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ORIGINAL ARTICLE

Parameterization of chlorophyll-specific phytoplankton absorption coefficients for productive lake waters

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ABSTRACT

We examined and parameterized chlorophyll-specific phytoplankton absorption coefficients [$a^*_{ph}(\lambda)$] for three turbid productive Estonian lakes on the basis of bio-optical measurements in 2005-2013. A new model parameterization was created that enables to reconstruct the spectra of $a^*_{ph}(\lambda)$ for turbid productive waters with the higher reliability than previous parameterizations for ocean and coastal waters. The coefficients $A(\lambda)$ and $B(\lambda)$ of our model differ from those found in seas, coastal waters and other types of lakes. For any water type separately the increase of total chlorophyll concentration accompanied with the decrease of a^*_{ph}. Our results showed significant seasonal differences between the model parameters due to diversity of the phytoplankton assemblages. This suggests that season-specific models should be developed and validated. Improving the modelling of chlorophyll-specific phytoplankton absorption spectra for hypertrophic lakes is still pending on the availability of a larger dataset, which includes simultaneous measurements of chlorophyll concentrations, phytoplankton absorption coefficients and phytoplankton species composition. Our results implied that total chlorophyll concentration is not a universal predictor of the magnitude of chlorophyll-specific phytoplankton absorption coefficient. The $a_{ph}(\lambda)$ models are also likely site and season dependent. Further research is needed for quantifying the role of accessory pigments and other optical constituents as well as the cell size of dominant algal species for considering their influence on the modelling outputs.

Key words: Phytoplankton absorption coefficient; in situ *data; laboratory analyses; lakes.*

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INTRODUCTION

The underwater light climate is formed as a result of the absorption and scattering of light by optically active constituents: phytoplankton, coloured dissolved organic matter, non-algal particles and water itself. Knowledge of phytoplankton absorption and its dependence on the concentration of chlorophyll-*a* as well as accessory pigments is fundamental in the refinement of bio-optical models (Arst and Kutser, 1994; Garver and Siegel, 1997; Kutser *et al*., 2001; Lee and Carder, 2004; Smyth *et al*., 2006; Pan *et al*., 2008; Binding *et al*., 2012). The bio-optical models are used in studying underwater light field but are primarily used in interpretation of remote sensing data. Many authors use the models to develop different band-ratio type algorithms (as collection sufficient amount of *in situ* data is too time consuming and expensive), but model inversion techniques retrieving chlorophyll-a, coloured dissolved organic matter (CDOM) and suspended matter concentration simultaneously are becoming more and more popular in aquatic remote sensing.

The chlorophyll-specific phytoplankton absorption coefficient [$a^*_{ph}(\lambda)$ - the amount of light absorbed by a unit of pigment quantity at different wavelengths] provides also information on phytoplankton community structure and is regarded as a key input parameter in primary production models (Longhurst *et al*., 1995; Westberry *et al*., 2005; Arst *et al*., 2008).

Decades of field studies have shown that $a^*_{ph}(\lambda)$ decreases with increasing chlorophyll concentrations due to the combined influence of the pigment composition and the so-called *package effect* (Yentsch and Phinney, 1989; Bricaud *et al*., 1995, 2004; Allali *et al*., 1997; Lohrenz *et al*., 2003; Stæhr *et al*., 2004). This effect depends both on algal cell size and intracellular pigment concentration, which in turn vary with the environmental factors: light availability, temperature and nutrient supply. Typically, eutrophic waters are dominated by large cells that harvest light with higher efficiency than small cells, which tend to be predominant in oligotrophic waters (Duysens, 1956). Differences in the shape of phytoplankton absorption spectra, however, refer to the changes in intracellular pigment composition (Stuart *et al*., 1998; Ciotti *et al*., 2002; Babin *et al*., 2003; Bricaud *et al*., 2004).

The spatial and temporal heterogeneity in the absorption and scattering properties of phytoplankton (Ahn *et al*., 1992; Kutser *et al*., 2006; Metsamaa *et al*., 2006) predicts that significant errors have to be expected if spectral bio-optical models are not optimized for a particular region or season. One possible approach to resolve this problem is to use parameterization of $a^*_{ph}(\lambda)$ variability.

Bricaud *et al*. (1995) recommended to represent $a^*_{ph}(\lambda)$ as a power function of total chlorophyll concentration (*TChl* – chlorophyll-*a* concentration including its metabolite phaeophytin-*a*):

$$a^*_{ph}(\lambda) = A(\lambda) \cdot [TChl]^{-B(\lambda)} \quad \text{(eq. 1)}$$

where $A(\lambda)$ and $B(\lambda)$ are wavelength-specific coefficients estimated from the measurements of optical properties of different algal species. The coefficient *A* reflects a^*_{ph} per *TChl* unit, while exponent *B* reflects deformations of a^*_{ph} spectrum with the increase of *TChl*. The dataset of Bricaud *et al*. (1995) included 815 spectra from oceanic waters, where total chlorophyll concentration ranged between 0.02 and 25 mg m^{-3}.

Strömbeck (2001) re-investigated this model for three relatively clear Swedish lakes and brackish archipelago waters near Stockholm. His parameterization covered almost the same range of total chlorophyll concentrations (0.8-33.1 mg m^{-3}) and the results were only a little different: the new *A* and *B* had at some wavelengths higher and at some wavelengths slightly lower values than those published by Bricaud *et al*. (1995). Stæhr and Markager (2004) provided a linear model of ln-transformed data for predicting $a^*_{ph}(\lambda)$ from total chlorophyll concentration. Their main goal was to elaborate the appropriate formula for a wider *TChl* range (0.03-88.1 mg m^{-3}) in estuarine, coastal and oceanic waters. However, only two of their study sites among twenty had total chlorophyll concentrations above 22.2 mg m^{-3}. Lately, a similar approach has been used also for 15 lakes in southern Finland (Ylöstalo *et al*., 2014), where *TChl* were in same range (Tab. 1). Ficek *et al*. (2012) and Yoshimura *et al.* (2012) proposed a $a^*_{ph}(\lambda)$ parameterizations for productive lake waters, where *TChl* values reached 336 mg m^{-3}. However, their new a^*_{ph} spectra did not correspond to each other. The model of Yoshimura *et al*. (2012) represented intensive pigment packaging in the region of 460-500 nm, while in the model of Ficek *et al*. (2012) the package effect was surprisingly weak, especially at maximum $a^*_{ph}(\lambda)$ in blue and red wavelength regions.

Our attempts to apply the above mentioned models for describing of $a^*_{ph}(\lambda)$ in some cyanobacteria-dominated lakes in Estonia were unsuccessful. Cyanobacteria are very common in lakes but rare in sea waters where the above mention models were parametrised. The accessory pigments of cyanobacteria, such as phycocyanin, has absorption properties that are different from those considered in the models parametrized for sea water (Kutser *et al*., 2006; Metsamaa *et al*., 2006). Also the physical and chemical conditions of inland waters are different from those in ocean, estuarine and coastal waters and that can influence the performance of the marine models in lakes.

Most of the parameterization algorithms for $a^*_{ph}(\lambda)$ are directed to the determination of $A(\lambda)$ and $B(\lambda)$ in the formulae similar to eq.1. As the existing models for $a^*_{ph}(\lambda)$ do not perform sufficiently well in eutrophic lake environment, the main aim of present study was to determine new $A(\lambda)$ and $B(\lambda)$ values for eq. 1 that could be used for productive turbid lakes. To achieve this goal, we used the data from three turbid productive lakes in Estonia to examine *TChl*-specific phytoplankton absorption and parameterized a simple model for describing it spectrally.

METHODS

Description of lakes

We studied three turbid productive Estonian lakes Peipsi, Võrtsjärv and Harku during ice-free periods (May-October) in 2005-2009 and 2011-2013. *In situ* and laboratory data were collected from 155 measurement points. Main morphometric characteristics, Secchi depth and optically active constituents of the studied lakes are shown in Tab. 2.

The submeridionally elongated Lake Peipsi (maximum length approximately 150 km and width 42 km) on the border of Estonia and Russia is shallow, turbid, biologically productive and surrounded by many wetland areas along its coast. The lake consists of three limnologically different parts: 1) the northernmost, largest and deepest (2611 km^2, mean depth 8.3 m) Lake Peipsi *sensu stricto* is moderately eutrophic; 2) the southern part, Lake Pihkva (708 km^2) is shallower (3.8 m) and hypertrophic; 3) very narrow strait-like Lake Lämmijärv (236 km^2, 2.3 m), connecting the former basins, has some dyseutrophic features (Nõges, 2001).

Tab. 1. The models of chlorophyll-specific phytoplankton absorption coefficient for lakes and selected ocean and coastal waters with the ranges of total chlorophyll concentration (TChl).

Author	Study site	TChl (mg m^{-3})
Bricaud *et al.*, 1995	Oceanic waters	0.02-25.0
Strömbeck, 2001	Archipelago waters near Stockholm and 3 relatively clear Swedish lakes	0.83-33.1
Stæhr and Markager, 2004	Estuarine, costal and oceanic waters	0.03-88.1
Ficek *et al.*, 2012	15 Pomeranian lakes, Poland	1.20-336.0
Yoshimura *et al.*, 2012	Lake Kasumiguara, Japan	36.6-214.4
Ylöstalo *et al.*, 2014	15 boreal lakes, southern Finland	1.80-94.7

While the access to Lake Pihkva (belongs almost entirely to Russia) is restricted by border regulations, no optical data were available for this part of the lake.

The phytoplankton community in Lake Peipsi is typical for large lowland lakes having some similarities to lakes Ladoga, Onega, Vänern and Vättern (Laugaste *et al*., 2008). Spring phytoplankton communities of Lake Peipsi are dominated by fast-growing species (diatoms, chrysophytes and cryptophytes), which are adapted to the steep gradients in temperature and light conditions. In Lake Peipsi *s.s*., the main species are *Aulacoseira islandica* (O. Müller) Simonsen and *Stephanodiscus neoastraea* Håk *et* Hickel whereas in Lämmijärv *Cyclotella spp*. and *Aulacoseira ambigua* (Grun. in Van Heurck) Simonsen are abundant (Alikas *et al*., 2010; Laugaste *et al*., 2010). In summer, the succession of cyanobacteria starts with Anabaena, then *Gloeotrichia echinulata* (J. S. Smith) P. Richter appears, followed by species of Microcystis. *Aphanizomenon flos-aquae* (L.) Ralfs prevails in the cyanobacterial community in August-September and in warm autumns even until November (Laugaste *et al*., 2008, 2013). As cyanobacteria typically contain accessory pigments (Stomp *et al*., 2007), the absorption properties measured in the present study characterize not only chlorophyll but also other pigments. Also note that *TChl* in our study means a sum of concentrations of chlorophyll-*a* and its metabolite phaeophytin-*a.*

Lake Võrtsjärv is a large and shallow non-stratified eutrophic lake in Central Estonia, well mixed by surface waves and currents. The lake has six main inflows, the outflowing River Emajõgi carries the waters to Lake Peipsi. Due to the restricted outflow, large seasonal and annual fluctuations of the water level are one of the most characteristic features of Lake Võrtsjärv. The absolute water level range of 3.1 m corresponds to a 2.4-fold difference in the mean depth affecting strongly the underwater light climate (Nõges and Nõges, 2012). Phytoplankton biomass is substantially higher in low-water years due to better water column illumination and increased release of phosphorus from resuspended bottom sediments (Nõges *et al*., 2003). Phytoplankton community in Lake Võrtsjärv is dominated by diatoms and cyanobacteria, accounting for more than two-third of the biomass during the ice-free period from May to October. The most common diatoms are from the genera of *Aulacoseira* and *Cyclotella,* cyanophytes are composed of *Limnothrix planktonica* (Woloszyńska) Meffert and *Limnothrix redekei* (Van Goor) Meffert, which are accompanied by *Planktolyngbya limnetica* (Lemmermann) Komárková-Legnerova *et* Cronberg. Cryptophytes and chrysophytes may become exceptionally abundant during a short period in spring (Nõges *et al*., 2010).

Lake Harku is located 3 km from the sea on the western border of the Estonian capital Tallinn (59º 25' N, 24º 37' E). Situated among the agricultural- and grasslands, the lake has received considerable nutrient enrichment and sewage runoff over the last 50 years of the 20th century (Lepane *et al*., 2004). During the growing season Lake Harku is characterized by heavy algal blooms, with extraordinarily high values of chlorophyll and total suspended matter concentrations: 398 mg m^{-3} and 82 g m^{-3}, respectively (Paavel, 2008). Spring phytoplankton in Harku composed of small-celled green algae from the genera *Pediastrum* (*P. duplex* Meyen, *P. boryanum* Meneghini) and *Scenedesmus* (*S. opoliensis P.* Richter, *S. acuminatus* Chodat, *S. spinosus* Chodat), while in summer mainly coccal forms of cyanobacteria *Microcystis* (*M. wesenbergii* Komárek, *M. viridis* Lemmermann) are abundant (Erm *et al*., 2002).

Samples collection and laboratory analyses

Water samples were collected from the surface layer (0.2 m) with a standard Ruttner water sampler (Hydrobios

Tab. 2. Morphometric data and bio-optical parameters of studied turbid Estonian lakes.

Parameter	Peipsi	Võrtsjärv	Harku
Area (km^2)	3555	270	1.64
Mean depth (m)	7.0	2.8	1.6
Maximum depth (m)	15	6.0	2.5
TChl (mg m^{-3})	19.8±13.0	51.2±14.2	160.3±85.1
Chl-a (mg m^{-3})	16.5±11.6	44.3±12.8	132.6±64.8
Phaeophytin-a (mg m^{-3})	3.5±2.8	5.9±4.6	26.4±42.6
TSM (g m^{-3})	7.4±4.8	17.2±5.8	36.2±15.7
a_{ph}(440) (m^{-1})	0.5±0.3	1.4±0.4	3.5±1.6
a_{CDOM} (380) (m^{-1})	9.1±3.0	9.3±2.3	13.7±3.5
Secchi depth (m)	1.5±0.6	0.7±0.3	0.4±0.2

Chl-a, concentration of chlorophyll-a; TSM, concentration of total suspended matter; Phaeophytin -a, concentration of phaephytin-a; Secchi depth, relative water transparency; TChl, chlorophyll-a concentration including its metabolite phaeophytin-a; a_{ph}(440), absorption coefficient of phytoplankton at wavelength 420 nm; a_{CDOM}(380), absorption coefficient of coloured dissolved organic matter at wavelength 420 nm.

GmbH, Kiel, Germany) and stored in the dark and cold for less than 10 h before filtering. Depending on particle concentration in the water 0.1-1 litre was filtered through GF/F-filters (Whatman). Phytoplankton pigments were extracted from the filters with 96% ethanol at 20°C for 24 hours and measured spectrometrically (Hitachi Ltd., Tokyo, Japan; Spectrophotometer model U-3010) both before and after acidification with dilute hydrochloride acid (ISO, 1992). Later, optical density values were converted respectively to chlorophyll-*a* and phaeophytin-*a* concentrations according to Lorenzen (1967) formulas. The sum of chlorophyll-a and phaeophytin-a concentrations is later called as total chlorophyll concentration and abbreviated as *TChl*.

The absorption coefficients of total particulate and non-algal material retained on GF/F filters were determined respectively before and after pigment bleaching with sodium hypochloride (Ferrari and Tassan, 1999) following the transmittance-reflectance technique (Tassan and Ferrari, 1995, 2002). Filters were scanned with a 2 nm step in wavelength region 400-700 nm using a dual beam UV-Visible spectrophotometer (Hitachi U-3010) equipped with an integrating sphere (60INTEGRATING SPHERE ACCY model 130-0632). Compared with the standard transmittance method, the integrating sphere attachment to a dual beam spectrometer offers a remarkable advantage, allowing the accurate correction for light backscattering by the particles. It should be considered, however, that the GF/F filter itself also strongly scatters light and therefore the absorption of a particle-filter aggregate is greater than *in situ* absorption of suspended particles. This phenomenon is called pathlength amplification and its correction is based on the empirical relationship of the optical density of particles in suspension and the optical density of the same amount of particles retained on GF/F filters (Tassan and Ferrari, 1995):

$$D_{\text{susp}}(\lambda) = 0.423 D_{\text{filter}}(\lambda) + 0.479 (D_{filter}(\lambda))^2 \quad \text{(eq. 2)}$$

The spectral absorption of total particulate material [$a_p(\lambda)$] and of non-algal particles [$a_{NAP}(\lambda)$] were calculated respectively from the optical densities of unbleached and bleached and the difference between them was assumed to reflect the absorption of phytoplankton pigments [$a_{ph}(\lambda)$]:

$$a_p(\lambda) = \frac{2.303\, D_{\text{susp}}(\lambda)}{V_{\text{filter}} / A_c}, \quad \text{(eq. 3)}$$

$$a_{ph}(\lambda) = a_p(\lambda) - a_{NAP}(\lambda) \quad \text{(eq. 4)}$$

The coefficient 2.303 is a factor for converting the natural logarithm to base-10 logarithm, V_{filter} is the volume of the filtered water (m^3) and A_c is the clearance area of the filter (m^2). The clearance area is defined as the area on the filter which is actively used during the filtration. As pigment bleaching with sodium hypochloride may affect the absorption of un-pigmented organic matter in the sample (Ferrari and Tassan, 1999), the determined $a_{ph}(\lambda)$ can include also some phaeopigments associated with particles other than living phytoplankton. Chlorophyll-specific phytoplankton absorption coefficient $a^*_{ph}(\lambda)$ was obtained by dividing $a_{ph}(\lambda)$ by the *TChl* concentration.

Aliquots for phytoplankton counts (250 ml, Lugol preserved) were analysed with inverted microscope (Ceti Versus, Belgium) under 100x and 400x magnification by using the Utermöhl (1958) technique. The biovolumes of each taxon were estimated by assuming the shape of the species to the closest geometric form (Wetzel and Likens, 1991), after which the biomass (wet weight) was calculated.

For determining the regression formulas and other statistical characteristics the Microsoft's Excel statistical analysis tool 'Data analysis' was used.

RESULTS

Variation of phytoplankton biomass and species composition

Seasonal dynamics of phytoplankton composition and biomass (BM) were estimated annually only for the years 2011-2013. Spring phytoplankton BM of Lake Peipsi and Lake Võrtsjärv was generally dominated by diatoms (Tab. 3). The exception was Lake Peipsi in 2011, when crypto- and chrysophytes were most abundant in biomass. This could be explained by the fact that in 2011 only the northern moderately eutrophic basin of Lake Peipsi was visited, while in 2012-2013 samples were taken also in southern more eutrophic regions. In Lake Harku cyanobacteria dominated in vernal phytoplankton biomass while diatoms were also rather abundant (40% of BM) in May of all the years.

During summer the share of cyanobacteria in the phytoplankton biomass of all lakes increased reaching average values of 60%, 65% and 71% in June, July and

Tab. 3. Seasonal ranges of phytoplankton biomass (wet weight, g m^{-3}) in studied turbid Estonian lakes.

Lake	Diatoms			Cyanobacteria		
	May	July	Sept	May	July	Sept
Peipsi	0.05-1.13	0.9-5.1	0.4-3.4	0.05-0.4	2.9-13.3	3.2-9.5
Võrtsjärv	2.5-11.0	2.8-8.6	3.4-7.7	1.2-3.7	12.5-33.5	6.2-20.7
Harku	1.0-4.6	1.28	2.4-4.9	1.5-8.1	50.6	33.3-89.5

August, respectively, and remained high until in autumn (53-89% in September and early October). The proportion of diatoms in summer and autumn ranged 2-60% and 2-34%, respectively. Chlorophytes formed less than 22% of phytoplankton biomass during the whole growing season.

The abundance of phytoplankton species in studied lakes changed from chryso- and cryptophytes dominance in May towards cyanobacteria prevalence during summer and autumn (Fig. 1). The most important species of cyanobacteria were *Planktolyngbya limnetica* in 2011 and *Limnothrix redekei* and *L. planktonica* in the subsequent years (2012-2013). Chlorophytes developed from late spring to early autumn and their abundance in lakes varied from 75 cells mL^{-1} (May) to 61050 cells mL^{-1} (September).

In Lake Harku *Scenedesmus spp.* was exceptionally abundant. Diatoms abundance peaked in July 2013, when the density *of Asterionella formosa* in Lake Peipsi rose up to 2454 cells mL^{-1}. However, generally diatoms constituted less than 13% of total plankton abundance in all studied lakes. Euglenophytes, dinophytes and xantophytes had very little contribution and no evident seasonal variation.

Variability of chlorophyll-specific phytoplankton absorption

Differences in phytoplankton absorption are related to species composition, pigment content and age of cells, availability of nutrients and light. The spectrum of a^*_{ph} has two maxima, in blue and red region. Our study showed that the variability of a^*_{ph} was greatest in the blue band with values ranging from 0.012 to 0.053 $m^2\ mg^{-1}$ at 440 nm. In the red region (676 nm) a^*_{ph} ranged between 0.007 and 0.037 $m^2\ mg^{-1}$ (Fig. 2).

The spectra had also the *shoulders* at 420, 490 and

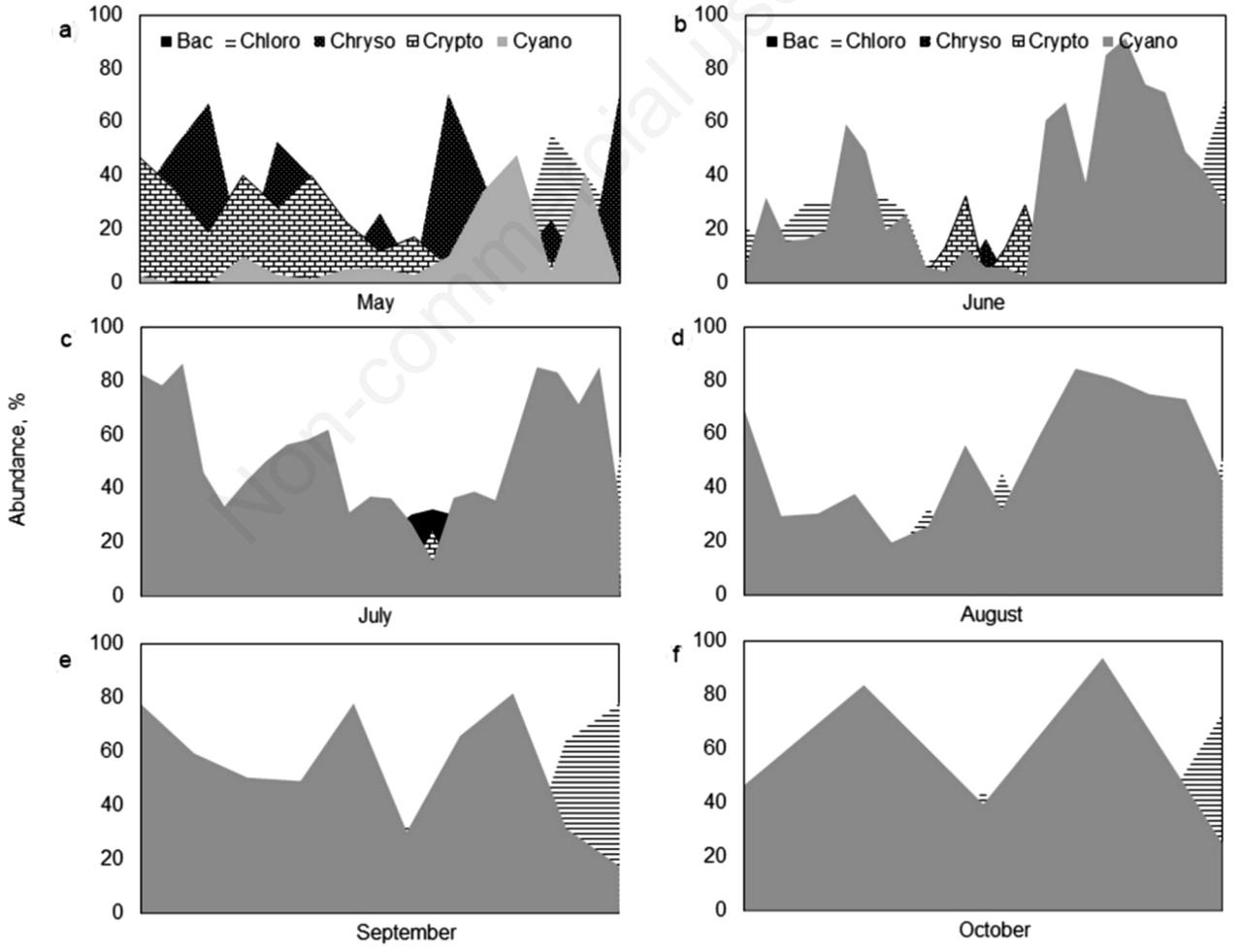

Fig. 1. Dynamics of phytoplankton communities in productive Estonian lakes described by percentages of abundance of major taxonomic assemblages (altogether 81 analyses in 2011-2013). Bac, Bacillariophyta; Chloro, Chlorophyta; Chryso, Chrysophyta; Crypto, Cryptophyta; Cyano, Cyanobacteria.

630 nm, associated with accessory pigments (respectively phaeophytins, carotenoids and phycocyanin). The blue to red ratio of $a^*_{ph}(\lambda)$ can be used as an indicator of phytoplankton size, with higher values (*e.g.*, $a^*_{ph}(440)/a^*_{ph}(676)$ >2.5) known to be associated with the dominance of small-sized populations (Stramski and Morel, 1990). This ratio in turbid productive Estonian lakes varied from 2.9 to 1.1, demonstrating approximately a 3-fold decrease when *TChl* increased from 2.7 to 315.4 mg m^{-3}.

Several authors (Yentsch and Phinney, 1989; Bricaud *et al*., 1995, 2004; Ciotti *et al*., 2002; Babin *et al*., 2003; Stæhr *et al*., 2004) found that $a^*_{ph}(\lambda)$ decreases with increasing total chlorophyll concentration and that was also demonstrated in three turbid Estonian lakes (Fig. 3). The greater dispersion of $a^*_{ph}(440)$ compared to $a^*_{ph}(675)$ is explained by the fact that in blue region the package effect as well cellular pigment content and composition have combined influence on a^*_{ph} while in the red band only the package effect is influential (Bricaud *et al*., 1995, 2004; Lohrenz *et al*., 2003; Stæhr *et al*., 2004).

Parameterization of chlorophyll-specific phytoplankton absorption

To parameterize phytoplankton absorption in the bio-optical models, coefficients $A(\lambda)$ and $B(\lambda)$ in eq. 1 were calculated from measured $a^*_{ph}(\lambda)$ spectra. The values of these parameters were tabulated with a 2 nm step over the range 400-700 nm (Tab. 4). Several studies (Bricaud *et al*., 1995; Strömbeck, 2001; Stæhr and Markager, 2004; Ficek *et al*., 2012; Yoshimura *et al*., 2012; Ylöstalo *et al*., 2014) have parametrized chlorophyll-specific phytoplankton absorption as power function of *TChl*. Spectra of the corresponding *A* and *B* coefficients (together with our results) are shown in Fig. 4.

In ocean, estuarine and coastal waters coefficient $A(\lambda)$ showed a maximum near 440 nm (Bricaud *et al*., 1995; Stæhr and Markager, 2004), whereas in turbid productive Estonian lakes it was shifted towards shorter wavelengths (Fig. 4). Such phenomenon indicates a presence of phaeopigments with a peak around 420 nm. In our lakes the contribution by phaeophytin-a varied between 0.5 and 94% (with an average 16.7%) of total chlorophyll concentration. Additionally, we demonstrated a spectral shoulder around 615-645 nm, which is a typical feature of cyanobacteria - characteristic to their phycocyanin pigment (Jeffrey and Vesk, 1997; Simis *et al*., 2005). In our study the coefficient $B(\lambda)$ had the highest values in the 600-660 nm region and the lowest in the green part of the spectrum, where a^*_{ph} was not correlated with total chlorophyll concentration (Fig. 4). At minimum a^*_{ph}, values of *B* became unstable and low and even negative in the 476-534 nm region. In Lake Mälaren in Sweden a similar tendency was observed between 580 nm and 635 nm (Strömbeck and Pierson, 2001).

To describe $A(\lambda)$ and $B(\lambda)$ coefficients for rather different spring and summer phytoplankton assemblages (Fig. 1 and Tab. 3) we analysed separately two datasets: 20 cases in May for spring and 70 cases in July for summer. In May the values of *A* at 400-440 nm were lower than those in

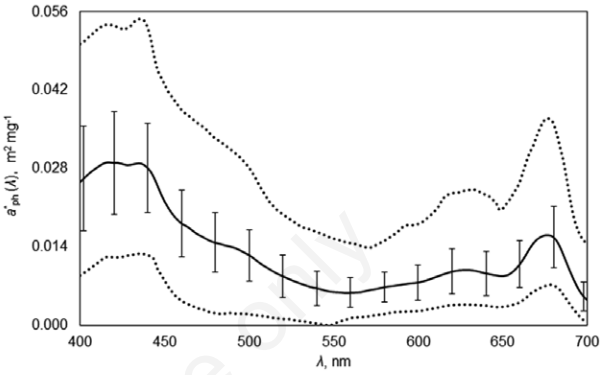

Fig. 2. Variability of chlorophyll-specific phytoplankton absorption coefficient [$a^*_{ph}(\lambda)$] measured in three productive Estonian lakes: minimum and maximum spectra (dotted), mean with standard deviations (solid).

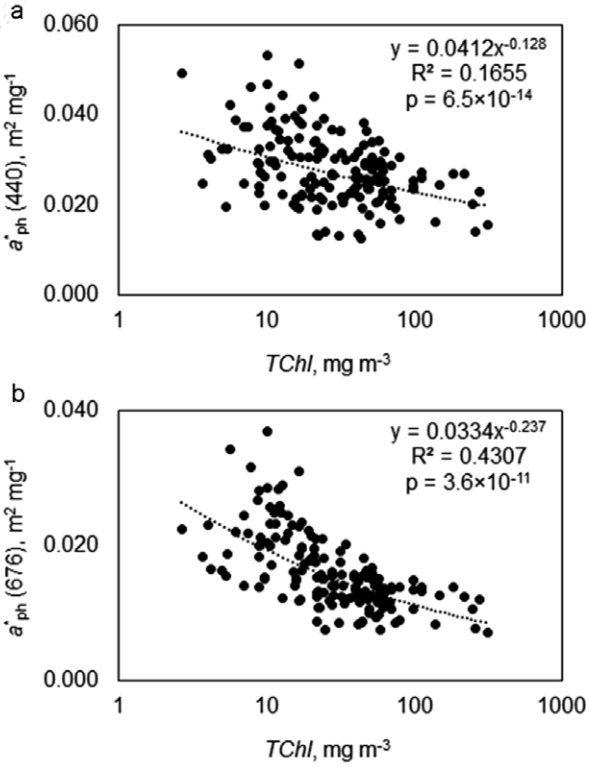

Fig. 3. Dependence of chlorophyll-specific phytoplankton absorption coefficient $a^*_{ph}(\lambda)$ on total chlorophyll concentrations (*TChl*, chlorophyll-*a* + phaeopigment-*a*) in turbid productive Estonian lakes: (a) at 440 nm and (b) at 676 nm.

July, indicating higher package effect and can be explained by the dominance of large cells in vernal phytoplankton. In summer small-celled cyanobacteria dominated, which harvest light with much lower efficiency in the red part of the spectrum the (absorption peak around 630 nm). The parameter $B(\lambda)$ also showed a large discrepancy between May and July, reflecting different pigment composition in vernal and summertime phytoplankton assemblages. The spectra of $a^*_{ph}(\lambda)$ in May, July and during the whole summer, measured *in situ* and calculated using of $A(\lambda)$ and $B(\lambda)$

Tab. 4. Spectral values of the numerical coefficients $A(\lambda)$ and $B(\lambda)$ for the parameterization of chlorophyll-specific phytoplankton absorption coefficient as a function of *TChl* in studied turbid Estonian lakes. The values of R^2 calculated are from power regression. N=155 is the number of water samples use for parameterization.

λ (nm)	A	B	R^2	λ (nm)	A	B	R^2
400	0.0483	0.2114	0.2889	488	0.0122	-0.0231	0.0026
402	0.0498	0.2127	0.3023	490	0.0121	-0.0216	0.0022
404	0.0506	0.2105	0.3055	492	0.0119	-0.0201	0.0021
406	0.0516	0.2104	0.3171	494	0.0117	-0.0198	0.0020
408	0.0526	0.2101	0.3244	496	0.0114	-0.0175	0.0020
410	0.0531	0.2079	0.3232	498	0.0113	-0.0151	0.0012
412	0.0534	0.2054	0.3210	500	0.0112	-0.0137	0.0005
414	0.0537	0.2025	0.3188	502	0.0109	-0.0123	0.0005
416	0.0534	0.1988	0.3150	504	0.0103	-0.0108	0.0009
418	0.0523	0.1950	0.3041	506	0.0098	-0.0121	0.0012
420	0.0516	0.1912	0.2988	508	0.0094	-0.0133	0.0011
422	0.0514	0.1873	0.2949	510	0.0091	-0.0146	0.0010
424	0.0503	0.1819	0.2842	512	0.0086	-0.0176	0.0013
426	0.0486	0.1724	0.2631	514	0.0082	-0.0207	0.0017
428	0.0472	0.1645	0.2488	516	0.0078	-0.0232	0.0020
430	0.0467	0.1602	0.2410	518	0.0075	-0.0247	0.0023
432	0.0462	0.1554	0.2316	520	0.0072	-0.0266	0.0025
434	0.0454	0.1495	0.2170	522	0.0069	-0.0282	0.0026
436	0.0446	0.1435	0.2024	524	0.0066	-0.0262	0.0025
438	0.0431	0.1361	0.1847	526	0.0064	-0.0243	0.0022
440	0.0412	0.1280	0.1655	528	0.0064	-0.0206	0.0013
442	0.0389	0.1193	0.1455	530	0.0062	-0.0160	0.0010
444	0.0363	0.1116	0.1260	532	0.0061	-0.0089	0.0004
446	0.0337	0.1060	0.1102	534	0.0060	-0.0018	0.0003
448	0.0311	0.0999	0.0949	536	0.0058	0.0053	0.0001
450	0.0287	0.0929	0.0785	538	0.0061	0.0165	0.0004
452	0.0264	0.0837	0.0604	540	0.0063	0.0278	0.0022
454	0.0246	0.0762	0.0471	542	0.0063	0.0343	0.0030
456	0.0229	0.0680	0.0354	544	0.0060	0.0329	0.0018
458	0.0217	0.0612	0.0274	546	0.0059	0.0314	0.0022
460	0.0204	0.0553	0.0188	548	0.0062	0.0310	0.0019
462	0.0198	0.0495	0.0168	550	0.0064	0.0626	0.0108
464	0.0193	0.0463	0.0149	552	0.0069	0.0830	0.0208
466	0.0181	0.0378	0.0092	554	0.0072	0.0986	0.0297
468	0.0169	0.0263	0.0043	556	0.0075	0.1077	0.0352
470	0.0162	0.0194	0.0023	558	0.0079	0.1271	0.0560
472	0.0157	0.0159	0.0015	560	0.0083	0.1395	0.0741
474	0.0149	0.0081	0.0004	562	0.0086	0.1482	0.0888
476	0.0141	-0.0015	0.0000	564	0.0090	0.1598	0.1097
478	0.0135	-0.0092	0.0005	566	0.0097	0.1715	0.1201
480	0.0130	-0.0144	0.0011	568	0.0103	0.1833	0.1556
482	0.0127	-0.0189	0.0018	570	0.0109	0.1967	0.1886
484	0.0124	-0.0216	0.0024	572	0.0115	0.2049	0.2126
486	0.0123	-0.0224	0.0031	574	0.0119	0.2108	0.2336

To be continued on next page

values from Tab. 4, show rather good correspondence in many cases while also discrepancies in the blue and red regions were observed (Fig. 5). Underestimation of a^*_{ph} in the blue region was generally accompanied by an overestimation of a^*_{ph} in the red region and *vice versa*. The mismatch between measured and modelled $a^*_{ph}(\lambda)$ values appeared mainly for low and extremely total high chlorophyll concentration, *e.g.*, a large discrepancy from measured and modelled a^*_{ph} spectra occurred in May, when *TChl* in Lake Peipsi was below 8 mg m^{-3} (Fig. 5a).

Since our database included only 13% of cases with *TChl* <10 mgm^{-3}, the seasonal models for such low *TChl* values cannot be fully reliable. In Lake Harku where vernal *TChl* reached up 113 mg m^{-3}, the parameterization for May gave rather good results (Fig. 5e) while the applicability of July model for summer months depended on the prevalence of cyanobacteria. A further study could help to decide whether the best option is to elaborate two separate parameterization for the blue and red regions of spectra or to use a model which takes into account also the variability of phytoplankton species composition. Total chlorophyll values above 150 mg m^{-3} were observed only in Lake Harku and in this *TChl* region both our seasonal models failed (Fig. 5f). As we did not find remarkable decrease of $a^*_{ph}(\lambda)$ with increase at *TChl* > 80 mg m^{-3} (Fig. 3), this explains the mismatch between measured and modelled $a^*_{ph}(\lambda)$ spectra for *TChl* values above 100 mgm^{-3} in Lake Harku.

Analysing the correspondence of measured and modelled a^*_{ph} values in blue (442 nm) and red (676 nm) wavelengths. We found that at 442 nm the determination coefficients (R^2) were remarkably lower than those at 676nm, except in May, when R^2(442) was 0.548 and R^2(676) was 0.325 (Fig. 6 and Tab. 5). The highest R^2 value (0.649) appeared in July at 676 nm. Generally R^2 values for May and July separately exceeded those calculated for the whole database, expressing the impact of

Tab. 4. Continued from previous page.

λ (nm)	A	B	R^2	λ (nm)	A	B	R^2
576	0.0124	0.2182	0.2580	640	0.0228	0.3007	0.4522
578	0.0131	0.2282	0.2856	642	0.0227	0.3010	0.4535
580	0.0137	0.2352	0.3097	644	0.0223	0.3009	0.4533
582	0.0142	0.2421	0.3325	646	0.0220	0.2994	0.4501
584	0.0147	0.2491	0.3434	648	0.0215	0.2953	0.4477
586	0.0152	0.2552	0.3605	650	0.0211	0.2909	0.4445
588	0.0157	0.2622	0.3758	652	0.0213	0.2890	0.4488
590	0.0162	0.2677	0.3828	654	0.0218	0.2870	0.4537
592	0.0168	0.2749	0.3923	656	0.0229	0.2868	0.4641
594	0.0172	0.2795	0.3977	658	0.0242	0.2847	0.4708
596	0.0176	0.2835	0.4059	660	0.0259	0.2837	0.4772
598	0.0178	0.2856	0.4089	662	0.0278	0.2812	0.4808
600	0.0181	0.2878	0.4124	664	0.0295	0.2746	0.4778
602	0.0187	0.2899	0.4169	666	0.0311	0.2676	0.4670
604	0.0191	0.2920	0.4187	668	0.0325	0.2606	0.4640
606	0.0197	0.2939	0.4244	670	0.0334	0.2550	0.4578
608	0.0203	0.2943	0.4256	672	0.0339	0.2488	0.4521
610	0.0208	0.2952	0.4291	674	0.0337	0.2426	0.4371
612	0.0214	0.2949	0.4295	676	0.0334	0.2374	0.4307
614	0.0218	0.2941	0.4307	678	0.0329	0.2337	0.4246
616	0.0223	0.2934	0.4334	680	0.0320	0.2313	0.4202
618	0.0228	0.2928	0.4344	682	0.0302	0.2284	0.4125
620	0.0233	0.2939	0.4382	684	0.0280	0.2295	0.4146
622	0.0236	0.2946	0.4400	686	0.0255	0.2356	0.4222
624	0.0240	0.2957	0.4437	688	0.0231	0.2454	0.4313
626	0.0241	0.2960	0.4460	690	0.0208	0.2580	0.4399
628	0.0242	0.2971	0.4494	692	0.0183	0.2703	0.4365
630	0.0244	0.2993	0.4521	694	0.0166	0.2932	0.4341
632	0.0243	0.2998	0.4538	696	0.0157	0.3325	0.4422
634	0.0240	0.2998	0.4536	698	0.0155	0.3770	0.4423
636	0.0235	0.3001	0.4496	700	0.0152	0.4183	0.4280
638	0.0230	0.3004	0.4495				

phytoplankton composition in different seasons. Phytoplankton in the analysed turbid lakes changed from chryso- and cryptophytes dominance in May to a predominance of small-celled cyanobacteria during whole summer. In July the determination coefficient of our a^*_{ph} model was much higher (R^2=0.65) in the red wavelength (676 nm) than in blue region (at 442 nm R^2=0.25) where a^*_{ph} values are affected by both pigment composition and packaging, but their relative importance is difficult to resolve. In our whole dataset the correspondence of a^*_{ph}(meas) *vs* a^*_{ph} (modelled) at 676 nm was a bit weaker (R^2=0.49) because of the larger variety of algal groups cell sizes. Chlorophyll-*a* content of cells varies between different phytoplankton groups and cyanobacteria, which prevailed in our study lakes in July and August, have more accessory pigments and less *Chl-a* per unit biovolume than other algae, *e.g.*, chlorophytes (Reynolds, 2006).

DISCUSSION

Chlorophyll-specific phytoplankton absorption in ocean, coastal and lake waters

In different water bodies chlorophyll-specific phytoplankton absorption coefficient values vary in large scale. In blue spectral region Bricaud *et al*. (1995) derived a range of $a^*_{ph}(440)$ between 0.01 and 0.18 m^2 mg^{-1} for ocean waters, whilst Stæhr and Markager (2004) extended this range to 0.015-0.194 m^2 mg^{-1} for estuarine

Tab. 5. Statistical analysis of the correspondence of the measured (x) and modelled (y) a^*_{ph} at 442 nm and 676 nm.

Data	R^2	SE	P	MRE (%)	N	Regression
442 nm						
All	0.195	0.0026	$3\cdot10^{-8}$	1.45	155	y=0.022+0.182x
May	0.548	0.0026	0.0003	2.22	20	y=0.015+0.442x
July	0.254	0.0035	$3\cdot10^{-5}$	3.76	70	y=0.020+0.247x
676 nm						
All	0.495	0.0025	$1\cdot10^{-22}$	3.23	155	y=0.087+0.459x
May	0.325	0.0013	0.011	2.25	20	y=0.011+0.417x
July	0.649	0.0031	$3\cdot10^{-15}$	4.63	70	y=0.007+0.621x

MRE, mean relative error.

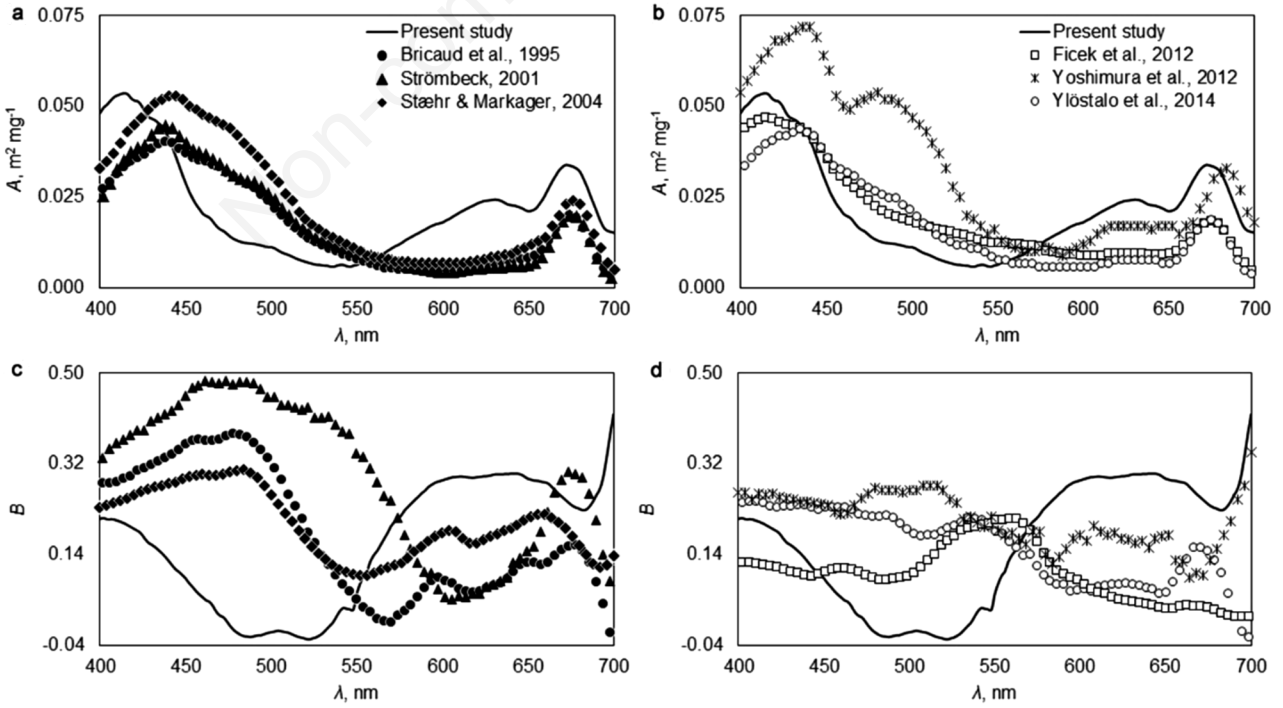

Fig. 4. Parameters *A* and *B* for modelling chlorophyll-specific phytoplankton absorption coefficient in different water bodies: (left column) for ocean, coastal and archipelago waters together with three clear Swedish lakes and (right column) for productive lakes.

and coastal waters. In lakes in southern Finland $a^*_{ph}(440)$ varied from 0.012 to 0.038 m^2 mg^{-1} (Ylöstalo *et al*., 2014) and in lakes Erken and Kasumigaura from 0.009 to 0.058 m^2 mg^{-1} (Strömbeck, 2001; Yoshimura *et al*., 2012). In the red spectral region the reported values in ocean, coastal waters and lakes have been quite similar (0.004-0.04 m^2 mg^{-1}) compared to those in blue region (Dekker, 1993; Le *et al*., 2009; Yoshimura *et al*., 2012; Perkins *et al*., 2014; references in Ylöstalo *et al*., 2014). In three turbid productive Estonian lakes a^*_{ph} values 0.012-0.053 m^2 mg^{-1} at 440 nm and 0.007-0.037 m^2 mg^{-1} at 676 nm were in same scale with the earlier studies.

The blue to red absorption ratios in the studied Estonian lakes (mean 1.81) were lower than in Lake Taihu (range 1.08-13.9; Le *et al.,* 2009), but comparable to those in the Baltic Sea (1.67-2.54; Seppälä *et al*., 2005) and other inland waters, like boreal lakes in Southern-Finland (1.10-2.38; Ylöstalo *et al*., 2014) and three clear-water lakes in Sweden (0.73-3.70; Strömbeck, 2001).

Comparison of parameterizations for ocean, coastal and lake waters

Several studies (Bricaud *et al*., 1995; Strömbeck, 2001; Stæhr and Markager, 2004; Ficek *et al*., 2012; Yoshimura *et al*., 2012; Ylöstalo *et al*., 2014) have parameterized chlorophyll-specific phytoplankton absorption as power function of *TChl* (Fig. 4).

In general, our parameter *A* spectrum had similar features with others -presence of two distinctive peaks at the blue and the red wavelengths in visible range,

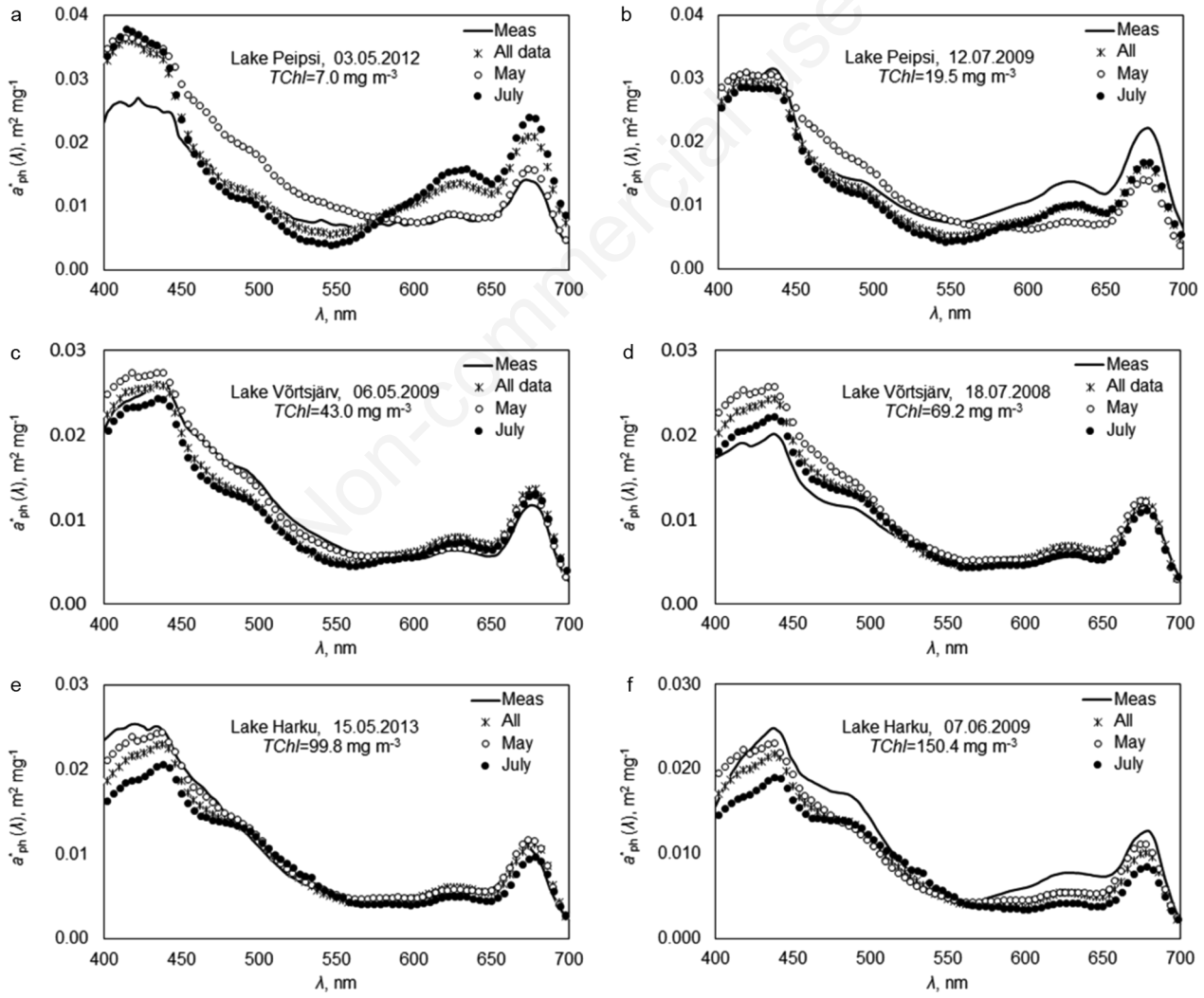

Fig. 5. Chlorophyll-specific phytoplankton absorption coefficient ($a^*_{ph}(\lambda)$) in three turbid productive Estonian lakes measured *in situ* and calculated on the basis of total chlorophyll (*TChl*) concentrations and $A(\lambda)$ and $B(\lambda)$ values from Tab. 4.

associated with the absorption of chlorophyll-a. However, few remarkable differences were also noticed. In our study the most pronounced inconsistency occurred around 630 nm, where various cyanobacterial pigments, like phycocyanin, are known to absorb (Simis *et al*., 2005) and the position of the blue peak of *A* appeared at 420 nm (Fig. 4) instead it common occurrence at 440 nm. This shift could be attributed to larger contribution of phaeophytin-a, that is characteristic to eutrophic waters, as its absorption peak is located at a shorter wavelength than that of chlorophyll-a (Bricaud *et al*., 1995). Such shifts of the peak location have been observed also in cryphytophyte-dominated lakes of southern Finland where peak of coefficient $A(\lambda)$ at 570 nm was attributed to large contribution of crypto-phycoerythrin pigment (Ylöstalo *et al*., 2014). In Lake Kasumiguara (Yoshimura *et al*., 2012) coefficient *A* had a shoulder between 485 nm and 505 nm (Fig. 4b) caused by various carotenoid pigments. The parameter $B(\lambda)$ shows also great differences between sea waters and lakes. The spectral behaviour of *B* for ocean, coastal and archipelago waters was rather similar (Fig. 4), but the magnitude was somewhat different, resulting from a weaker package effect in brackish archipelago waters (Strömbeck, 2001). The small shoulder around 660 nm of the *B* spectra (Bricaud *et al*., 1995; Stæhr and Markager, 2004) could appear in the presence of *Prochlorococcus*, species, which have been observed mainly in oligotrophic waters (Partensky *et al*., 1993).

Influence of the package effect on the parameterization of $a^*_{ph}(\lambda)$

According to IOCCG (2000), phytoplankton populations found in oligotrophic waters have higher $a^*_{ph}(\lambda)$ values than those in eutrophic waters. The package effect increases when either the cell size or the pigment concentration of the cellular material increases, as a result of depressing phytoplankton absorption at all wavelengths and flattening the a^*_{ph} spectrum (Yentsch and Phinney, 1989; Cleveland, 1995; Bricaud *et al*., 1995, 2004). Our parameterization predicted approximately 2-time variation of $a^*_{ph}(440)$ when total chlorophyll varied in the range of 5-240 mg m^{-3} (Fig. 7b). In the range of 580-700 nm the values of a^*_{ph} at *TChl*=5 mg m^{-3} were much bigger than those at higher *TChl* (30-240 mg m^{-3}). It should be considered, however, that our database comprised only samples of total chlorophyll values less than 5 mg m^{-3} and that could at least partly explain the discrepancy of $a^*_{ph}(\lambda)$ at *TCh l*=5 mg m^{-3} from those at greater *TChl* values. For any water type separately the increase of *TChl* accompanied by the decrease of $a^*_{ph}(\lambda)$, except in the some parts of spectrum, where the change of absorption due to total chlorophyll concentration was very small (Fig. 7 c-j). One should consider that for modelling $a^*_{ph}(\lambda)$ both the variation range of total chlorophyll concentrations and the contribution of different *TChl* values are important. For example, in northern Polish lakes (Ficek *et al*., 2012) the variation range of *TChl* was comparable to those in three productive Estonian lakes, whilst the average values of chlorophyll concentrations were rather different, respectively 26.9 and 42.5 mg m^{-3} and that probably caused also the different results of modelling.

Applicability of the parameterizations of phytoplankton absorption spectra for different aquatic environments

Comparison of different modelling results indicated their dependence on the physical and chemical conditions in the aquatic environments as well as on the phytoplankton pigment composition, which in lakes are divergent

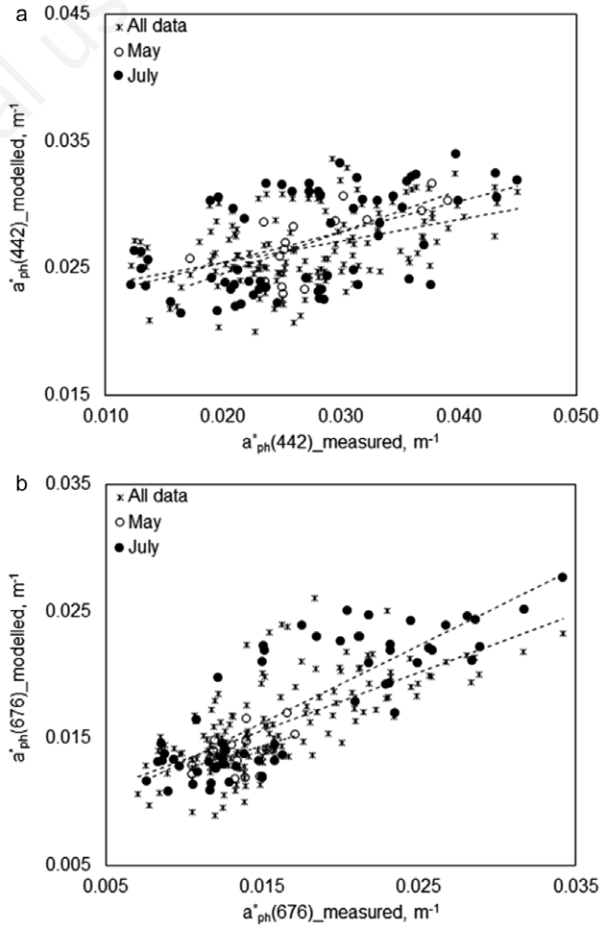

Fig. 6. Modelled *vs* measured chlorophyll-specific phytoplankton absorption coefficient ($a^*_{ph}(\lambda)$) for turbid productive Estonian lakes. Months in the legend are corresponding to the seasonal models used for parameterization of $a^*_{ph}(\lambda)$. The corresponding statistical characteristics are shown in Tab. 5.

from those in ocean and coastal waters. For instance, we cannot use the results of Bricaud *et al*. (1995) on eutrophic lakes as their $A(\lambda)$ and $B(\lambda)$ parameterization was limited to the *TChl* values up to 25 mg m^{-3}. Outside this upper boundary an abnormal increase of $a^*_{ph}(\lambda)$ in the spectral region of 500-600 nm was observed (Fig. 8 c,e,g,i). Similarly, the model of the Stæhr and Markager (2004) did not perform well in the conditions of total chlorophyll values above 100 mg m^{-3}. For this parameterization the artificial shoulder was shifted towards shorter wavelengths (Fig. 8 e,g,i). In three relatively clear Swedish lakes together with brackish archipelago waters in Stockholm (Strömbeck, 2001) the spectral behaviour of $a^*_{ph}(\lambda)$ was rather similar to those in ocean and coastal waters (Fig. 8). Consequently, all the three parameterizations mentioned above (Bricaud *et al*., 1995; Strömbeck, 2001; Stæhr and Markager, 2004) predict much lower chlorophyll-specific phytoplankton absorption than those observed in turbid productive lakes.

The largest discrepancy in parameterizations of *lake models* was observed for *TChl* values below 5 mg m^{-3} (Fig. 8a), which could be explained by the fact that in these parameterizations the contribution of such a low total chlorophyll concentrations were almost negligible. Additionally, we have to take into account that our databased comprised only four samples of *TChl* values less than 5 mg m^{-3}. A good coincidence - especially in the red part of the spectrum – was noticed (almost for all models) in cases, when *TChl* was around 30 mg m^{-3} (Fig. 8). For higher total chlorophyll values our parameterization

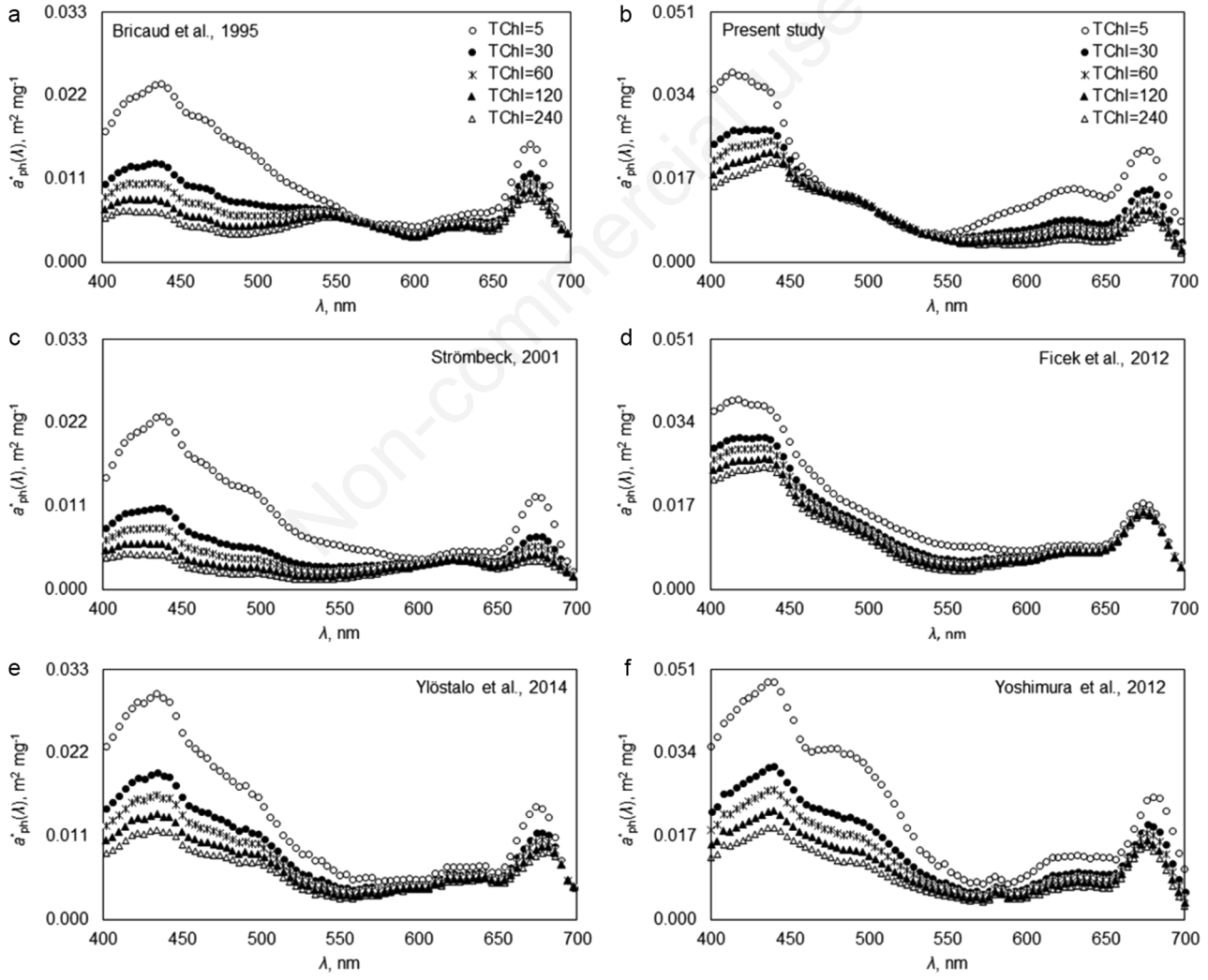

Fig. 7. Spectral distribution of $a^*_{ph}(\lambda)$ for *TChl* concentrations between 5 mg m^{-3} and 240 mg m^{-3}. Left column: for ocean, brackish archipelago and clear inland waters; right column: for productive lakes.

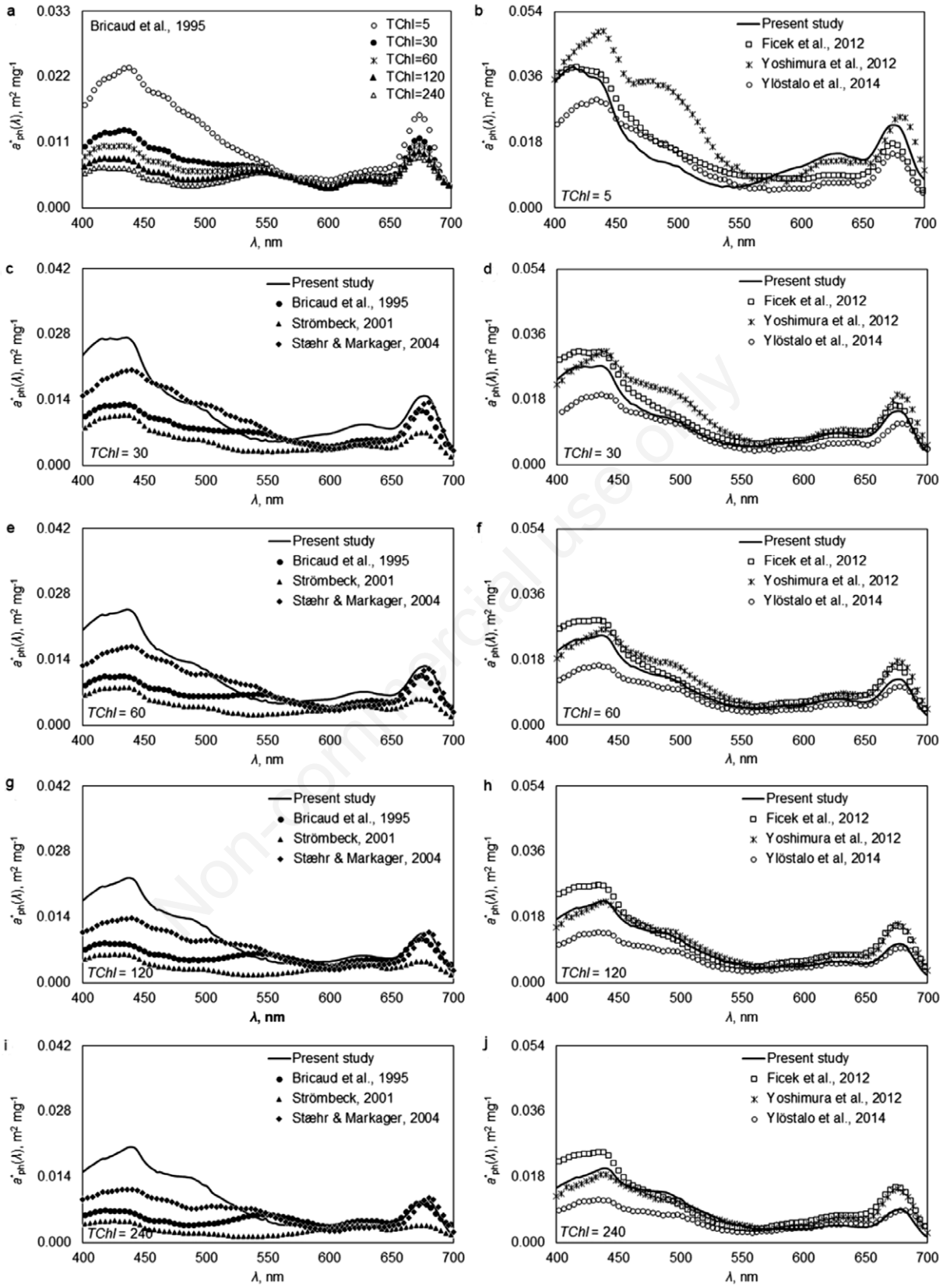

Fig. 8. Chlorophyll-specific phytoplankton absorption spectra for various values of total chlorophyll concentration (from 5 to 240 mg m^{-3}), calculated using eq. 1 with the spectral values of parameters $A(\lambda)$ and $B(\lambda)$ recommended by cited authors and modelled in present study.

had similar features to several studies (Fig. 8f), but in different spectral regions: in the blue absorption band with the results by Yoshimura *et al*. (2012) and in the red part of spectrum with results by Ylöstalo *et* al. (2014). The compatibility with Polish lakes (Ficek *et al*., 2012) was noticed mainly between 490-550 nm. It seems that the improvement of the parameterization of $a^*_{ph}(\lambda)$ spectra for productive and hypertrophic lakes needs a larger dataset, which includes simultaneous measurements of total chlorophyll concentrations, phytoplankton absorption coefficients and - as revealed in the current study - phytoplankton species composition of these inland waters.

In the present study we investigated the chlorophyll-specific phytoplankton absorption coefficients and how to predict these spectra in the case of turbid productive lakes. However, bio-optical models that are used to simulate water reflectance spectra require also the spectra of backscattering coefficient (Gordon *et al*., 1988). Phytoplankton backscattering coefficient spectra are usually smooth with decrease towards longer wavelengths (Ahn *et al*., 1992; Kutser, 2004; Vaillancourt *et al*., 2004; Metsamaa *et al*., 2006). The exception could be cyanobacteria, which have gas vesicles in their cells that may backscatter light selectively. Note, the published backscattering coefficient spectra for cyanobacteria (Ahn *et al*., 1992; Kutser, 2004; Metsamaa *et al*., 2006) do not have high enough spectral resolution in order to determine that with great certainty. Absorption coefficient of CDOM decreases exponentially with increasing wavelength and absorption and backscattering properties of water molecules and mineral particles are spectrally smooth (Kutser *et al*., 2001). Consequently, in eutrophic lakes the specific absorption coefficient, studied by us, is the most important factor determining the shape of water reflectance spectra. The approach proposed by Bricaud *et al.* (1995) has been used in semi-analytical reflectance models for nearly two decades (Kutser, 1997; Kutser *et al*., 2001). However, the results of our study should help to improve the performance of the semi-empirical and radiative transfer models also requiring $a^*_{ph}(\lambda)$ as an input parameter.

CONCLUSIONS

In the present paper we examined and parameterized a model that allows calculating the chlorophyll-specific phytoplankton absorption coefficient spectra for turbid lakes. This kind of models should be developed and validated for improving remote sensing algorithms, estimation of primary production and retrieval of phytoplankton community structure from optical data. The coefficients $A(\lambda)$ and $B(\lambda)$ of our model differ from those found in sea, coastal waters and other types of lakes. For any water type separately the increase of total chlorophyll concentration accompanied with the decrease of a^*_{ph}. Our results showed significant seasonal differences between the model parameters due to diversity of the phytoplankton assemblages. This suggests that season-specific models should be developed and validated. Improving the modelling of chlorophyll-specific phytoplankton absorption spectra for productive and hypertrophic lakes is still pending on the availability of a larger dataset, which includes simultaneous measurements of chlorophyll concentrations, phytoplankton absorption coefficients and phytoplankton species composition of inland waters. Our results implied that total chlorophyll concentration is not a universal predictor of the magnitude of chlorophyll-specific phytoplankton absorption coefficient. The $a^*_{ph}(\lambda)$ models are also likely site and season dependent. Further research is needed for quantifying the role of accessory pigments and other optical constituents as well as the cell size of dominant algal species for considering their influence on the modelling outputs.

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