





DISSERTATIONES BIOLOGICAE UNIVERSITATIS TARTUENSIS  
**142**

**BIRGOT PAAVEL**

Bio-optical properties of turbid lakes

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 at the University of Tartu on April 21, 2008 by the Council of the Faculty of Science and Technology, University of Tartu

Supervisors: Dr. Helgi Arst  
University of Tartu  
Faculty of Science and Technology,  
Estonian Marine Institute, University of Tartu

Prof. Toomas Saat,  
University of Tartu  
Faculty of Science and Technology,  
Estonian Marine Institute, University of Tartu

Opponent: Dr. Susanne Kratzer,  
Department of Systems Ecology,  
University of Stockholm, Sweden

Commencement: on 18 June 2008 at 10.15, Room 301, Vanemuise St. 46,  
Tartu.



Toetab Euroopa Liit



Eesti Riiklik Arengukava

The doctoral studies and the publication of the current thesis was supported by the Doctoral School of Ecology and Environmental Sciences created under the auspices of European Union Social Fund structural funds measure

*1.1. Educational System Supporting the Flexibility and Employability of the Labor force and Providing Opportunities of Lifelong Learning for All.*

ISSN 1024–6479

ISBN 978–9949–11–860–1 (trükis)

ISBN 978–9949–11–861–8 (PDF)

Autoriõigus Birgot Paavel, 2008

Tartu Ülikooli Kirjastus

[www.tyk.ee](http://www.tyk.ee)

Tellimus nr. 175

# CONTENTS

LIST OF ORIGINAL PUBLICATIONS .....	6
1. INTRODUCTION.....	8
2. REVIEW OF THE LITERATURE.....	10
2.1. Inherent optical properties .....	10
2.2. Apparent optical properties.....	14
3. MATERIAL AND METHODS .....	16
3.1. Study areas .....	16
3.2. <i>In situ</i> measurements.....	17
3.3. Laboratory measurements and methods.....	19
4. RESULTS AND DISCUSSION .....	21
4.1. Optically active substances in the water and correlation analyses ....	21
4.2. Contribution of different water constituents to the total absorption and attenuation of light.....	26
4.3. Absorption of solar light in the water caused by tripton.....	32
4.4. Estimation of the slope of the scattering coefficient spectra .....	35
4.5. Parameters for estimating the transparency and optical quality of the water .....	37
4.6. A model for calculating the spectra of diffuse attenuation coefficient using <i>in situ</i> measured data at three wavelengths .....	42
4.7. Application of the data on bio-optical parameters for modelling the photosynthesis primary production.....	44
5. CONCLUSIONS.....	46
REFERENCES .....	49
SUMMARY IN ESTONIAN .....	56
ACKNOWLEDGEMENTS .....	59
ORIGINAL PUBLICATIONS.....	61

## LIST OF ORIGINAL PUBLICATIONS

The present thesis is based on the following papers, which are referred to by their Roman numerals in the text. The papers are reproduced by kind permission of the publishers Boreal Environment Research (I), Estonian Academy of Sciences (II, III), IWA Publishing (IV) and Springer Science and Business Media (V, VI).

- I Reinart, A., Paavel, B., Pierson, D. & Strömbeck, N. 2004. Inherent and apparent optical properties of Lake Peipsi, Estonia. *Boreal Envir. Res.*, 9(5): 429–445.
- II Reinart, A., Paavel, B. & Tuvikene, L. 2004. Effects of coloured dissolved organic matter on the attenuation of photosynthetically active radiation in Lake Peipsi. *Proc. Estonian Acad. Sci., Biol. Ecol.*, 53 (2): 88–105.
- III Paavel, B., Arst, H., Reinart, A. & Herlevi, A. 2006. Model calculations of diffuse attenuation coefficient spectra in lake waters. *Proc. Estonian Acad. Sci., Biol. Ecol.*, 55(1): 61–81.
- IV Paavel, B., Arst, H. & Herlevi, A. 2007. Dependence of spectral distribution of inherent optical properties of lake waters on the concentrations of different water constituents. *Nordic Hydrology*, 38(3): 265–285.
- V Paavel, B., Arst, H. & Reinart, A. 2008. Variability of bio-optical parameters in two North-European large lakes. *Hydrobiologia*, 599(1): 201–211.
- VI Arst, H., Nõges, T., Nõges, P. & Paavel, B. 2008. Relationship of phytoplankton *in situ* primary production, chlorophyll concentration and underwater irradiance in turbid lakes. *Hydrobiologia*, 599(1): 169–176.

## AUTHOR'S CONTRIBUTION

**Publication (I):** Birgot Paavel took part in field works in Lake Peipsi and was responsible for laboratory analysis. She also participated in the processing of the results. Don Pierson and Niklas Strömbeck were responsible for comparison material, i.e. measurements in Swedish lakes Vänern and Vättern.

**Publication (II):** Anu Reinart was the principal author of this paper. Birgot Paavel was helping in field work and made data analyses as well as calculations connected with them. Lea Tuvikene was responsible for the underwater irradiance measurements with radiometer BIC–2104.

**Publication (III):** The idea of “C-model” belongs to Helgi Arst. Birgot Paavel made calculations using this model and estimations of its suitability. She was also the principal author of the manuscript.

**Publication (IV):** Birgot Paavel was mainly responsible of the data analysis. Helgi Arst made some part of these analyses. Preparation of the manuscript was performed together. As initial data for this study we used the database (measurements with the underwater spectrometer ac-9) of Antti Herlevi (University of Helsinki).

**Publication (V):** Birgot Paavel was responsible for all measurements in lakes Peipsi and Võrtsjärv, processing the results and for the preparation of the manuscript.

The work was supervised by Helgi Arst and Anu Reinart.

**Publication (VI):** The principal author of the manuscript is Helgi Arst. Tiina Nõges and Peeter Nõges were responsible for the results concerning primary production. Birgot Paavel measured the bio-optical properties of the lakes.

# I. INTRODUCTION

At the current stage the bio-optical properties of oceanic waters have been extensively analyzed (e.g. Jerlov, 1976; Prieur & Sathyendranath, 1981; Gordon & Morel, 1983; Sathyendranath *et al.*, 1989; Kirk, 1994; Bricaud *et al.*, 1995b; Bricaud *et al.*, 2004) and detailed studies on the optical parameters of coastal and estuarine regions have been recently presented (Babin *et al.*, 2003; Magnuson *et al.*, 2004; Gallegos, 2005; Gallegos *et al.*, 2005; Doxaran *et al.*, 2006). On the other hand, turbid productive inland lakes have received less attention despite their importance as freshwater supplies and recreational areas.

Optical properties, however, play a major role in the ecological structure and function of lakes, which are likely to be highly sensitive to climate changes (Schindler *et al.*, 1990; Vincent *et al.*, 1998) as well as local changes in land use (Goldman, 1988; Rae *et al.*, 2001). Typical problems include increases in lake productivity, decreases in water transparency and increased frequency and severity of algal blooms (Dokulil & Teubner, 2003).

Among the different types of water bodies, lakes deserve special attention because they are multicomponential waters where optically active substances (OAS: phytoplankton, tripton and coloured dissolved organic matter) may vary in type and amount within short distances and time intervals. The concentrations of the OAS observed in lakes are often notably higher than those in the open ocean (Dekker, 1993; Kirk, 1994; Herlevi, 2002b; Arst, 2003). The relative values of OAS can differ, too: in one lake the dominating substance may be the coloured dissolved organic matter, in another lake – phytoplankton. Inspection of published data on lakes throughout the world reveals that the concentrations of OAS and diffuse attenuation coefficient of light can differ by more than one hundred fold (Kirk, 1994; Lindell *et al.*, 1999; Arst, 2003). However, the database on the bio-optical properties of lakes should not be limited to the concentrations of OAS, but also the attenuation of solar light in the water is of importance. The radiation penetrating into water is subject to absorption and scattering, forming an underwater light field, while some small part of radiation is scattering back to space. Light conditions in water are important for primary production, species composition and the depth distribution of submerged phytoplankton, likewise in the application of optical measurement systems in monitoring water quality and interpretation of remote sensing images. Absorption and scattering coefficients of light beam are called inherent optical properties (IOP) as they depend only on the medium, while optical properties depending also on the surrounding light field (e.g. Secchi disk depth, diffuse attenuation coefficient) are called apparent optical properties (AOP) (Mobley, 1994).

Nowadays optical remote sensing has become a useful tool for monitoring spatial and temporal properties of the aquatic environment. However, in coastal waters and lakes there are some difficulties concerning the quantitative



interpretation of satellite data, consequently, *in situ* measurements retain their value. Each database (even for 1–2 lakes) helps build a mosaic for describing global variability in the optical properties of lakes and elucidates the connections between types of lakes and environmental as well as climatic conditions.

The main objectives of the present work were: (1) collecting and analysing the data on inherent and apparent optical properties of the water in North-European lakes; (2) estimation of the relative contribution of different OAS in formation of absorption and scattering properties of the lake waters; (3) investigation and modelling the spectra of the diffuse attenuation coefficient in lakes. It led to the following studies:

- Description of the spatial-temporal variations of water properties and estimation of the general relationships between the OAS and optical parameters.
- Determination of the contribution of each water constituent to total values of absorption and attenuation coefficients for some narrow spectral intervals in the photosynthetically active region of the spectrum (PAR, 400–700 nm) as well as for the whole PAR-band.
- Estimation of the values and variability of the specific absorption coefficient for tripton in the PAR region.
- Calculation of the slopes of the scattering coefficient spectra and analyzing their variability (seasonal change, dependence on the concentrations of OAS).
- Elaboration of a model for determining the full spectra of the diffuse attenuation coefficient in the PAR region on the basis of *in situ* measured data at three narrow wavebands.
- Collection of a database from *in situ* measured bio-optical parameters (including primary production) that should be suitable for building the models of the photosynthesis primary production.

In the present work a database about three turbid Estonian lakes (Peipsi, Võrtsjärv and Harku) was collected and the variations of bio-optical properties in these lakes were studied. For comparing the results with other North-European lakes we analysed the water samples collected from 20 southern Swedish lakes, 14 Estonian lakes and 15 southern Finnish lakes. The inherent and apparent optical properties were also compared with those obtained from two large clear-water Swedish lakes, L. Vänern and L. Vättern. The results obtained in this study definitely have a special importance, because the data of optical properties published for productive lakes are rather few in number and they could be used for the further development of remote sensing algorithms in turbid and humic water bodies.

## 2. REVIEW OF THE LITERATURE

Natural waters contain a heterogeneous mixture of dissolved and particulate matter, which are both optically significant and highly variable in type and concentration. The bulk optical properties of water are divided into two classes, inherent optical properties and apparent optical properties. Inherent optical properties (IOP) depend solely on the substances within the aquatic medium and not on the illumination conditions. By contrast, the apparent optical properties (AOP) depend both on the medium and on geometric structure of the ambient light field.

### 2.1. Inherent optical properties

The inherent optical properties of relevance in this thesis are the absorption coefficient  $a$  (which determines the exponential rate of decay of flux per unit pathlength of light in the medium, and per unit incident flux, due to the process of absorption), and the scattering coefficient  $b$ , which defines similarly the exponential rate of decay of flux due to scattering (Preisendorfer, 1976; Dera, 1992; Kirk, 1994). The beam attenuation coefficient,  $c(\lambda)$  measures the extinction of a narrow beam of light and this extinction is due to processes of absorption and scattering:

$$c(\lambda) = a(\lambda) + b(\lambda). \quad (2.1)$$

All these properties are defined for collimated, monochromatic flux incident normally on the medium, and traversing an infinitesimally thin layer of the medium. The inherent optical parameters are additive over the different optically active substances of the medium (Prieur & Sathyendranah, 1981; Kirk, 1994; Arst, 2003). For example, for total absorption coefficient,  $a$ :

$$a(\lambda) = a_w(\lambda) + a_{CDOM}(\lambda) + a_{ph}(\lambda) + a_t(\lambda), \quad (2.2)$$

where the terms on the right-hand side of this equation represent absorption by water, coloured dissolved organic material (CDOM), phytoplankton and tripton, respectively. A similar expression can be written for the attenuation and the scattering coefficients, although coloured dissolved organic matter would not be expected to contribute to scattering (i.e.  $b_{CDOM} = 0$ ). The terms  $a_{ph}(\lambda)$  and  $a_t(\lambda)$  are assumed to be proportional to the concentration of the material, so  $a_{ph}(\lambda) = a'_{ph}(\lambda)C_{chl}$  and  $a_t(\lambda) = a'_t(\lambda)C_t$ , where  $a'_{ph}(\lambda)$  and  $a'_t(\lambda)$  are correspondingly the specific absorption coefficients and  $C$  means concentration. Usually the biomass of phytoplankton is expressed through concentration of

chlorophyll *a* (also the version chlorophyll *a* + phaeophytin *a* is used), assuming their good correlation relationships. The term  $a_{CDOM}(\lambda)$  in Eq. (2.2) remain the same (the concentration of CDOM is not used). The reason is that in natural waters CDOM is not identifiable as a distinct molecule, but it is a rather indeterminate mixture of dissolved organic substances (Dera, 1992). Using analytical methods it is extremely difficult to determine individual organic compounds therein (Dera, 1992). Investigations of numerous researchers have shown that optical determination of CDOM has apparent advantages over chemical analysis techniques (Bricaud *et al.*, 1981; Baker & Smith, 1982; Kopelevich, 1983a; Davies-Colley & Vant, 1987; Ferrari & Tassan, 1991).

A more detailed description (together with the formulas) of light attenuation, absorption and scattering coefficients, corresponding to all OAS are presented also in **I**, **II** and **IV**.

#### *Pure water*

The absorption characteristics of pure water ( $a_w$ ) may be considered invariant, although the optical properties of pure water have themselves been reanalysed (Irvine & Pollack, 1968; Hale & Querry, 1973; Morel & Prieur, 1977; Smith & Baker, 1981; Kopelevich, 1983a; Pope & Fry, 1997; Morel *et al.*, 2007). Comparing different publications we can see that the values  $a_w(400)$  vary from  $0.006 \text{ m}^{-1}$  to  $0.058 \text{ m}^{-1}$ , and the values of  $a_w(650)$  from  $0.29 \text{ m}^{-1}$  to  $0.45 \text{ m}^{-1}$ . These differences in the blue-green region of the spectrum can be relevant in studies of clear ocean waters, but not in turbid waters, while the differences in the red region can influence the results of calculations for any type of water. We used the data by Pope & Fry (1997). Scattering by pure water is very small, varying markedly with wavelength (in accordance with  $\lambda^{-n}$  where  $n$  changes from 4 to 4.32 (Kirk, 1994).

#### *Coloured dissolved organic matter*

Both fresh and saline waters contain varying concentrations of dissolved organic material (DOM), which plays a major role in the aquatic medium as carbon and energy sources for the microbial food web, and for consumers at higher trophic levels that feed on microbes or on DOM directly. The optically active fraction of dissolved organic matter, known as coloured dissolved organic matter “CDOM” are a group of organic dissolved substances, consisting of humic and fulvic acids. They may have a local origin (autochthonous material), for example from degradation of phytoplankton cells and other organic particles, or they may be advented to a locality from a distant source (allochthonous material). The coloured dissolved organic matter is photochemically active and so it influences the spectral underwater regime. CDOM is assumed to be fully dissolved (i.e. it does not contain particles that cause scattering) and considered to be non-scattering.

There is excellent agreement in the spectral form of absorption by coloured dissolved organic matter reported in various publications (e.g. Unoki *et al.*, 1978; Bricaud *et al.*, 1981; Bukata *et al.*, 1981; Davies-Colley & Vant, 1987; Roesler *et al.*, 1989; Gallegos *et al.*, 1990). According to these studies absorption spectra of CDOM can be expressed as an exponent function:

$$a_{CDOM}(\lambda) = a_{CDOM}(\lambda_0) e^{(-S_{CDOM}(\lambda_0 - \lambda))}, \quad (2.3)$$

where  $\lambda_0$  is a reference wavelength and  $S$  is an empirically-determined slope of the exponential curve. The reference wavelength is usually chosen between 380 and 400 nm. For a wide range of seawaters,  $S$  has been found to vary between about 0.010 and 0.020 nm<sup>-1</sup> (Baker & Smith, 1982; Davies-Colley & Vant, 1987; Kirk, 1994; as referenced in Reinart, 2000). The average value for Finnish and Estonian lakes has been found to be 0.016–0.017 nm<sup>-1</sup> by Sipelgas *et al.* (2003).

### *Phytoplankton*

Phytoplankton consists of ubiquitous, microscopic, free-floating organisms found in the illuminated surface layer (there organisms receive sufficient photosynthetically active radiation for photosynthetic processes) of freshwater and marine ecosystems. They are the single-celled plants that form the base of the aquatic food chain, and they are important component of the global carbon cycle. Thousands of phytoplankton species, with characteristic sizes, shapes and physiological properties, are known to exist in the aquatic environment, and their species composition and concentration can change with time and space. These absorbing pigments are not evenly distributed within phytoplankton cells, but are localized into small “packages” (chloroplasts), which are distributed nonrandomly throughout the cell. This localized distribution of pigments means that the spectral absorption by a phytoplankton cell, or by a collection of cells in water, is “flatter” (has less pronounced peaks and reduced overall absorption) than if the pigments were uniformly distributed throughout the cell, or throughout the water (Mobley, 1994). This so-called “pigment packaging effect” is a major source of both inter- and intra-species variability in spectral absorption by phytoplankton. Another source of variability in addition to chlorophyll *a* concentration and packaging is changes in pigment composition, since each pigment displays a characteristic absorption curve. Typical absorption spectra have a maximum in the blue part of spectrum (440–500 nm), and a second maximum in the red part (650–680 nm) (Bidigare *et al.*, 1990).

Variability in specific absorption coefficient of phytoplankton  $a'_{ph}(\lambda)$  is analysed by Bricaud *et al.* (1995a) using a dataset including 815 spectra and covering the chlorophyll concentration range 0.02–25 mg m<sup>-3</sup>. Empirical relationships between  $a'_{ph}(\lambda)$  and  $C_{chl}$  were calculated using the power function:

$$a'_{ph}(\lambda) = A(\lambda)C_{Chl}^{-B(\lambda)}, \quad (2.4)$$

where  $A(\lambda)$  and  $B(\lambda)$  are positive, wavelength-dependent parameters tabulated on the basis of laboratory measurements of optical properties of different algae species. The equation takes into account the pigment packing effect which causes the phytoplankton specific absorption coefficient to be smaller in case of larger cells and large intercellular chlorophyll concentrations.

Phytoplankton cells and colonies also scatter light, influencing the total scattering properties of aquatic medium (Bricaud *et al.*, 1983). The scattering properties vary from one species to another. Assuming that the scattering of light is caused mainly by phytoplankton, different authors have found several algorithms for describing the corresponding scattering coefficient,  $b(z, \lambda)$ . The general equation is the following:

$$b(z, \lambda) = M_1 [C_{Chl}(z)]^{M_2} \left( \frac{550}{\lambda} \right)^{M_3}, \quad (2.5)$$

where  $M_1$  is the scattering coefficient at the 550 nm wavelength. Gordon & Morel (1983) obtained  $M_1 = 0.3$ ,  $M_2 = 0.62$  and  $M_3 = 1$ . However, Morel (1980) obtained a slightly different value of  $b(550)$ , with  $M_1 = 0.12$  and  $M_2 = 0.63$  (these values were used also in Sathyendranath *et al.* (1989)). According to Dekker (1993)  $M_1 = 0.17(0.12)$  and  $M_2 = 1$ .

### *Tripton*

Tripton consists of non-living suspended material in the water (organic and inorganic particles). Non-living organic particles are called detritus. These particles are assumed to have biological origin (produced when phytoplankton die and their cells break apart, and when zooplanktons graze on phytoplankton and leave cell fragments and fecal pellets). However, detrital material may also have other sources e.g., resuspension of organic matter from the bottom, river and land drainage. Inorganic particles (the second component of tripton) may include minerals, such as fine clay, silt particles, sand, or precipitates such as iron and manganese hydroxides and calcium carbonate. It is recognized that these particles can significantly affect light penetration especially in turbid and coastal waters, where their concentration can be substantially high as a result of large river discharges, heavy sediment load and long and short range transport of atmospheric particulates followed by dry deposition.

The spectrum of tripton absorption coefficient  $a_t(\lambda)$  can be described by an exponential function that increases toward short wavelength, similarly to CDOM (see Eq. 2.3) However the value of the slope ( $S_t$ ) is different. Measurements performed by several authors give the values for this slope in the

range 0.006 to 0.016 nm<sup>-1</sup> (Kishino *et al.*, 1986; Maske & Haardt, 1987; Iturriaga & Siegel, 1988; Morrow *et al.*, 1989; Roesler *et al.*, 1989; Bricaud & Stramski, 1990; Gallegos *et al.*, 1990).

The scattering properties of tripton are predominately caused by the inorganic fraction. Few spectral measurements exist but theory and investigations suggested that wavelength dependence of scattering can be expressed by a  $\lambda^{-n}$  law, with the exponent  $n$  varying between 0 and 1 (Morel & Preiur, 1977; Gallie & Murtha, 1992; Jupp *et al.*, 1994).

Usually not tripton, but the concentration of total suspended matter is measured (by its dry weight). There are ways for separating tripton (described in Hoogenbloom & Dekker (1997), Kutser *et al.* (2001) and in IV).

## 2.2. Apparent optical properties

The apparent optical properties depend mainly on the inherent optical properties of the water, but to a certain extent they are also dependent on irradiance conditions existing at any instant in the water body, chiefly on the directional distribution of the incoming irradiance. In fact they are properties of the light field, which under the incident solar radiation stream is established within the water body. The main corresponding parameters are Secchi disk depth, underwater irradiance (also underwater quantum irradiance), diffuse attenuation coefficient, irradiance reflectance and average cosine (Dera, 1992; Kirk, 1994).

We do not describe the well-known measurements with Secchi depth. Submersible light sensors measure irradiance,  $E$ , in units of radiant power per unit area (W m<sup>-2</sup>) or flux of photons (quantum irradiance),  $q$ , per unit area (quanta m<sup>-2</sup> s<sup>-1</sup> or in  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ). Sensors itself may be fixed so they look up, measuring downwelling irradiance or they may look down, measuring upwelling irradiance.

In order to obtain the values of integral irradiance in some spectral range (from wavelength  $\lambda_1$  to  $\lambda_2$ ), the respective integral has to be determined:

$$E(\lambda_1, \lambda_2) = \int_{\lambda_1}^{\lambda_2} E(\lambda) d\lambda. \quad (2.6)$$

The respective formula for quantum irradiance is:

$$q_{\lambda_1, \lambda_2} = \int_{\lambda_1}^{\lambda_2} E_d(\lambda) \frac{\lambda}{hc_0} d\lambda. \quad (2.7)$$

Here  $h = 6.6255 \times 10^{-34}$  J s is Planck's constant and  $c_0 = 2.9979 \times 10^8$  m s<sup>-1</sup> is the velocity of light in vacuum.

In marine optics and biology an important wavelength region is 400–700 nm, which represents visible light and determines the energy conditions of photosynthesis. The waveband 400–700 nm is called the photosynthetically active region, PAR, and respective irradiances are then  $E_{PAR}$  and  $q_{PAR}$ .

The values of  $E_{PAR}$  (planar irradiance) were measured by a sensor taking irradiance from the upper or lower hemisphere in the water (Dera, 1992; Kirk, 1994; Arst, 2003). However, due to the fact that the algal cells are illuminated from all directions, for primary production calculations we need scalar quantum irradiance ( $q_{0,PAR}(z)$ ). It can be measured using a spherical quantum sensor, which takes radiation from all directions (Kirk, 1994; Sosik, 1996).

A useful variable for characterizing the vertical decrease of natural light in water bodies is the diffuse attenuation coefficient ( $K_d$ ). The index “ $d$ ” means that we consider the downwelling irradiance. The general equations used to define  $K_d(z, \lambda)$  are shown in Dera (1992), Kirk (1994), Arst (2003) and in **III**.

In the optically unstratified water body  $K_d$  practically does not depend on depth and the underwater irradiance can be calculated by the following formula:

$$E_d(z, \lambda) = E_d(-0, \lambda)e^{-K_d(\lambda)z}, \quad (2.8)$$

where  $K_d$  can be considered also as diffuse attenuation coefficient averaged over the layer from 0 to  $z$ . When  $z$  is measured in metres,  $K_d$  is expressed in  $\text{m}^{-1}$ . To determine the diffuse attenuation coefficient, in practice, a semilog plot of irradiance results vs. depth has to be applied and the value of  $K_d$  can be found as the slope of the mean straight line through these points.

Equation 2.8 is derived for monochromatic radiation; it works quite well for narrow spectral intervals, but gives only approximate results for integral radiation (Kirk, 1994; Arst *et al.*, 2000).

### 3. MATERIAL AND METHODS

#### 3.1. Study areas

We have a rather large database about five lakes: L. Peipsi, L. Võrtsjärv, L. Harku (all in Estonia), L. Vättern and L. Vänern (both in Sweden). These lakes are quite different from each other as their limnological type varies from ultra-oligotrophic to hypertrophic. Main morphometric data and typical variation of Secchi disk values are presented in Table 1.

**Table 1.** Trophic type, main morphometric data, and typical variation of Secchi depth ( $z_{SD}$ ) in three Estonian lakes and two Swedish lakes.

<i>Lake</i>	<i>Trophic type</i>	<i>Area</i> ( $km^2$ )	<i>Average</i> <i>depth (m)</i>	<i>Maximum</i> <i>depth (m)</i>	$z_{SD}^1$ (m)
Peipsi	Meso/eutrophic	3555	7.0	15	0.4–4.8
Võrtsjärv	Eutrophic	270	2.8	6.0	0.2–1.0
Harku	Hypertrophic	1.64	2.0	2.5	0.1–1.0
Vänern	Oligotrophic	5648	27	106	2.0–7.9
Vättern	Ultraoligotrophic	1856	40	128	6.0–15.0

<sup>1</sup> Data from long time monitoring

Our main investigation object was Lake Peipsi (**I, II, V, VI**) on the border of Estonia and Russia, which is the fourth largest lake in Europe. Lake Peipsi is a relatively shallow lake consisting of three parts: (1) the northernmost, largest and deepest (average depth 8.3 m) L. Peipsi *sensu stricto* (Peipsi *s.s.*) is unstratified and mesotrophic/eutrophic; (2) the southernmost part, L. Pihkva, is shallower (5.3 m) and hypertrophic and (3) narrow L. Lämmijärv (2.3 m), connecting the first two, is close to hypertrophic (Nöges, 2001). About 240 rivers and streams fall into L. Peipsi and there is only one outflow, the Narva River, carrying the water from L. Peipsi to Gulf of Finland. Therefore lake feeding is realised in extent of 84% by inflowing rivers and 16% by precipitation falling onto the lake surface (Mäemets, 1977). Due to L. Peipsi shallowness and large surface area it may be sensitive to possible climate changes.

Lake Võrtsjärv (**V, VI**) is a large shallow non-stratified eutrophic lake within the boundaries of Estonia. More than 20 rivers, streams and ditches bring their waters into L. Võrtsjärv. There is only one out-flowing river, Suur-Emajõgi, which carries waters to L. Peipsi. The underwater light climate is strongly affected by the water level fluctuations. Phytoplankton biomass is significantly lower in years of high water level and the changes are unrelated to nutrient loading. In low-water years better water column illumination and increased release of phosphorus from resuspended bottom sediments results in subs-



tentially higher phytoplankton biomass than in high-water years (Nõges *et al.*, 2002).

Lake Harku (VI) is located within the borders of the Estonian capital Tallinn and was separated from sea by neotectonic uplift about 2000 years ago. The lake is small and hypertrophic, with extraordinarily high values of chlorophyll and total suspended matter concentrations (maxima  $398 \text{ mg m}^{-3}$  and  $82 \text{ g m}^{-3}$ , respectively) and the very small values of Secchi depth (minimum 0.1 m). The maximum integrated primary production, measured by us, was  $435 \text{ mg C m}^{-2} \text{ h}^{-1}$ .

Lake Vänern (I, II, V) is the third largest lake in Europe. This lake is situated in central Sweden and is divided into two basins by a shallow archipelago. Its water quality is classified as moderately nutrient-rich, and measurements of algal biomass indicate oligotrophic conditions (Willén, 2001a). In L. Vänern the bloom of phytoplankton in spring (May–early June) is often more pronounced than the second bloom in August. This lake can also have rather intense colour (Strömbeck, 2001).

The second largest in Sweden, Lake Vättern (I, II, V), is the fifth largest lake in Europe (Kvarnäs, 2001). It is about 20 km east of L. Vänern and comprises only one rather narrow basin (width less than 15 km). It has a relatively small watershed, and seasonal variations in discharge from the tributaries have very little impact on the lake's water quality. Ultraoligotrophic conditions prevail in this lake (Willén, 2001a).

In our study we used (as the initial data for calculations) also the parameters measured in nine Estonian and six Finnish lakes (III, IV). The dataset was obtained during a co-operation project (SUVI, 1995–2005) between the Department of Geophysics, University of Helsinki and Estonian Marine Institute. The lakes were located in the area with geographical coordinates ranging from  $57^{\circ}\text{N}$  to  $63^{\circ}\text{N}$  and from  $22^{\circ}\text{E}$  to  $29^{\circ}\text{E}$ . The dataset includes different types and sizes of water bodies in the boreal ecoregion varying from clear oligotrophic lakes to very turbid hypertrophic lakes.

### 3.2. *In situ* measurements

Measurements of the optical properties of lake waters involved *in situ* measurements of underwater irradiance and collection of water samples for subsequent laboratory analyses.

As a part of project SUVI (Herlevi *et al.*, 1999; Herlevi, 2002a,b) the attenuation and absorption coefficients of light in the water were measured using the instrument ac-9 (WET Labs. Inc., 1995). It is a dual path absorption and attenuation meter, measuring  $a$  and  $c$  simultaneously at nine different wavelengths (412, 440, 488, 510, 532, 555, 650, 676 and 715 nm (beginning from 2000 the channel 532 was replaced by 630 nm). The dataset of ac-9

contains the vertical profiles of parameters determined with very small depth-step (1–2 cm) down to 2–6 m in a lake. However, the depth-variation of variables in our lakes was only 2–3% (Herlevi *et al.*, 1999; Herlevi, 2002b) and we used the averaged values for the layer of 0.5–1 m. The total scattering coefficient cannot be measured directly, but is calculated as the difference between attenuation and absorption.

The spectral downwelling and upward irradiances ( $E_d(z)$  and  $E_u(z)$ ,  $\text{W m}^{-2} \text{nm}^{-1}$ ) were profiled in the water column using the spectroradiometer LI-1800 UW. This instrument measures the irradiance spectra over 300–1100 nm in air and 350–850 nm in water with the spectral resolution of 2 nm. The manufacturer is LI-COR Corporation (Lincoln, Nebraska, USA). The description of this instrument as well as the measurement methods are presented in Herlevi (2002b). Usually  $E_d(\lambda)$  decreased very quickly with depth (especially in the blue region of the spectrum) and irradiance values were beyond the sensitivity limit of the spectrometer ( $3 \times 10^{-5} \text{ W m}^{-2} \text{nm}^{-1}$ ). In clear water lakes it was possible to determine 6–7 spectra at different depth, but in turbid lakes the number of spectra was usually 3. In very turbid waters the whole spectrum was obtained only in the upper thin layer.

We had at our disposal also another instrument, BIC-2104 (Biospherical Instruments Inc.), allowing to measure the profiles of underwater irradiance in three bands (centred at 412, 555, 665 nm), and the integral irradiance in the PAR region. This instrument is easy to handle and suitable for measurements even in very shallow water (at least  $\sim 20$  cm). Using BIC-2104, we performed measurements, the results of which are described in **II**. Data were collected continuously during lowering and lifting the instrument, stored together with the respective depth (precision  $\pm 2$  cm) and temperature data into a laptop computer. In **III** (for modelling the spectra of diffuse attenuation coefficient) as well as in **IV**, (for investigation of the relationships between inherent optical properties and water constituents) we used the ac-9 data obtained by Herlevi (1999; 2002a,b).

In lakes Peipsi, Võrtsjärv and Harku also the scalar and downwelling planar irradiances (in PAR band of the spectrum) were measured using LI-COR sensors (LI-COR, Inc., 1984): LI-193 SA for scalar irradiance and LI-192 SA for the downwelling irradiance (Jewson *et al.*, 1984; Bowling & Tyler, 1985). Both sensors separately calibrated for quantum irradiance. In the air the quantum irradiance of  $4.6 \mu\text{mol s}^{-1} \text{m}^{-2}$  corresponds to a radiative energy of  $1 \text{ W m}^{-2}$  but in the water this relationship depends on the optical properties of the water (Reinart *et al.*, 1998). Incident PAR irradiance was measured by the LI-192 SA just before submerging it into the water and after the underwater measurements and with an air pyronometer LI-192 SA (range 400–1100 nm) during the measurement.

Water samples were collected either from surface layer (**I**, **II**, **III**, **IV**, **V**) and/or as depth-integrated, i.e. water taken from the whole water column with

an interval of 0.5 m was mixed in one bigger tank (V–VI). A standard water sampler was used and the samples were stored in the dark and cold less than 7h before filtering. The relative transparency of water was measured using Secchi disk during the time of sampling.

### 3.3. Laboratory measurements and methods

On arrival at the laboratory the water samples from each lake were filtered either through Whatman GF/C (during co-operation project SUVI, in III and IV) or Whatman GF/F filters (other studies). The corresponding pore sizes of these filters are 1.2  $\mu\text{m}$  and 0.7  $\mu\text{m}$ . The concentration of chlorophyll *a* was determined by filtering 0.5–1 litres of water through one of these filters, extracting pigments with hot ethanol (90%, 75°C) and measuring absorption coefficients at the wavelengths of 665 and 750 nm. In SUVI studies the value of  $C_{Chl}$  was calculated according to the Lorenzen (1967) method but in I, II the chlorophyll *a* and phaeophytin *a* concentrations were measured according to the ISO standard method (ISO 10260, 1992 (E)). In V–VI the concentration of chlorophyll *a* was estimated in parallel by both methods. The concentration of total suspended matter,  $C_{TSS}$ , was measured gravimetrically after filtration of the same amount of water through pre-weighed and pre-combusted (103–105 °C for 1 h) filters; the inorganic fraction,  $C_{SPIM}$ , was measured after combustion at 550 °C for 30 min. The organic fraction  $C_{SPOM}$  was determined by subtraction of  $C_{SPIM}$  from  $C_{TSS}$  (ESS method 340.2, 1993).

The “spectrometric” attenuation coefficients of light,  $c^*(\lambda)$  and  $c_f^*(\lambda)$ , were determined respectively from unfiltered and filtered (filters pore size was 0.7  $\mu\text{m}$ ) water samples. Note that more correct results could be obtained when the filters with pore size 0.2  $\mu\text{m}$  were used (Lindell *et al.*, 1999). However, we could not use these filters because the water of many lakes was so rich in particles that it would have clogged up the fine filters. The variable  $c^*(\lambda)$  was obtained as the difference  $c(\lambda) - c_d(\lambda)$ , where  $c(\lambda)$  and  $c_d(\lambda)$  are the beam attenuation coefficients for natural and distilled water, respectively. The term ‘spectrometric attenuation coefficient’ needs explanation. As known (Zaneveld *et al.*, 1992; Bricaud *et al.*, 1995b), the experimental determination of the true values of the beam attenuation coefficient ( $c$ ) is complicated. Theoretically, the beam transmittance should contain no contribution from scattered light, but in reality small-angle forward scattering does reach the detector. The measured transmittance then exceeds the theoretical value and the attenuation coefficient determined from the measured transmittance is smaller than the true value. Actually, the direct spectrophotometer reading,  $c^*(\lambda)$ , is the following:

$$c^*(\lambda) = c(\lambda) - Fb(\lambda) - c_d(\lambda), \quad (3.1)$$

where  $b(\lambda)$  is the light-scattering coefficient and  $F$  is a coefficient showing the contribution of small-angle forward scattering to the radiation measured by the spectrophotometer.

We performed our laboratory measurements with a commercial Hitachi U1000 spectrophotometer at a spectral interval of 10 nm in the PAR (photo-synthetically active radiation) band, 400–700 nm. Unfortunately, the value of  $F$  for this instrument is not known and therefore we refer to the measurement result not as a ‘beam attenuation coefficient’, but as a ‘spectrometric’ attenuation coefficient. Arst *et al.* (1996, 1999a,b) found that although  $c^*(\lambda)$  differs from the true beam attenuation coefficient, the averaged value over the PAR region,  $c_{PAR}^*$ , can be used for characterizing the optical quality and transparency of water at different depths.

The absorption coefficient of CDOM is usually determined from the attenuation coefficient spectra of filtered water,  $c_f^*(\lambda)$ . Note that the variable  $c_f^*(\lambda)$  is not identical to  $a_{CDOM}(\lambda)$  because some very small inorganic particles and colloids also pass through the filter and the water may remain a scattering medium even after filtration (Bricaud *et al.*, 1995b; Sipelgas *et al.*, 2003; Arst, 2003). In this case we need a correction, the general relationship of which is given in Bricaud *et al.* (1981). However, in the blue part of the spectrum the differences are small, about 2–8% (Sipelgas *et al.*, 2003). For  $c_f^*(\lambda)$  Eq. (3.1) is also valid, but the term  $Fb(\lambda)$  is considerably smaller due to the decrease in scattering after filtration.

In regard to apparatus and methods **I**, **II** form an exception, where absorption by coloured dissolved organic matter ( $a_{CDOM}$ , called also  $a_{ys}$ ) was measured with a spectrometer (PERKIN ELMER Lambda 40 UV/VIS, in the range 300–900 nm) in water filtered through Millipore 0.2  $\mu\text{m}$  filter, in a 10 cm cuvette against distilled water and corrected for residual scattering according to Davis-Colley & Vant (1987).

The total particulate absorption,  $a_p(\lambda)$ , was measured with a spectrometer (PERKIN ELMER Lambda 40 UV/VIS in the range 400–750 nm) with the Whatman GF/F filter pad technique (summary of the method is given in Lindell *et al.*, 1999) and using later depigmentation with sodium hypochloride (Tassan & Ferrary, 1995), which separates phytoplankton pigment absorption  $a_{ph}(\lambda)$  and the absorption by the rest of particles,  $a_t(\lambda)$  (tripton).

## 4. RESULTS AND DISCUSSION

### 4.1. Optically active substances in the water and correlation analysis

Lakes are multicomponent systems where the optical parameters of the water depend on the concentrations of all three optically active substances. The amount of OAS changes from lake to lake, but additionally their temporal changes are observed, caused by phytoplankton blooms as well as springtime increase of dissolved organic matter (associated with snowmelt runoff) or changes in concentration and type of suspended particles (associated with river discharge or resuspension). The variations in the amount of OAS (as well as the variations of underwater light field) are essential factors in the formation of the ecological status of lakes. Information about OAS is needed also to build remote sensing models for optically complex waters (Kutser *et al.*, 2001; Dall'Olmo & Gitelson, 2005) which have to be parameterized and validated using *in situ* data (Pierson & Strömbeck, 2000; Darecki & Stramski, 2004; Kutser *et al.*, 2006; Metsamaa *et al.*, 2006).

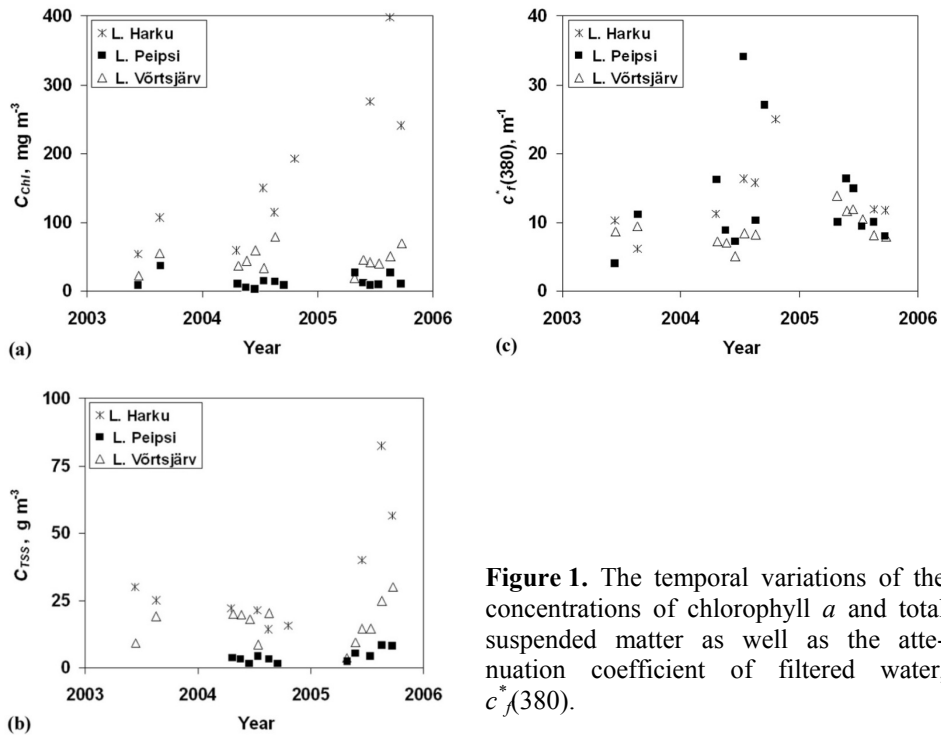
The results obtained by us (Paavel, 2004; I–VI) demonstrate a large variability in optically active substances in different types of lakes. Our main study sites were lakes Peipsi, Võrtsjärv and Harku in Estonia (I–II and V–VI). Additionally we analysed water samples collected from 20 turbid southern Swedish lakes (Paavel, 2004 and II), 14 Estonian lakes and 15 southern Finnish lakes (dataset described in II–IV). The measured water parameters were also compared with those obtained from two clear-water Swedish lakes, L. Vänern and L. Vättern (I, II, V).

The average values of observed concentrations of OAS and Secchi disk depth (without L. Võrtsjärv and L. Harku) are presented in Table 2. These data were taken from Paavel (2004) and I, except for L. Peipsi, where the whole dataset obtained from 2001–2005 is used (look also V). According to the parameter  $C_{TSS}$ , L. Peipsi falls in the same range with small Estonian and Finnish lakes (30 lakes), but this parameter was significantly higher for the two Swedish large lakes, L. Vänern and L. Vättern. The main reason is that due to its shallowness L. Peipsi is frequently well mixed, especially in the conditions of strong winds when resuspensions of sediments from the bottom occur. The differences between  $a_{CDOM}(400)$  are smaller in comparison with of those between  $C_{chl}$  in lakes.

**Table 2.** Mean values and respective standard deviations for some bio-optical parameters in lake waters during measurements campaigns in 1994–2005.

	<i>Peipsi</i> * N=238	<i>Vänern</i> • N=48	<i>Vättern</i> • N=22	<i>Swedish</i> ♣ N=20	<i>Finnish</i> ♣ N=63	<i>Estonian</i> ♣ N=54
$C_{Chl}$ , mg m <sup>-3</sup>	23.5±17.3	3.9±1.2	2.0±0.5	2.2±3.0	13.7±14.2	20.8±20.4
$C_{TSS}$ , g m <sup>-3</sup>	7.3±5.8	1.2±0.4	0.6±0.6	3.0±2.6	5.9±7.3	6.6±5.6
$C_{SPIM}$ , g m <sup>-3</sup>	3.1±3.0	0.6±0.2	0.2±0.1	1.1±2.0	0.3±0.2*	1.2±1.5*
$C_{SPOM}$ , g m <sup>-3</sup>	4.6±3.7	0.6±0.4	0.3±0.2	1.9±1.3	3.2±1.7*	2.2±1.6*
$a_{CDOM}(400)$ , m <sup>-1</sup>	4.6±2.6	2.5±1.1	0.5±0.2	8.3±5.3	6.6±2.8	3.8±3.6
$z_{SD}$ , m	1.7±0.7	4.0±0.6	9.0±0.4	2.3±1.3	2.4±1.6	2.7±1.8
* Measurements 2001–2005			• Measurements in 1999 and 2002			
♣ Measurements 1994–2003			♣ Measurements in 2003			

The temporal variations of OAS were examined during 2003–2005 in lakes Peipsi, Võrtsjärv and Harku (the corresponding sampling stations were Varnja, Limnology and Harku). Simultaneously also the underwater irradiance and primary production profiles were measured. In 2003 we had field trips only in June and August, in 2004–2005 in different months from April to September. Altogether there were 37 measurement days, 14 in L. Peipsi, 14 in L. Võrtsjärv and 9 in L. Harku. The measurement series were planned twice a day (about 11:00–13:00 and 15:00–17:00), but sometimes due to the weather conditions or technical problems some data were missing or not acceptable. The values of the annual variations of OAS were obtained averaging the results of two series in each measurement day (Fig. 1). In this figure the amount of CDOM is described using the attenuation coefficient of filtered water at the wavelength 380 nm ( $c^*_\lambda(380)$ ). The range of variations and corresponding mean values of OAS for the stations Varnja in L. Peipsi and Limnology in L. Võrtsjärv (some data for L. Võrtsjärv in 1995–2002 were added) are also presented in Table 2 in V and Fig. 2 in V.



**Figure 1.** The temporal variations of the concentrations of chlorophyll *a* and total suspended matter as well as the attenuation coefficient of filtered water,  $c^*(380)$ .

The seasonal behaviour of all three parameters in L. Peipsi and L. Võrtsjärv is irregular, and with no apparent long-term trend (Fig. 1). A noticeable increase of concentration of chlorophyll *a* and total suspended matter from 2003 to 2005 was observed only in L. Harku (Fig. 1a,b). The data collected at three stations showed that  $C_{chl}$  values in all lakes were highest during the intensive algal blooms that occurred in late summer (Fig. 1), which is typical of turbid lakes situated in agricultural and rural areas (Marshall & Peters, 1989). Extraordinarily high values of chlorophyll and total suspended matter concentrations, mainly in the second half of the chlorophyll growing period (maxima 398  $\text{mg m}^{-3}$  and 82  $\text{g m}^{-3}$ , respectively), were observed in L. Harku. (Fig. 1a,b).

The considerable increase of CDOM in L. Peipsi in July and September 2004 was due to summer rainfall, which resulted in intensive inflow from rivers to the lake. The low  $c^*(380)$  (and conclusively, also small  $a_{CDOM}(380)$ ) values in April 2005 corresponded to a very severe winter, when snowmelt runoff peaks were shifted from April to early May (Fig. 1). According to these parameters, L. Peipsi, L. Võrtsjärv and L. Harku fall in the same range as the Estonian lakes investigated previously (Arst, 2003).

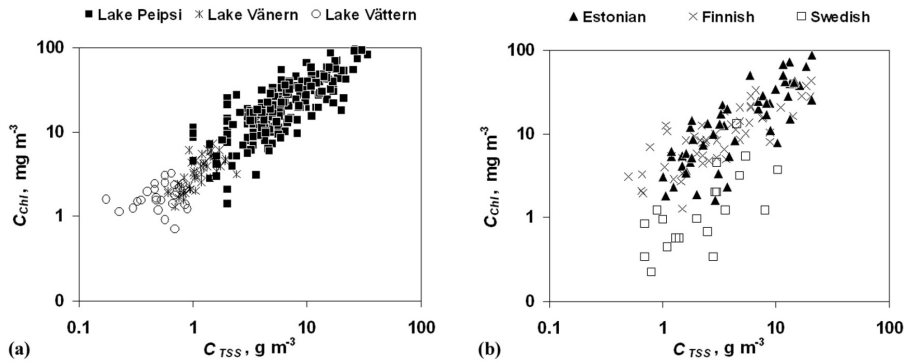
During our measurement campaigns we also examined the spatial variability of OAS in the north-south direction in Lake Peipsi (Table 3 in V). L. Peipsi is a large lake (area 3,555  $\text{km}^2$ ) and the concentrations of OAS vary noticeably

when comparing its three different parts. The general trend was the increase of OAS from the northern part of L. Peipsi towards its southern part (Table 3 in V). The spatial distribution of OAS is influenced also by inflow from rivers. The Velikaya River (entering L. Pihkva) accounts for about 50% and the Suur-Emajõgi River (entering L. Peipsi *s.s.*) for 39% of the inflowing water to L. Peipsi as a whole (Laugaste & Yastremskij, 2000). Since these large, strongly eutrophied rivers are major inflows in the southern coast of L. Peipsi, the concentrations of all three OAS were high especially near the mouths of the Rivers Suur-Emajõgi and Velikaya (Fig. 2 in II and Table 3 in V). The relatively high concentrations of  $C_{Chl}$  and  $C_{TSS}$  in the southern area of L. Peipsi were probably caused also by the fact that the measurements were performed in the period of algal bloom. The spatial distribution of OAS can vary with time. For instance, the average value of  $C_{Chl}$  in 2003 (the water samples were taken only in the Estonian side of L. Peipsi *s.s.* and L. Lämmijärv) was  $12.7 \pm 14.8 \text{ mg m}^{-3}$  (Paavel, 2004), which is substantially smaller than usual in this lake (Table 2).

In my study the correlation between different OAS measured in Estonian, Finnish and Swedish lakes was investigated (I–VI). According to Paavel (2004) and I there is a strong relationship ( $R^2=0.74$ ) between the concentrations of total suspended matter and chlorophyll *a* over all three large European lakes (Fig. 2a), indicating that generally suspended matter contains a large amount of phytoplankton cells. However, in case of low values of  $C_{Chl}$  and  $C_{TSS}$  they did not correlate anymore, partly because of uncertainty of the weighting method. Thus, separately in lakes Vänern and Vättern the corresponding determination coefficients were only 0.35 and 0.03 (in L. Peipsi it was 0.64). High values of  $C_{TSS}$  can be caused by high amounts of biomass or suspended solids, which both are typical of shallow eutrophic lakes. According to Laugaste *et al.* (1996) there is a strong seasonal and spatial variation in the composition of suspended particles, for example because of cyanobacteria blooms in the southern area of L. Peipsi (L. Pihkva) in late summer, but in L. Peipsi *s.s.* diatoms may cause high water turbidity even in November. The results of Paavel (2004) describing the regressions  $C_{Chl}$  vs.  $C_{TSS}$  for small lakes are presented in Fig. 2b. For chlorophyll-rich Estonian and Finnish lakes the values of  $R^2$  were much higher than those in small Swedish lakes ( $R^2$  was respectively 0.63, 0.64 and 0.17).

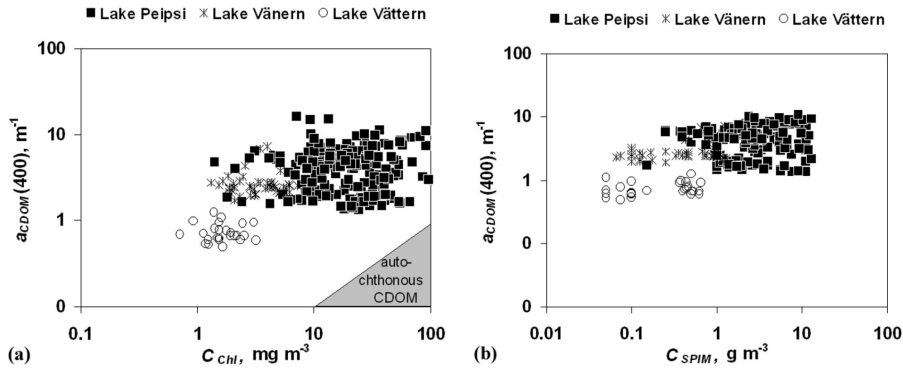
Using the database collected in L. Peipsi during 2001–2005 and in L. Võrtsjärv during 2003–2005 the determination coefficients of the regression  $C_{Chl}$  vs.  $C_{TSS}$  were correspondingly 0.64 and 0.44 (Table 4 in V). The low value of  $R^2$  for L. Võrtsjärv can be caused by the fact that this lake is noticeably shallower than L. Peipsi (mean depths 2.8 and 7 m) and in the conditions of strong wind the resuspensions of sediments from the bottom occur, which does not depend on the biological activity of the water.





**Figure 2.** Relationship between total suspended matter and chlorophyll *a* concentration in: (a) three European large lakes; (b) small lakes in Estonia, Finland and Sweden (according to Paavel (2004) and I).

Coloured dissolved organic matter may be produced in a lake itself or transported from the drainage area. Based on the relationship between  $a_{CDOM}$  and  $C_{ChI}$  (Fig. 3a) in Estonian lakes (L. Võrtsjärv and L. Harku are not shown), similarly to L. Vänern and L. Vättern, the coloured dissolved organic matter was clearly of allochthonous origin, referring to the relationship from Davies-Colley & Vant (1987). The correlative relationship between inorganic matter and CDOM in lakes Vänern and Vättern (Fig. 3b) showed that  $C_{SPIM}$  values were somewhat higher than the values of  $a_{CDOM}(400)$ , which usually refers to samples from river mouths or shallower areas close to the shore of lakes. In L. Peipsi the maximum values of  $a_{CDOM}(400)$  obtained in I were up to  $11 \text{ m}^{-1}$  (measured in the mouth of the River Suur-Emajõgi and in narrow L. Lämmijärv), but taking into account all measurements made during 2001–2005 it was  $16 \text{ m}^{-1}$ . The values of  $C_{SPIM}$  may be rather high everywhere over L. Peipsi, as they depend more on the depth and wind conditions than on inflows in shallow lakes (Nõges *et al.* 1996).



**Figure 3.** Absorption coefficient of light by coloured dissolved organic matter,  $a_{CDOM}(400)$ , as: (A) a function of chlorophyll  $a$  concentration; and (B) a function of inorganic suspended matter (according to I).

## 4.2. Contribution of different water constituents to the total absorption and attenuation of light

There are numerous publications where the absolute values of total and/or substance-specific absorption, scattering and attenuation coefficients are presented, both for the PAR region and for different wavelengths. However, we could find only a few studies where the contributions of different components of aquatic medium to total  $a$  (or  $c$ ) are assessed (Kirk, 1980, 1994; McKee *et al.*, 2002). This kind of information allows comparing the water bodies from the point of view of relative importance of water constituents in formation of inherent optical properties in different lakes and times.

The contributions of different components of aquatic medium to total  $a$  and  $c$  were estimated in Paavel (2004), I and IV. In the first two studies the necessary data were obtained from laboratory analyses, in IV I used additionally the *in situ* measurements made by the instrument ac-9 (Herlevi *et al.*, 1999; Herlevi, 2002). However, it is rather hard to distinguish  $b_{ph}$  and  $b_t$  from  $b$  spectra. For this reason, we did not separate the contribution of the scattering by different OAS, and only the total contribution.

In I the values of absorption coefficients by different water constituents were determined by measurements with a laboratory spectrometer. Then the ratios  $a_w/a$ ,  $a_{ph}/a$ ,  $a_{CDOM}/a$ , and  $a_t/a$  were calculated for three wavebands, 400–450, 550–650 and 670–700 nm, and for the whole PAR region.

The averaged values of contributions of water, CDOM, phytoplankton and tripton to the total spectral absorption coefficient for North-European large lakes (L. Peipsi, L. Vänern and L. Vättern) as well for some small Estonian and Finnish lakes for three wavebands are presented in Table 3. These results are

taken from Paavel (2004) as it covers more lakes than the database used in I. Note that the results showing percentage of absorption by the water, CDOM and particles for different water types in L. Peipsi, are also presented in Table 4 in I.

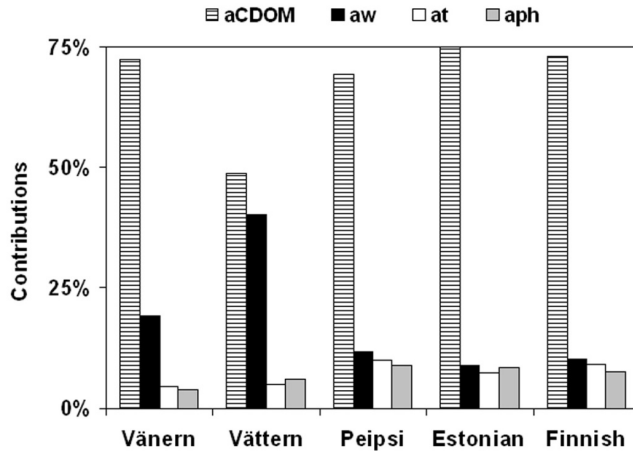
Coloured dissolved organic matter (CDOM) is certainly the most essential absorbing component in all investigated lakes. Its influence is especially high in the blue region of spectra, where the corresponding percentage is more than 80% (Table 3). Beginning from 550 nm absorption by pure water quickly increases. If in the waveband 550–650 nm the absorption of CDOM and water are still comparable, then at the end of the PAR region the contribution of CDOM is apostatized and the main absorber is water itself (Table 3). The phytoplankton and tripton absorb mostly up to 15% of the radiance in Estonian and Swedish lakes, while Finnish lakes form an exception where  $a_{ph}$  and  $a_t$  at the waveband 550–650 nm are respectively 24% and 22% (Table 3).

**Table 3.** Averaged values of contributions of optically active components to the total absorption coefficient at three wavebands (by Paavel, 2004 and I).

<i>Lakes</i>	<i>Vättern</i>	<i>Vänern</i>	<i>Peipsi</i>	<i>Estonian</i>	<i>Finnish</i>
Pure water					
400–450 nm	0.3%	0.2%	0.2%	0.2%	0.1%
550–650 nm	48%	69%	40%	29%	32%
670–700 nm	86%	89%	81%	72%	74%
Coloured dissolved organic matter					
400–450 nm	91%	83%	83%	85%	85%
550–650 nm	46%	26%	39%	55%	51%
670–700 nm	9%	4%	5%	12%	9%
Phytoplankton					
400–450 nm	3%	9%	6%	7%	6%
550–650 nm	2%	3%	12%	10%	24%
670–700 nm	5%	4%	11%	15%	14%
Tripton					
400–450 nm	5%	9%	10%	8%	9%
550–650 nm	2%	3%	9%	13%	22%
670–700 nm	1%	0%	2%	1%	3%

The averaged values of contributions of CDOM, water, tripton and phytoplankton to the total spectral absorption coefficient in the PAR region are shown in Fig. 4. Only in L. Peipsi and small Estonian and Finnish lakes the absorption by pure water are comparable with that of phytoplankton and tripton. In Swedish large lakes the amount of organic and mineral particles as well their

contribution to light absorption is smaller. In ultraoligotrophic L. Vättern the main factors of light absorption are dissolved organic matter and pure water, the effects of which are equivalent, respectively 49% and 40%. In L. Vänern the average absorption by CDOM (73%) is even higher than in L. Peipsi (average 64%), but the effect of particles is more than two times smaller (8% in L. Vänern and 19% in L. Peipsi). In small lakes, as well L. Peipsi, the influence of particles in light absorption is to some extent higher than the influence of pure water itself.



**Figure 4.** Contributions of phytoplankton, CDOM, pure water and tripton to the total absorption coefficients in the PAR region (Paavel 2004).

In **IV** the total absorption coefficients (as well attenuation and scattering coefficients) were obtained from the results of the instrument ac-9 (Herlevi *et al.*, 1999; Herlevi, 2002b). The following ratios were calculated: (1)  $a_w/a$ ,  $a_{ph}/a$ ,  $a_{CDOM}/a$  and  $a_t/a$ , (2)  $a_w/c$ ,  $a_{ph}/c$ ,  $a_{CDOM}/c$  and  $a_t/c$ , (3)  $b/c$ . The calculations were performed for eight wavelengths of ac-9 and for the whole PAR region (look at Eqs. 2.3–2.4 and Eq. 5 in **IV**). The spectral values of absorption coefficients of pure water were taken from Pope & Fry (1997). The database consists, similarly to Paavel (2004), of small Estonian and Finnish lakes, but the lakes are different. Two examples describing results for four individual cases are shown in Figs. 5 and 6 (look also at Figs. 3 and 4 in **IV** as well as at Table 4 in **IV**). These contributions change from lake to lake and can be very different for 440 and 676 nm (especially  $a_{CDOM}/a$  and  $a_w/a$ ). With two exceptions (L. Paukjärv & L. Koorküla Valgjärv) contribution of  $a_{ph}$  for 676 nm exceeds markedly that for 440 nm (Table 4 in **IV**). At the wavelength 440 nm the value of  $a_{ph}/a$  changes from 3.2% to 13% and  $a_{CDOM}/a$  from 56% to 90%. The values of  $a_w/a$  (and their absolute change) are small. At the wavelength 676 nm  $a_{ph}/a$  changes from 8.1% to 35%,  $a_{CDOM}/a$  from 1.6% to 11% and  $a_w/a$  from 39% to 82%. The numerical

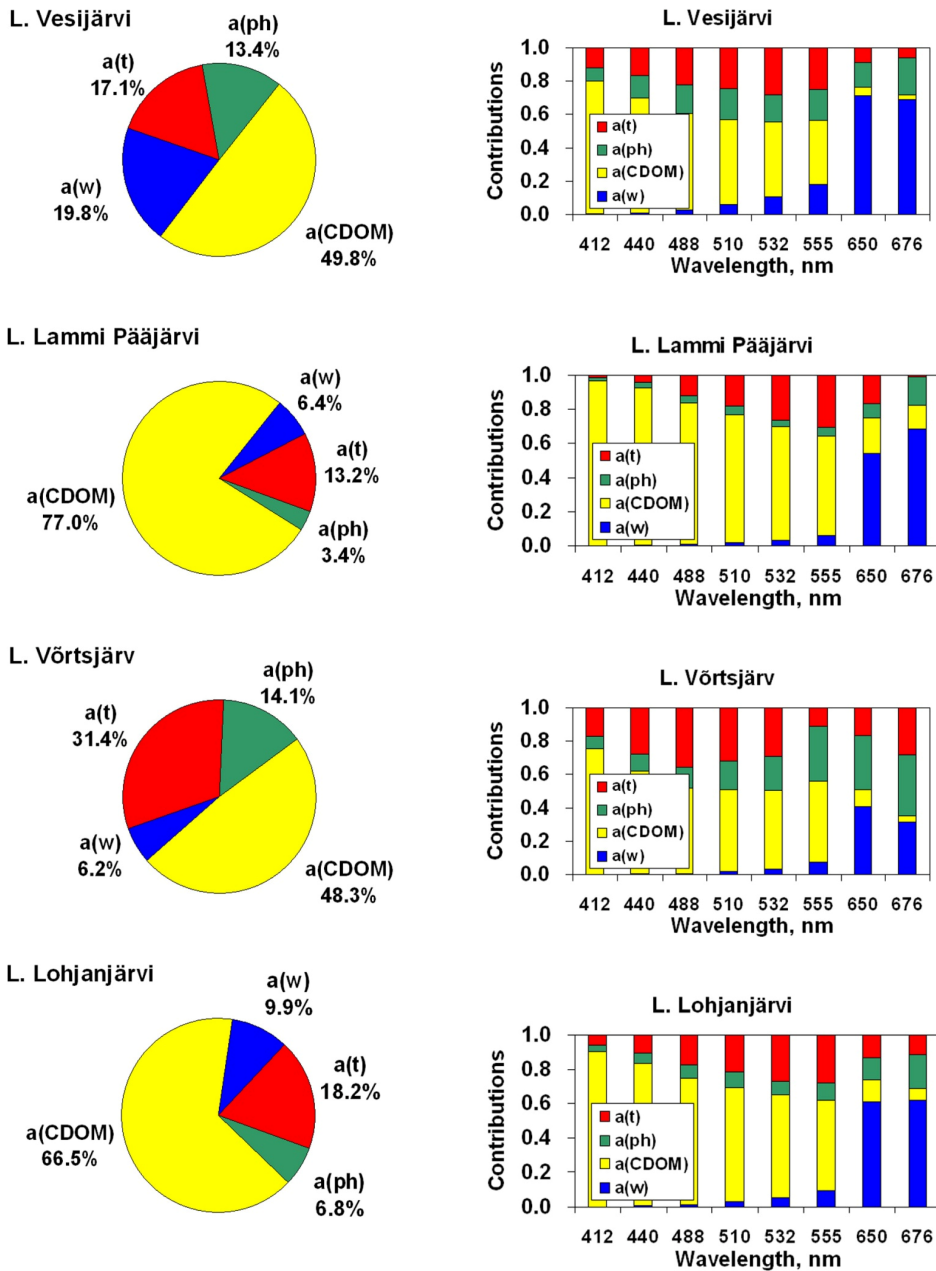
values of  $a_t/a$  have to be accepted with caution, but surely their highest contributions in three most turbid lakes (L. Tuusulanjärvi, L. Vörtsjärv and L. Ülemiste) are logical.

The contributions of OAS to  $a$  and  $c$  at different wavelengths, as well as those for the entire PAR region (Figs. 5 and 6) are to some extent in correspondence with the optical types of lakes (Reinart *et al.*, 2003; Arst 2003). According to Fig. 5, the value of  $a_{w,PAR}/a_{PAR}$  is almost 20% in L. Vesijärvi, but only about 6% in L. Vörtsjärv and L. Lammi Pääjärvi. The contribution of CDOM ( $a_{CDOM,PAR}/a_{PAR}$ ) is about 50% in L. Vesijärvi and L. Vörtsjärv, to some extent higher in L. Lohjanjärvi (65%), but in L. Lammi Pääjärvi it reaches 77%. The values of  $a_{ph,PAR}/a_{PAR}$  and  $a_{CDOM,PAR}/a_{PAR}$  are the highest in L. Vesijärvi and L. Vörtsjärv (14%), but only 7% in L. Lohjanjärvi and 3.4% in L. Lammi Pääjärvi. As can be expected, the ratio  $a_{t,PAR}/a_{PAR}$  is highest in shallow and turbid L. Vörtsjärv (30%), but almost similar in the other three lakes (13%–18%).

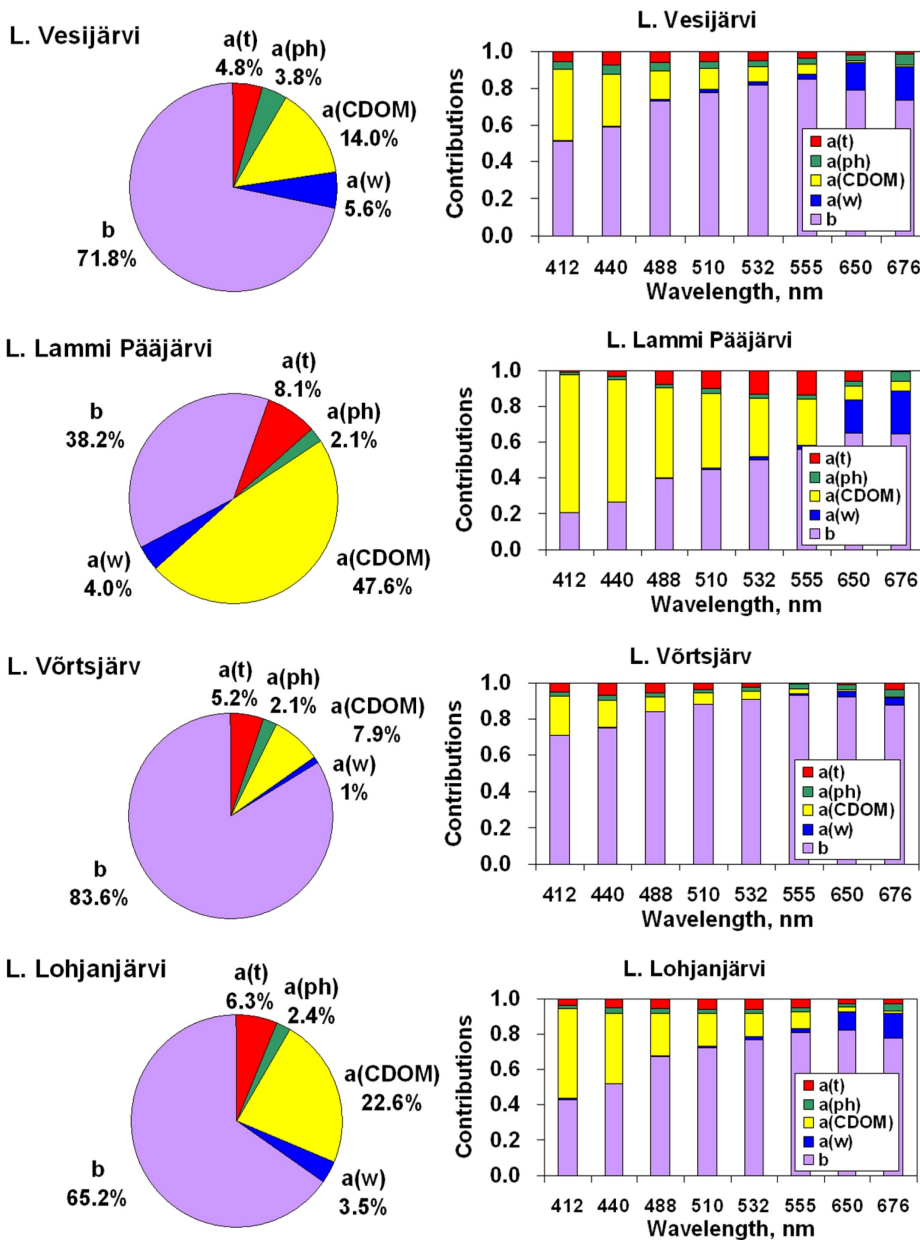
The values of  $b_{PAR}/c_{PAR}$  also vary from lake to lake: in L. Vörtsjärv it is 84%, in L. Vesijärvi 72%, in L. Lohjanjärvi 65% and in L. Lammi Pääjärvi only 38% (Fig. 6). In our very turbid lakes (L. Vörtsjärv, L. Tuusulanjärvi, L. Ülemiste) the scattering coefficient can be rather high (typical values of  $b(412\text{ nm})$  in these lakes were 10–26  $\text{m}^{-1}$ )(IV). Kirk (1981, 1994) presented the values of  $b_{PAR}$  for five Australian freshwater lakes, with a minimum of 1.5  $\text{m}^{-1}$  and a maximum of 59.8  $\text{m}^{-1}$ . So, there are lakes with very high values of scattering coefficient and correspondingly, the ratio  $b/c$  is relatively high. For the cases shown in Fig. 6, the values of  $b_{PAR}$  were between 1.9 and 12.3  $\text{m}^{-1}$ .

There is not much data of other authors for comparing with our results. Kirk (1980, 1994) presents some estimations of the contribution of 1) water itself, 2) soluble fraction, and 3) particulate fraction to absorbed PAR quantum irradiance for coastal-oceanic, estuarine and inland waters (altogether 12 cases). For inland waters the contribution of the water itself was in the range 6%–39%, the contributions of soluble and particulate fractions varied correspondingly 7.5%–60.4% and 5.2%–86.6%. The general agreement with the results of I and IV is good, but our turbid lakes show to some extent lower values of  $a_{w,PAR}/a_{PAR}$  and higher values of  $a_{CDOM,PAR}/a_{PAR}$ .

In McKee *et al.* (2002) the measurements and radiative transfer modelling were performed in a Scottish fjord, Loch Elive (down to 40 m). This water body is different from most of our shallow lakes, but three lakes (L. Paukjärv, L. Koorküla Valgjärv and L. Nohipalu Valgjärv) showed rather similar values of chlorophyll and coloured dissolved organic matter content. In Loch Elive the contributions of water, CDOM and phytoplankton (obviously together with tripton) to the total absorption in PAR were correspondingly 36%, 44% and 20%. For our clear-water lakes we obtained similar results, except that the contribution of CDOM in lakes was higher than that in the fjord.



**Figure 5.** Contributions of phytoplankton, CDOM, water and tripton to the total absorption coefficient  $a$  (calculated correspondingly as  $a_w/c$ ,  $a_{ph}/c$ ,  $a_{CDOM}/c$  and  $a_t/c$ ) for eight wavelengths and also for the PAR region. In the figure the abbreviations  $a_{ph}$ ,  $a_{CDOM}$ ,  $a_w$ ,  $a_t$  and  $b$  were used.



**Figure 6.** Contributions of  $a_{ph}$ ,  $a_{CDOM}$ ,  $a_w$ ,  $a_t$  and scattering coefficient  $b$  to the total attenuation coefficient  $c$  (calculated correspondingly as  $a_w/c$ ,  $a_{ph}/c$ ,  $a_{CDOM}/c$ ,  $a_t/c$  and  $b/c$ ) for eight wavelengths and the PAR region. In the figure the abbreviations  $a_{ph}$ ,  $a_{CDOM}$ ,  $a_w$ ,  $a_t$  and  $b$  were used.

### 4.3. Absorption of solar light in the water caused by tripton

Particulate attenuation can be decomposed into contributions from phytoplankton (“chlorophyllous” particles) and from other particulate material, tripton (“nonchlorophyllous” particles). Tripton consists of non-living suspended material in the water (organic and inorganic particles). Non-living organic particles are called detritus. These particles are assumed to have biological origin (produced when phytoplankton die and their cells break apart, and when zooplanktons graze on phytoplankton and leave cell fragments and fecal pellets). However, detrital material may also have other sources e.g., resuspension of organic matter from the bottom, river and land drainage. The second component of tripton, inorganic particles may include minerals, such as fine clay, silt particles, sand, or precipitates such as iron and manganese hydroxides and calcium carbonate. Note that different authors have different definitions for tripton (Kishino *et al.*, 1985; Nelson & Robertson, 1993; Tassan & Ferrari, 1995; Hoogenboom & Dekker, 1997). Rather often nonchlorophyllous material is equated with detritus, obviously supposing that the contribution of mineral particles in tripton is very small.

Usually data exist on total particulate absorption (Kirk & Tyler, 1986; Bowling *et al.*, 1986; Oliver, 1990; Alvarez-Cobelas, 1991), but these studies do not provide direct information about tripton absorption itself because of confounding contributions by phytoplankton. Measurements of phytoplankton and tripton absorption, in turbid productive inland waters are even more limited. Most published data have been collected from European lakes (Duarte *et al.*, 2000; Pierson & Strömbeck, 2000; Kutser *et al.*, 2001; Simis *et al.*, 2005), although oligotrophic and mesotrophic lakes in North America have been investigated (Bukata *et al.*, 1979; Weidemann *et al.*, 1985; Weidemann & Bannister, 1986; Bergmann *et al.*, 2004). Thus, the assessment of the numerical values of absorption of light by suspended particles as well as of the corresponding specific absorption coefficients is complicated and is still one of the most difficult problems in the building of the remote sensing models.

One of the main tasks of my research was to extend the current understanding of variations in specific absorption coefficients of tripton, and the potential diversity in their spectral signatures (**I**, **IV**). The values of tripton absorption coefficients were determined in two ways: (1) measuring the total particulate absorption with a spectrometer and using later depigmentation with sodium hypochloride, which separates phytoplankton and tripton absorptions (**I**), and (2) estimated as a residual on the basis of Eq. 2.2 (Eq. 5 in **IV**). In the last case the total absorption coefficient was obtained from the results of the instrument ac-9, and the values  $a_{ph}$  and  $a_{CDOM}$  were estimated using Eqs. 2.3 and 2.4). The spectral values of absorption coefficients of pure water are considered as known data and were taken from Pope and Fry (1997).



It is generally accepted that the spectrum of tripton absorption coefficient  $a_t(\lambda)$  can be described by an exponential function which increases toward shorter wavelengths:

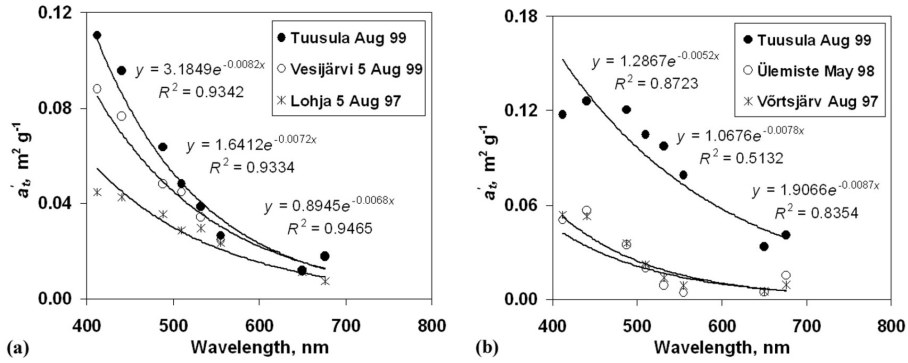
$$a_t(\lambda) = a_t(\lambda_0) \exp[-t(\lambda - \lambda_0)]. \quad (4.1)$$

Here  $\lambda_0$  is a reference wavelength, and  $t$  is an empirically determined slope of the exponential curve. When the concentration of tripton in the water ( $C_t$ ) is known, we can estimate corresponding specific absorption coefficient  $a'_t(\lambda) = a_t(\lambda)/C_t$ .

In Paavel (2004) the values of  $a'_t(400 \text{ nm})$  were estimated for two Swedish lakes (L. Vänern and L. Vättern), for L. Peipsi (Estonia) and for some small Estonian and Finnish lakes. The results obtained were between 0.11 and 0.20  $\text{m}^2 \text{g}^{-1}$ . Partially the same database (L. Peipsi, L. Vänern and L. Vättern) was used in I. The numerical values of the tripton absorption coefficient ( $a_t(400)$ ) for these lakes were correspondingly  $0.72 \pm 0.50$ ,  $0.13 \pm 0.17$  and  $0.05 \pm 0.03 \text{ m}^{-1}$ . The slope  $t$  varies only a little: from 0.012 to 0.014  $\text{nm}^{-1}$ , increasing with the water transparency.

According to the results of IV for small Estonian and Finnish lakes the values of  $a_t$  at the wavelength of 412 nm were mostly between 0.02 and 0.8  $\text{m}^{-1}$ . For comparison we have several values of  $a_t(412)$  measured in other studies. In the Baltic Sea in summer 1998 Darecki *et al.* (2003) got the values of  $a_t(412)$  mostly up to 0.65  $\text{m}^{-1}$  (the maximum was 1  $\text{m}^{-1}$ ). For Lake Peipsi  $a_t(412)$  ranged from 0.18 to 0.95  $\text{m}^{-1}$ , which was about six times higher than  $a_t(412)$  for large Swedish lakes, L. Vänern and L. Vättern (0.05–0.16  $\text{m}^{-1}$ ) (Paavel, 2004 and I). The variability of  $a_t$  can be explained by the fact that it depends not only on absorptive properties of tripton, but also on its concentration in the water.

Some examples of the spectral variation of specific absorption coefficients of tripton,  $a'_t$ , calculated by Eqs. 5 and 6 in IV, are shown in Fig. 7. Four spectra in this figure are characterized by a high determination coefficient and a rather stable value of the exponent  $t$ , which was between 0.0068 and 0.0082  $\text{nm}^{-1}$ . However, there is a group of measurements, where the maximum value of  $a'_t$  is at the wavelength 440 nm, the value of  $R^2$  is lower (sometimes even less than 0.5) and the values of  $a'_t$  at 532 and 555 nm are very small (Fig. 7b). As one can expect, the numerical values of  $a'_t$  were very variable (see also Table 3 in IV). Naturally, the slope of the exponent is the same for  $a_t$  and  $a'_t$ .



**Figure 7.** Some examples of the spectral distribution of  $a'_t(\lambda)$ , calculated by Eqs. 5 and 6 in I, using the results of *in situ* and laboratory measurements as initial data: (a) shows the trendlines fitting well with the measurement results, (b) the points showing the spectral distribution of  $a'_t(\lambda)$  are rather irregular.

On the basis of ac-9 measurements we could estimate  $a'_t(400)$  only very approximately (by extrapolation), using trendlines of the  $a'_t(\lambda)$  spectra (IV). According to these data (I),  $a'_t(400)$  varies between 0.050 and 0.176  $\text{m}^2 \text{g}^{-1}$ . When comparing these results with those of Paavel (2004) (from 0.11 to 0.20  $\text{m}^2 \text{g}^{-1}$ ) we see that there is only partial coincidence. However, such a discrepancy is not surprising taking into account the dependency of  $a'_t$  on the refractive index of particles and their size distribution (Mikkelsen, 2002). The values of  $a'_t(532)$  varied from 0.013 to 0.098  $\text{m}^2 \text{g}^{-1}$ , but this can be explained not only by variability of tripton constituents, but also by errors of results obtained. We could not find a good correlation between the values of  $a'_t(532)$  and the concentration of tripton,  $C_t$ . However, using the Microsoft Excel Data Analysis program we found a rather good relationship between  $a'_t(532)$  and exponent  $t$  (for linear regression  $R^2 = 0.584$ , standard error (SE) = 0.00092  $\text{m}^2 \text{g}^{-1}$ ,  $p = 1.42 \times 10^{-6}$ ).

The slope of the absorption coefficient spectra of tripton,  $t$ , for investigated North-European lakes (I, IV) was rather independent from time and place of sampling, varying from 0.0060 to 0.014  $\text{nm}^{-1}$  (with two exceptions, the lower boundaries being 0.0044 and 0.0052  $\text{nm}^{-1}$ ). It is in agreement with the data for a large range of waters, where  $t$  varied in the range of 0.006–0.016  $\text{nm}^{-1}$  (Roesler *et al.*, 1989; Bricaud & Stramski, 1990; Strömbeck & Pierson, 2001; Darecki *et al.*, 2003).

#### 4.4. Estimation of the slope of the scattering coefficient spectra

A special problem in marine optics is the description of the spectral distribution of the scattering coefficient. As was mentioned before, there are algorithms describing the scattering of light by phytoplankton (Eq. 2.5). However, the relevant scatterers are also detritus and mineral particles. Usually the spectrum of total scattering coefficient,  $b(\lambda)$ , describing the summary influence of all OAS, is considered. Rather often the spectral invariance of  $b$  is stated (Jerlov (1974) for Baltic Waters; Bukata *et al.* (1979) for Lake Ontario; Phillips & Kirk (1984) for Australian waters). Unfortunately, only a few spectral measurements exist, but the theory (Morel & Prior, 1977) and investigations (Dekker, 1993; Jupp *et al.*, 1994; Herlevi *et al.*, 1999) suggest that scattering is relatively high at short wavelengths and lower at high wavelengths, following a power law,  $\lambda^{p_b}$ , (see Eq. 11 in IV). The crucial parameter is the slope  $p_b$ , the numerical values of which vary noticeably (Morel & Prior, 1977; Kopelevich, 1983b; Dekker, 1993; Kirk, 1994; Gould & Arnone, 1998; Herlevi *et al.*, 1999; Herlevi, 2002b; Gallegos *et al.*, 2005). Sometimes even contradictory results on its dependence on water turbidity were presented — some authors show a decrease, others an increase of  $p_b$  with increasing the turbidity.

The objectives of my work were to describe seasonal variation of  $p_b$  (comparing May/June and August data) and to estimate its dependence on the concentrations of optically active substances (IV). The initial data ( $b(\lambda)$  at eight wavelengths in the PAR region) were taken from the database of the project SUVI (Herlevi *et al.*, 1999; Herlevi, 2002b). The slope  $p_b$  was determined using the power function trendline through these points. In most cases the determination coefficient was high ( $R^2 > 0.94$ ). The values of  $p_b$  varied in large range, being between 0.32 and 2.53, the average value was 0.847 ( $N = 73$ ,  $SE = 0.439$ ) (IV). The parameter  $p_b$  was also determined from our measurements in L. Peipsi (I). The average value for exponent  $p_b$  for L. Peipsi was  $1.01 \pm 0.16$  (Table 5 in I), which is slightly lower than that estimated in large Swedish lakes Vättern and Vänern (1.25–1.45) by Strömbeck (2001). Note that for lake waters the value  $p_b = 0.8$  is often used in practice (Herlevi *et al.*, 1999; Herlevi, 2002b; Arst, 2003).

In three Finnish and two Estonian lakes we found distinguishable differences between  $p_b$  averaged for May/June and for August (Fig. 7 in IV). The early summer values are rather variable, from 0.44 to 2.1, but in August  $p_b$  varies only from 0.33 to 0.66. Gallegos *et al.* (2005) also found a seasonal trend for  $p_b$  characterized by relatively high values in early spring and declines during the summer bloom. The reason why the wavelength dependence of the scattering coefficient is larger in spring than in late summer could be the different size and type of particles in water.

It was rather problematic to assume that we can find the connections between the values of slope  $p_b$  and the concentrations of OAS. We had no success in finding a good correlation between  $p_b$  and the concentration of any single OAS, although multiple regression between  $p_b$  and three OAS jointly can give rather high determination coefficients. To predict this slope, the best results were obtained using multiple linear regression module of STATISTICA 6.0 (StatSoft Inc., 2001) including the measured OAS values as well as their pairwise products ( $C_{chl}C_{TSS}$ ,  $C_{chl}c_f^*(380)$  and  $C_s c_f^*(380)$ ) in the analysis. Forward stepwise method was applied to select the best fitting model. The regression formula obtained is following:

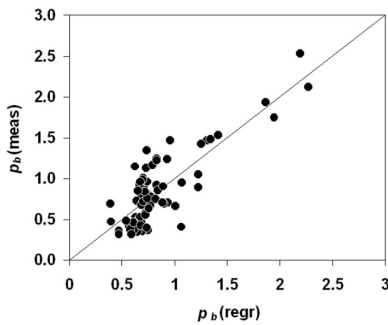
$$p_b = 0.7964 + 0.00964C_{TSS}c_f^*(380) - 0.0453C_s - 0.0124C_{chl}. \quad (4.2)$$

The units  $C_{TSS}$ ,  $C_{chl}$  and  $c_f^*$  are  $\text{mg l}^{-1}$ ,  $\text{mg m}^{-3}$  and  $\text{m}^{-1}$ , respectively. The statistical parameters of this regression were  $N = 73$ ,  $R^2 = 0.668$ , SE of estimate = 0.259,  $p < 0.000001$ , with all variables and intercept being highly significant ( $p < 0.001$ ). The comparison of  $p_b(\text{meas})$  and  $p_b(\text{regr})$  is presented in Fig. 8. These results show that, to some extent, the slope of the scattering coefficient spectrum depends all at once on the concentrations of three OAS.

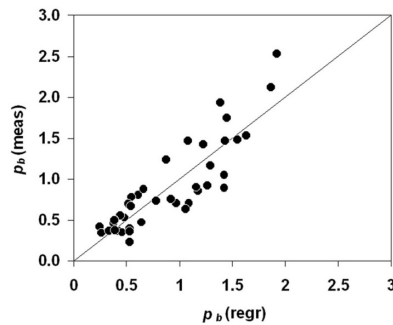
However, using the data only for five Finnish lakes (L. Lammi Pääjärvi, L. Lohjanjärvi, L. Päijänne, L. Tuusulanjärvi and L. Vesijärvi) a simple linear multiple regression gave a rather high value of  $R^2$  (Fig. 9). The corresponding regression formula was:

$$p_b = 0.212 + 0.0492C_{TSS} - 0.0306C_{chl} + 0.0922c_f^*(380), \quad (4.3)$$

where  $N = 41$ ,  $R^2 = 0.764$ , SE = 0.27 and  $p < 0.001$ .



**Figure 8.** Comparison of  $p_b$  values, derived from ac-9 measurements and calculated by regression formula (equation 4.2).



**Figure 9.** Comparison of  $p_b(\text{meas})$  and  $p_b(\text{calc})$ , computed by Eq. 4.3 (only the data of L. Päijänne, L. Vesijärvi, L. Lammi Pääjärvi, L. Lohjanjärvi and L. Tuusulanjärvi were used).

## 4.5. Parameters for estimating the transparency and optical quality of the water

The different lake field programmes, carried out in 1994–2005 in Estonian, Finnish and Swedish lakes (Paavel, 2004; **I–VI**) included: (1) the parameters determined from water samples, like the concentrations of optically active substances (described already in chapter 4.1), (2) the values of spectrometric attenuation coefficient of light between 400–700 nm, and corresponding attenuation coefficient in the photosynthetically active region,  $c_{PAR}^*$ ; (3) the apparent optical properties obtained from measurements *in situ*. In the last case the main characteristics are Secchi depth,  $z_{SD}$ , and the diffuse attenuation coefficient (spectral and also for the whole PAR region, respectively  $K_d(\lambda)$  and  $K_{d,PAR}$ ). On the basis of these data the temporal variations of  $z_{SD}$ ,  $c_{PAR}^*$  and  $K_{d,PAR}$  were described and the general relationships between OAS and other parameters were investigated.

The laboratory measurements giving us the parameters  $c^*(\lambda)$  and  $c_{PAR}^*$  as well as underwater irradiance measurements with sensors LI-1800 UW and LI-192 SA were described in the chapter 3. From underwater irradiance measurements also the depth-averaged diffuse attenuation coefficient of PAR,  $K_{d,PAR}$ , was determined (**V–VI**). For this we used a semi-logarithmic plot of  $E_{d,PAR}$  (**I–III**) or  $q_{PAR}$  (**V–VI**) vs. depth and calculated  $K_{d,PAR}$  as the slope of the least-square regression line through these points. It has been shown that in addition to  $z_{SD}$  and  $K_{d,PAR}$ , also  $c_{PAR}^*$  is a rather good indicator of the optical quality of the water (Arst, 2003).

The temporal variations of characteristics  $z_{SD}$ ,  $c_{PAR}^*$  and  $K_{d,PAR}$  during 2003–2005 were examined in lakes Peipsi, Võrtsjärv and Harku (the corresponding sampling stations were Varnja, Limnology and Harku). As told before (section 4.1), in 2003 we had field trips only in June and August and during 2004–2005 in different months from April to September. Two consecutive measurement series of all parameters (including water samples and primary production) were planned for each day, the first before or at midday and the second in the afternoon, but sometimes due to the weather conditions or technical problems some results were missing or not acceptable. Altogether we got reliable data from 53 field and 68 laboratory series. For describing the seasonal variations of parameters we averaged the results of two series in each measurement day (Fig. 4.5.1).

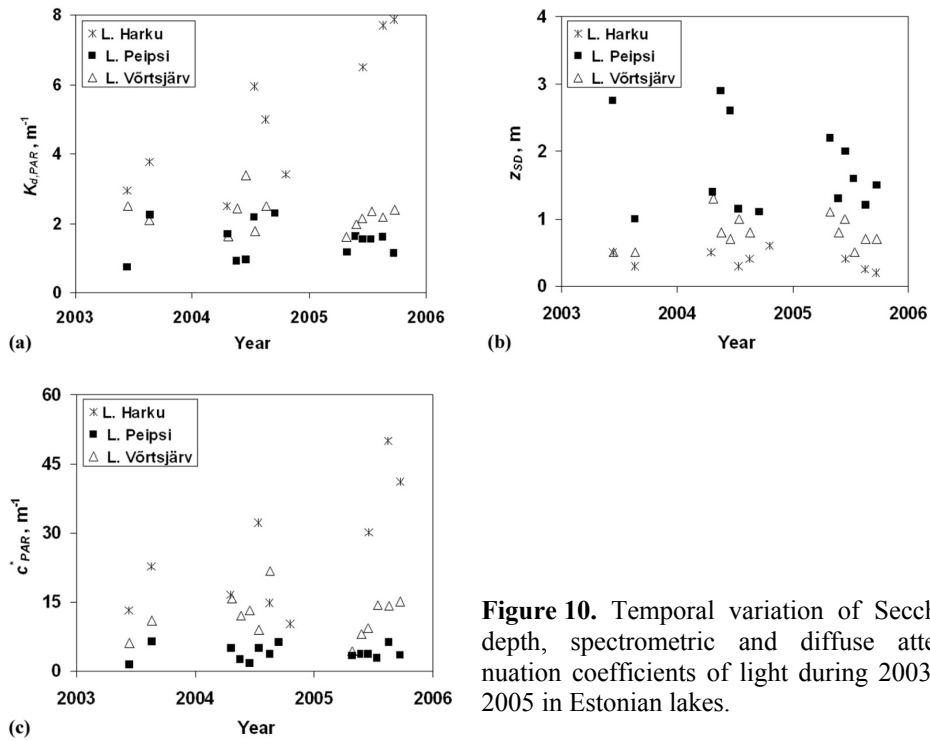
The analysis of the data showed that the seasonal behaviour of  $K_{d,PAR}$  (and also  $z_{SD}$  and  $c_{PAR}^*$ ) was closely related to the variations in OAS. The lowest  $K_{d,PAR}$  values (from 0.74 to 1.70 m<sup>-1</sup>) in Peipsi were observed in spring and summer, but by the end of August (in some years even in September)  $K_{d,PAR}$  had increased to 2.28 m<sup>-1</sup>, mainly due to phytoplankton blooms (Fig. 4.5.1a). We have additional data on  $K_{d,PAR}$  obtained on the basis of measurements with a four-channel instrument BIC-2104 in L. Peipsi *s.s.* and Lämmijärv. During

a field campaign in 2003  $K_{d,PAR}$  varied from 0.89 to 3.76 m<sup>-1</sup> (II). In spring  $K_{d,PAR}$  values in Võrtsjärv and Harku varied from 1.60 to 2.50 m<sup>-1</sup>, but they increased in late summer and autumn up to 7.80 m<sup>-1</sup> in Harku (in lake Võrtsjärv the maximum together with results in 1995–2002 was 3.80 m<sup>-1</sup>, V). Note that in September 1996, when the Secchi depth in L. Võrtsjärv was only 0.15 m, an extremely high value of  $K_{d,PAR}$ , equal to 6.5 m<sup>-1</sup>, was observed (Fig. 3b in V).

In general, the values of  $c_{PAR}^*$  showed a seasonal dynamics similar to  $K_{d,PAR}$ , but sometimes their behaviours conflicted. The reason can be that  $K_{d,PAR}$ , unlike  $c_{PAR}^*$ , depends on the angular distribution of irradiance (Figs. 10a,c). However, a trend of increasing  $C_{Chl}$  in Harku from 2003 to 2005 is clearly expressed both in  $c_{PAR}^*$  and  $K_{d,PAR}$  (Fig. 1a and Fig. 10a,c).

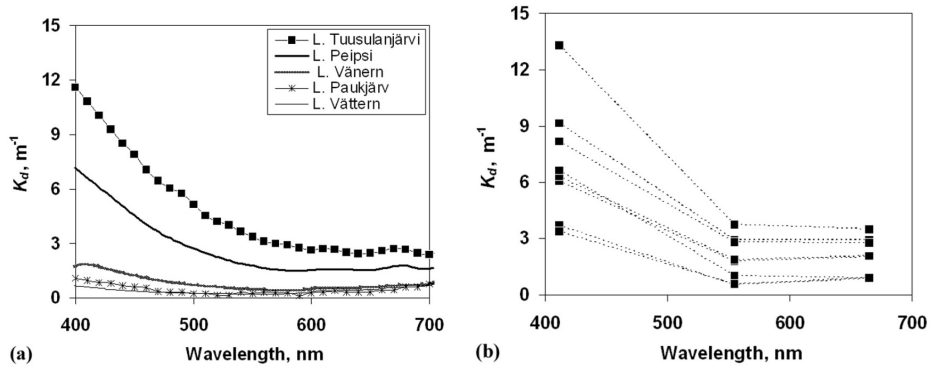
We can compare the vernal diffuse attenuation coefficients in the eutrophic Estonian lakes with that measured in the Swedish lakes Vänern and Vättern during spring 2002. In L. Peipsi we obtained the values of  $K_{d,PAR}$  from 0.74 and 1.70 m<sup>-1</sup> and in L. Võrtsjärv from 1.60 to 2.44 m<sup>-1</sup>. In L. Vänern and L. Vättern the  $K_{d,PAR}$  values were respectively 0.71 and 0.33 m<sup>-1</sup>. Water in the deep Swedish lakes is more transparent than in the shallow Estonian lakes; it contains fewer nutrients because the rivers bring less organic matter from the rocky upland catchments into these lakes (Willen, 2001b). On the contrary, the Estonian lakes are frequently surrounded by wetlands.

Due to the remarkable turbidity of L. Peipsi, L. Võrtsjärv and L. Harku the Secchi depth values are low (up to 3 m, mostly below 1.5 m) (Fig. 10b). The seasonal dynamics of water transparency in different parts of L. Peipsi in 2003 is also described in Figs. 2 and 3 (respectively, for the period 1992–2003 and year 2003) in I. The clearest water was observed in the northwestern corner of L. Peipsi *s.s.*, Secchi depth was to some extent lower in L. Lämmijärv, and the lowest in L. Pihkva. The River Suur-Emajõgi brings large amounts of humic matter into the lake from the surrounding bog areas, which makes the water close to the river inflow brownish and usually less transparent than the water in the deeper parts of L. Peipsi *s.s.* (II). According to Lindpere *et al.* (1991) in L. Peipsi *s.s.* Secchi depth depends primarily on the development of phytoplankton, while in L. Lämmijärv and L. Pihkva it depends also on the amount of humic substances. The values of  $z_{SD}$  found in Paavel (2004) in Estonian and Finnish lakes vary from 7 m in oligotrophic L. Nohipalu Valgjärv down to 0.15 m in L. Võrtsjärv, which was unusually turbid because of extremely low water level in 1996.



**Figure 10.** Temporal variation of Secchi depth, spectrometric and diffuse attenuation coefficients of light during 2003–2005 in Estonian lakes.

All optically active components affect irradiance attenuation in the water in a different manner, therefore the spectra of  $K_d(\lambda)$  give more information about the underwater light field than  $K_{d,PAR}$ . Some examples of these spectra were chosen to show the variability in different types of lakes (Fig. 11). In L. Peipsi the spectral diffuse attenuation coefficient was measured only in 2003 (thin lines in Fig. 5b in II) as well as during the field campaign in 2005 (the corresponding average is presented in Fig. 11a). The values of  $K_d(\lambda)$  are notably higher than the averaged spectra from lakes Vättern, Vänern and Paukjärv. L. Paukjärv represents the lowest  $K_d$  values measured during expeditions in Estonia and Finland 1994–2000 (Fig. 11a). However,  $K_d$  values measured at three wavelengths with a spectrometer BIC-2104 (in 2003) show that attenuation in shallow areas of L. Peipsi is sometimes comparable with most turbid waters (e.g. L. Tuusulanjärvi) (Fig. 11b).

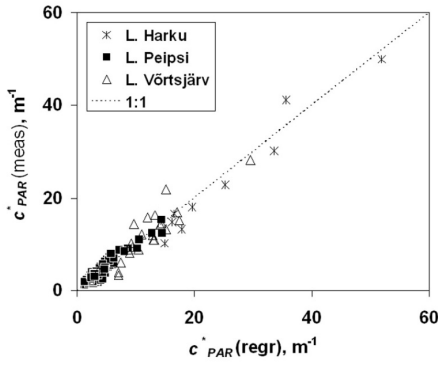


**Figure 11.** Examples of diffuse attenuation coefficient spectra: (a) average measured in different lakes; (b) measured in different sampling stations in L. Peipsi (in 2003) by BIC-2104.

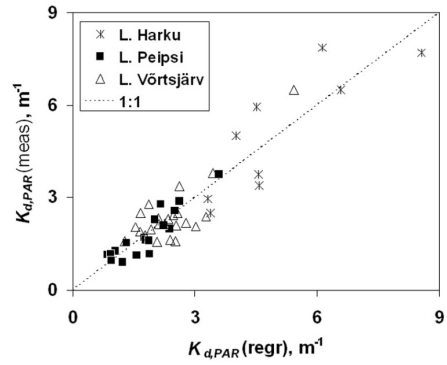
We investigated also the correlation relationships between OAS and optical characteristics of the water. It was done using databases separately for three turbid Estonian lakes, Peipsi, Võrtsjärv and Harku (Eqs. 2–5 in V). The determination coefficients of the regression predicting  $K_{d,PAR}$  from different OAS were in most cases only 0.25–0.35. The regression formulas predicting  $c_{PAR}^*$  as a function of each OAS separately are shown for lakes Peipsi and Võrtsjärv in Table 4 in V. The parameter  $c_{PAR}^*$  correlated well with the concentrations of chlorophyll and total suspended matter. The corresponding determination coefficients were relatively high for all three lakes (from 0.64 and 0.76), but the correlation  $C_{Chl}$  vs.  $C_{TSS}$  was good only for L. Peipsi and L. Harku (0.64 and 0.67, respectively). The correlation  $c_{PAR}^*$  vs.  $c_{\lambda(380)}^*$  was weak for all three lakes (in L. Võrtsjärv it was actually negative). The reasons can be: (1) the relative temporal change of  $c_{\lambda(380)}^*$  is noticeably smaller than the relative variations in phytoplankton concentration; (2) the parameter  $c_{\lambda(380)}^*$  usually decreases slightly from spring to autumn, but in turbid lakes a strong growth of  $C_{Chl}$  is observed towards the phytoplankton bloom in August–September (Erm *et al.*, 2002). Note that the contribution of  $c_{\lambda}^*(\lambda)$  to the scattering coefficient is extremely small.

Since the water transparency is influenced simultaneously by all three OAS together, we also determined corresponding multiple regressions, predicting  $c_{PAR}^*$  or  $K_{d,PAR}$ . The regression formulas obtained and the corresponding statistical characteristics for L. Peipsi and L. Võrtsjärv are shown in V. The values of  $R^2$  for  $c_{PAR}^*$  (Eqs. 2 and 4 in V) are higher than those for  $K_{d,PAR}$  (Eqs. 3 and 5 in V). The reason is that  $K_{d,PAR}$  depends not only on the concentrations of substances, but also on the angular distribution of irradiance. The relationships  $c_{PAR}^*(\text{meas})$  vs.  $c_{PAR}^*(\text{regr})$  and  $K_{d,PAR}(\text{meas})$  vs.  $K_{d,PAR}(\text{regr})$  are presented in Fig. 12 and Fig. 13.





**Figure 12.** Relationship between measured and calculated (from multiple regression analyses) spectrometric attenuation coefficient in Peipsi (all stations), in Võrtsjärv (Limnology Station) and in Harku (Harku Station).



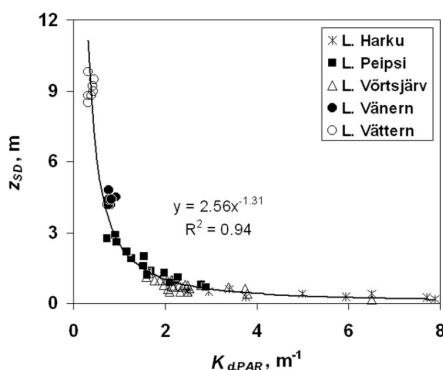
**Figure 13.** Relationship between measured and calculated (from multiple regression analyses) diffuse attenuation coefficient values in lakes Peipsi, Võrtsjärv and Harku.

The relationship  $z_{SD}$  vs.  $K_{d,PAR}$  found for three Estonian lakes and two Swedish lakes on the basis of our data (I,V) is shown in Fig. 14. These results show that this relationship can be described by a power function with an exponent of 1.31. This value is rather close to those obtained by Davies-Colley & Vant (1988), Koenings & Edmundson (1991) (the exponent is 1) and also by Reinart & Nõges (2004) for various Estonian lakes (1.35).

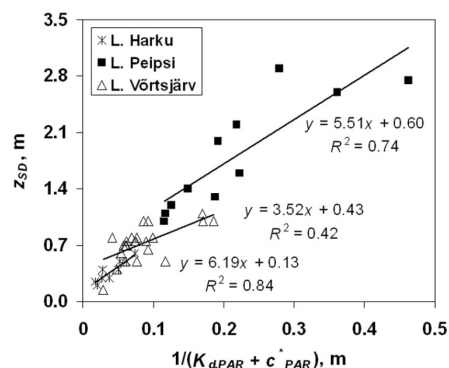
In Kirk (1994) the connection between  $z_{SD}$  and  $K_{d,PAR}$  is described in the following way:

$$z_{SD} = \frac{C}{K_{d,PAR} + c_{PAR}} \quad (4.5.1)$$

where  $C$  is a constant ranging from 8.7 to 9.4 (estimated for coastal waters and New Zealand lakes). We tried to determine the value of  $C$  for L. Peipsi, L. Võrtsjärv and L. Harku (Varnja, Limnology and Harku Stations), using not  $c_{PAR}$ , but  $c_{PAR}^*$  (i.e. the attenuation caused by pure water was not taken into account). This hardly influences the result, because in turbid waters the contribution of pure water is very small, 1–4%. Using the database “three lakes together” we got the regression formula  $z_{SD} = 6.67/(K_{d,PAR} + c_{PAR}^*) + 0.20$ . In this equation the constant  $C$  was lower than that presented in Kirk (1994) and there was also an intercept in our algorithm. The determination coefficient  $R^2$  was 0.85, but when to determining these regressions separately for L. Peipsi, L. Võrtsjärv and L. Harku, the values of  $R^2$  were correspondingly 0.74, 0.42 and 0.84 (Fig. 15). The reason of the low value of  $R^2$  in L. Võrtsjärv may be the small range of variation in  $z_{SD}$  and  $K_{d,PAR}$  in our database.



**Figure 14.** Relationship between the values of Secchi disk depth and diffuse attenuation coefficient in five North-European lakes (for Estonian lakes the data for all stations are included).



**Figure 15.** Relationship  $z_{SD}$  vs.  $1/(K_{d,PAR} + c^*_{PAR})$ , separately for lakes Peipsi, Võrtsjärv and Harku.

#### 4.6. A model for calculating the spectra of diffuse attenuation coefficients using *in situ* measured data at three wavelengths

Spectral distribution of solar radiation in water bodies is of interest for identifying optically active substances, marine biology and remote sensing of aquatic environment. The light attenuation accordance with depth is characterized by the spectral diffuse attenuation coefficient,  $K_d(\lambda)$  which is calculated on the basis of measured vertical profiles of downward irradiance  $E_d(\lambda)$ . However, quite often occur situations where  $K_d(\lambda)$  data for the whole spectrum (400–700 nm) are not available (sensors having only few wavebands in the PAR region, unsuitable weather conditions, and negligible small irradiance in the blue region of the spectrum in very turbid waters occur).

Reinart & Herlevi (1999) presented an analytical form for spectra of  $K_d(\lambda)$ , suitable for different types of lakes. The model allows calculating the spectra of  $K_d(\lambda)$  (with 10 nm step over the range of 400–700 nm) on the basis of measured irradiance profile in one reference wavelength. It was quantified on the basis of spectral measurements of underwater light using the spectroradiometer LI-1800 UW (LI-COR, Inc., 1984). Then, using statistical methods, an algorithm and its spectral parameters were found suitable for recreating the diffuse attenuation coefficient spectra for a water body on the basis of known values of  $K_d(490)$ , i.e.  $\lambda_r = 490$  nm was taken as a reference wavelength. The final equation and respective spectral coefficients (for the PAR region) are shown in Eq. 5 in **III** and Table 1 in **III**.

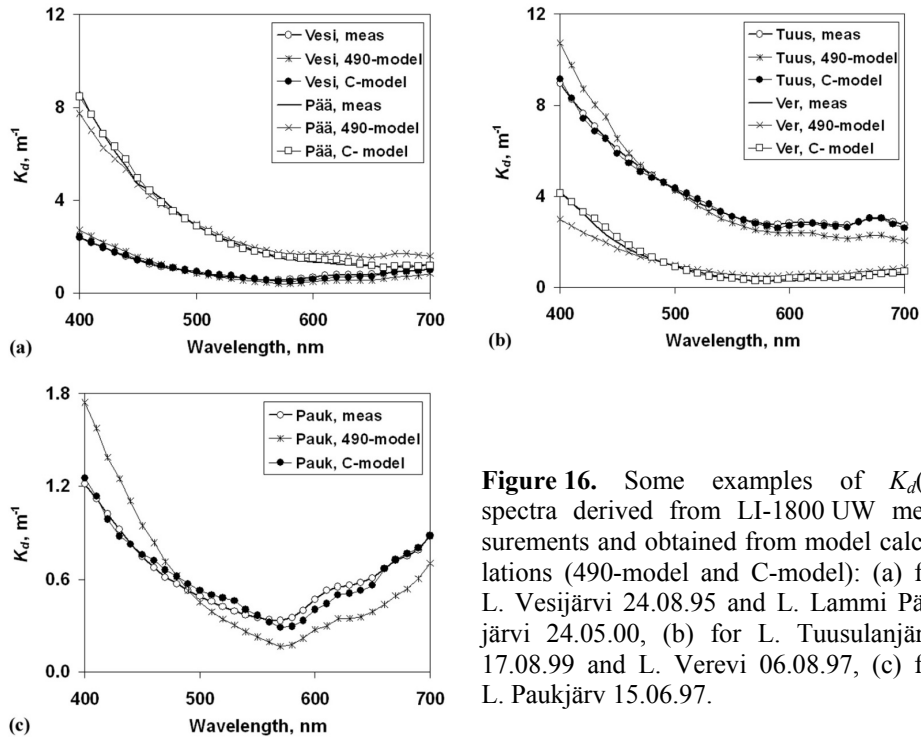
In many individual cases, the results obtained using the so-called 490-model were in good accordance with the measured values in the whole PAR region, but often some discrepancies in the blue and red regions were observed. Usually an overestimation of  $K_d(\lambda)$  in the blue region is accompanied by an underestimation of  $K_d(\lambda)$  in the red region, and vice versa (Fig. 16c). For this reason the purpose of the present study was to elaborate a new improved method (we call it C-model), for recreating the  $K_d(\lambda)$  spectra utilizing its values in the centres of three different wavebands of BIC-2104 radiometer (412, 555, 665 nm). Here we used Eq. 6 from **III** and the same parameters,  $J(\lambda_r)$  and  $M(\lambda_r)$  as shown in Table 1 in **III**. Since these parameters were presented with a 10 nm step, their values, necessary for BIC-2104 wavelengths, were determined by linear interpolation and then three different spectra were derived according to each  $\lambda_r$ . As can be expected, the first reference wavelength gives best coincidence with the measured spectra in the band of 400–440 nm, the second in 520–600 nm, and the third in 640–700 nm (Fig. 6 in **III**). This leads to the idea to create a computing program where in some wavebands the results by the model of Reinart & Herlevi (1999) are used, but in the “intermediate wavebands” the values of diffuse attenuation coefficient should be determined as a function of  $K_d(\lambda)$  for two neighbouring wavebands. Let’s name the new, “combined” model the C-model. The computing system of the C-model is presented in **III**.

For estimating the suitability of the C-model the statistical characteristics of regression  $K_d(\text{meas})$  vs.  $K_d(\text{C-model})$  for 14 wavelengths in the PAR region of the spectrum were calculated. The intercept was taken equal to zero and the regression formula for  $K_d(\text{meas})$  vs.  $K_d(\text{C-model})$  was in the form  $y = Dx$ . Coefficient  $D$  varied from 0.997 to 1.016,  $R^2$  from 0.977 to 0.998 and the mean relative error was between  $-0.032$  and  $0.021 \text{ m}^{-1}$  (Table 3 in **III**). Performing integration from 400 to 700 nm, we can compare the values  $K_{d,PAR}(\text{meas})$  and  $K_{d,PAR}(\text{C-model})$ . The conclusion is that the C-model allows to determine also the values of  $K_{d,PAR}$  with high accuracy (the regression formula is  $y = 1.001x$ ,  $R^2 = 0.9986$ , and the SE is  $0.0604 \text{ m}^{-1}$ ) (**III**).

Some examples describing the spectra of  $K_d(\lambda)$  obtained using the 490-model, the C-model, and the respective results derived from LI-1800 UW measurements, are shown in Fig. 16 (Fig. 7 in **III**). From the four spectra shown in Figs. 16a,b three demonstrate the case where the C-model gives values very close to the measured ones, but where the 490-model does not work so well in the blue and red regions of spectra (lakes Pääjärvi, Tuusulanjärvi, and Verevi). For L. Vesijärvi not only the C-model spectra are close to the measured ones, but also the 490-model gives good results (absolute errors are very low, **III**). However, sometimes low absolute errors correspond to rather high relative errors, as is seen when comparing the 490-model spectra with the measured ones (L. Paukjärv in Fig. 16c). Note that there were 14 cases (from 82) where

all models (for 4 reference wavelengths separately and C-model) gave extremely good coincidence with measured spectrum.

One can ask whether the model based on the  $K_d(\lambda)$  values at three wavelengths (like the C-model) is necessary at all, because we can try to recreate the spectra in the form of a trendline through three (reference) points. Our studies showed, Fig. 8 in **III**, that in the region 400–580 nm at least three trendlines (power function, exponential and square polynom) describe these spectra rather well, but at longer wavelengths the differences can be notable (depending on water type).



**Figure 16.** Some examples of  $K_d(\lambda)$  spectra derived from LI-1800 UW measurements and obtained from model calculations (490-model and C-model): (a) for L. Vesijärvi 24.08.95 and L. Lammi Pääjärvi 24.05.00, (b) for L. Tuusulanjärvi 17.08.99 and L. Verevi 06.08.97, (c) for L. Paukjärv 15.06.97.

## 4.7. Application of the data on bio-optical parameters for modelling the photosynthesis primary production

The main aim of productivity measurements in aquatic ecosystems is the better understanding of the food web relationships and functioning of these ecosystems. Traditional methods of measuring primary production are based on the gas exchange that occurs during the photosynthetic process, and determine either the rate of oxygen release or carbon dioxide uptake by plants. Both methods measure the instantaneous rate of photosynthesis during short

(1–2 h) exposures. Due to changing light conditions the planktonic photosynthesis has a pronounced daily dynamics. In order to acquire integrated results over longer time periods (days, months, years), many consecutive measurements of instantaneous photosynthesis rate should be carried out and integrated. However, this time consuming method cannot be used for routine measurements, so the introduction of bio-optical model calculations could solve the problem.

Our ultimate purpose is to build a model for computing primary production in the water based on the values of photosynthetically absorbed radiation and quantum yield of carbon fixation (VI, Smith *et al.*, 1989 and Arst *et al.*, 2006). For this model we need (as initial parameters) the spectral values of incident quantum irradiance and the corresponding diffuse attenuation coefficient, as well as chlorophyll *a* concentration in the water. In 2003–2005 we measured numerous *in situ* primary production profiles, corresponding solar irradiances (incident and underwater) and chlorophyll *a* values from three shallow, turbid lakes (Secchi depth less than 3 m) in Estonia, L. Peipsi, L. Võrtsjärv and L. Harku (Arst *et al.*, 2006; VI).

The results concerning optical parameters and chlorophyll *a* concentration are shown in previous sections. As an additional study, the underwater downwelling planar ( $q$ ) and scalar ( $q_0$ ) quantum PAR irradiances were measured and compared (VI). In all cases  $q_0 > q$ , the relative differences were 25–45% for L. Peipsi, 30–55% for L. Võrtsjärv and about 65% in L. Harku. This result is important, because due to the fact that the algal cells are illuminated from all directions primary production calculations should be performed using the data of underwater scalar quantum irradiance (Kirk 1994, Sosik 1996). Analysing the whole dataset, we can conclude that the three turbid lakes investigated can differ greatly not only in the values of optically active substances,  $K_{d,PAR}$  and  $z_{SD}$ , but also in biological productivity,  $P(z)$ . Typical profiles of  $P(z)$  from the lakes usually showed a minimum at the water surface due to inhibition, then an increase to a maximum at some depth, followed by decreasing production with depth (Arst *et al.*, 2006; VI). There can be some exceptions: in low illumination the maximum of  $P(z)$  curve is located at or near the surface. Similarly to  $C_{Chl}$ , the primary production integrated over depth ( $P_{int}$ ) had the maximum values in August, but decreased in September because the incoming irradiation decreased. From these three lakes, L. Harku is a really exceptional, extremely turbid lake, with maximum values of  $C_{Chl}$ ,  $K_{d,PAR}$  and  $P_{int}$  respectively  $398 \text{ mg m}^{-3}$ ,  $7.7 \text{ m}^{-1}$  and  $435 \text{ mg C m}^{-2} \text{ h}^{-1}$  (Arst *et al.*, 2006; VI).

## CONCLUSIONS

During 1994–2005 an extensive database of the bio-optical properties of North-European lakes was collected and their variations were examined. The main study sites were Lake Peipsi, Lake Võrtsjärv and Lake Harku (in Estonia), which all were turbid lakes with mean Secchi depth below 3 m. The additional measurements have been performed in 20 southern Swedish lakes, in 14 Estonian lakes and in 15 southern Finnish lakes (mostly small lakes). The inherent and apparent optical properties were also compared with those obtained from two clear-water large Swedish lakes, Lake Vänern and Lake Vättern.

**The results presented in this thesis can be summarized as follows:**

1. The data obtained by underwater radiation measurements and analyses of water samples demonstrated a large variability in water constituents as well as in optical characteristics measured in different types of lakes (e.g. the diffuse attenuation coefficient varied from  $0.92$  to  $7.8\text{ m}^{-1}$  and the values of chlorophyll *a* concentration from  $0.71$  to  $398\text{ mg m}^{-3}$ ). The differences between the lakes exceeded the temporal/spatial variations of water properties found separately in one lake. There are thousands of lakes over the world: our results show that these lakes can have diverse waters and belong to different limnological/optical classes.
2. Investigation of the temporal variations of optical characteristics in lakes Peipsi, Võrtsjärv and Harku during 2003–2005 (one sampling station in each lake) showed that the apparent long-term trend in the temporal changes of the water parameters was observed only in L. Harku. However, in all lakes the variability of bio-optical properties was connected with the season and the biological activity of water. There was also some spatial change in the OAS and diffuse attenuation coefficient from north to south in Peipsi.
3. The contributions of different water constituents of aquatic medium to total absorption and attenuation coefficients (both spectral and for the PAR region) were estimated in several lakes (L. Peipsi, L. Võrtsjärv, L. Vättern, L. Vättern and small Estonian and Finnish lakes). They changed from lake to lake, depending strongly on wavelength. In most lakes the main absorber was coloured dissolved organic matter (its stake to the total value of *a* was especially high in the blue region of spectra, and varies from 48% to 77% in case of PAR). The contributions of phytoplankton and tripton were noticeably smaller: in the PAR region their variations were correspondingly 3–15% and 4–32%, depending on the optical type of the water. The contribution of the total scattering coefficient to the total attenuation coefficient also varied from lake to lake (e.g. in eutrophic L. Võrtsjärv the ratio  $b_{PAR}/c_{PAR}$  was 84%, but in L. Lammi Pääjärvi (rich in CDOM) it was only 38%).

4. The slope of the specific absorption coefficient spectra of tripton,  $a'(\lambda)$ , varied between 0.0060 and 0.0109 nm<sup>-1</sup>, which is a little lower in comparison with the data by other authors (0.006–0.016 nm<sup>-1</sup>). Together with our earlier data (Paavel, 2004) we got the variability of  $a'(400)$  between 0.11 and 0.20 m<sup>2</sup> g<sup>-1</sup>. The reasons for this variability can be the different composition of tripton and there can also be some seasonal changes.
5. The slope of scattering coefficient spectra ( $p_b$ ) varied in a large range, being between 0.32 and 2.53, the average value was 0.847. It is in good agreement with the value of 0.8, which is often used for lake waters in the publications of other authors. In some cases we found some seasonal change of  $p_b$  (for five lakes from eleven). We had no success in finding a good correlation between  $p_b$  and the concentration of some single OAS. However the multiple regression between  $p_b$  and three OAS jointly gave a rather high determination coefficient ( $R^2(\text{adjusted}) = 0.655$ , SE = 0.259,  $p < 0.000001$ ). This result can count as unique, because we could not find comparable data from other publications.
6. One part of the present work is the correlation analysis. We determined the multiple regressions between the diffuse attenuation coefficient  $K_{d,PAR}$  and all OAS together and got good correlations both for L. Peipsi (Station Varnja) and L. Võrtsjärv (respectively  $R^2 = 0.82$ , SE = 0.37 m<sup>-1</sup> and  $R^2 = 0.73$ , SE = 0.58 m<sup>-1</sup>). The multiple regression between the spectrometric attenuation coefficient  $c^*_{PAR}$  and all three OAS in Varnja station (L. Peipsi) also gave a high determination coefficient (0.89) and SE = 0.84 m<sup>-1</sup>. However, considering the regressions between  $c^*_{PAR}$  and each OAS separately we got  $R^2$  equal to 0.72, 0.70 and 0.24 (respectively for chlorophyll, suspended particles and CDOM). Quite similar results were obtained for L. Võrtsjärv. This illustrates the additive effects of all OAS on the optical properties of the water and confirms that the best estimation of  $K_{d,PAR}$  and  $c^*_{PAR}$  can be made using data on all three OAS. Additionally, the regression  $z_{SD}$  vs.  $K_{d,PAR}$  was investigated (three Estonian and two large Swedish lakes together). The trendline of this relationship was a power function with the exponent 1.31,  $R^2 = 0.94$ .
7. We elaborated a new method (named C-model) that allows recreating the spectrum of  $K_d(\lambda)$  on the basis of its measured values at three wavelengths (we chose 412, 555 and 665 nm, which are the centres of three wavebands of the underwater spectrometer BIC-2104). The reliability of this model was assessed using of 84 series of  $K_d(\lambda)$  spectra, including additionally the databases of other authors. We determined the regression formulas and statistical characteristics of the correlation  $K_d(\text{meas})$  vs.  $K_d(\text{C-model})$  for 11 wavebands covering the interval 400–700 nm. The coefficient  $D$  in the regression formula  $y = Dx$  for different wavebands varied between 0.989 and 1.016, the determination

coefficient  $R^2$  from 0.977 to 0.998 and the SE from 0.047 to 0.219  $\text{m}^{-1}$ . Comparison of the values  $K_{d,PAR}(\text{meas})$  and  $K_{d,PAR}(\text{C-model})$  gave the regression formula  $y = 1.001x$ ,  $R^2 = 0.999$  and  $\text{SE} = 0.0604 \text{ m}^{-1}$ . Thus, our C-model allows to determine  $K_{d,PAR}$ , and also to reconstruct the spectra of  $K_d$ , with high reliability.

8. We observed a large variability (both within and between lakes) of the relative differences between underwater planar and scalar quantum irradiance in the PAR region, ranging from 25% to 65%. This result is relevant due to the fact that the algal cells are illuminated from all directions. Consequently, the calculations of primary production should be performed using the data of underwater scalar quantum irradiance. According to our study turbid lakes can be very different not only by water properties, but also by their biological productivity.
9. The results obtained in this study definitely have an importance because: (1) a database describing the bio-optical properties of different type of lakes is collected; (2) they could be used for deriving the algorithms of optical remote sensing models; and (3) they are necessary for model calculations of primary production in lakes



## REFERENCES

- Alvarez-Cobelas, M. 1991. Optical Limnology of a Hypertrophic Gravel-Pit Lake. *Internationale Revue Der Gesamten Hydrobiologie*, 762: 213–223.
- Arst, H. 2003. *Optical Properties and Remote Sensing of Multicomponental Water Bodies*. Springer, Praxis Publishing, Springer, Chichester, UK.
- Arst, H., Paavel, B. & Nöges, T. 2006. Optical properties and primary production in three North-European turbid lakes. *Proceedings of the XVIII Ocean Optics Conference: XVIII Ocean Optics Conference*; Montreal, Canada; 9–13 October, 2006, 1–9. (CD-ROM)
- Arst, H., Reinart, A., Erm, A. & Hussainov, M. 2000. Influence of depth-dependence of the PAR diffuse attenuation coefficient on the computation of downward irradiance in different water bodies. *Geophysica*, 36: 129–139.
- Arst, H., Erm, A., Kallaste, K., Mäekivi, S., Reinart, A., Nöges, P. & Nöges, T. 1999a. Investigation of Estonian and Finnish lakes by optical measurements in 1992–97. *Proc. Estonian Acad. Sci. Biol. Ecol.*, 48: 5–24.
- Arst, H., Erm, A., Kutser, T. & Reinart, A. 1999b. Optical remote sensing and contact measurements in Estonian and Finnish lakes in 1992–98. *Fourth Workshop on Physical Processes in Natural Waters, 13–17 September, Roosta, Estonia*, 105–110.
- Arst H., Mäekivi, S., Kutser, T. Reinart, A., Blanco-Sequeiros A. & Virta, J. 1996. Optical investigation of Estonian and Finnish lakes. *Lakes & Reservoirs: Research & Management*, 2: 187–198.
- Babin, M., Stramski, D., Ferrari, G. M., Claustre, H., Bricaud, A., Obolensky, G. & Hoepffner, N. 2003. Variations in the light absorption coefficients of phytoplankton, nonalgal particles, and dissolved organic matter in coastal waters around Europe. *J. Geophys. Res.*, 108(C7), 3211, doi:10.1029/2001JC000882.
- Baker, K. S. & Smith, R. C. 1982. Bio-optical classification and model of natural waters. *Limnol. Oceanogr.*, 27: 500–509
- Bergmann, T., Fahnenstiel, G., Lohrenz, S., Millie, D. & Schofield, O. 2004. Impacts of a recurrent resuspension event and variable phytoplankton community composition on remote sensing reflectance. *J. Geophys. Res.*, 109, C10S15, doi:10.1029/2002JC001575.
- Bidigare, R. R., Ondrusek, E. O., Morrow, J. H. & Kiefer, D. A. 1990. *In vivo* absorption properties of algal pigments. *Proc. SPIE, Ocean Optics X*, 1302: 290–302.
- Bowling, L. C., Steane, M. C. & Tyler, P. A. 1986. The spectral distribution and attenuation of underwater irradiance in Tasmanian inland waters. *Freshw. Biol.*, 16: 313–335.
- Bowling, L. C. & Tyler, P. A. 1985. The underwater light-field of lakes with marked physiochemical and biotic diversity in the water column. *J. Plankton Res.*, 34: 69–77.
- Bricaud, A., Claustre, H., Ras, J. & Oubelkheir, K. 2004. Natural variability of phytoplanktonic absorption in oceanic waters: Influence of the size structure of algal populations. *J. Geophys. Res.*, 109, C11010, doi:10.1029/2004JC002419.
- Bricaud, A., Babin, M., Morel, A. & Claustre, H. 1995a. Variability in the chlorophyll-specific absorption coefficients of natural phytoplankton: Analysis and parameterisation. *J. Geophys. Res.*, 100: 13,321–13,332.

- Bricaud, A., Roesler, C. & Zanevald, J. R. V. 1995b. *In situ* methods for measuring the inherent optical properties of ocean waters. *Limnol. Oceanogr.*, 40: 393–410.
- Bricaud, A. & Stramski, D. 1990. Spectral absorption coefficients of living phytoplankton and nonalgal biogenous matter: A comparison between the Peru upwelling area and the Sargasso Sea. *Limnol. Oceanogr.*, 35: 562–585.
- Bricaud, A., Morel, A. & Prieur, L. 1983. Optical efficiency factors of some phytoplankters. *Limnol. Oceanogr.*, 28: 816–832.
- Bricaud, A., Morel, A. & Prieur, L. 1981. Absorption by dissolved organic matter in the sea (yellow substance) in the UV and visible domains. *Limnol. Oceanogr.*, 26: 43–53.
- Bukata, R. P., Jerome, J. H., Bruton, J. E., Jane, S. C. & Zwick, H. H.. 1981. Optical water quality model of Lake Ontario. 1. Determination of optical cross sections of organic and inorganic particulates in Lake Ontario. *Appl. Optics*, 20: 1696–1703.
- Bukata, R. P., Jerome, J. H., Bruton, J. E. & Jain, S. C. 1979. Determination of inherent optical properties of Lake Ontario coastal waters. *Appl. Optics*, 18: 3926–3932.
- Dall’Olmo, G. & Gitelson, A. A. 2005. Effect of bio-optical parameter variability on the remote estimation of chlorophyll-*a* concentration in turbid productive waters: experimental results. *Appl. Optics*, 44: 412–422.
- Darecki, M. & D. Stamski, 2004. An evaluation of MODIS and SeaWiFS bio-optical algorithms in the Baltic Sea. *Rem. Sens. Environ.*, 89: 326–350.
- Darecki, M., Weeks, A., Sagan, S., Kowalczyk, P. & Kaczmarek, S. 2003. Optical characteristics of two contrasting Case 2 waters and their influence on remote sensing algorithms. *Cont. Shelf Res.*, 23: 237–250.
- Davies-Colley, R. J. & Vant, W. N. 1988. Estimates of optical properties of water from Secchi disk depths. *Water Resources Bulletin* 24: 1329–1335.
- Davies-Colley, R. J. & Vant, W. N. 1987. Absorption of light by yellow substance in freshwater lakes. *Limnol. Oceanogr.*, 32, 416–425.
- Dekker, A. G. 1993. *Detection of optical water quality parameters for eutrophic waters by high resolution remote sensing*. PhD thesis. Free University, Amsterdam.
- Dera, J. 1992. *Marine Physics*. PWN, Warszawa and Elsevier, Amsterdam.
- Dokulil, M. & Teubner, K. 2003. Klimaeinfüsse auf Seen in Europe (CLIME). *Österreichs Fischerei*, 56: 176–180.
- Doxaran, D., Cherukuru, N. & Lavender, S. 2006. Apparent and inherent optical properties of turbid estuarine waters: measurements, empirical quantification relationships and modelling. *Appl. Optics*, 45: 2310–2324.
- Duarte, C. M., Agusti, S. & Kalff, J. 2000. Particulate Light Absorption and the Prediction of Phytoplankton Biomass and Planktonic Metabolism in Northeastern Spanish Aquatic Ecosystems. *Can. J. Fish. Aquat. Sci.*, 57: 25–33.
- Erm, A., Arst, H., Nõges, P., Nõges, T., Reinart, A. & Sipelgas, L. 2002. Temporal variations in bio-optical properties of four North Estonian lakes in 1999–2000. *Geophysica*, 38: 89–111.
- ESS method, 340.2. 1993. Total suspended solids, Mass balance, Volatile suspended solids. *Environmental Sciences Section*, 3: 189–192.
- Ferrari, G. M. & Tassan, S. 1991. On the accuracy of determining light absorption by “yellow substance” through measurements of induced fluorescence. *Limnol. Oceanogr.*, 36, 777–786.
- Gallegos, C. L. 2005. Optical water quality of a blackwater river estuary: the Lower St. Johns River, Florida, Usa. *Estuar. Coast. Shelf Sci.*, 63: 57–72.

- Gallegos, C. L., Jordan, T. E., Hines, A. H. & Weller, D. E. 2005. Temporal variability of optical properties in a shallow, eutrophic estuary: Seasonal and interannual variability. *Estuar. Coast. Shelf Sci.*, 64: 156–170.
- Gallegos, C. L., Corell, D. L. & Pierce, J. W. 1990. Modeling spectral diffuse attenuation, absorption, and scattering coefficients in a turbid estuary. *Limnol. Oceanogr.*, 35: 1486–1502.
- Gallie, E. A. & Murtha, P. A. 1992. Specific absorption and backscattering spectra for suspended minerals and chlorophyll *a* in Chilko Lake, British Columbia. *Rem. Sens. Environ.*, 39: 103–118.
- Goldman, C. R. 1988. Primary productivity, nutrients, and transparency during the early onset of eutrophication in ultra-oligotrophic Lake Tahoe, California-Nevada. *Limnol. Oceanogr.*, 33: 1321–1333.
- Gordon, H. & Morel, A. 1983. *Remote assessment of ocean colour for interpretation of satellite visible imagery, a review. Lecture notes on coastal and estuarine studies*. R. T. Barber, C. N. K. Mooers, M. J. Bowman, B. Zeitzel (eds.), Springer-Verlag, New York.
- Gould, R. W. Jr. & Arnone, R. A. 1998. Three-dimensional modeling of inherent optical properties in a coastal environment coupling ocean colour imagery and *in situ* measurements. *Int. J. Remote Sens.*, 19: 2141–2159.
- Hale, G. M. & Querry, M. R. 1973. Optical constants of water in the 200 nm to 200  $\mu$ m wavelength region. *Appl. Optics*, 12: 557–562.
- Herlevi, A. 2002a. A study of scattering, backscattering and a hyperspectral reflectance model for boreal waters. *Geophysica*, 38: 113–132.
- Herlevi, A. 2002b. *Inherent and Apparent Optical Properties in Relation to Water Quality in Nordic Waters*. PhD Thesis. Report Series in Geophysics, 45, University of Helsinki, Division of Geophysics.
- Herlevi, A., Virta, A., Arst, H. & Erm, A. 1999. Results of light absorption/attenuation measurements in Finnish and Estonian lakes in summer 1997. *Proc. Estonian Acad. Sci. Biol. Ecol.*, 48: 46–62.
- Hoogenboom, J. & Dekker, A. G. 1997. Simulation of the medium-resolution imaging spectrometer (MERIS) performance for detecting chlorophyll-*a* over turbid inland waters. *Proc. SPIE*, 2963: 440–447.
- Irvine, W. M. & Pollack, J. B. 1968. Infrared optical properties of water and ice spheres. *Icarus*, 8: 324–360.
- ISO 10260. 1992(E). *Water quality – Measurements of biochemical parameters – Spectrophotometric determination of chlorophyll-*a* concentration*. (Geneva, Switzerland: ISO): 1–6
- Itturiaga, R. & Siegel, D. 1988. Microphotometric characterization of phytoplankton and detrital absorption properties in the Sargasso Sea. *Limnol. Oceanogr.*, 34: 1706–1726.
- Jerlov, N. G. 1976. *Marine Optics*, Elsevier, Amsterdam.
- Jerlov, N. G. 1974. *Optical Aspects of Oceanography*, Academic, New York.
- Jewson, D. H., Talling, J. F., Dring, M. J., Tilzer, M. M., Heaney, S. I. & Gunningham, C. 1984. Measurements of photosynthetically available radiation in freshwater: comparative tests of some current instruments used on studies of primary production. *J. Plankton Res.*, 6: 259–273.

- 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. *Aust. J. Mar. Freshw. Res.*, 45: 801–828.
- Kirk, J. T. O. 1994. *Light and Photosynthesis in Aquatic Ecosystems*. Cambridge, University Press, Cambridge.
- Kirk, J. T. O. 1981. Estimation of the scattering coefficient of natural waters using underwater irradiance measurements. *Aust. Mar. Freshwater Res.*, 32: 533–539.
- Kirk, J. T. O. 1980. Spectral absorption properties of natural waters: contribution of the soluble and particulate fraction to light absorption in some inland waters of south-eastern Australia. *Aust. Mar. Freshwater Res.*, 31: 287–296.
- Kirk, J. T. O. & Tyler, P. A. 1986. The spectral absorption and scattering properties of dissolved and particulate components in relation to the underwater light field of some tropical Australian freshwaters. *Freshw. Biol.*, 16: 573–583.
- Kishino, M., Okami, N., Takahashi, M. & Ichimura, S. 1986. Light utilization and quantum yield of phytoplankton in a thermally stratified sea. *Limnol. Oceanogr.*, 31: 557–566.
- Kishino, M., Takahashi, M., Okami, N. & Ichimura, S. 1985. Estimation of the spectral absorption coefficients of phytoplankton in the sea. *Bull. Mar. Sci.*, 37: 634–642.
- Koenings, J. P. & Edmundson, J. A. 1991. Secchi disk and photometers estimates of light regimes in Alaskan lakes: Effects of yellow color and turbidity. *Limnol. Oceanogr.*, 36: 91–105.
- Kopelevich, O. V. 1983a. Factors determining the optical properties of seawater – *Optics of the ocean*, Nauka, Moscow, 1: 150–166. (in Russian).
- Kopelevich, O. V. 1983b. A few-parameter model of the optical properties of seawater. *Optics of the ocean*, Nauka, Moscow, 1: 208–234. (in Russian).
- Kutser, T., Vahtmäe, E. & Martin, G. 2006. Assessing suitability of multispectral satellites for mapping benthic macroalgal cover in turbid coastal waters by means of model simulations. *Estuar. Coast. Shelf Sci.*, 67: 521–529.
- Kutser, T., Herlevi, A., Kallio, K. & Arst, H. 2001. A hyperspectral model for interpretation of passive optical remote sensing data from turbid lakes. *Sci. Total Environ.* 268: 47–58.
- Kvarnäs, H. 2001. Morphometry and hydrology of the four large lakes of Sweden. *Ambio*, 30: 467–474.
- Laugaste, R. & Yastremskij, V. V. 2000. Role of inflows in the phytoplankton compositions of Lake Peipsi. *Proc. Estonian Acad. Sci. Biol. Ecol.*, 49: 19–33.
- Laugaste, R., Yastremskij, V. V. & Ott, I. 1996. Phytoplankton of lake Peipsi-Pihkva: a species composition, biomass and seasonal dynamics. *Hydrobiologia*, 338: 49–62.
- LI-COR, Inc. 1984. *LI-1800 UW, Underwater Spectral Instruction Manual*. Lincoln, Nebraska, USA.
- Lindell, T., Pierson, D., Premazzi, G. & Zilioli, E. (eds). 1999. *Manual for monitoring European lakes using remote sensing techniques*. Office for Official Publication of European Communities, Luxembourg.
- Lindpere, A., Starast, H., Milius, A. & Saan, T. 1991. Quantitative changes of water composition in Lake Peipsi-Pihkva in 1985–1989. *Proc. Estonian Acad. Sci. Biol. Ecol.*, 1: 86–92.
- Lorenzen, C J., 1967. Determination of chlorophyll and phaeopigments; spectro-photometric equations. *Limnol. Oceanogr.* 12: 343–346.

- Magnuson, A., Harding, L.W., Mallonee, M.E. & Adolf, J.E. 2004. Bio-Optical Model for Chesapeake Bay and the Middle Atlantic Bight. *Estuar. Coast. Shelf Sci.*, 61: 403–424.
- Marshall, C. T. & Peters, R. H. 1989. General patterns in the seasonal development of chlorophyll a for temperate lakes. *Limnol. Oceanogr.* 34: 856–867.
- Maske, H. & Haardt, H. 1987. Quantitative in vivo absorption spectra of phytoplankton: Detrital absorption and comparison with fluorescence excitation spectra. *Limnol. Oceanogr.*, 32: 620–633.
- McKee, D., Cunningham, A. & Jones, K. J. 2002. Optical and hydrographic consequences of freshwater runoff during spring phytoplankton growth in a Scottish fjord. *J. Plankton Res.*, 24: 1163–1171.
- Metsamaa, L., Kutser, T. & Strömbeck, N. 2006. Recognising cyanobacterial blooms based on their optical signature: a modelling study. *Boreal Envir. Res.*, 11: 493–506.
- Mikkelsen, O. A. 2002. Variation in the projected surface area of suspended particles: Implications for remote sensing assessment of TSM. *Rem. Sens. Environ.*, 1: 23–29.
- Mobley, C. D. 1994. Light and Water. Radiative Transfer in Natural Waters. Academic Press, San Diego.
- Morel, A. 1980. In-water and remote measurements of ocean color. *Boundary-Layer Meteorol.*, 18: 177–201.
- Morel, A., Gentili, B., Claustre, H., Babin, M., Bricaud, A., Ras, J. & Tie'che, F. 2007. Optical properties of clearest natural waters. *Limnol. Oceanogr.*, 52: 217–229.
- Morel, A. & Prieur, L. 1977. Analysis of variations in ocean color. *Limnol. Oceanogr.*, 22: 709–722.
- Morrow, J. H., Chamberlin, W. S. & Kiefer, D. A. 1989. A two-component description of spectral absorption by marine particles. *Limnol. Oceanogr.*, 34: 1500–1509.
- Mäemets, A. 1977. Estonian lakes and their protection. Valgus, Tallinn. (in Estonian).
- Nelson, J. R. & Robertson, C. Y. 1993. Detrital spectral absorption: laboratory studies of visible light effects on phytodetritus absorption, bacterial spectral signal, and comparison to field measurements. *J. Mar. Res.*, 51: 181–207.
- Nõges, T., Järvet, A., Laugaste, R., Loigu, E., Leisk, Ü., Tõnno, I. & Nõges, P. 2002. Consequences of Catchments Processes and Climatic Changes on the Ecological Status of Large Shallow Temperate Lakes. *Symposium on Conservation, Restoration and Management of Aquatic Ecosystems. Venue, Dec 9–13, 2002. Bangalore: TTY:* 159–171.
- Nõges, T. (ed.) 2001. *Lake Peipsi. Meteorology, hydrology, hydrochemistry*. Sulemees Publishers, Tartu, Estonia.
- Nõges, T., Haabermann, J., Jaani, A., Laugaste, R., Lokk, S., Mäemets, A., Nõges, P., Pihu, E., Starast, H., Timm, T. & Virro, T. 1996. General description of Lake Peipsi-Pihkva. *Hydrobiologia*, 338: 1–9.
- Oliver, R. L. 1990. Optical Properties of Waters in the Murray-Darling Basin, South-Eastern Australia. *Aust. J. Mar. Freshw. Res.*, 41: 581–601.
- Paavel, B. (2004). *Optical Properties of Lake Peipsi Waters*. MSc thesis, University of Tartu. (in Estonian).
- Phillips, D. M. & Kirk, J. T. O. 1984. Study of the spectral variation of absorption and scattering in some Australian coastal waters. *Aust. J. Mar. Res.*, 35: 635–644.
- Pierson, D. C. & Strömbeck, N. 2000. A Modelling approach to evaluate preliminary remote sensing algorithms: Use of water quality data from Swedish Great Lakes. *Geophysics*, 36: 177–202.

- Pope, M. & Fry, E. S. 1997. Absorption spectrum (380–700 nm) of pure water: II. Integrating cavity measurements. *Appl. Optics*, 36: 8710–8723.
- Preisendorfer, R. W. 1976. *Hydrologic optics*, Vol. I. *Introduction*, U. S. Department of Commerce National Oceanic and Atmospheric Administration, Environment Research Laboratory, Honolulu.
- Prieur, L. & Sathyendranath, S. 1981. An optical classification of coastal and oceanic water based on the specific absorption curves of phytoplankton pigments, dissolved organic matter, and other particulate materials. *Limnol. Oceanogr.*, 26: 671–689.
- Rae, R., Howard-Williams, C., Hawes, I., Schwarz A. M. & Vincent, W. F. 2001. Penetration of solar ultraviolet radiation into New Zealand lakes: Influence of dissolved organic carbon and catchment vegetation. *Limnology* 2: 79–89.
- Reinart, A. 2000. *Underwater light field characteristics in different types of Estonian and Finnish lakes*. Dissertationes Geophysicales Universitatus Tartuensiss, 11, Tartu University Press, Tartu.
- Reinart, A. & Nõges, P. 2004. Light conditions in lake Võrtsjärv. *Lake Võrtsjärv*, Haberman, J., Pihu, E. & Raukas A. (eds), Estonian Encyclopedia Publishers, Tallinn: 141–149.
- Reinart, A., Herlevi, A., Arst, H. & Sipelgas, L. 2003. Preliminary optical classification of lakes and coastal waters in Estonia and South-Finland. *J. Sea Res.*, 49: 357–366.
- Reinart, A. & Herlevi, A. 1999. Diffuse attenuation coefficient in some Estonian and Finnish lakes. *Proc. Estonian Acad. Sci. Biol. Ecol.*, 48: 267–283.
- Reinart, A., Arst, H., Blanco-Sequeiros, A. & Herlevi, A. 1998. Relation between underwater irradiance and quantum irradiance in dependence on water transparency at different depths in the water bodies. *J. Geophys. Res.* 103: 7749–7752.
- Roesler, C. S., Perry, M. J. & Carder, K. L. 1989. Modeling *in situ* phytoplankton absorption from total absorption spectra in productive inland marine waters. *Limnol. Oceanogr.*, 34: 1510–1523.
- Sathyendranath, S., Prieur, L. & Morel, A. 1989. A three-component model of ocean colour and its application to remote sensing of phytoplankton pigments in coastal waters. *Int. J. Remote Sensing*, 10: 1373–1394.
- Schindler, D. W., Beaty, K. W., Fee, E. J., Cruikshank, D. R., DeBruyn, E. R., Findlay, D. L., Linsey, G. A., Shearer J. A., Stainton, M. P. & Turner, M. A. 1990. Effect of climatic warming on lakes of central boreal forest. *Science* 250: 967–970.
- Simis, S. G. H., Peters, S. W. M. & Gons, H. J. 2005. Remote Sensing of the Cyanobacterial Pigment Phycocyanin in Turbid Inland Water. *Limnol. Oceanogr.*, 50: 237–245.
- Sipelgas, L., Kallio, K., Arst, H., Erm, A., Oja, P. & Soomere, T. 2003. Optical properties of dissolved organic matter in Finnish and Estonian lakes. *Nord. Hydrol.*, 34: 361–386.
- Smith, R. C., Prezelin, B. B., Bidigare, R. R. & Baker, K. S. 1989. Bio-optical modeling of photosynthetic production in coastal waters. *Limnol. Oceanogr.*, 34: 1524–1544.
- Smith, R. C. & Baker, K. S. 1981. Optical properties of the clearest natural waters (200–800 nm). *Appl. Optics*, 20: 177–184.
- Sosik, H. M. 1996. Bio-optical modeling of primary production: consequences of variability in quantum yield and specific absorption. *Mar. Ecol. Prog. Ser.*, 143: 225–238.

- Strömbeck, N. 2001. *Water quality and optical properties of Swedish lakes and coastal waters in relation to remote sensing*. Comprehensive Summaries of Uppsala Dissertations from Faculty of Science and Technology, 633. Uppsala.
- Strömbeck, N. & Pierson, D. C. 2001. The effects of variability in the inherent optical properties on estimations of chlorophyll a by remote sensing in Swedish freshwaters. *Sci. Total Environ.*, 268: 123–137.
- Tassan, S. & Ferrari, G. M. 1995. An alternative approach to absorption measurements of aquatic particles retained on filters. *Limnol. Oceanogr.*, 40: 1358–1368.
- Unoki, S., Okami, N., Kishino, M. & Sugihara, S. 1978. *Optical Characteristics of Sea Water at Tokyo Bay*. Science and Technology Agency Report, Japan.
- Vincent, W. F., Laurion I. & Pienitz, R. 1998. Arctic and Antarctic lakes as optical indicators of global change. *Ant. Glaciol.*, 27: 691–696.
- Weidemann, A. D. & Bannister, T. T. 1986 Absorption and Scattering Coefficients in Irondequoit Bay. *Limnol. Oceanogr.*, 31: 567–583.
- Weidemann, A. D., Bannister, T. T., Effler, S. W. & Johnson, D. L. 1985. Particulate and Optical Properties During CaCO<sub>3</sub> Precipitation in Otisco Lake. *Limnol. Oceanogr.*, 30: 1078–1083.
- Willén, E. 2001a. Phytoplankton and water quality characterization: Experiences from the Swedish large lakes Mälaren, Hjälmaren, Vättern and Vänern. *Ambio*, 30: 529–537.
- Willén, E. 2001b. Four decades of research on the Swedish large lakes Mälaren, Hjälmaren, Vättern and Vänern: the significance of monitoring and remedial measures for a sustainable society. *Ambio* 30: 458–466.
- Zaneweld, J. R. V., Kitchen, J. C., Bricaud, A. & Moore, C. 1992. Analysis of *in situ* spectral absorption meter data. *Proc. SPIE, Ocean Optics II*, 1750: 187–200.

## SUMMARY IN ESTONIAN

### Eutrofeerunud järvede bio-optilised omadused

Veekogude ökosüsteemide seisund ja areng on mõjutatud paljude biootiliste ja abiootiliste tegurite poolt, kusjuures looduslikud ja inimtekkelised protsessid on erineva intensiivsuse ja kestusega. Neil protsessidel on kompleksne mõju, seetõttu on toimemehhanismide ja “põhjus-tagajärg” seoste väljaselgitamine äärmiselt keeruline.

Veekogude uurimine optilistel meetoditel (k.a. optiline kaugseire) kujutab endast laialtkasutatavat ja kiiresti arenevat uurimissuunda kogu maailmas. Viimastel aastatel on uurimuste põhirõhk kandunud avaookeanilt rannikuvetele ja järvedele, kus optiliselt aktiivsete ainete (OAS: lahustunud värvunud orgaaniline aine, fütoplankton, hõljum) sisaldus on oluliselt suurem kui ookeanis. Nendes vetes on OAS omadused ja hulgad ajas ja ruumis niivõrd varieeruvad, et mõõtmiste tegemine vee kvaliteedi määramiseks nõuab märgatavalt paremaid tehnilisi võimalusi.

Vaatamata sellele, et tänapäeval on vee kvaliteedi hindamisel laialt levinud meetodiks muutunud satelliitidele paigutatud optiliste sensorite kasutamine, pole veekeskonna uurimine *in situ* mõõtmiste abil kaotanud oma tähtsust. Satelliituuringud annavad rahuldavaid tulemusi ookeanide jaoks, kuid ranniku- ja sisevete puhul pole ookeanide kaugseire algoritmid enamasti kasutatavad. Traditsioonilised meetodid (veeproovide võtmine, nende laboratoorne töötlemine ja kiirguse mõõtmine veealuste sensorite abil jne.) on küll kallid ja aeganõudvad, et hankida piisavalt palju andmeid kogu järve ulatuses, kuid ka episoodiliste uuringute abil saadud tulemused lubavad meil hinnata veekogu bio-optiliste omaduste sesoonset ja ruumilist muutlikkust. Kahtlemata on sellised andmed vajalikud algmaterjalina järvede bio-optilisel modelleerimisel. Nagu teada võimaldab bio-optiline mudel analüüsida niihästi veesisese valgusvälja kujunemist (oluline veeorganismide elutegevuse seisukohalt) kui ka valguse hajumist veest atmosfääri (oluline satelliituuringute algoritmide väljatöötamiseks eutrofeerunud veekogude regulaarses seires).

Käesoleva dissertatsiooni põhieesmärkideks olid: (1) koguda ja analüüsida *in situ* mõõtmiste andmebaas kolme eutrofeerunud Eesti järve (Harku, Peipsi, Võrtsjärv) bio-optiliste omaduste kohta ning võrrelda tulemusi andmetega, mis saadud kahel Rootsi suurjärvel (Vänern ja Vättern) ning teistel Eesti, Soome ja Rootsi väikejärvedel; (2) hinnata erinevate optiliselt aktiivsete ainete osakaalu veekeskonna valgustneelavate ja -hajutavate omaduste formeerumisel; (3) valguse difuusse hajumiskoeffitsiendi ning tema spektraalse jaotuse mõõtmine ja modelleerimine.



### **Töö tulemusena leiti järgmist:**

Välitöödel ja laborianalüüside käigus kogutud andmed näitasid uuritavate järvede bio-optiliste omaduste suurt muutlikkust (kiirguse difuusne nõrgenemiskoeffitsient ja klorofüll *a* kontsentratsioon varieerusid vastavalt vahemikes 0.92 kuni 7.8 m<sup>-1</sup> ja 0.71–398 mg m<sup>-3</sup>), kusjuures mõõdetud parameetrite muutused järvelt-järvele ületasid oluliselt muutusi ühe järve erinevate osade piires.

Peipsis, Võrtsjärves ja Harkus (igas järves üks mõõtejaam) aastatel 2003–2005 mõõdetud kiirgusparameetrid ja optiliselt aktiivsete ainete hulgad näitasid pikaajalist tõusu ainult Harkus, samas kui bioloogilise aktiivsuse muutus (näiteks veeõitseng suve lõpus) tõi kaasa optiliste parameetrite muutuse kõigis eelpool mainitud järvedes. Korduvad mõõtmised aastatel (2001–2005) kogu Peipsi järve akvatooriumil näitasid optiliste karakteristikute ajalis-ruumilist varieerumist, kuid ühtlasi oli märgata nende väärtuste kasvutrendi põhjast lõuna suunas, kuhu suubuvad järve peamised reostajad Velikaya ja Emajõgi.

Kasutades esmaste optiliste parameetrite vaheliste seoste algoritme leiti iga OAS osakaal summaarse nõrgenemis- ja neeldumiskoeffitsiendi formeerumisel. Neid osakaale hinnati nii instrumendi ac-9 kaheksa spektraalkanali jaoks eraldi kui ka kogu fotosünteesiliselt aktiivses piirkonnas (PAR, 400–700 nm). Leiti, et osakaalud sõltusid oluliselt lainepikkusest ja muutusid ka järvelt-järvele. Selgus ka, et limnoloogilise klassifikatsiooni järgi sarnastel järvedel võivad vastavad osakaalud oluliselt erineda.

Valguse erineeldumiskoeffitsient, mis põhjustatud triptonist (detriit ja mineraalosakesed) on väheuuritud parameeter, kuid ta on vajalik veekeskkonna modelleerimisel ja optilise kaugseire algoritmide väljatöötamisel. Lainepikkusel 400 nm varieerusid selle optilise karakteristikute väärtused Eesti ja Rootsi suurjärvedes (Peipsi, Vänern ja Vättern) ning Eesti ja Soome väikejärvedes vastavalt vahemikes 0.11–0.20 m<sup>2</sup> g<sup>-1</sup> ning 0.050–0.176 m<sup>2</sup> g<sup>-1</sup>. Erinevuse põhjuseid tuleks ilmselt otsida nii triptoni koostisest kui ka tema osakeste suuruse varieeruvusest. Samas oli kõikides uuritud järvede triptoni erineeldumiskoeffitsiendi spektraalkõverate kuju üsna sarnane. Tema spektrit iseloomustav tõusuparameeter muutus vahemikus 0.006–0.011 nm<sup>-1</sup> olles veidi väiksem teiste autorite poolt saadud vastavatest tulemustest (0.006–0.016 nm<sup>-1</sup>).

Valguse hajumiskoeffitsiendi spektraalne käik sõltub veekeskkonna omadustest ja enamasti kirjeldatakse seda sõltuvust lainepikkuse astmefunktsioonina. Uuritavates Eesti, Soome ja Rootsi järvedes olid vastava astmenäitaja väärtused vahemikus 0.32 kuni 2.53 (keskmine väärtus 0.847), kusjuures üheteistkümnest järvest viiel leiti antud parameetri sõltuvus aastaajast. See tulemus on lähedane üldkasutatava väärtusega 0.8. Käesolevas töös ei õnnestunud küll leida seost astmenäitaja ja iga OAS kontsentratsiooni vahel eraldi, kuid antud optilise karakteristikute mitmene regressioon kõikide OAS korraga andis korregeeritud determinatsioonikoeffitsiendiks 0.665. Viimast tulemust võib lugeda unikaalseks, kuna meil ei õnnestunud leida vastavaid võrdlusmaterjale teiste autorite publikatsioonidest.

Valguse nõrgenemisele vees avaldavad samaaegselt mõju kõik optiliselt aktiivsed ained. Mitmese regressiooni võrrandeid spektrofotomeetrilise ja difuusse nõrgenemiskoeffitsiendi ning kõigi kolme OAS vahel iseloomustasid Peipsil determinatsioonikoeffitsiendid 0.89 ja 0.84; Võrtsjärvel olid need väärtused vastavalt 0.82 ja 0.73. Väiksemad  $R^2$  väärtused, mida vaadeldi difuusse nõrgenemiskoeffitsiendi jaoks, tulenevad ilmselt asjaolust et viimane sõltub lisaks OAS kontsentratsioonidele ka vette langeva kiirguse nurkjaotusest.

Töös on testitud ja täiustatud mudeleid, mis on väljatöötatud difuusse nõrgenemiskoeffitsiendi spektrite määramiseks fotosünteesiliselt aktiivse kiirguse piirkonnas (PAR, 400–700 nm) juhul kui mõõtmisandmed on olemas 1–3 lainepikkuse jaoks. Uute mõõtmiste baasil testiti Reinarti ja Herlevi (1999) poolt välja töötatud "ühepunktimudelit", mis võttis aluseks difuusse nõrgenemiskoeffitsiendi väärtused lainepikkusel 490 nm. Uue versioonina on käesolevas töös välja töötatud nn. C-mudel, mis kasutab algandmetena veealuse spektromeetri BIC-2104 kolme kanali (412, 555 ja 665 nm) mõõtmisandmetest saadud difuusse nõrgenemis-koeffitsiendi väärtusi. C-mudelit hinnati statistilise analüüsi abil ja osutus, et see võimaldab saada difuusse nõrgenemiskoeffitsiendi spektreid, mis on väga lähedased mõõdetutele. Vahemiku 400–700 nm piires keskmistatud difuusse nõrgenemiskoeffitsiendi väärtusi on aga suure täpsusega võimalik määrata mõlema mudeli abil.

Veealused kiirgusmõõtmised kvantkiirguse sensoritega näitasid, et relatiivne erinevus samaaegselt mõõdetud skalaarse ja tasapinnalise kiiritustiheduse vahel on 25%–65%, sõltudes järve tüübist ja sügavusest vees. Antud erinevus on oluline, kuna vetikarakk neelab talle igast suunast langevat kiirgust. Viimasest tuleneb järeldus, et primaarproduktiooni vertikaalse profiili mudel-arvutused peavad baseeruma skalaarse kiiritustiheduse andmetel. Meie uuringud kinnitasid teavet, et järved erinevad teineteisest mitte üksnes vee optiliste omaduste, vaid ka bioloogilise produktiivsuse poolest.

## ACKNOWLEDGEMENTS

I express my sincere gratitude to my supervisor Dr. Helgi Arst for friendly, supportive and constructive guidance during my studies as well as valuable comments and suggestion throughout the preparation of the thesis.

I would also like to thank to my co-supervisor Prof. Toomas Saat for his support and for giving me the possibility to start my student years working in Estonian Marine Institute, University of Tartu.

I am very thankful to my former supervisor Anu Reinart for introducing me the world of underwater optics as well as for her advice from the very beginning of my fieldworks and laboratory analyses.

I wish to thank Dr. Don Pierson (Department of Limnology, University of Uppsala) for letting us use their working group equipment for L. Peipsi expeditions as well as for the opportunity to work in their laboratory and study the techniques of absorption measurements of particulate matter (phytoplankton and tripton) .

I owe much to Tõnu Feldmann, Antti Herevi, Kersti Kangro, Tiit Kutser, Evi Lill, Tiina Nõges, Niklas Strömbeck, Lea Tuvikene, Ilmar Tõnno for their pleasant teamwork on the expeditions and for kindly providing data used in the present thesis.

My special thanks to Ants Erm and Medhat Hussainov for the assistance on the technical issues and to Annika Pung for editing the English manuscript.

My sincerest thanks belong to my mother for always being most understanding and supportive. My warmest thoughts go to the memory of my father – I wish that we could have kept you for longer.

This study has been supported by the EU Marie Curie Fellowship, contract No HPMF-CT-2001-01284, the Estonian Science Foundation (Grants 5594, 5738 and 6814), the Swedish National Space Board (Grants 169/02 and 132/02) and the Academy of Finland.



## **PUBLICATIONS**





Reinart, A., Paavel, B., Pierson, D. & Strömbeck, N. 2004.  
Inherent and apparent optical properties of Lake Peipsi, Estonia.  
*Boreal Envir. Res.*, 9(5): 429–445.





Reinart, A., Paavel, B. & Tuvikene, L. 2004.  
Effects of coloured dissolved organic matter on the attenuation  
of photosynthetically active radiation in Lake Peipsi.  
*Proc. Estonian Acad. Sci., Biol. Ecol.*,  
53 (2): 88–105.



Paavel, B., Arst, H., Reinart, A. & Herlevi, A. 2006.  
Model calculations of diffuse attenuation coefficient spectra in lake waters.  
*Proc. Estonian Acad. Sci., Biol. Ecol.*, 55(1): 61–81.



Paavel, B., Arst, H. & Herlevi, A. 2007.  
Dependence of spectral distribution of inherent optical properties of  
lake waters on the concentrations of different water constituents.  
*Nordic Hydrology*, 38(3): 265–285.

v

Paavel, B., Arst, H. & Reinart, A. 2008  
Variability of bio-optical parameters in two North-European  
large lakes. *Hydrobiologia*, 599(1): 201–211.



VI

Arst, H., Nõges, T., Nõges, P. & Paavel, B. 2008.  
Relationship of phytoplankton *in situ* primary production, chlorophyll  
concentration and underwater irradiance in turbid lakes.  
*Hydrobiologia*, 599(1): 169–176.

# CURRICULUM VITAE

## Birgot Paavel

Date of birth: April 18, 1980  
Citizenship: Estonia  
Address: Estonian Marine Institute, University of Tartu,  
10a Mäealuse Street, Tallinn 12618, Estonia  
Phone: +372 511 4555  
Fax: +372 671 8900  
E-mail: birgot.paavel@ut.ee

## Education

1986–1998 Pärnu Koidula Gymnasium  
1998–2002 University of Tartu, Faculty of Physics and Chemistry,  
*BSc* in physics  
2002–2004 University of Tartu, Faculty of Physics and Chemistry,  
Institute of Environmental Physics,  
*MSc* in environmental physics  
2004–2008 University of Tartu, Faculty of Science and Technology,  
Institute of Ecology and Earth Sciences,  
*PhD* studies in hydrobiology

## Professional experience

2004–2005 Estonian Marine Institute, University of Tartu, engineer  
2004–present University of Tartu, Faculty of Science and Technology,  
Estonian Marine Institute, University of Tartu,  
Research Fellow

## Scientific activity

Main topics: inherent and apparent optical properties, optically active  
substances  
Total number of publications: 7

# CURRICULUM VITAE

## Birgot Paavel

Sünniaeg: 18. aprill 1980  
Kodakondsus: Estonian  
Aadress: Tartu Ülikooli Eesti Mereinstituut, Mäealuse 10a ,  
Tallinn 12618  
Telefon: +372 511 4555  
Faks: +372 671 8900  
E-mail: birgot.paavel@ut.ee

## Hariduskäik

1986–1998 Pärnu Koidula Gümnaasium  
1998–2002 Tartu Ülikool, Füüsika-keemiateaduskond, *BSc* füüsikas  
2002–2004 Tartu Ülikool, Füüsika-keemiateaduskond,  
Keskkonnafüüsika instituut, *MSc* keskkonnafüüsikas  
2004–2008 Tartu Ülikool, Loodus-ja tehnoloogiateaduskond,  
Ökoloogia ja Maateaduste Instituut,  
doktorantuur hüdrobioloogias

## Teenistuskäik

2004–2005 Tartu Ülikooli Eesti Mereinstituut, insener  
2004–praeguseni Tartu Ülikool, Loodus-ja tehnoloogiateaduskond,  
Tartu Ülikooli Eesti Mereinstituut, teadur

## Teadustöö

Peamised töösuunad: esmased ja tuletatud optilised parameetrid, optiliselt  
aktiivsed ained  
Publikatsioone: 7

## 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 Käär.** The development of an automatic online dynamic fluorescence-based pH-dependent fiber optic penicillin flowthrough 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 environmental conditions. Tartu, 1994, 119 p.
13. **Mati Reeben.** Regulation of light neurofilament gene expression. Tartu, 1994, 108 p.
14. **Urmas Tartes.** Respiration rhythms 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 temperate 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 micro-organisms 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 grassland plant species. Tartu, 1998, 78 p.
38. **Olavi Kurina.** Fungus gnats in Estonia (*Diptera: Bolitophilidae, Kero-platidae, Macroceridae, Dityomyiidae, 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<sub>3</sub> and CO<sub>2</sub> on wheat, clover and pasture. Tartu, 1999, 123 p.
53. **Ljudmilla Timofejeva.** Electron microscopical analysis of the synaptone-mal 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 transla-tional 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 popula-tions: 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 invasions 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 Northern temperate forests. Tartu, 2002. 126 p.
72. **Rita Hõrak.** Regulation of transposition of transposon Tn4652 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<sub>2</sub> 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 Tn4652 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 Tn4652 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.