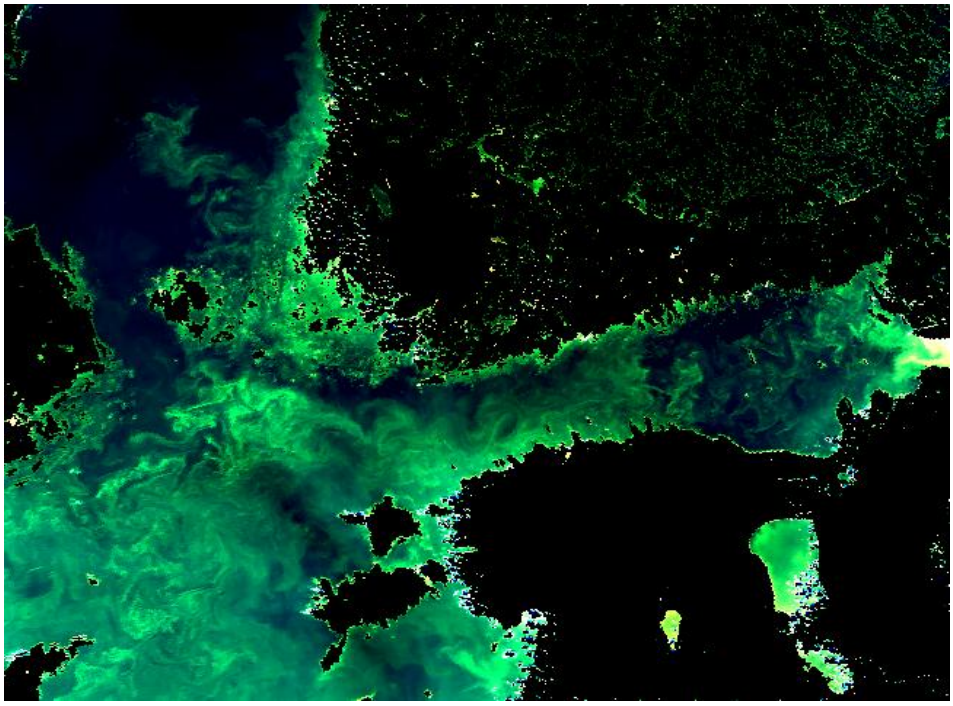

Figure 2. MODIS Aqua false colour RGB 1 km resolution image of cyanobacterial bloom (green coloured area) in the Gulf of Finland (the Baltic Sea) on the 7th of August 2007.

1.5. Thesis objectives

In an ideal case the development of algorithms and methods for recognition and quantitative mapping of the potentially harmful cyanobacterial blooms should be carried out on the bases of *in situ* data. However, as mentioned above, the blooms can be extremely patchy both spatially and temporally. Collecting statistically significant amount of data about the properties of cyanobacterial blooms may require many years as there are years when the blooms do not occur and the blooms may occur in places where research vessels do not reach, and outside the planned cruise schedule.

The above mentioned reasons gave the idea to use modelling as a primary approach in the current thesis. The models require knowledge about specific optical properties of the phytoplankton species present in the studied water area (in this thesis the Baltic Sea) as well as information on specific properties of other optically active substances and variability in their concentrations. Laboratory and *in situ* data used in this thesis were collected both by the author

and her colleagues. This thesis also includes some additional results from unpublished *in situ* data.

The first objective of the thesis was to determine if it is possible to separate waters dominated by cyanobacteria from those dominated by other types of phytoplankton using remote sensing methods. The first part of this study (Paper **I**) was carried out for hyperspectral sensors. There are currently no hyperspectral sensors that could provide daily coverage of extended marine areas. Therefore, the second part of the study (Paper **II**) was carried out taking into account the spectral resolution of sensors that can provide such coverage and could therefore be suitable for operative monitoring of cyanobacterial blooms.

The second objective of the thesis was to study the possibility of quantitative mapping of cyanobacterial blooms by means of remote sensing. The suitability of different available remote sensing sensors was assessed using model simulations (papers **I, II** and **III)**.

A modelling study (Paper **III**) was carried out to determine the possibility of using the MODIS 250 m data also for quantitative mapping of cyanobacterial biomass besides being useful in monitoring presence and dynamics of cyanobacterial blooms. MODIS sensors on Terra and Aqua satellites currently provide the highest revisit times (up to four times per day) making these sensors the most suitable for operative monitoring of water quality. Separating the cyanobacterial blooms from turbidity plumes is not possible using a single band. However, there are circumstances where it is almost certain that the elevated water leaving signal is caused by cyanobacterial bloom.

Unlike most phytoplankton species cyanobacteria can regulate their buoyancy and move in the water column. This may have an impact on measurable remote sensing signal and our ability to estimate cyanobacterial biomass by means of remote sensing. A modelling study (Paper **IV**) was carried out to determine the possible effect of inhomogeneous vertical distribution of cyanobacterial biomass on remote sensing signal.

Bio-optical and radiative transfer models that are used to simulate water reflectance spectra have to be parameterised for the specific water body under investigation. The backscattering coefficient was the least known inherent optical property of the Baltic Sea. Therefore, there was a need to study variability of this parameter in the Baltic Sea waters (Paper **V**).

2. MATERIAL AND METHODS

2.1. Study area

The Baltic Sea (Fig. 3.) is one of the biggest brackish water bodies in the world. The tides are hardly noticeable and the depths are generally low (average ~50 m). The average salinity in the Baltic Sea is 8–10 PSU, which is conditioned by river inflow, high amount of rainfall and poor exchange of the water with an ocean through shallow Danish straits.

As the result of its seclusion the Baltic Sea has turned from being oligotrophic water to eutrophic water in the course of time and is very sensitive to the inflow of pollution and other biological and chemical matters. High amount of nutrients is the main character of europhication, which expresses in the extent and frequency of phytoplankton blooms. Those blooms cause the organic matter's increase of quantity. Oxygen depletion may result when blooms decay, which has a negative influence on the benthic habitat and the fish (Voipio, 1981).

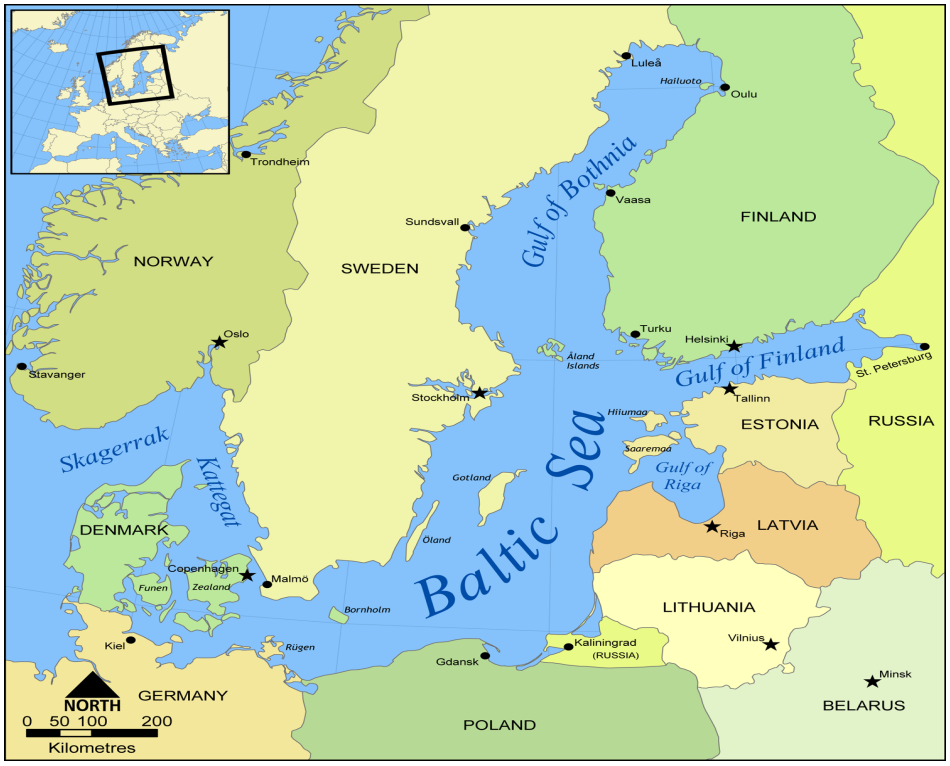

Figure 3. Map of the Baltic Sea (Salleman 2008).

Baltic Sea waters are affected by seasonal variations in chlorophyll concentration – chlorophyll *a* may even sometimes rise up to hundreds of mg m^{-3}. There are essentially two annual blooms in the Baltic Sea. The spring bloom takes place from early March up to May depending on the area and year. The main phytoplankton groups forming the spring bloom are diatoms and dinoflagellates. The cyanobacterial blooms occur mainly in late summer, from July to September. The main summer bloom forming nitrogen-fixing cyanobacteria species is: *Aphanizomenon flos-aquae*, *Nodularia spumigena* and *Anabaena ssp*. (Öström, 1976; Niemistö *et al*., 1989). These blooms can cover areas of more than 100 000 km^2 (Kahru 1997), affecting recreation, ecosystem integrity, human and animal health. In addition there can be regional algal blooms earlier or later in the summer, depending on the weather and the nutrients available in the water.

2.2. Optical modelling

Two different modelling approaches were used in this study. First a semi-empirical model was used to calculate the reflectance spectra of the optically deep water just above the water surface. The basics of the model are taken from the results of Monte Carlo studies by Gordon *et al*. (1975) and Kirk (1994). The diffuse component of remote sensing reflectance was calculated using the following equation:

$$R(0+\lambda) = 0.544(-0.629\mu_0 + 0.975)\frac{b_b(\lambda)}{a(\lambda)+b_b(\lambda)} \qquad (1),$$

where r (0+λ) is reflectance just above the water surface, μ_0 is the cosine of solar zenith angle, $b_b(\lambda)$ is the total backscattering coefficient and $a(\lambda)$ is the total absorption coefficient.

It is assumed that there are three optically active components in the water: phytoplankton, coloured dissolved organic matter (CDOM), and suspended matter. Under these conditions the total spectral absorption coefficient, $a(\lambda)$, is described by:

$$a(\lambda) = a_w(\lambda) + a^*_{Ph}(\lambda)C_{Chl} + a_{CDOM}(\lambda) + a^*_{SM}(\lambda)C_{SM}\ , \qquad (2),$$

where a_w is the absorption coefficient of pure water, $a^*_{Ph}(\lambda)$ is the chlorophyll-specific spectral absorption coefficient of phytoplankton, $a_{CDOM}(\lambda)$ is the spectral absorption coefficient of CDOM, and $a^*_{SM}(\lambda)$ is the mass-specific absorption coefficient of suspended matter. C_{Chl} and C_{SM} are concentrations of chlorophyll *a* and total suspended matter.

The total spectral backscattering coefficient $b_b(\lambda)$ can be described:

$$b_b(\lambda) = 0.5b_w(\lambda) + b^*_{b,Ph}(\lambda)C_{Chl} + b^*_{b,SM}(\lambda)C_{SM}\ , \qquad (3),$$

where b_w is the scattering coefficient of pure water and it is assumed that the backscattering probability is 50% in pure water. $b^*_{b,Ph}$ is chlorophyll-specific backscattering coefficient of phytoplankton and $b^*_{b,SM}$ is suspended sediment specific spectral backscattering coefficient of suspended matter. The detailed description of this model can be found in the papers **I** and **II**.

The modelling was carried out for two distinctly different water types. Water type 1 is CDOM rich waters near a river estuary and water type 2 represents water parameters typical in the open Baltic Sea area. The suspended matter and CDOM values were selected based on *in situ* measurements. Specific absorption spectra of thirteen different phytoplankton species, including cyanobacteria, were used (more detailed description in the papers **I** and **II**).

The Hydrolight 4.2 radiative transfer code (Mobley and Sundman, 2001) was used to study the effect of uneven vertical distribution of cyanobacteria on the remote sensing signal. The simulations were performed for waters with different chlorophyll *a* content and vertical distribution of cyanobacteria. The real vertical distribution of cyanobacteria in bloom conditions is practically unknown. Therefore, we used different hypothetical vertical distributions (Fig. 4.). Wind speed was taken to be 2 ms^{-1} so that cyanobacteria are capable of migrating vertically in the water column. The solar zenith angle was assumed to be 30° which is typical for the time around midday in the July-August period when the cyanobacterial blooms occur in the Baltic Sea. Four different chlorophyll concentration ranges and six vertical distributions were used in the model simulation. Detailed description is presented in **IV**.

2.3. Laboratory measurements

Several authors (Davies-Colley *et al.* 1986, Ahn *et al.* 1992, Subramaniam *et al.* 1999) have presented the specific absorption and scattering coefficients of different phytoplankton species. However, the specific optical parameters of the Baltic Sea phytoplankton species (including cyanobacteria) were virtually unknown. Niklas Strömbeck from University of Uppsala carried out the laboratory measurements describing the optical parameters of five phyto-plankton cultures (three cyanobacteria species) present in the three largest Swedish lakes and the Baltic Sea. Detailed descriptions of the laboratory work are given in the papers **I** and **II**. Laboratory measurements results are presented on the different level in the papers **I, II, III** and **IV**.

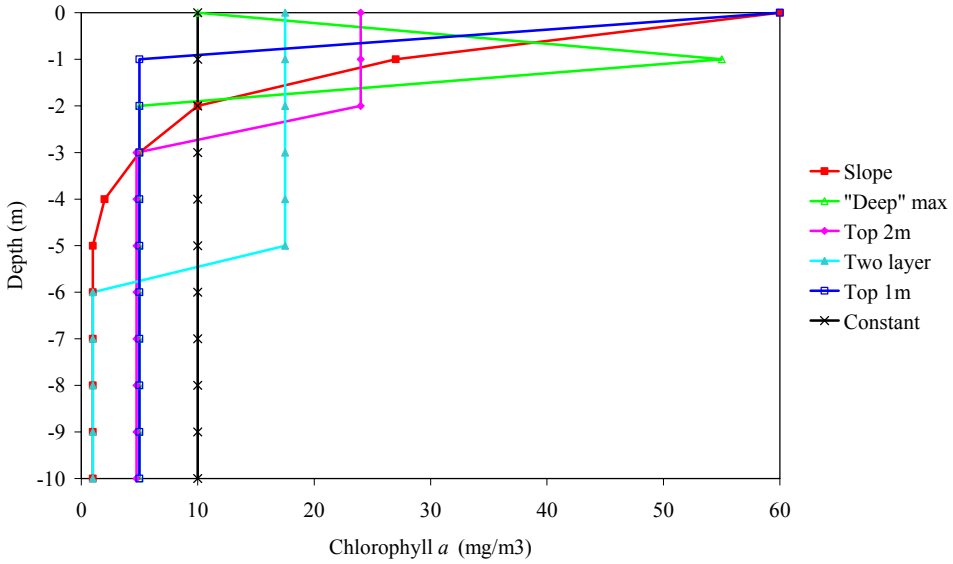

Figure 4. Vertical distributions of chlorophyll *a* used in the model simulations. SL=slope, exponentially decreasing concentration; DM=''Deep'' max, where most of the cyanobacteria were located at depths between 1 and 2 m; 2m= top 2m, most cyanobacteria located in the top 2 m; 2L=two layers, where the top 5 m had a high concentration of cyanobacteria and the following 5 m had a low concentration of cyanobacteria; 1m=top 1m, most cyanobacteria located in the top 1 m; and Co=constant, for a mixed surface water.

2.4. *In situ* data

All the measurements presented in the paper **V**, were collected in 2005 and 2006. The optical backscattering meter HydroScat-6 (HOBILabs) was used in the different regions of the Baltic Sea and some lakes. Concentrations of chlorophyll *a*, CDOM and total suspended matter were measured from the water samples taken at each station where the HydroScat measurements were carried out.

Some unpublished fieldwork results are used in this thesis to assure the modelling results. Measurements of above-water reflectance were collected in August 2007, during the Finnish Institute of Marine R/V "Aranda" cruise on the Baltic Sea. Exact dates and station locations can be found in table 1. All the stations were monitored by using two TrioS RAMSES spectrometers. One of the spectrometers measured downwelling irradiance and one measured up-welling radiance in spectral range 310–1130 nm. Water reflectance was calculated of this data. In order to understand the formation of water colour (reflectance) due to different concentrations of optically active substances

(phytoplankton, CDOM, suspended matter) we also collected water samples for chlorophyll (Tab. 1), CDOM and total suspended sediments. Filtration and laboratory analyses were carried out using methods described by Paavel (2008).

Table 1. Dates and locations of the stations monitored. *In situ* measured chlorophyll concentrations for the each station are presented (laboratory measurements were carried out by B. Paavel). Stations were monitored during on R/V "Aranda" cruise on the Baltic Sea.

STATION	DATE	LATITUDE	LONGITUDE	C_{chl} (mg/m^3)
39A	06.08.2007	60.04.013 N	024.58.822 E	3.8
LL4A	06.08.2007	60.00.995 N	026.04.852 E	4.5
LL3A	07.08.2007	60.04.057 N	026.20.778 E	9.2
LL3B	07.08.2007	60.04.033 N	026.20.769 E	7.1
LL6A	08.08.2007	59.55.001 N	025.01.810 E	5.9
LL7	08.08.2007	59.50.790 N	024.50.270 E	7.1
GF1	08.08.2007	59.42.291 N	024.40.950 E	5.0
LL12	09.08.2007	59.29.010 N	022.53.814 E	5.2
LL 12A	09.08.2007	59.28.993 N	022.53.921 E	7.3
LL13	09.08.2007	59.22.001 N	022.27.809 E	5.0
LL8	10.08.2007	59.46.011 N	024.25.811 E	43.1

3. RESULTS OVERVIEW AND GENERAL DISCUSSION

3.1. Recognizing cyanobacterial bloom by means of remote sensing

Simulating reflectance spectra of the Baltic Sea waters requires knowledge about specific optical properties of the phytoplankton species that are present in the Baltic Sea. Chlorophyll specific absorption coefficient spectra of three cultured cyanobacteria species *Aphanizomenon flos-aquae*, *Nodularia spumigena*, *Anabaena circinalis* and two other cultured phytoplankton species *Cyclotella cryptica* (*Diatomophyceae*), *Scenedesmus obliqus* (*Chlorophyceae*) were measured in the laboratory by N. Strömbeck and the results are presented in papers **I**, **II** and **III**.

A cyanobacterial specific pigment, phycocyanin, absorption feature (*in vivo* maximum at 627 nm, Dekker *et al.* 1992) was clearly seen in the results. Also the specific backscattering coefficient of cyanobacteria was higher than that of other phytoplankton species. Decreasing backscattering towards longer wavelengths was more significant in case of cyanobacteria. The same trends were also observed by Ahn *et al*. (1992) (for detail see paper **I**).

A bio-optical model described in paper **I** was used to simulate reflectance spectra. Bio-optical model simulations were carried out for two different waters types: CDOM-rich coastal and typical characteristic open Baltic Sea waters. Just above the water surface reflectance $R(0+\lambda)$ (Eq. 1.) spectra were calculated for chlorophyll *a* concentrations from 1 mg/m^3 to 300 mg/m^3, with different increments described in paper **I**. Measured absorption- and backscattering coefficients from all phytoplankton species studied by N. Strömbeck, and those presented in the paper by Ahn *et al*. (1992), were used.

The phycocyanin absorption feature of all cyanobacteria species are also detectable in modelled reflectance spectra (Fig. 5.), simulated for remote sensing instruments. However, cellular pigment concentration of phycocyanin can be expected to fluctuate for changing nutrient and light environments (Tandeau de Marsac, 1977) and this can also cause variability of phycocyanin specific optical features.

In typical waters of open Baltic Sea area remote sensing instruments with sufficient spectral resolution (10 nm or better) and high radiometric sensitivity can be used for recognition and quantitative mapping of cyanobacteria as absorption by phycocyanin is causing specific feature in reflectance spectra that is characteristic to cyanobacteria only. However, an exception among all modelled phytoplankton species was *Isochrysis galbana* (Prymnesiophyceae) (specific optical properties presented in Ahn *et al*., 1992). Reflectance spectrum of this species is similar to those of cyanobacteria i.e. there is absorption feature near 630 nm. This is probably caused by chlorophylls c_1 and c_2, which are the

major pigments (> 10%) of the total chlorophylls in the phytoplankton class Prymnesiophyceae (Jeffrey and Vesk, 1996). Chlorophylls c_1 and c_2 have absorption peaks near 628 and 630 nm, respectively (Jeffrey and Vesk, 1996). However, Cyanophyceae and Prymnesiophyceae sp. usually do not occur in similar aquatic environments. Therefore, separating cyanobacterial blooms from waters dominated by other algae should not be a problem provided that the amount of cyanobacteria is high enough. Two other phytoplankton species, *Emiliania huxleyi* and *Hymenomonas elongata*, studied by Ahn *et al*. (1992) also belong to the prymnesiophyceae. There was no significant absorption feature near 630 nm neither in the measured absorption coefficient spectra nor modelled reflectance spectra of these two species.

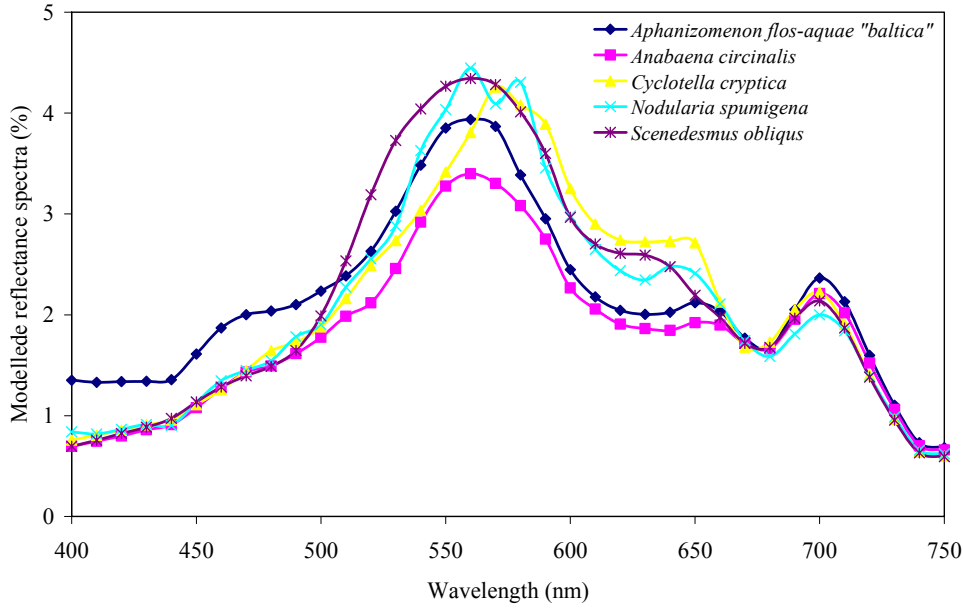

Figure 5. Modelled reflectance spectra of five cultured phytoplankton species, including three cyanobacterial species (*Aphanizomenon flos-aquae "baltica"*, *Anabaena circinalis* and *Nodularia spumigena*). Modelling was carried out using the following concentrations of optically active substances: C_{chl} = 30 mg/m^3; C_{SM} = 2 mg/l; $a_{CDOM(380)}$ = 1,5 m^{-1}. The phycocyanin absorption feature (max near 620 nm) is clearly seen in reflectance spectra of cyanobacteria.

Estimation for the open Baltic Sea waters (paper **I**) show that the concentration of chlorophyll *a* has to be 8–10 mg/m^3 before the phycocyanin absorption feature becomes detectable in reflectance spectra of hyperspectral instruments with sufficient signal to noise ratio. Therefore, it is unlikely that remote sensing can be used for early warning of emerging potentially harmful

cyanobacterial blooms as chlorophyll concentrations higher than 4 mg/m^3 are already considered as bloom in the Baltic Sea.

It is important to point out that the specific absorption and backscattering coefficients were measured on pure algae cultures. Very intensive blooms may be dominated by a single species but usually the natural assemblages consist of several species. Consequently, the optical properties specific to cyanobacteria may be shadowed and even higher concentration of biomass is needed before waters dominated by cyanobacteria can be recognised by their spectral signature.

In order to back up these modelling results an example of *in situ* optical measurements is presented. The variability in water reflectance spectra measured ~20 cm above the water surface is shown in Fig. 6. Surface bloom was visually noticed in station LL8. It is also clearly seen in reflectance spectrum as it appears in high values at near-infrared wavelengths. The reflectance spectrum of the station LL8 shows a clear minimum in reflectance around 620–630 nm caused by phycocyanin absorption, and a characteristic peak near 650 nm typical for cyanobacteria.

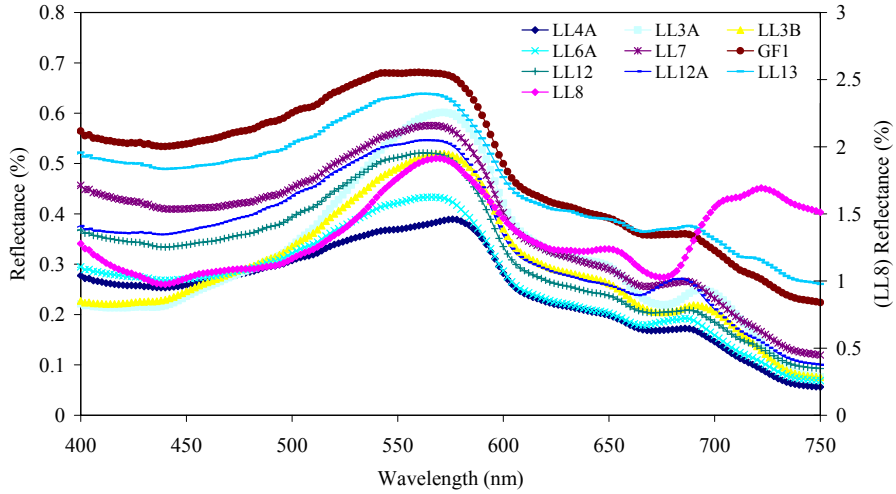

Figure 6. Reflectance spectra measured ~20 cm above the water surface at ten stations monitored during cruise on the Baltic Sea with R/V "Aranda" in August 2007. A surface bloom was visually noticed at station LL8 (chlorophyll concentration 43.1 mg/m^3).

These features also occur in case of subsurface blooms if cyanobacteria are present in high enough quantity (chlorophyll *a* at least 8–10 mg/m^3 according to our model simulations **I**). Concentration of chlorophyll *a* almost reached this level also in some other stations. However, the spectral features typical to cyanobacteria are not so clear in the reflectance spectra collected in these stations. It was detected in the laboratory that cyanobacteria were not the only

species present species in the bloom (personal comment by Maija Huttunen). This suggests that the actual concentrations where cyanobacteria become optically separable from other phytoplankton species can be even higher in some cases. It probably depends of the species that occur in the same bloom and environmental conditions. Also the condition of photosynthetic rate and energy transfer between different pigments of the bloom forming cyanobacterial species has an important impact on their optical signature.

It is shown in paper **II** that multispectral sensors like ALI and Landsat are unlikely capable of separating the Baltic Sea waters dominated by cyanobacteria species (Fig. 7.) as their spectral band configuration does not allow detecting absorption features caused by phycocyanin (present primarily in cyanobacteria) or any other spectral features that are characteristic to cyanobacteria only. Vincent *et al*. (2004) have shown that it is possible to map phycocyanin concentration in lake waters using Landsat. However, the spectral bands of Landsat are so wide that both the absorption feature around 620–630 nm and peak at 650 are within the same spectral band. Increasing biomass should cause deepening in the absorption feature and increase of the peak at 650 nm. As a result the increasing biomass of cyanobacteria may cause decrease, increase or no change in radiance measured in this particular band (630–690 nm). The results of Vincent *et al*. (2004) can be explained with correlation of concentration of phycocyanin with some other water characteristic (e.g. transparency or turbidity) in the Landsat data. Similar effects may also occur in other cases.

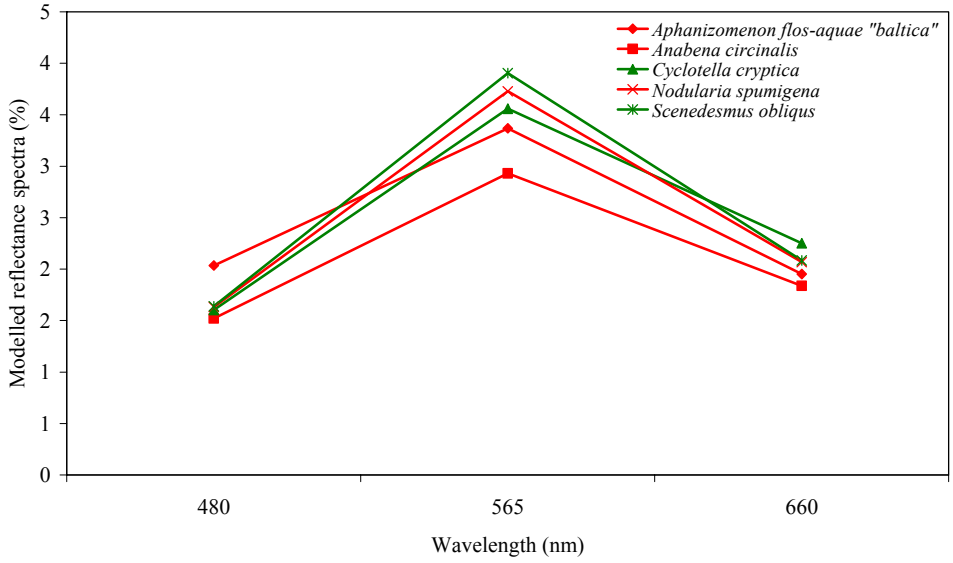

Figure 7. Modelled reflectance spectra of five cultured phytoplankton species (including three cyanobacterial species – red lines) using ALI band configuration. Modelling was carried out using the following concentrations of optically active substances: C_{chl} = 30 mg/m^3; C_{SM} = 2 mg/l; $a_{CDOM(380)}$ = 1,5 m^{-1}.

MERIS bands 6 (615–625 nm) and 7 (660–670 nm) allow detecting phycocyanin absorption feature near 620–630 nm and a small peak in reflectance spectra near 650 nm characteristic only to waters dominated by cyanobacteria (Fig. 8.). Other MERIS bands useful for detecting phytoplankton are band 8 (677,5–685 nm) where the chlorophyll *a* absorption feature occurs, and band 9 (703,75–713,75 nm) at wavelengths where there is often a peak in reflectance spectra of waters which contain the high concentration of phytoplankton.

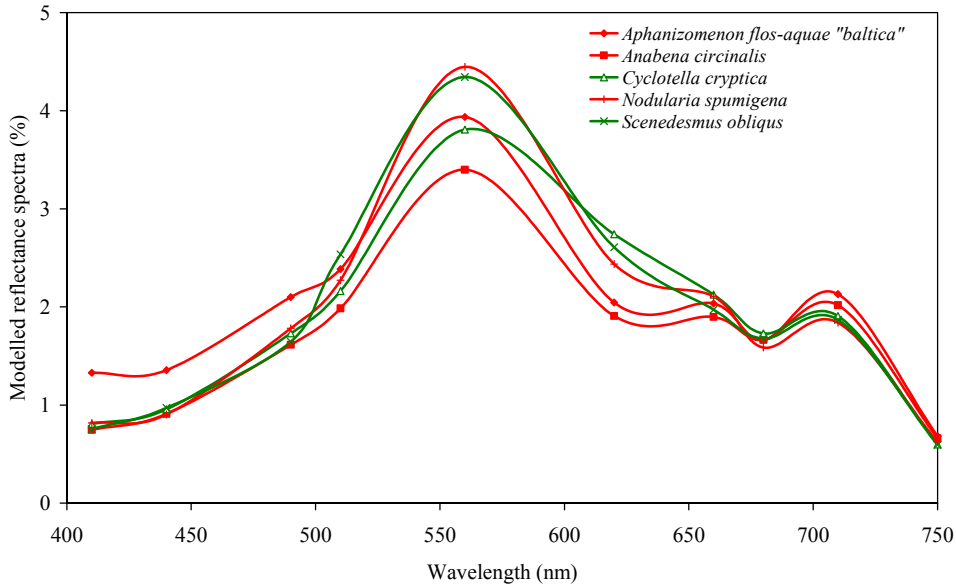

Figure 8. Modelled reflectance spectra of five cultured phytoplankton species (including three cyanobacterial species – red lines) using MERIS band configuration. Cyanobacteria specific pigment phycocyanin absorption feature (620 nm) is noticeable. Modelling was carried out using the following concentrations of optically active substances: C_{chl} = 30 mg/m^3; C_{SM} = 2 mg/l; $a_{CDOM(380)}$ = 1,5 m^{-1}.

MERIS can potentially be used to identify cyanobacteria if they are present in relatively large quantities. Detection of emerging blooms may not be possible because the phycocyanin absorption feature becomes detectable by MERIS when chlorophyll *a* concentrations reach values around 10–30 mg/m3 (depending on species) which are much higher than the level of chlorophyll which is considered as bloom condition in the Baltic Sea (4 mg/m3).

However the only data available regularly (up to 4 times per day) and with sufficient spatial resolution for coastal waters are MODIS band 1 (620 nm) and band 2 (842 nm) imagery with 250 m spatial resolution. Those bands were designed for mapping land, cloud, and aerosol boundaries, not for water environments. Pure water is a medium whose absorbance increases with

increasing wavelength at wavelengths beyond 580–590 nm. As a result the water leaving signal is very small already at wavelengths < 600 nm (Kirk, 1994) and almost negligible at wavelengths of MODIS band 1 in the case of clear natural waters (oceans, alpine lakes).The large amount of a suspended sediments or phytoplankton in turbid waters increases backscattering of light to the level where the water leaving signal in MODIS band 1 is not negligible any more. Hu *et al.* (2004) showed that MODIS band 1 can be used to map total suspended matter concentrations in coastal waters.

Model simulations (paper **III)** show that MODIS band 1 is sensitive to changes in the concentration of cyanobacteria and can be used for quantitative mapping during cyanobacterial blooms. The relationship between MODIS band 1 and the concentration of cyanobacteria is nonlinear. It is relatively easier to estimate the chlorophyll concentration in *Nodularia spumigena* bloom than in *Anabaena circinalis* or *Aphanizomenon flos-aquae* blooms as an increase in the concentration of *Nodularia* increases the reflectance the most strongly of the three bloom-forming cyanobacteria species studied. It should be kept in mind that the possibilities of using these results in accurate mapping of cyanobacterial biomass are limited as it is not possible to confirm the reason of increased signal using a single spectral band. Both high concentration of mineral particles and phytoplankton may cause the increase in the remote sensing signal. Single band algorithms can only be used if there is auxiliary information that confirms presence of cyanobacterial blooms as the main source of increased reflectance.

3.2. Impact of cyanobacteria vertical distribution on remote sensing signal

Mapping of the extent of surface cyanobacterial blooms with remote sensing is straightforward, but recognizing waters dominated by cyanobacteria mixed throughout the water column and quantitative mapping of cyanobacterial biomass with remote sensing is more complicated. It has been shown (Gordon and Clark, 1980; Stramska and Stramski, 2005) that vertical distribution of phytoplankton has an impact on the remotely sensed signal. However, these studies tend to concentrate on oceanic waters and on the impact of the deep (around 100 m) chlorophyll maximum on global chlorophyll algorithms (based on the blue-green ratio). An important fact is also that unlike most phytoplankton species, some cyanobacteria can regulate their buoyancy and move vertically in the water column (Walsby *et al.* 1995). This may cause problems in developing remote sensing algorithms for quantitative mapping of cyanobacteria.

Results obtained with Hydrolight 4.2 radiative transfer modelling (paper **IV**) show that variability in reflectance spectra due to different vertical distributions of cyanobacteria was significant. The highest reflectance values occur when most of the cyanobacteria are close to the water surface, for example in the case

of vertical distributions where the concentration of chlorophyll *a* is decreasing exponentially with depth (Slope) or when most of the cyanobacteria are in the top 1 m (Top 1m). "Deep" maximum (Deep Max) distribution also gave higher reflectance values during low concentrations of cyanobacteria. It must be noted here that unlike in ocean waters we considered biomass maximum between 1–2 m as a "deep maximum" (e.g. the maximum below the immediate surface layer). The reflectance spectra of a uniformly mixed water column are significantly lower than those of uneven vertical distributions in all cases for the three species studied and all modelled concentration ranges.

It indicates a strong need in *in situ* data concerning the real vertical distribution of the cyanobacterial biomass in the water column. Water sampling methods that can adequately reveal the vertical structure of the cyanobacterial distribution have to be used during blooms to get data that is suitable for developing reliable remote sensing methods for quantitative mapping of cyanobacteria. A single depth measurement or a mixed water sample of chlorophyll *a* may often be unsuitable for calibrating satellite data from cyanobacterial bloom areas.

Some possible cyanobacterial vertical distribution *in situ* results can be found in paper **V**. A certain stratification pattern was observed in the Pakri Bay near the Port of Paldiski (Fig. 9.). The cyanobacterial bloom was visually noticeable in the water. However the vertical distribution of particles was bimodal with one maximum near the water surface and the second near thermocline. It is likely that both maxima were caused by cyanobacteria, but it may have happened that the first maximum was caused by cyanobacteria and the second maximum by other phytoplankton species.

Accumulations of cyanobacteria were also observed in the northern part of the Baltic Proper where measurements were carried out (Fig. 10.). Unfortunately, it is practically impossible to measure surface accumulations with HydroScat (and other instruments) as the instrument disturbs natural stratification of cyanobacteria. It must also be noted that most of the cyanobacteria were in the top 3–4 meters of the water column as seen from the HydroScat measurement. It is important to note that the noisiness of the vertical profile was probably caused by aggregations of cyanobacteria, which are too large (from millimetres to centimetres) for the optical instrument to accurately measure. Aggregations in front of the instrument window gives high backscattering values and water between the aggregations (containing unicellular cyanobacteria) gives comparatively low backscattering values.

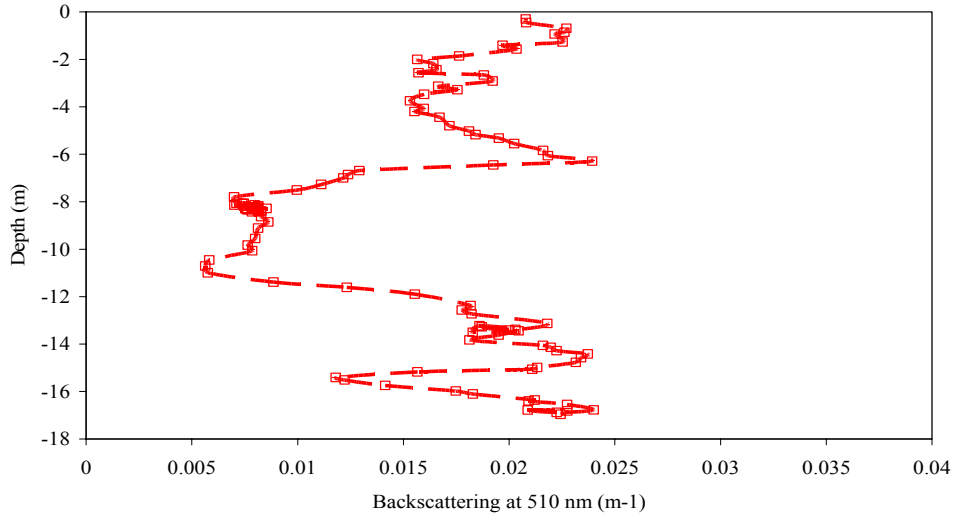

Figure 9. Vertical distribution of particles in the water column during visually detected cyanobacterial bloom in the Pakri Bay (near the Port of Paldiski, in Gulf of Finland). Data collected in July 2005.

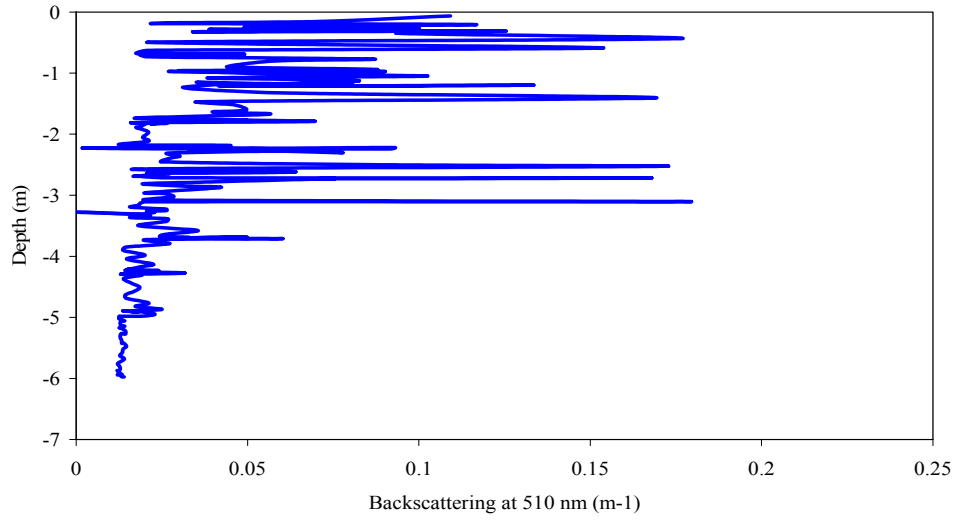

Figure 10. Vertical distribution of particles in the water column during visually detected cyanobacterial bloom in the Baltic Proper area. Data collected in August 2006.

SUMMARY

On the global scale cyanobacteria are common inhabitants of pristine aquatic and terrestrial environments. Natural populations of these organisms may be found everywhere and they influence environment and humanity in several ways. Remote sensing might be the only method providing sufficient information on cyanobacterial blooms in their spatial and temporal variability. However, there are still several limitations and uncertainties in the applications where remote sensing is used.

One approach to finding a solution to ocean colour remote sensing problems is using modelling. The model-based approaches show the feasibility of different optical and remote sensing instrumentation measurements. When *in situ* measurements of optical parameters are not available, the empirical proxy may be used or the parameter is allowed to vary and be optimized by the model. Always has to be taken into account that the models give results that support very extreme and so called ideal conditions, which are difficult to find in the nature. Nevertheless, the results of modelling may be useful for drawing the attention to the possibilities of how the problems that might arise (e.g which remote sensing and fieldwork instruments could be used and which presumptions should be kept in mind in those studies) could be solved in the future.

In the present thesis bio-optical and radiative transfer models were used to show the remote sensing capabilities in pure culture conditions in the Baltic Sea area. Remote sensing instruments with sufficient spectral resolution (10 nm or better) and high radiometric sensitivity may be used for recognition and quantitative mapping of cyanobacteria. The absorption by phycocyanin is causing an appearance of a special feature in reflectance spectra that is typical to only cyanobacteria and can be detected with sufficient spectral resolution instruments. Estimation and some *in situ* data for the typical open Baltic Sea waters show that the concentration of chlorophyll *a* should be around 8–10 mg/m^3 so that the phycocyanin absorption feature would become detectable in reflectance spectra. However, in reality the chlorophyll concentrations can also be higher in order to have the phycocyanin absorption feature be detectable. The precise results depend on the bloom composition and the state of the phytoplankton species in that bloom. MERIS with suitable spectral bands could be a useful tool for detecting waters dominated by cyanobacteria and estimating phytoplankton biomass in blooms. MERIS bands 6 and 7 (620 and 665 nm respectively) allow detecting phycocyanin absorption feature around 620 nm.

The vertical distributions of cyanobacteria also have a significant influence on remote sensing. The variability in reflectance spectra due to modelled different vertical distributions of cyanobacteria was significant in both cases of lower and higher concentrations of cyanobacterial biomass. Knowledge about the vertical distribution of cyanobacteria can help developing remote sensing algorithms and methods for quantitative mapping of cyanobacteria, likewise it

can even be used to validate the existing remote sensing algorithms. Using a single depth water sample for calibration and validation of remote sensing algorithms in some cases might lead to incorrect results.

The results of this study indicate that there is a strong need for *in situ* studies on cyanobacterial blooms. First of all, the optical properties of natural phytoplankton assemblages in the Baltic Sea are not known. The second set of problems is related to the knowledge of the vertical distribution of cyanobacteria in bloom conditions. Using phycocyanin and chlorophyll *a* fluorometers together in profiling the water column should reveal variability in stratification of cyanobacteria and how it is related to remote sensing signal.

One of the issues related to the stratification of cyanobacteria is the depth of penetration of reflected sunlight. The layer from which the remote sensing signal is coming may be very thin if cyanobacteria reach very high quantities near the water surface. The optical properties of extremely dense cyanobacterial blooms differ significantly from moderate blooms because the light passing through them is more scattered than in the "normal" situations. The *in situ* sampling methodology should be changed when collecting data for calibration/ validation of remote sensing. Point samplings should be replaced by measurements that take into account both vertical and horizontal heterogeneity of biomass in cyanobacterial blooms. This also concerns all other studies carried out in seas and lakes where cyanobacterial blooms occur as it is not possible to evaluate representativeness of a random single sample in situations where phytoplankton biomass is varying in orders of magnitude within small horizontal and vertical distances.

Appropriate technical equipment may help to carry out these measurements. However, as already mentioned in the Introduction of the thesis, intensive cyanobacterial blooms do not occur every year. Cyanobacterial blooms may occur in areas not reachable by vessels, or at times when vessels are not available. These blooms are also extremely heterogeneous both horizontally and vertically.

The capabilities of the aircraft mounted sensors should be studied as well. These sensors have better viewing angle and spectral band combination than satellite remote sensing sensors, which are important qualities in such extreme heterogenous environments like cyanobacterial blooms.

Consequently, collecting the statistically significant amount of information about cyanobacterial blooms may take many years. Optical modelling can be a useful tool for developing remote sensing methods for quantitative mapping of cyanobacterial blooms. However, the models are only useful when we have good knowledge on the cyanobacterial blooms and other natural conditions.

REFERENCES

Ahn Y.-H., Bricaud A. & Morel A. (1992). Light backscattering efficiency and related properties of some phytoplankters. *Deep-Sea Research*, 39, 1835–1855.

Anderson D.M. (2003). Phytoplankton blooms. *Encyclopaedia of Ocean Sciences*, 2179–2192.

Bryant D.A. (1986). The cyanobacterial photosynthetic apparatus: comparison to those of higher plants and photosynthetic bacteria. Pages 423–500 in: T. Platt, W.K.W. Li eds. *Photosynthetic Picoplankton.* Canadian Bulletin of Fisheries and Aquatic Sciences, 214.

Capone D.G. & Subramaniam A. (2005). Seeing microbs from space. *ASM News,* 71(4), 179–186.

Codd G.A. (1998). Cyanobacterial blooms and toxins in fresh-, brackish and marine waters. Pages 13–17 in: B. Reguera, J. Blanco, M.L. Fernàndez, T. Wyatt eds. *Harmful Algae, Proceedings of the VIII International Conference on Harmful Algae, Vigo, Spain 25–29 June 1997.* Vigo: Xunta de Galicia and Intergovernmental Oceanographic Commission of UNESCO.

Darecki, M. & Stramski, D. (2004). An evaluation of MODIS and SeaWiFS bio-optical algorithms in the Baltic Sea. *Remote sensing of Environment,* 89, 326–350.

Davies-Colley R. J., Pridmore R. D. & Hewitt, J. E. (1986). Optical properties of some freshwater phytoplanktonic algae. *Hydrobiology,* 133, 165–178.

Dekker A.G., Malthus T.J. & Seyhan E. (1991). Quantitative modelling of inland water-quality for high-resolution mss systems. *IEEE Transactins on Geoscience and Remote Sensing,* 29, 89–95.

Dekker A.G., Malthus T.J. & Goddijn L.M. (1992). Monitoring cyanobacteria in eutrophic waters using airborne imaging spectroscopy and multispectral remote sensing systems. *Proceedings of 6th Australasian Remote Sensing Conference,* 1, 204–214.

Ferguson A.J.D., Pearson M.J. & Reynolds C.S. (1996). Eutrophication of natural waters and toxic algal blooms. In: R.E. Hester, R.H. Harrison eds. *Agricultural Chemicals and the Environment. Issues in Environmental Science and Technology 5.* The Royal Society of Chemistry, Cambridge.

Fogg G.E., Stewart W.D.P., Fay P. & Walsby A.E. (1973). *The Blue-Green Algae.* Academic Press, London.

Gieskes W.W. (1991). Algal pigment fingerprints: clue to taxon specific abundance, productivity, and degradation of phytoplankton in seas and oceans. Pages 61–99 in: Demers S. ed. *Particle analysis in oceanography. NATO ASI Series. Vol G27.* Springer-Verlag, Berlin, Germany.

Golubic S. & Soeng-Joo L. (1999). Early cyanobacterial fossil record: preservation, palaeoenvironments and identification. *European Journal of Phycology,* 34, 339–348.

Gordon H.R., Brown O.B. & Jacobs, M.M. (1975). Computed relationships between the inherent and apparent optical properties of a flat, homogenous ocean. *Applied Optics,* 14, 417–427.

Gordon H.R. & Clark D.K. (1980). Remote sensing optical properties of a stratified ocean: an improved interpretation. *Applied Optics,* 19, 598–600.

Håkanson B.G. & Moberg M. (1994). The algal bloom in the Baltic during July and August 1991, as observed from NOAA weather satellites. *International Journal of Remote Sensing,* 15, 963–965.

Hu C., Chen Z., Clayton T. D., Swarzenski P., Brock J. C. & Muller-Karger F. E. (2004). Assessment of estuarine water-quality indicators using MODIS medium-resolution bands: initial results from Tampa Bay, FL. *Remote Sensing of Environment*, 93, 423–441.

Jeffrey S.W. & Vesk M. (1996). Introduction to marine phytoplankton and their pigment signatures. In: S.W. Jeffrey, R.F.C. Mantoura, S.W. Wright eds. *Phytoplankton pigments in oceanography: guidelines to modern methods.* UNESCO.

Joint I. & Groom B. (2000). Estimation of phytoplankton production from space: Current status and future potential of satellite remote sensing. *Journal of Experimental Marine Biology and Ecology,* 250, 233–255.

Jupp D.L.B., Kirk J.T.O. & Harris G.P. (1994). Detection, identification and mapping of cyanobacteria–using remote sensing to measure the optical quality of turbid inland waters. *Australian Journal of Marine and Freshwater Research,* 45, 801–828.

Kahru M., Leppänen J.-M. & Rud O. (1993). Cyanobacterial blooms cause heating of the sea surface. *Marine Ecolocy – Progress Series,* 101, 1–7.

Kahru M. (1997). Using satellites to monitor large-scale environmental change in the Baltic Sea. Pages 43–61 in M. Kahru, C.W. Brown eds. *Monitoring algal blooms: New techniques for detecting large-scale environmental change.* Springer-Verlag.

Kahru M., Leppänen J.-M., Rud O. & Savchuk O.P. (2000). Cyanobacteria blooms in the Gulf of Finland triggered by saltwater inflow into the Baltic Sea. *Marine Ecolocy – Progress Series,* 207, 13–18.

Kirk J.T.O. (1994). *Light and photosynthesis in aquatic ecosystems.* 2nd ed. Cambridge University Press.

Kutser T. (2004). Quantitative detection of chlorophyll in cyanobacterial blooms by satellite remote sensing. *Limnology and Oceanography,* 49, 2179–2189.

Lee T., Tsuzuki M., Takeuchi T., Yokoyama K. & Karube I. (1994). In vivo fluorometric method for early detection of cyanobacterial waterblooms. *Journal of Applied Phycology,* 6, 489–495.

Lillesand T. & Kiefer R. (1999). *Remote Sensing and Image Interpretation.* 4th Edition, John Wiley & Sons Inc.

Lotter A.F. (2001). The paleolimnology of Soppensee (Central Switzerland), as evidenced by diatom, pollen, and fossil-pigment analyses. *Journal of Paleolimnology*, 25, 65–79.

Millie D.F., Paerl H.W. & Hurley J.P. (1993). Microalgal pigment assessments using high-performance liquid chromatography: a synopsis of organismal and ecological applications. *Canadian Journal of Fisheries and Aquatic Sciences,* 50, 2513–2527.

Mobley C.D. & Sundman L.K. (2001). *Hydrolight 4.2 Users' Guide*. Sequoia Scientific.

Niemistö L., Rinne I., Melvasalo T. & Niemi Å. (1989). Blue-green algae and their nitrogen fixation in the Baltic Sea in 1980, 1982 and 1984. *Meri*, 17, 1–59.

Paavel P. (2008). *Bio-optical properties of turbid lakes*. Dissertationes Biologicae Universitatis Tartuensis, Tartu.

Rantajärvi E., Olsonen R., Hällfors S., Leppänen J.-M. & Raateoja M. (1998). Effect of sampling frequency on detection of natural variability in phytoplankton: Unattended high-frequency measurements on board ferries in the Baltic Sea. *ICES Journal of Marine Scince,* 55, 697–704.

Reinart A. & Kutser T. (2006) Comparsion of different satellite sensors in detecting cyanobacterial bloom events in the Baltic Sea. *Remote Sensing of Environment*, 102, 74–85.

Richardson L.L. (1996). Remote Sensing of Algal Bloom Dynamics. *BioScience,* 46 (7), 492–501.

Rowan K.S. (1989). *Photosynthetic pigments of algae*. Cambridge University Press, Cambridge, UK.

Seppälä J., Ylöstalo P., Kaitala S., Hällfors S., Raateoja M. & Maunula P. (2007). Ship-of-opportunity based phycocyanin fluorescence monitoring of filamentous cyanobacteria bloom dynamics in the Baltic Sea. *Estuarine, Coastal and Self Science*, 73, 489–500.

Siegel H., Gerth M., Neumann T. & Doerrfer R. (1999). Case studies on phytoplankton blooms in coastal and open waters of the Baltic Sea using Coastal Zone Colour Scanner data. *International Journal of Remote Sensing*, 20, 1249–1264.

Siegel H. & Gerth M. (2000). Remote-sensing studies of the exceptional summer of 1997 in the Baltic Sea: the warmest August of the century, the Oder flood, and phytoplankton blooms. In: D. Halpern ed. *Satellites, oceanography and society.* Elsevier Science.

Siegel H., Gerth M., Ohde T. & Heene T. (2005). Ocean color remote sensing relevant water constituents and optical properties of Baltic Sea. *International Journal of Remote Sensing*, 26 (2), 315–330

Simis S.G.H., Peters S.W.M. & Gons H.J. (2005). Remote sensing of the cyanobacterial pigment phycocyanin in turbid inland water. *Limnology and Oceanogaphy,* 50 (1), 237–245.

Simis S.G.H., Ruiz-Verdú A., Domínguez J.A., Peña-Martinez R., Peters S.W.M. & Gons H.J. (2007). Influence of phytoplankton pigment composition on remote sensing of cyanobacterial biomass. *Remote Sensing of Environment,* 106, 414–427.

Smayda T.J. (1997). Harmful algal blooms: Their ecophysiology and general relevance to phytoplankton blooms in the sea. *Limnology and Oceanography*, 42, 1137–1153.

Stramska M. & Stramski D. (2005). Effects of non-uniform vertical profile of chlorophyll concentration on remote-sensing reflectance of the ocean. *Applied Optics,* 44, 1735–1747.

Subramaniam A., Carpenter E.J., Karentz D. & Falkowski P.G. (1999). Optical properties of the marine diazotrophic cyanobacteria *Trichodesmium* spp.; I Absorption and spectral photosynthetic characteristics. *Limnology and Oceanography*, 44, 608–617.

Subramaniam A., Kratzer S., Carpenter E.J. & Söderbäck E. (2000). Remote sensing and optical in-water measurements of a cyanobacteria bloom in the Baltic Sea. *Proceedings of the Sixth International Conference on Remote Sensing for Marine and Coastal Environments,* Charleston, South Carolina.

Sutcliffe D.W. & Jones J.G. (1992). *Eutrophication: Research and Application to Water Supply*. Freshwater Biological Association, Windermere, England.

Svejkovsky J. & Shandley J. (2001). Detection of offshore plankton blooms with AVHRR and SAR imagery. *International Journal of Remote Sensing,* 22, 471–485.

Tandeu de Marsac N. (1977). Occurrence and nature of chromatic adoptions in cyanobacteria. *Journal of Bacteriology,* 130, 82–91.

Ting C.S., Rocap G., King J. & Chisholm S.W. (2002). Cyanobacterial photosynthesis in the oceans: the origins and significance of divergent light-harvesting strategies. *Trends in Microbiology,* 10, 134–142.

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. (2007). Internal ecosystem feedbacks enchance nitrogen-fixing cyanobacteria blooms and complicate management in the Baltic Sea. *Ambio*, 36 (2), 186–194.

Vepsäläinen J., Pyhälahti T., Rantajärvi E., Kallio K., Pertola S., Stipa T., Kiirikki M., Pulliainen J. & Seppälä J. (2005). The combined use of optical remote sensing data and unattended flow-through fluorometer measurements in the Baltic Sea. *International Journal of Remote Sensing*, 26(2), 261–282.

Vincent R.K., Qin X., McKay R.M.L., Miner J., Czajkowski K., Savino J. & BridgemanT. (2004). Phycocyanin detection from LANSAT TM data for mapping cyanobacterial blooms in Lake Erie. *Remote Sensing of Environment,* 89, 381–392.

Viskari P.J. & Colyer C.L. (2003). Rapid extraction of phycobiliproteins from cultured cyanobacteria samples. *Analytical Biochemistry,* 319, 263–271.

Voipio A. (1981) The Baltic Sea. *Elsevier Oceanography Series*, 30.

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.

Waterbury J.B., Watson S.W., Guillard R.R.L. & Brand L.E. (1979). Widespread occurrence of a unicellular, marine, planktonic cyanobacterium. *Nature*, 277, 293–294.

Öström B. (1976). Fertilisation of the Baltic by nitrogen fixation in the blue-green algae *Nodularia spumigena*. *Remote Sensing of Environment,* 4, 305–310.

SUMMARY IN ESTONIAN

Mudelhinnang parandamaks kaugseire kasutamist tsüanobakterite tuvastamisel ja kvatitatiivsel seirel

Tsüanobakterite õitsengud esinevad peaaegu igal suvel, kattes sageli rohkem kui 100 000 km^2 Läänemere pinnast (Kahru, 1997). Fütoplanktoni hulka vees on vaja teada näiteks mere primaarprodukstsiooni ja vee kvaliteedi hindamiseks. Lisaks võivad tsüanobakterite toksiinid esile kutsuda erinevat tüüpi probleeme nii inimestel, kaladel kui loomadel ning põhjustada majanduslikku kahju olulistes mere-äärsetes rekreatsioonipiirkondades. Seetõttu on potentsiaalselt toksiliste tsüanobakterite õitsengute avastamine ja seire olulise tähtsusega.

Merekeskkonna seire Eesti rannikuvetes põhineb veeproovide uurimisel, mida kogutakse piiratud arvul (kuni 35) mõõtejaamadest kord aastas ning suurema sagedusega (kaks korda kuus) mõõtejaamadest, mida on kokku 12. On selge, et nii väikese arvu mõõtejaamade ning suure ajalise intervalliga tehtud mõõtmiste abil ei ole võimalik adekvaatselt hinnata muutusi fütoplanktoni biomassis, seda eriti fütoplanktoni õitsengute ajal.

Üheks võimaluseks koguda detailsemat informatsiooni fütoplanktoni hulga kohta on kasutada regulaarliinidel sõitvaid reisi- ja kaubalaevu, varustades need automaatsete mõõtesüsteemidega. Võrreldes punktmõõtmistega, suureneb sellise meetodi kasutamisel mõõtmiste sagedus ja enamasti ka uuritav ala, kuid selle piiranguks on vetikate biomassi hindamine vaid laevateede alal ja vaid ühelt fikseeritud sügavuselt.

Fütoplanktoni hulka meres on võimalik tuvastada ka erinevate satelliitide või lennuvahenditel paiknevate kaugseire sensorite abil. Kui kaugseire meetoditel on tsüanobakterite õitsengute ulatuse hindamine suhteliselt levinud, milleks võib kasutada väga erinevaid sensoreid, siis õitsengute biomassi hindamine on senini lahendamata probleem.

Antud töö eesmärgiks oli välja selgitada:

- kas vee heleduskoefitsiendi spektrite järgi on tsüanobaktereid kaugseire meetodite abil võimalik eristada teistest fütoplanktoni liikidest
- kui suur peaks sellisel juhul olema tsüanobakterite hulk vees
- millise spektraalse ning ruumilise lahutusvõimega peaksid olema selleks kasutatavad kaugseire sensorid
- kas satelliidi MODIS spektrikanaleid 1 ja 2 saab kasutada tsüanobakerite biomassi hindamiseks
- millist mõju avaldab kaugseire signaalile tsüanobakterite ebaühtlane vertikaalne jaotus

Kuna tsüanobakterite õitsengud on ajas ja ruumis väga varieeruvad, siis võib nende uurimine *in situ* mõõtmiste abil võtta aastaid või isegi aastakümneid. Sellepärast on käesolevas töös põhiliselt kasutatud mudelarvutusi, mis

baseeruvad labori ja *in situ* mõõtmistel ning võimaldavad simuleerida kaugseire sensoritega mõõdetavat signaali väga erinevates tingimustes.

Töö tulemusena leiti, et piisava spektraalse lahutusvõimega (10 nm või vähem) ja kõrge tundlikkusega kaugseire instrumendid võimaldavad tsüanobakterite tuvastamist ainult tsüanobakteritele omase fükobiliproteiini, fükotsüaniini, kaudu (artikkel **I**). Fükotsüaniin neelab valgust kitsas lainepikkuste vahemikus (620–630 nm), mis tekitab vee heleduskoefitsiendi spektris lokaalse miinimumi. See miinimum on kaugseire abil tuvastatav juhul kui tsüanobakterite hulk vees on piisavalt suur.

Mõned fütoplanktoni liigid (*Prymnesiophyceae* sp.) võivad sisaldada suuremal määral klorofülli c_1 ja c_2 ning seetõttu põhjustavad vee heleduskoefitsiendi spektris muutuseid, mis on sarnased fükotsüaniini tekitatud mõjule. Kuid teadaolevalt tsüanobakterid ja *Prymnesiphyceae* sp. liigid üldjuhul ühes ja samas looduslikus keskkonnas ei esine. Seega ei tohiks tsüanobakterite tuvastamine kaugseire meetoditel olla võimatu.

Mudelarvutuste tulemused näitavad (artikkel **I**), et Läänemere avaosale sarnaste optiliste omadustega vees peaks klorofüll *a* kontsentratsioon olema vähemalt 8–10 mg/m^3, et fükotsüaniini põhjustatud neeldumine oleks vee heleduskoefitsiendi spektris tuvastatav hüperspektraalsete instrumentidega. Seega, antud tulemuste põhjal ei saaks tuvastada potentsiaalselt toksilisi tsüanobakterite õitsenguid Läänemeres väga varases faasis kuna klorofüll *a* kontsentratsiooni üle 4 mg/m^3 loetakse siin juba õitsenguks. Üksikud olemasolevad *in situ* mõõtmistulemused aga näitavad, et identifitseerimine võib esineda ka suuremate konsentratsioonide juures, sõltuvalt õitsengu koosluse moodustavatest liikidest ja tsüanobakterite fotosünteetilisest aktiivsusest.

Multispektraalsete sensoritega satelliitide, nagu ALI, Landsat ja MODIS, abil ei ole võimalik tsüanobaktereid teistest fütoplanktoni liikidest eristada kuna nendel sensoritel puuduvad 630 ja 650 nm piirkonnas spektrikanalid (artikkel **II**). Satelliitidest on vaid MERIS'el tsüanobakterite avastamiseks sobivad spektrikanalid.

Tsüanobakterite õitsengute ulatuse operatiivseks seireks on hetkel sobivaim satelliit MODIS (kuni 4 pilti päevas). MODIS'e spektraalsete tulemuste järgi ei saa küll otseselt identifitseerida tsüanobakterite poolt domineeritavaid veemasse, kuid näiteks õitsengute ulatuse määramine on täiesti teostatav. Lisaks on satelliidil MODIS kaks spektrikanalit 250-meetrilise ruumilise lahutusega. Selline ruumilise lahutuse ja ajalise sageduse kombinatsioon on hetkel parim, mille abil tagada operatiivset seiret. Käesoleva töö modelleerimistulemused (artikkel **III**) näitavad, et kuigi MODIS'e esimene spektrikanal ei ole ette nähtud vee kaugseireks, saab siiski selle abil kaardistada tsüanobakterite õitsengute ulatust ja hinnata biomassi. Antud tulemused on aga peamiselt teoreetilised ja ei ole reaalsetes mõõtmistes kasutatavad.

Erinevalt teistest fütoplanktoni liikidest on tsüanobakterid suutelised reguleerima oma ujuvust ning kogunevad tihti veepinna alla või moodustavad pinnal ujuvaid kogumeid. Modelleerimistulemused (artikkel **IV**) näitasid, et

tsüanobakterite vertikaalsel jaotusel võib olla väga oluline mõju vee heleduskoefitsiendi spektritele ja ka kaugseire abil saadud biomassi hinnangutele. Tsüanobakterite biomassi uurimiseks ja/või kaugseire algoritmide välja töötamiseks tsüanobakterite biomassi hindamisel on oluline teada tsüanobakterite vertikaalset jaotust veesambas ning ei ole õige kasutada ühest sügavusest kogutud või segatud veeproovi. Kuna käesolevas töös kasutatud mudelid vajavad reaalsetel mõõtmistulemustel põhinevaid sisendeid, siis uuriti Läänemere vee optilisi omadusi nii *in situ* mõõtmiste kui laborimõõtmiste abil. Artiklis **V** on uuritud tagasihajumiskoefitsiendi muutlikust Läänemeres. Lisaks on töös kasutatud ka seni avaldamata *in situ* mõõtmiste tulemusi.

Tuginedes väitekirja tulemustele võib välja tuua mõningad töösuunad, mis vajaksid esmajärjekorras arendamist. Kuna käesoleva töö järeldused on tehtud ideaalsetes kasvutingimustes paiknenud puhaste vetikakultuuride optilistel omadustel, siis oleks kindlasti vaja samast aspektist uurida looduslike fütoplanktoni koosluse optilisi omadusi. Tsüanobakterite õitsengute uurimisel oleks vajalik muuta veeproovide kogumise strateegiat. Detailsemalt peaks uurima tsüanobakterite ning teiste fütoplanktoni liikide vertikaalset jaotust tsüanobakterite õitsengute ajal. Kaugseire osas, eriti rannikuvetes, tuleks koguda andmeid ka lennuvahenditel paiknevate sensorite abil, kuna need on suure spektraalse ja ruumilise lahutusega. Kuna kaugseire algoritmide edasiseks väljatöötamiseks vajaliku materjali kogumine võib vaid merel teostatavate mõõdistuse baasil võtta aega aastakümneid, siis seetõttu jääb ka tulevikus väga oluline osa modelleerimisele.

ACNOWLEDGEMENTS

I am grateful to my supervisor Tiit Kutser who introduced remote sensing and water optics to me and guided me with his good and encouraging ideas to writing my doctor's thesis. I thank Ele Vahtmäe who has joyfully helped me get through all the tough moments of my studies. I would like to express great gratitude to Niklas Strömbeck, who performed the laboratory works.

I thank all the employees of the Estonian Marine Institute (University of Tartu), Tartu Observatory and Marine Systems Institute (Tallinn University of Technology) who have supported and helped me in completion of this thesis.

For a pleasant co-operation I want to thank Arnold Dekker and the team of Environmental Remote Sensing Group in the CSIRO Land and Water as well as Giuseppe Zibordi and Jean-François Berthon from the Joint Research Centre (European Commission). I also want to thank the team of research vessel "Aranda" and the employees of the Finnish Institute of Marine Research who have helped me in the fieldwork and with the laboratory work.

My warmhearted gratitude belongs to my family and friends. I am happy to have you beside me. I am grateful to my dear Mait who has supported me by being patient and cheerful when I was struggling through some difficult moments of my work and studies. I thank my dear mother who has always supported and encouraged me in everything. My very special thanks go to my little sister Anneli who is always there for me and who also helped me with the linguistic proofreading of this thesis.

The laboratory analysis on inherent optical properties of different phytoplankton species was supported by Swedish National Space Board grant 131/03. Author's scholarship was funded by the Estonian Science Foundation grant 6051 and the study in general was funded by the research grant 0712699s05 of Estonian Ministry of Education and Research.

Last but not least I am grateful to the POGO-IOC-SCOR, to the Baltic Sea Regional Project (BSRP), to the Kristjan Jaak fellowship program and to the Doctoral School of Ecology and Environmental Sciences for several scholarships, which have helped me to complete my studies.

PUBLICATIONS

CURRICULUM VITAE

Liisa Metsamaa

Date of birth:	December 11, 1981
Citizenship:	Estonian
Address:	Estonian Marine Institute, University of Tartu, Mäealuse 10a, Tallinn 12618, Estonia
Phone:	+372 5098951
Fax:	+372 6718900
E-mail:	liisa.metsamaa@sea.ee

Education

1988–2000	Saue Gymnasium
2000–2004	Tallinn Pedagogical University, Faculty of Mathematics and Natural Science, *BSc* in marine biology
2004–2005	University of Tartu, Faculty of Biology and Geography, Institute of Zoology and Hydrobiology, *MSc* in hydrobiology.
2005–2009	University of Tartu, Faculty of Science and Technology, Institute of Ecology and Earth Sciences, PhD studies in hydrobiology.

Professional experience

2005–2006	Estonian Marine Institute, University of Tartu, Department of Remote Sensing and Marine Optics, engineer.
2006– present	Estonian Marine Institute, University of Tartu, Department of Remote Sensing and Marine Optics, research fellow.

Scientific activity

Main topics:	Study the possible usage of ocean color remote sensing for qualitative and quantitative mapping of cyanobacteria in the Baltic Sea.

Publications

Kutser, T., **Metsamaa**, **L.**, Strömbek, N. & Vahtmäe, E. 2006. Monitoring cyanobacterial blooms by satellite remote sensing. *Estuarine, Coastal and Shelf Science*, 67: 303–312

Kutser, T., **Metsamaa**, **L.**, Vahtmäe, E. & Strömbeck, N. 2006. On suitability of MODIS 250 m resolution band data for quantitative mapping cyanobacterial blooms. *Proceedings of Estonian Academy of Sciences. Biology-Ecology*, 55(4): 318–328

Kutser T., Vahtmäe E. & **Metsamaa** L. 2006. Spectral library of Estonian coastal water bottom types. *Proceedings of Estonian Academy of Sciences. Biology-Ecology*, 55(4): 329–340

Metsamaa, L., Kutser, T. & Strömbeck, N. 2006. Recognising cyanobacterial blooms based on their opticale signature: a modelling study. *Boreal Environment Research,* 11(6): 493–506

Kutser, T., Vahtmäe, E., Roelfsema, C.M. & **Metsamaa, L.** 2007. Photo-library method for mapping seagrass biomass. *Estuarine, Coastal and Shelf Science*, 75: 559–563

Kutser, T., **Metsamaa, L.**, Vahtmäe, E. & Aps, R. 2007. Operative monitoring of the extent of dredging plumes in coastal ecosystems using MODIS satellite imagery. *Journal of Coastal Research*, SI50: 180–184

Kutser, T., **Metsamaa, L.** & Dekker, A.G. 2008. Influence of the vertical distribution of cyanobacteria in the water column on the remote sensing signal. *Estuarine, Coastal and Shelf Science*, 78: 649–654

Kutser, T., Hiire, M., **Metsamaa, L.**, Vahtmäe, E., Paavel, B. & Aps, R. 2009. Field measurements of spectral backscattering coefficient of the Baltic Sea and boreal lakes. *Boreal Environment Research,* 14: 305–312

Kutser, T., Paavel, B., **Metsamaa, L.** & Vahtmäe, E. 2009. Mapping coloured dissolved organic matter concentration in coastal waters. *International Journal of Remote Sensing*, (in press)

ELULOOKIRJELDUS

Liisa Metsamaa

Sünniaeg:	11.detsember 1981
Kodakondsus:	Eestlane
Aadress:	Tartu Ülikooli Eesti Mereinstituut, Mäealuse 10a, Tallinn 12618
Telefon:	+372 5098951
Faks:	+372 6718900
E-mail:	liisa.metsamaa@sea.ee

Hariduskäik

1988–2000	Saue Gümnaasium
2000–2004	Tallinna Pedagoogikaülikool, Matemaatika ja loodusteaduste teaduskond, *BSc* bioloogias (merebioloog-keskkonnaspetsialist)
2004–2005	Tartu Ülikool, Bioloogia-geograafiateaduskond, Zooloogia ja Hüdrobioloogia Instituut, *MSc* hüdrobioloogias.
2005–2009	Tartu Ülikool, Loodus- ja tehnoloogiateaduskond, Ökoloogia ja Maateaduste Instituut, *PhD* hüdrobioloogias.

Teenistuskäik

2005–2006	Tartu Ülikooli Eesti Mereinstituut, kaugseire ja mereoptika osakond, insener.
2006– praeguseni	Tartu Ülikooli Eesti Mereinstituut, kaugseire ja mereoptika osakond, teadur.

Teadustegevus

Peamised uurimissuunad:	Tsüanobakterite tuvastamine ja jälgimine kaugseire meetodite abil Läänemeres.

DISSERTATIONES BIOLOGICAE UNIVERSITATIS TARTUENSIS

1. **Toivo Maimets**. Studies of human oncoprotein p53. Tartu, 1991, 96 p.
2. **Enn K. Seppet**. Thyroid state control over energy metabolism, ion transport and contractile functions in rat heart. Tartu, 1991, 135 p.
3. **Kristjan Zobel**. Epifüütsete makrosamblike väärtus õhu saastuse indikaatoritena Hamar-Dobani boreaalsetes mägimetsades. Tartu, 1992, 131 lk.
4. **Andres Mäe**. Conjugal mobilization of catabolic plasmids by transposable elements in helper plasmids. Tartu, 1992, 91 p.
5. **Maia Kivisaar**. Studies on phenol degradation genes of *Pseudomonas* sp. strain EST 1001. Tartu, 1992, 61 p.
6. **Allan Nurk**. Nucleotide sequences of phenol degradative genes from *Pseudomonas sp.* strain EST 1001 and their transcriptional activation in *Pseudomonas putida.* Tartu, 1992, 72 p.
7. **Ülo Tamm**. The genus *Populus* L. in Estonia: variation of the species biology and introduction. Tartu, 1993, 91 p.
8. **Jaanus Remme**. Studies on the peptidyltransferase centre of the *E.coli* ribosome. Tartu, 1993, 68 p.
9. **Ülo Langel**. Galanin and galanin antagonists. Tartu, 1993, 97 p.
10. **Arvo Käärd**. The development of an automatic online dynamic fluorescense-based pH-dependent fiber optic penicillin flowthrought biosensor for the control of the benzylpenicillin hydrolysis. Tartu, 1993, 117 p.
11. **Lilian Järvekülg**. Antigenic analysis and development of sensitive immunoassay for potato viruses. Tartu, 1993, 147 p.
12. **Jaak Palumets**. Analysis of phytomass partition in Norway spruce. Tartu, 1993, 47 p.
13. **Arne Sellin**. Variation in hydraulic architecture of *Picea abies* (L.) Karst. trees grown under different enviromental conditions. Tartu, 1994, 119 p.
13. **Mati Reeben**. Regulation of light neurofilament gene expression. Tartu, 1994, 108 p.
14. **Urmas Tartes**. Respiration rhytms in insects. Tartu, 1995, 109 p.
15. **Ülo Puurand**. The complete nucleotide sequence and infections *in vitro* transcripts from cloned cDNA of a potato A potyvirus. Tartu, 1995, 96 p.
16. **Peeter Hõrak**. Pathways of selection in avian reproduction: a functional framework and its application in the population study of the great tit (*Parus major*). Tartu, 1995, 118 p.
17. **Erkki Truve**. Studies on specific and broad spectrum virus resistance in transgenic plants. Tartu, 1996, 158 p.
18. **Illar Pata**. Cloning and characterization of human and mouse ribosomal protein S6-encoding genes. Tartu, 1996, 60 p.
19. **Ülo Niinemets**. Importance of structural features of leaves and canopy in determining species shade-tolerance in temperature deciduous woody taxa. Tartu, 1996, 150 p.

20. **Ants Kurg**. Bovine leukemia virus: molecular studies on the packaging region and DNA diagnostics in cattle. Tartu, 1996, 104 p.
21. **Ene Ustav**. E2 as the modulator of the BPV1 DNA replication. Tartu, 1996, 100 p.
22. **Aksel Soosaar**. Role of helix-loop-helix and nuclear hormone receptor transcription factors in neurogenesis. Tartu, 1996, 109 p.
23. **Maido Remm**. Human papillomavirus type 18: replication, transformation and gene expression. Tartu, 1997, 117 p.
24. **Tiiu Kull**. Population dynamics in *Cypripedium calceolus* L. Tartu, 1997, 124 p.
25. **Kalle Olli**. Evolutionary life-strategies of autotrophic planktonic microorganisms in the Baltic Sea. Tartu, 1997, 180 p.
26. **Meelis Pärtel**. Species diversity and community dynamics in calcareous grassland communities in Western Estonia. Tartu, 1997, 124 p.
27. **Malle Leht**. The Genus *Potentilla* L. in Estonia, Latvia and Lithuania: distribution, morphology and taxonomy. Tartu, 1997, 186 p.
28. **Tanel Tenson**. Ribosomes, peptides and antibiotic resistance. Tartu, 1997, 80 p.
29. **Arvo Tuvikene**. Assessment of inland water pollution using biomarker responses in fish *in vivo* and *in vitro.* Tartu, 1997, 160 p.
30. **Urmas Saarma**. Tuning ribosomal elongation cycle by mutagenesis of 23S rRNA. Tartu, 1997, 134 p.
31. **Henn Ojaveer**. Composition and dynamics of fish stocks in the gulf of Riga ecosystem. Tartu, 1997, 138 p.
32. **Lembi Lõugas**. Post-glacial development of vertebrate fauna in Estonian water bodies. Tartu, 1997, 138 p.
33. **Margus Pooga**. Cell penetrating peptide, transportan, and its predecessors, galanin-based chimeric peptides. Tartu, 1998, 110 p.
34. **Andres Saag**. Evolutionary relationships in some cetrarioid genera (Lichenized Ascomycota). Tartu, 1998, 196 p.
35. **Aivar Liiv**. Ribosomal large subunit assembly *in vivo*. Tartu, 1998, 158 p.
36. **Tatjana Oja**. Isoenzyme diversity and phylogenetic affinities among the eurasian annual bromes (*Bromus* L., Poaceae). Tartu, 1998, 92 p.
37. **Mari Moora**. The influence of arbuscular mycorrhizal (AM) symbiosis on the competition and coexistence of calcareous crassland plant species. Tartu, 1998, 78 p.
38. **Olavi Kurina**. Fungus gnats in Estonia (*Diptera: Bolitophilidae, Keroplatidae, Macroceridae, Ditomyiidae, Diadocidiidae, Mycetophilidae*). Tartu, 1998, 200 p.
39. **Andrus Tasa**. Biological leaching of shales: black shale and oil shale. Tartu, 1998, 98 p.
40. **Arnold Kristjuhan.** Studies on transcriptional activator properties of tumor suppressor protein p53. Tartu, 1998, 86 p.

41. **Sulev Ingerpuu.** Characterization of some human myeloid cell surface and nuclear differentiation antigens. Tartu, 1998, 163 p.
42. **Veljo Kisand.** Responses of planktonic bacteria to the abiotic and biotic factors in the shallow lake Võrtsjärv. Tartu, 1998, 118 p.
43. **Kadri Põldmaa.** Studies in the systematics of hypomyces and allied genera (Hypocreales, Ascomycota). Tartu, 1998, 178 p.
44. **Markus Vetemaa.** Reproduction parameters of fish as indicators in environmental monitoring. Tartu, 1998, 117 p.
45. **Heli Talvik.** Prepatent periods and species composition of different *Oesophagostomum* spp. populations in Estonia and Denmark. Tartu, 1998, 104 p.
46. **Katrin Heinsoo.** Cuticular and stomatal antechamber conductance to water vapour diffusion in *Picea abies* (L.) karst. Tartu, 1999, 133 p.
47. **Tarmo Annilo.** Studies on mammalian ribosomal protein S7. Tartu, 1998, 77 p.
48. **Indrek Ots.** Health state indicies of reproducing great tits (*Parus major*): sources of variation and connections with life-history traits. Tartu, 1999, 117 p.
49. **Juan Jose Cantero.** Plant community diversity and habitat relationships in central Argentina grasslands. Tartu, 1999, 161 p.
50. **Rein Kalamees.** Seed bank, seed rain and community regeneration in Estonian calcareous grasslands. Tartu, 1999, 107 p.
51. **Sulev Kõks.** Cholecystokinin (CCK) — induced anxiety in rats: influence of environmental stimuli and involvement of endopioid mechanisms and erotonin. Tartu, 1999, 123 p.
52. **Ebe Sild.** Impact of increasing concentrations of O_3 and CO_2 on wheat, clover and pasture. Tartu, 1999, 123 p.
53. **Ljudmilla Timofejeva.** Electron microscopical analysis of the synaptonemal complex formation in cereals. Tartu, 1999, 99 p.
54. **Andres Valkna.** Interactions of galanin receptor with ligands and G-proteins: studies with synthetic peptides. Tartu, 1999, 103 p.
55. **Taavi Virro.** Life cycles of planktonic rotifers in lake Peipsi. Tartu, 1999, 101 p.
56. **Ana Rebane.** Mammalian ribosomal protein S3a genes and intron-encoded small nucleolar RNAs U73 and U82. Tartu, 1999, 85 p.
57. **Tiina Tamm.** Cocksfoot mottle virus: the genome organisation and translational strategies. Tartu, 2000, 101 p.
58. **Reet Kurg.** Structure-function relationship of the bovine papilloma virus E2 protein. Tartu, 2000, 89 p.
59. **Toomas Kivisild.** The origins of Southern and Western Eurasian populations: an mtDNA study. Tartu, 2000, 121 p.
60. **Niilo Kaldalu.** Studies of the TOL plasmid transcription factor XylS. Tartu 2000. 88 p.

61. **Dina Lepik.** Modulation of viral DNA replication by tumor suppressor protein p53. Tartu 2000. 106 p.
62. **Kai Vellak.** Influence of different factors on the diversity of the bryophyte vegetation in forest and wooded meadow communities. Tartu 2000. 122 p.
63. **Jonne Kotta.** Impact of eutrophication and biological invasionas on the structure and functions of benthic macrofauna. Tartu 2000. 160 p.
64. **Georg Martin.** Phytobenthic communities of the Gulf of Riga and the inner sea the West-Estonian archipelago. Tartu, 2000. 139 p.
65. **Silvia Sepp.** Morphological and genetical variation of *Alchemilla L.* in Estonia. Tartu, 2000. 124 p.
66. **Jaan Liira.** On the determinants of structure and diversity in herbaceous plant communities. Tartu, 2000. 96 p.
67. **Priit Zingel.** The role of planktonic ciliates in lake ecosystems. Tartu 2001. 111 p.
68. **Tiit Teder.** Direct and indirect effects in Host-parasitoid interactions: ecological and evolutionary consequences. Tartu 2001. 122 p.
69. **Hannes Kollist.** Leaf apoplastic ascorbate as ozone scavenger and its transport across the plasma membrane. Tartu 2001. 80 p.
70. **Reet Marits.** Role of two-component regulator system PehR-PehS and extracellular protease PrtW in virulence of *Erwinia Carotovora* subsp. *Carotovora*. Tartu 2001. 112 p.
71. **Vallo Tilgar.** Effect of calcium supplementation on reproductive performance of the pied flycatcher *Ficedula hypoleuca* and the great tit *Parus major,* breeding in Nothern temperate forests. Tartu, 2002. 126 p.
72. **Rita Hõrak.** Regulation of transposition of transposon Tn*4652* in *Pseudomonas putida*. Tartu, 2002. 108 p.
73. **Liina Eek-Piirsoo.** The effect of fertilization, mowing and additional illumination on the structure of a species-rich grassland community. Tartu, 2002. 74 p.
74. **Krõõt Aasamaa.** Shoot hydraulic conductance and stomatal conductance of six temperate deciduous tree species. Tartu, 2002. 110 p.
75. **Nele Ingerpuu.** Bryophyte diversity and vascular plants. Tartu, 2002. 112 p.
76. **Neeme Tõnisson.** Mutation detection by primer extension on oligonucleotide microarrays. Tartu, 2002. 124 p.
77. **Margus Pensa.** Variation in needle retention of Scots pine in relation to leaf morphology, nitrogen conservation and tree age. Tartu, 2003. 110 p.
78. **Asko Lõhmus.** Habitat preferences and quality for birds of prey: from principles to applications. Tartu, 2003. 168 p.
79. **Viljar Jaks.** p53 — a switch in cellular circuit. Tartu, 2003. 160 p.
80. **Jaana Männik.** Characterization and genetic studies of four ATP-binding cassette (ABC) transporters. Tartu, 2003. 140 p.
81. **Marek Sammul.** Competition and coexistence of clonal plants in relation to productivity. Tartu, 2003. 159 p

82. **Ivar Ilves.** Virus-cell interactions in the replication cycle of bovine papillomavirus type 1. Tartu, 2003. 89 p.
83. **Andres Männik.** Design and characterization of a novel vector system based on the stable replicator of bovine papillomavirus type 1. Tartu, 2003. 109 p.
84. **Ivika Ostonen.** Fine root structure, dynamics and proportion in net primary production of Norway spruce forest ecosystem in relation to site conditions. Tartu, 2003. 158 p.
85. **Gudrun Veldre.** Somatic status of 12–15-year-old Tartu schoolchildren. Tartu, 2003. 199 p.
86. **Ülo Väli.** The greater spotted eagle *Aquila clanga* and the lesser spotted eagle *A. pomarina*: taxonomy, phylogeography and ecology. Tartu, 2004. 159 p.
87. **Aare Abroi.** The determinants for the native activities of the bovine papillomavirus type 1 E2 protein are separable. Tartu, 2004. 135 p.
88. **Tiina Kahre.** Cystic fibrosis in Estonia. Tartu, 2004. 116 p.
89. **Helen Orav-Kotta.** Habitat choice and feeding activity of benthic suspension feeders and mesograzers in the northern Baltic Sea. Tartu, 2004. 117 p.
90. **Maarja Öpik.** Diversity of arbuscular mycorrhizal fungi in the roots of perennial plants and their effect on plant performance. Tartu, 2004. 175 p.
91. **Kadri Tali.** Species structure of *Neotinea ustulata*. Tartu, 2004. 109 p.
92. **Kristiina Tambets.** Towards the understanding of post-glacial spread of human mitochondrial DNA haplogroups in Europe and beyond: a phylogeographic approach. Tartu, 2004. 163 p.
93. **Arvi Jõers.** Regulation of p53-dependent transcription. Tartu, 2004. 103 p.
94. **Lilian Kadaja.** Studies on modulation of the activity of tumor suppressor protein p53. Tartu, 2004. 103 p.
95. **Jaak Truu.** Oil shale industry wastewater: impact on river microbial community and possibilities for bioremediation. Tartu, 2004. 128 p.
96. **Maire Peters.** Natural horizontal transfer of the *pheBA* operon. Tartu, 2004. 105 p.
97. **Ülo Maiväli.** Studies on the structure-function relationship of the bacterial ribosome. Tartu, 2004. 130 p.
98. **Merit Otsus.** Plant community regeneration and species diversity in dry calcareous grasslands. Tartu, 2004. 103 p.
99. **Mikk Heidemaa.** Systematic studies on sawflies of the genera *Dolerus, Empria,* and *Caliroa* (Hymenoptera: Tenthredinidae). Tartu, 2004. 167 p.
100. **Ilmar Tõnno.** The impact of nitrogen and phosphorus concentration and N/P ratio on cyanobacterial dominance and N_2 fixation in some Estonian lakes. Tartu, 2004. 111 p.
101. **Lauri Saks.** Immune function, parasites, and carotenoid-based ornaments in greenfinches. Tartu, 2004. 144 p.

102. **Siiri Rootsi.** Human Y-chromosomal variation in European populations. Tartu, 2004. 142 p.
103. **Eve Vedler.** Structure of the 2,4-dichloro-phenoxyacetic acid-degradative plasmid pEST4011. Tartu, 2005. 106 p.
104. **Andres Tover.** Regulation of transcription of the phenol degradation *pheBA* operon in *Pseudomonas putida*. Tartu, 2005. 126 p.
105. **Helen Udras.** Hexose kinases and glucose transport in the yeast *Hansenula polymorpha*. Tartu, 2005. 100 p.
106. **Ave Suija.** Lichens and lichenicolous fungi in Estonia: diversity, distribution patterns, taxonomy. Tartu, 2005. 162 p.
107. **Piret Lõhmus.** Forest lichens and their substrata in Estonia. Tartu, 2005. 162 p.
108. **Inga Lips.** Abiotic factors controlling the cyanobacterial bloom occurrence in the Gulf of Finland. Tartu, 2005. 156 p.
109. **Kaasik, Krista.** Circadian clock genes in mammalian clockwork, metabolism and behaviour. Tartu, 2005. 121 p.
110. **Juhan Javoiš.** The effects of experience on host acceptance in ovipositing moths. Tartu, 2005. 112 p.
111. **Tiina Sedman.** Characterization of the yeast *Saccharomyces cerevisiae* mitochondrial DNA helicase Hmi1. Tartu, 2005. 103 p.
112. **Ruth Aguraiuja.** Hawaiian endemic fern lineage *Diellia* (Aspleniaceae): distribution, population structure and ecology. Tartu, 2005. 112 p.
113. **Riho Teras.** Regulation of transcription from the fusion promoters generated by transposition of Tn*4652* into the upstream region of *pheBA* operon in *Pseudomonas putida*. Tartu, 2005. 106 p.
114. **Mait Metspalu.** Through the course of prehistory in india: tracing the mtDNA trail. Tartu, 2005. 138 p.
115. **Elin Lõhmussaar.** The comparative patterns of linkage disequilibrium in European populations and its implication for genetic association studies. Tartu, 2006. 124 p.
116. **Priit Kupper.** Hydraulic and environmental limitations to leaf water relations in trees with respect to canopy position. Tartu, 2006. 126 p.
117. **Heili Ilves.** Stress-induced transposition of Tn*4652* in *Pseudomonas Putida.* Tartu, 2006. 120 p.
118. **Silja Kuusk.** Biochemical properties of Hmi1p, a DNA helicase from *Saccharomyces cerevisiae* mitochondria. Tartu, 2006. 126 p.
119. **Kersti Püssa.** Forest edges on medium resolution landsat thematic mapper satellite images. Tartu, 2006. 90 p.
120. **Lea Tummeleht.** Physiological condition and immune function in great tits (*Parus major* l.): Sources of variation and trade-offs in relation to growth. Tartu, 2006. 94 p.
121. **Toomas Esperk.** Larval instar as a key element of insect growth schedules. Tartu, 2006. 186 p.

122. **Harri Valdmann.** Lynx (*Lynx lynx*) and wolf (*Canis lupus*) in the Baltic region: Diets, helminth parasites and genetic variation. Tartu, 2006. 102 p.
123. **Priit Jõers.** Studies of the mitochondrial helicase Hmi1p in *Candida albicans* and *Saccharomyces cerevisia*. Tartu, 2006. 113 p.
124. **Kersti Lilleväli.** Gata3 and Gata2 in inner ear development. Tartu, 2007. 123 p.
125. **Kai Rünk.** Comparative ecology of three fern species: *Dryopteris carthusiana* (Vill.) H.P. Fuchs, *D. expansa* (C. Presl) Fraser-Jenkins & Jermy and *D. dilatata* (Hoffm.) A. Gray (Dryopteridaceae). Tartu, 2007. 143 p.
126. **Aveliina Helm.** Formation and persistence of dry grassland diversity: role of human history and landscape structure. Tartu, 2007. 89 p.
127. **Leho Tedersoo.** Ectomycorrhizal fungi: diversity and community structure in Estonia, Seychelles and Australia. Tartu, 2007. 233 p.
128. **Marko Mägi.** The habitat-related variation of reproductive performance of great tits in a deciduous-coniferous forest mosaic: looking for causes and consequences. Tartu, 2007. 135 p.
129. **Valeria Lulla.** Replication strategies and applications of Semliki Forest virus. Tartu, 2007. 109 p.
130. **Ülle Reier**. Estonian threatened vascular plant species: causes of rarity and conservation. Tartu, 2007. 79 p.
131. **Inga Jüriado**. Diversity of lichen species in Estonia: influence of regional and local factors. Tartu, 2007. 171 p.
132. **Tatjana Krama.** Mobbing behaviour in birds: costs and reciprocity based cooperation. Tartu, 2007.
133. **Signe Saumaa.** The role of DNA mismatch repair and oxidative DNA damage defense systems in avoidance of stationary phase mutations in *Pseudomonas putida.* Tartu, 2007. 172 p.
134. **Reedik Mägi**. The linkage disequilibrium and the selection of genetic markers for association studies in european populations. Tartu, 2007. 96 p.
135. **Priit Kilgas.** Blood parameters as indicators of physiological condition and skeletal development in great tits (*Parus major*): natural variation and application in the reproductive ecology of birds. Tartu, 2007. 129 p.
136. **Anu Albert**. The role of water salinity in structuring eastern Baltic coastal fish communities. Tartu, 2007. 95 p.
137. **Kärt Padari.** Protein transduction mechanisms of transportans. Tartu, 2008. 128 p.
138. **Siiri-Lii Sandre.** Selective forces on larval colouration in a moth. Tartu, 2008. 125 p.
139. **Ülle Jõgar.** Conservation and restoration of semi-natural floodplain meadows and their rare plant species. Tartu, 2008. 99 p.
140. **Lauri Laanisto.** Macroecological approach in vegetation science: generality of ecological relationships at the global scale. Tartu, 2008. 133 p.
141. **Reidar Andreson**. Methods and software for predicting PCR failure rate in large genomes. Tartu, 2008. 105 p.

142. **Birgot Paavel.** Bio-optical properties of turbid lakes. Tartu, 2008. 175 p.
143. **Kaire Torn.** Distribution and ecology of charophytes in the Baltic Sea. Tartu, 2008, 98 p.
144. **Vladimir Vimberg.** Peptide mediated macrolide resistance. Tartu, 2008, 190 p.
145. **Daima Örd.** Studies on the stress-inducible pseudokinase TRB3, a novel inhibitor of transcription factor ATF4. Tartu, 2008, 108 p.
146. **Lauri Saag.** Taxonomic and ecologic problems in the genus *Lepraria* (*Stereocaulaceae*, lichenised *Ascomycota*). Tartu, 2008, 175 p.
147. **Ulvi Karu.** Antioxidant protection, carotenoids and coccidians in greenfinches – assessment of the costs of immune activation and mechanisms of parasite resistance in a passerine with carotenoid-based ornaments. Tartu, 2008, 124 p.
148. **Jaanus Remm.** Tree-cavities in forests: density, characteristics and occupancy by animals. Tartu, 2008, 128 p.
149. **Epp Moks.** Tapeworm parasites *Echinococcus multilocularis* and *E. granulosus* in Estonia: phylogenetic relationships and occurrence in wild carnivores and ungulates. Tartu, 2008, 82 p.
150. **Eve Eensalu.** Acclimation of stomatal structure and function in tree canopy: effect of light and CO_2 concentration. Tartu, 2008, 108 p.
151. **Janne Pullat**. Design, functionlization and application of an *in situ* synthesized oligonucleotide microarray. Tartu, 2008, 108 p.
152. **Marta Putrinš.** Responses of *Pseudomonas putida* to phenol-induced metabolic and stress signals. Tartu, 2008, 142 p.
153. **Marina Semtšenko.** Plant root behaviour: responses to neighbours and physical obstructions. Tartu, 2008, 106 p.
154. **Marge Starast.** Influence of cultivation techniques on productivity and fruit quality of some *Vaccinium* and *Rubus* taxa. Tartu, 2008, 154 p.
155. **Age Tats.** Sequence motifs influencing the efficiency of translation. Tartu, 2009, 104 p.
156. **Radi Tegova.** The role of specialized DNA polymerases in mutagenesis in *Pseudomonas putida.* Tartu, 2009, 124 p.
157. **Tsipe Aavik.** Plant species richness, composition and functional trait pattern in agricultural landscapes – the role of land use intensity and landscape structure. Tartu, 2008, 112 p.
158. **Kaja Kiiver.** Semliki forest virus based vectors and cell lines for studying the replication and interactions of alphaviruses and hepaciviruses. Tartu, 2009, 104 p.
159. **Meelis Kadaja.** Papillomavirus Replication Machinery Induces Genomic Instability in its Host Cell. Tartu, 2009, 126 p.
160. **Pille Hallast.** Human and chimpanzee Luteinizing hormone/Chorionic Gonadotropin beta (*LHB/CGB*) gene clusters: diversity and divergence of young duplicated genes. Tartu, 2009, 168 p.

161. **Ain Vellak.** Spatial and temporal aspects of plant species conservation. Tartu, 2009, 86 p.
162. **Triinu Remmel.** Body size evolution in insects with different colouration strategies: the role of predation risk. Tartu, 2009, 168 p.
163. **Jaana Salujõe.** Zooplankton as the indicator of ecological quality and fish predation in lake ecosystems. Tartu, 2009, 129 p.
164. **Ele Vahtmäe.** Mapping benthic habitat with remote sensing in optically complex coastal environments. Tartu, 2009, 109 p.