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ECOLOGY

Development and application of a phytoplankton primary production model for well-mixed lakes

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Abstract. For estimations of the ecological state of a lake and its future trends, data on seasonal and long-term variations of primary production are most necessary. The methods of in situ measurements of production are time consuming, rather complicated, and very expensive. Bio-optical model calculations provide a good alternative here. A semi-empirical model for estimating phytoplankton primary production (Arst et al., 2008, *Aquatic Biology*, Vol. 3, No. 1, pp. 19–30) allows calculating the vertical profiles and areal (integrated over water column) values of primary production using chlorophyll *a* concentration, incident irradiance, and light attenuation coefficient in the water. In the present study this model was developed further by elaborating its automated version. It enables performing rapid and greatly replicated estimations of the circumstantial variability of phytoplankton primary production at hourly intervals from morning to evening and as daily and monthly sums based on a table of initial parameters and depths. For demonstrating the practical application of the model we calculated primary production in two large eutrophic North-European lakes (Võrtsjärv and Peipsi), using a database collected during four warm months in 2009 (123 days in both lakes).

Key words: limnology, phytoplankton, primary production, model calculations, eutrophic lakes.

INTRODUCTION

The productivity of lakes is of great importance in the estimation of their ecological state and for predicting its development in the future. Because of changing light conditions, planktonic photosynthesis has a pronounced diel pattern. In order to acquire integrated results over longer time periods (days, months, years), many consecutive measurements of instantaneous photosynthesis rate should be carried out. In some studies (Joniak et al., 2003; Yoshida et al., 2003; Forget et al., 2007) the values of daily primary production integrated over the photic zone have been estimated from in situ incubations, often using the radioactive ^{14}C method suggested in (Steeman Nielsen, 1952). However, in situ methods give reliable results only in oligotrophic waters. In eutrophic and hypertrophic waters incubations cannot be performed over long periods (e.g. from morning to evening) because part of the ^{14}C taken up in photosynthesis is respired (Lancelot & Mathot, 1986) or releases as extracellular products (Møller Jensen, 1985). In general, the method of in situ measurements is time consuming, rather complicated, and very expensive.

Bio-optical model calculations provide an alternative to the time-consuming ^{14}C method. Modelling is especially important in turbid waters of high productivity where the abrupt light gradient may cause large errors when traditional field methods are applied. Several studies have estimated primary production from light intensity and abundance of phytoplankton pigments (e.g. Smith et al., 1989; Sosik, 1996). When primary production is modelled for longer than diurnal timescales, diel variations of light intensity are commonly ignored and the mean daily photosynthetically available

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irradiance (PAR) is used to estimate primary production. This approach can produce a significant error if the model does not explicitly account for light saturation and the irradiance during part of the day is higher than that needed for the maximum possible growth rate (Robson, 2005).

Two versions (spectral and integral) of a semi-empirical model were elaborated in Arst et al. (2008a) for the calculation of the vertical profiles of primary production, $P(z)$, in lakes. These models are suitable for calculating the primary production for well-mixed lakes, where chlorophyll *a* (Chl *a*) concentration (C_{chl}) and the diffuse attenuation coefficient of light do not change (or change only slightly) with depth. The models work only for ice-free conditions. To elaborate a model for estimating the primary production under the ice we should have to know the optical properties of the ice cover. The basic equation of these models describes primary production ($P(z)$ in mg C m^{-3} h^{-1}) as a function of photosynthetically absorbed radiation and quantum yield of carbon fixation (Smith et al., 1989). The main difference between the spectral and integral models resides in the data on underwater irradiance and specific absorption coefficient of Chl *a* (spectral or integral). Quantification and verification of these models was performed using in situ measurements of primary production profiles and simultaneously measured bio-optical parameters (C_{chl}, diffuse attenuation coefficient, incident solar irradiance, and downwelling irradiance in the wavelength range of 400–700 nm) in three turbid well-mixed Estonian lakes (Peipsi (Estonian part), Võrtsjärv, and Harku) in 2003–2005 (Arst et al., 2008a).

In this study the modelled and measured vertical profiles of primary production and also its areal values were compared. Statistical analysis of the regressions *P*(meas) vs *P*(mod) was performed (and the corresponding tables and figures are shown) in (Arst et al., 2008a). The data obtained proved that our models gave rather reliable estimations of primary production in the turbid, well-mixed lakes. Both models allow estimation of the instantaneous primary production profiles, $P(z)$, and the areal (water-column-integrated) production, P_{int}, and, consequently, also their daily dynamics and daily and monthly totals. The models are based on the fact that in well-mixed lakes only incident irradiance varies noticeably, and often irregularly during a day, but the other initial parameters of the model usually change rather slowly over time (Reinart and Nõges, 2004; Arst et al., 2008b; Paavel et al., 2008; Nõges et al., 2011). Thus, for the estimation of the temporal dynamics of primary production in a lake, daily data are needed on incoming PAR irradiance combined with at least episodic measurements of C_{chl} and the diffuse attenuation coefficient in the water (Arst et al., 2008a).

The objectives of the present study were (a) to further develop the models by Arst et al. (2008a) and (b) to demonstrate the application of the upgraded and automated models in practice, using the database collected during four warm months (May–August) in two eutrophic lakes. In the present study we used the integral version of the primary production model. We present here quantitative estimates of the daily variability of phytoplankton primary production profiles as well as areal values (daily and monthly sums) of the production in the observed lakes as the results of the application of the automated model.

MATERIALS AND METHODS

Short description and automation of the calculation model

Basic algorithms of a primary production model (two versions, spectral and integral) were derived and their quantification and verification were performed by Arst et al. (2008a). In the present study, we demonstrate the application of the automated version of the integral primary production model. As the detailed description of this model is presented elsewhere (Smith et al., 1989; Arst et al., 2008a), we give here only some basic equations. The main equation is the following (Smith et al., 1989; Arst et al., 2008a):

$$P(z) = \Psi Q_{0,\text{PAR}}(z) F_{\text{PAR}}(z), \tag{1}$$

where $P(z)$ is primary production at a depth z (in mg C m^{-3} h^{-1}); Ψ is the factor 12 000 for converting moles of carbon to milligrams of carbon; $Q_{0,\text{PAR}}(z)$ is photosynthetically absorbed scalar irradiance (in Einst m^{-2} h^{-1}), following the usage in (Smith et al., 1989) at depth z; and $F_{\text{PAR}}(z)$ is the quantum yield of carbon fixation (mol C Einst^{-1}) in the wavelength range of 400–700 nm. In the case of the integral model:

$$Q_{0,\text{PAR}}(z) \approx q_{0,\text{PAR}}(z) a_{\text{ph,PAR}}, \tag{2}$$

and

$$a_{\text{ph,PAR}} = \int_{400}^{700} a'_{\text{ph}}(\lambda) C_{\text{chl}} d\lambda \Big/ \int_{400}^{700} d\lambda. \tag{3}$$

Here $q_{0,\text{PAR}}(z)$ is the underwater scalar irradiance (in Einst m^{-2} h^{-1}) in the wavelength range of 400–700 nm (PAR) at depth z, λ is the wavelength (in nm), $a_{\text{ph,PAR}}$ is the averaged over the PAR region absorption coefficient of phytoplankton (in m^{-1}), and $a'_{\text{ph}}(\lambda)$ is the sequence of specific absorption coefficients of phytoplankton at wavelengths λ (in m^2 mg^{-1}). For the calculation of $a'_{\text{ph}}(\lambda)$ we used an algorithm presented by Bricaud et al. (1995):

$$a'_{\text{ph}}(\lambda) = A(\lambda) C_{\text{chl}}^{-B(\lambda)}, \tag{4}$$

where the specific absorption coefficient $a'_{\rm ph}(\lambda)$ is calculated taking into account the "package effect" (Morel and Bricaud, 1981; Kirk, 1994; Bricaud et al., 1995). Here A and B are positive, wavelength-dependent parameters, as tabulated in Bricaud et al. (1995).

The parameter $F_{\rm PAR}(z)$ was computed according to the algorithms presented in Arst et al. (2008a):

$$F_{\rm PAR}(z) = \frac{F_{\max}}{(1 + Mq_{\rm PAR}(z))^n}, \quad (5)$$

where $F_{\max} = 0.08$ mol C Einst^{-1}, $q_{\rm PAR}(z)$ is the underwater planar irradiance at depth z (in Einst m^{-2} h^{-1}), M and n are parameters that we presumed to depend on the incident irradiance and on the bio-optical characteristics of the water body. For moderately turbid lakes (diffuse attenuation coefficient, $K_{\rm d,PAR}$, from 0.7 to 7 m^{-1}) the parameters M and n for the integral model (taken from Arst et al., 2008a) are presented in Table 1. In the case of the spectral model, $n = 3$ and the algorithms for M are different (Arst et al., 2008a). The results of the calculations are the values of $P(z)$ in mg C m^{-3} h^{-1} and areal production, $P_{\rm int}$, in mg C m^{-2} h^{-1}. The daily sums are calculated from the hourly sums from morning to evening, and the monthly sums from the daily sums.

The integral version of the primary production model needs (as initial data) an irradiance estimate for the entire PAR spectrum (the spectral values of the incident irradiance and diffuse attenuation coefficient are not necessary). In (Arst et al., 2008a) the quantification and verification of this model were performed using primary production profiles that were episodically measured during 2003–2005 in three Estonian lakes (Peipsi, Võrtsjärv, Harku), using in situ incubations and the radioactive ^{14}C method (Steeman Nielsen, 1952). Altogether we collected 53 measured profiles of $P(z)$, which were used as model validation by Arst et al. (2008a). According to statistical comparison, the spectral model is preferable, but the differences were rather small: the regressions P(measured) vs P(calculated) for spectral and integral models (L. Peipsi and L. Võrtsjärv together) gave R^2(adj) of 0.919 and 0.856, respectively (Arst et al., 2008a). However, the integral model is more suitable because there is no need for the spectral data of the incident irradiance and diffuse attenuation coefficient.

The models presented in (Arst et al., 2008a) give a possibility of getting quite reliable results on the vertical profiles and the corresponding areal (integrated over water column) values of the production. The automation of both versions (spectral and integral) of the primary production models, developed in the present study, allows performing rapid estimations of the circumstantial variability of phytoplankton primary production at hourly intervals from morning to evening and as daily and monthly sums during a few seconds of calculation time. The computations are realized in the Microsoft Excel® environment and are based on a table of initial parameters and depths (it is possible to calculate for 20 depths, beginning from $z = 0$, the depth interval depending on the transparency of the water).

Study sites

We calculated production in two large eutrophic North-European lakes, Võrtsjärv and Peipsi, using a new database collected during May–August 2009 (123 days in both lakes). We chose these lakes because (a) they are good examples of a eutrophic lake, (b) we have continuous measurements of incoming solar radiation at their locations, and (c) repeated measurements of water parameters were conducted during May–August 2009 (13 field trips to L. Võrtsjärv and 12 trips to L. Peipsi).

Lake Võrtsjärv (270 km^2, mean depth 2.8 m, maximum depth 6 m, coordinates of our station 58°13′N, 26°06′E) is the largest lake belonging entirely to Estonia. The shallow lake is well mixed: regular monitoring has shown that phytoplankton concentration is practically unchanged with depth. Its water is optically turbid (in summer conditions the Secchi depth, $z_{\rm SD}$, usually varies from 0.3 to 1.6 m), and the underwater light climate is strongly affected by the water level and ice conditions (Reinart and Nõges, 2004; Nõges and Nõges, 2006; Arst et al., 2008c). The diffuse attenuation coefficient for the PAR region (400–700 nm), $K_{\rm d,PAR}$, is normally between 1.5 and 3.8 m^{-1} (only in September 1996, after a very dry summer, $z_{\rm SD}$ was as low as 0.15 m and $K_{\rm d,PAR}$ was 6.5 m^{-1}) (Reinart and Herlevi, 1999; Arst et al., 2008c). The range of $C_{\rm chl}$ in ice-free conditions is 20–102 mg m^{-3} (Paavel et al., 2008). Lake Võrtsjärv fits the definition of a hard-water eutrophic lake (Mäemets, 1977).

Table 1. Regression formulas for the parameter M and the value of n (in Eq. 5) for the integral model of primary production taken from Arst et al. (2008a). The incident irradiance $q_{\rm PAR}(z = 0)$ is in Einst m^{-2} h^{-1}, $C_{\rm chl}$ in mg m^{-3}, and $K_{\rm d,PAR}$ in m^{-1}; SE is the standard error

$C_{\rm chl}$, mg m^{-3}	M	R^2	SE	p	n
$C_{\rm chl} < 35$	$1.99 + 0.028q_{\rm PAR}(z = 0) - 0.154K^{2.5}_{\rm d,PAR}$	0.883	0.22	<0.0001	2
$C_{\rm chl} = 35–100$	$1.58 - 0.138q_{\rm PAR}(z = 0) - 0.0025C_{\rm chl}$	0.669	0.15	<0.0001	2

Lake Peipsi is a large (2611 km^2), shallow (mean depth 8.3 m, maximum depth 12.9 m) well-mixed lake on the border of Estonia and Russia. It is the fourth largest lake in Europe. According to Arst et al. (2008c), its z_{SD} varies in summer from 0.4 to 4.8 m, the values of $K_{d,PAR}$ are between 0.74 and 2.58 m^{-1}, and C_{chl} varies between 1.8 and 37 mg m^{-3}. Lake Peipsi is defined as a large unstratified eutrophic lake with oligohumic water of medium hardness (Jaani, 2001). The coordinates of our measurement point in L. Peipsi were approximately 58°50′N, 27°06′E.

Measurements of the initial parameters of the model

Incident solar irradiance in the PAR region $(q_{PAR}(z=0))$ was recorded from morning to evening from May to the end of August 2009. For L. Peipsi the data were provided by Tiirikoja Actinometric Station (Estonian Meteorological and Hydrological Institute). At L. Võrtsjärv we used a Yanishevsky pyranometer (Kondratyev, 1965) on a roof near the coastal station where the water samples were taken. The results in W m^{-2} were converted to Einst m^{-2} h^{-1}. The readings of irradiance were obtained at two minute intervals, but primary production was calculated as hourly averages.

The values of underwater planar quantum irradiance $(q_{PAR}(z))$ were determined as $q_{PAR}(z) = (1-r)q_{PAR}(z=0)\exp(-K_{d,PAR}z)$ and later converted to scalar quantum irradiance $q_{0,PAR}(z)$ (Arst et al., 2008a). Here $q_{PAR}(z=0)$ is the incoming irradiance at the water surface, and r is the reflectance that was assumed to equal 0.06.

Spectra of the beam attenuation coefficient in the 350–700 nm wavelength range for filtered and unfiltered water samples were obtained with a U-3010 laboratory spectrophotometer (Hitachi High-Technologies Corporation). These results allowed derivation of not only the spectral values of the diffuse attenuation coefficient but also $K_{d,PAR}$ (Arst et al., 2002; Arst, 2003).

Relative transparency of water (z_{SD}, m) was determined with a Secchi disk. The concentration of chlorophyll *a* (C_{chl}, in mg m^{-3}) was measured in depth-integrated water samples according to Lorenzen (1967). Water samples were taken at 1 m depth intervals and pooled. Both Peipsi and Võrtsjärv are polymictic lakes and do not stratify during the ice-free season (Jaani, 2001; Laas et al., 2012), therefore the pooled water was assumed to reflect C_{chl} in the whole water column.

As C_{chl} and $K_{d,PAR}$ change rather gradually at our sampling stations in lakes Peipsi and Võrtsjärv, we assumed that these parameters for the intervals between measurements during the field trips could be estimated by linear interpolation. It was also assumed that although C_{chl} and $K_{d,PAR}$ change from day to day (Figs 1 and 2), they are approximately constant during each day. These approximations and the hourly averages of $q_{PAR}(z=0)$ from the actinometric data for each day serve as the initial data necessary for phytoplankton primary production calculations.

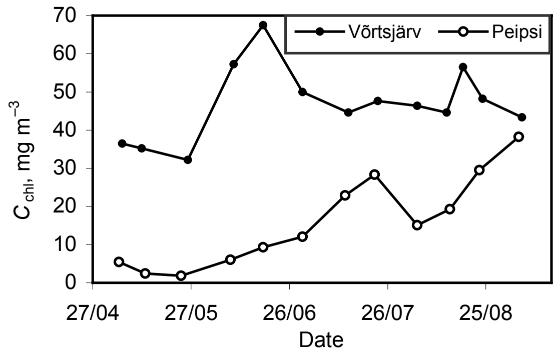

Fig. 1. Measured (circles) and interpolated (lines) values of C_{chl} in summer 2009.

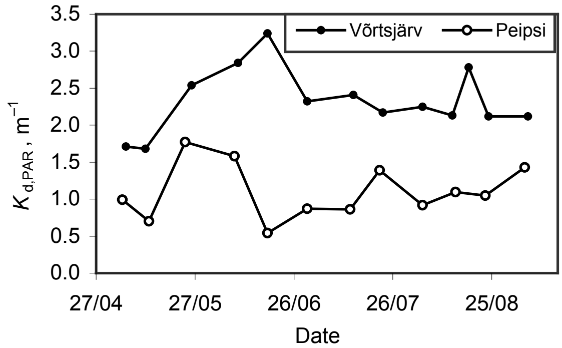

Fig. 2. Measured (circles) and interpolated (lines) values of $K_{d,PAR}$ in summer 2009 (Kauer, 2012).

RESULTS

We determined the vertical profiles of primary production for 20 depths (in L. Võrtsjärv from 0 to 3 m and in L. Peipsi from 0 to 7 m). The $P(z,t)$ values (t denotes time) presented in this paper were simulated by the model. The purpose of the models was to determine primary production ($P(z,t)$, areal values, daily and monthly sums) in cases when in situ measurements were not performed. The validation of the model results with measured data was accomplished and published earlier by Arst et al. (2008a) and by Nõges et al. (2011).

The diurnal variability of the hourly values of $P(z,t)$ for four days in L. Peipsi and for four days in L. Võrtsjärv is shown as contour plots in Figs 3 and 4, respectively. The existing data set allows for such

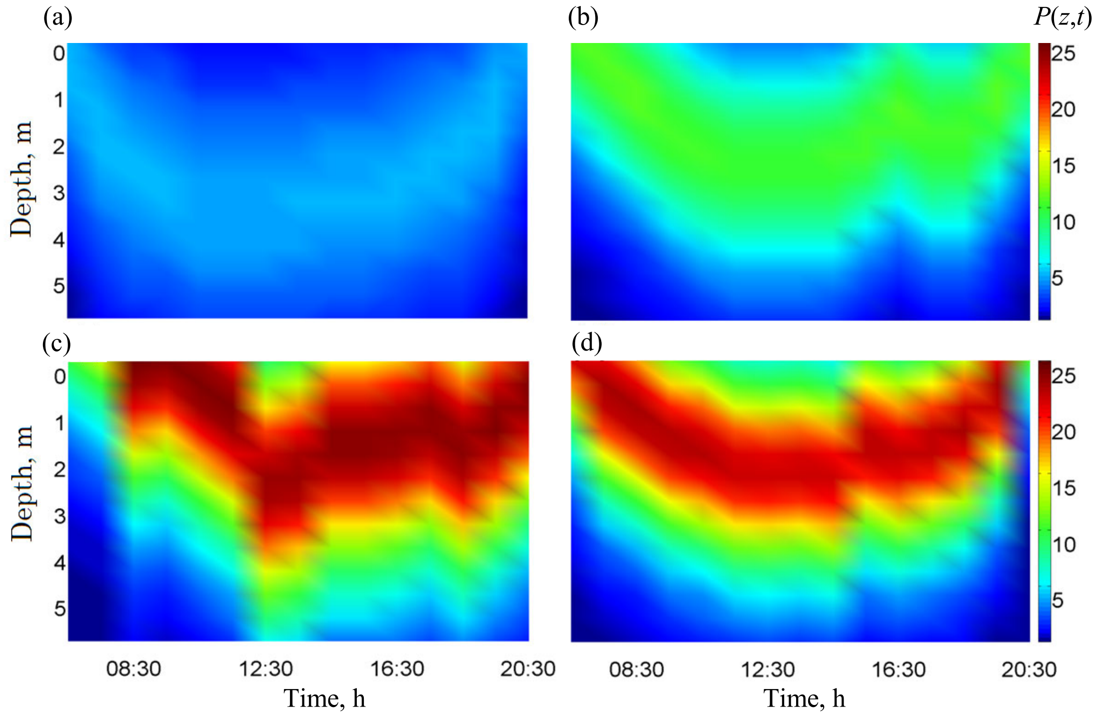

Fig. 3. Dependence of primary production $P(z, t)$ (in mg C m^{-3} h^{-1}) on time and depth calculated for Lake Peipsi: (a) 13.05.2009; (b) 14.06.2009; (c) 13.07.2009; and (d) 15.08.2009. The values of $P(z, t)$ correspond to different colours (Kauer, 2012).

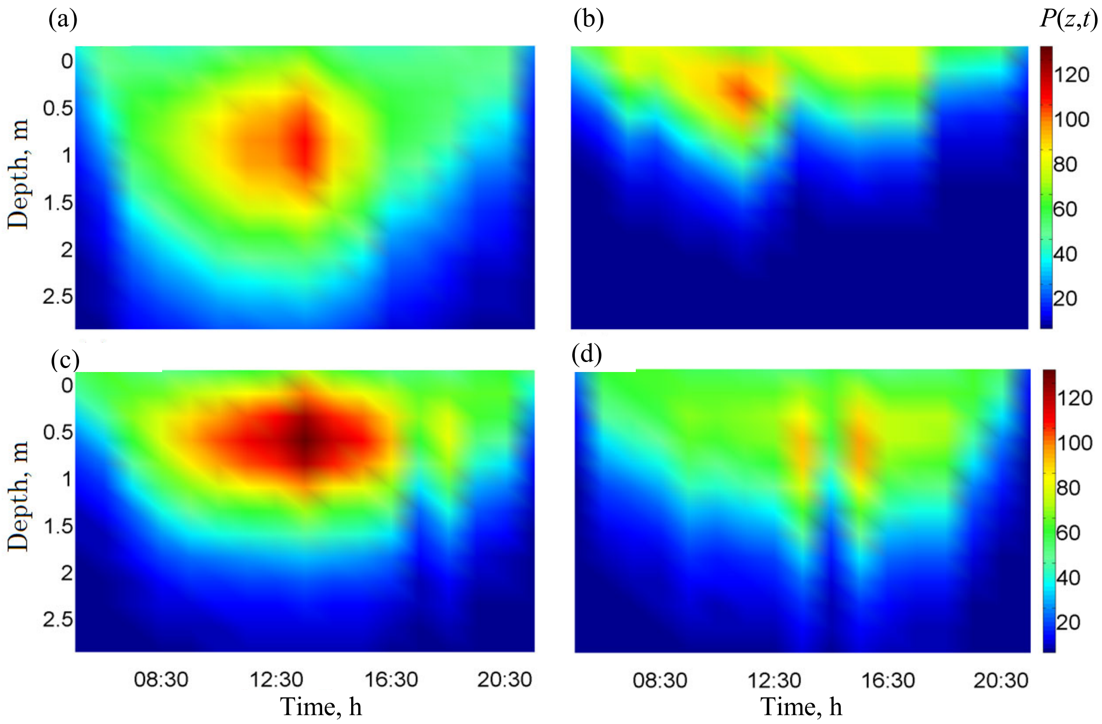

Fig. 4. Dependence of primary production $P(z, t)$ (in C mg m^{-3} h^{-1}) on time and depth calculated for Lake Võrtsjärv: (a) 12.05.2009; (b) 13.06.2009; (c) 14.07.2009; and (d) 13.08.2009. The values of $P(z, t)$ correspond to different colours (Kauer, 2012).

calculations for 123 days in each lake (not shown). We chose only some cases to demonstrate the variability of $P(z,t)$ in different seasonal and weather conditions.

Because C_{chl} and $K_{\mathrm{d,PAR}}$ were taken to be constant for each day, the temporal variations of $P(z,t)$ during a day were caused only by changes of the incoming irradiance. When this irradiance was low, the maximum of $P(z,t)$ was located near the water surface (morning and evening in all figures, most of the day in Fig. 3c and Fig. 4b and d); on cloudless days the maximum of $P(z,t)$ was observed at noon and it was located at 1 to 3 m depth (Fig. 4a and c). However, for some other cloudless days this maximum in L. Peipsi was at a depth of 4–5 m. Note that for L. Peipsi the scale of $P(z,t)$ was taken from 0 to 25 mg C m^{-3} h^{-1}, but for L. Võrtsjärv it was from 0 to 125 mg C m^{-3} h^{-1}. Thus, the numerical values represented by the same colours in the figures for the two lakes are different.

The daily sums of the areal (integrated over the water column) primary production for both lakes (separately for each month) are presented in Fig. 5 and the respective monthly sums in Fig. 6. According to our calculations for the whole observation period, L. Peipsi showed the minimum P_{int}(day) of 100 mg C m^{-2} day^{-1} and the maximum value of 1390 mg C m^{-2} day^{-1}. For L. Võrtsjärv the corresponding values were 780 and 2338 mg C m^{-2} day^{-1}. Especially marked differences between daily P_{int}(Peipsi) and P_{int}(Võrtsjärv) were observed in May. The production changed irregularly from day to day whereas different illumination conditions predominantly influenced the temporal variability of P_{int}(day). The monthly variations were greater in L. Peipsi, the monthly sums of production increasing from May to late summer (Fig. 6). In L. Võrtsjärv the differences between months were smaller; the maximum of P_{int}(month) was observed for July, and both in May and August primary production was by about 12–14% smaller than in July (Fig. 6). As we expected, primary production depended in general on C_{chl}. That dependence was greater when the relative difference between C_{chl}(max) and C_{chl}(min) in a lake was high (Fig. 1). Averaged over four months, C_{chl} in L. Peipsi was 14.3 mg m^{-3} and in L. Võrtsjärv 46.8 mg m^{-3}. In L. Peipsi the ratio $(C_{\mathrm{chl}}(\max) - C_{\mathrm{chl}}(\min))/C_{\mathrm{chl}}(\mathrm{average})$ was equal to 2.32, but in L. Võrtsjärv it was only 0.75. The determination coefficient R^2 of the regression P_{int}(day) vs C_{chl} was 0.81 for L. Peipsi and 0.03 for L. Võrtsjärv. For this reason the substantial trend over summer of P_{int}(day) and P_{int}(month) is clearly seen in L. Peipsi, but not in L. Võrtsjärv (Figs 5 and 6).

At in situ primary production measurements daily values are calculated using an empirical equation relating P_{int} (in mg C m^{-2} day^{-1}) to P_{int} at midday (in mg C m^{-2} h^{-1}):

$$P_{\mathrm{int}}(\mathrm{day}) = P_{\mathrm{int}}(\mathrm{midday}) / (0.230 - 890 \times 10^{-5}\,\mathrm{DL}), \quad (6)$$

where DL is the length of daylight in hours. This equation was obtained from the measurements in

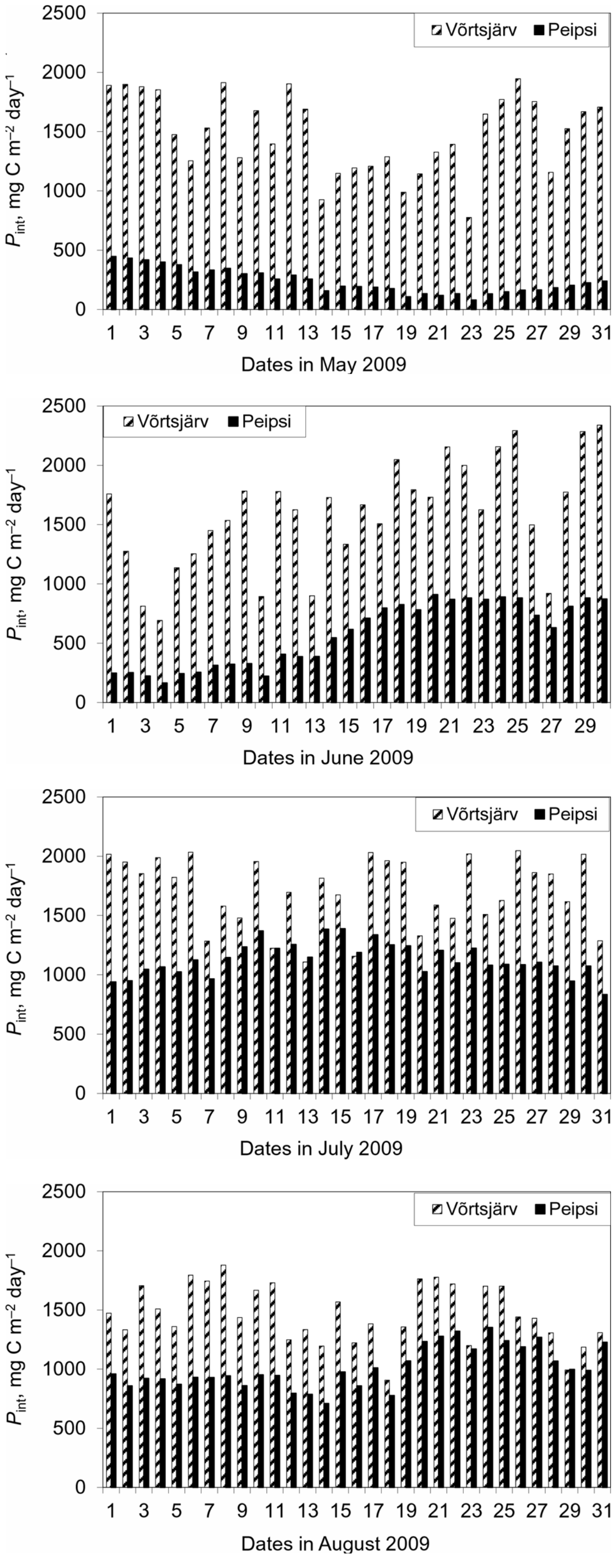

Fig. 5. Daily sums of the areal primary production (P_{int}) in summer 2009 in lakes Peipsi and Võrtsjärv.

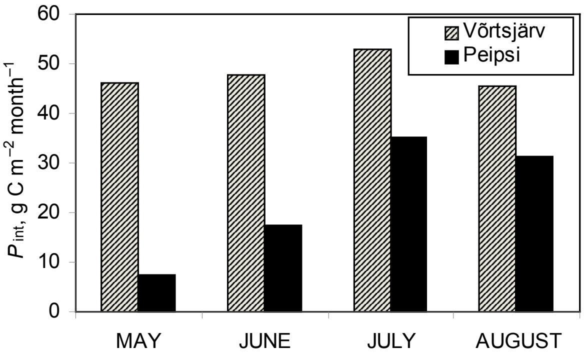

Fig. 6. Monthly sums of the areal primary production ($P_{\rm int}$) in lakes Peipsi and Võrtsjärv in summer 2009 (Kauer, 2012).

L. Võrtsjärv by Nõges and Nõges (1998), and later used by Nõges and Kangro (2005) and Nõges et al. (2011). Relying on our model results we compared the values of $P_{\rm int}$(day) with the corresponding results calculated with Eq. (6). For L. Peipsi our model results always exceeded those obtained by Eq. (6). The differences were mostly 20–25%, but the maximum difference was 50% and the minimum 4%. For L. Võrtsjärv these differences were substantially more variable. In some cases Eq. (6) gave lower values of $P_{\rm int}$(day) (the maximum was 50%), but in other cases Eq. (6) gave higher values of $P_{\rm int}$(day) (the maximum was 33%). In both lakes these differences depended on the values of $P_{\rm int}$(midday) in comparison with the other values of $P_{\rm int}$ during the day.

DISCUSSION

The presented results demonstrate the efficiency of our primary production model for calculating the variability of the primary production profiles during a day, and also the daily and monthly sums of $P_{\rm int}$ for a large database. Although our results (Figs 3–6) describe $P(z,t)$ and $P_{\rm int}$ for a relatively short period (123 days in four months), they allowed evaluation of the variations of the productivity in two different lakes. From the irregular diurnal variability of $P(z,t)$ during a day and of $P_{\rm int}$ during a month (Figs 3–5) we can conclude that, besides the other factors (water properties, optically active substances), primary production is markedly influenced by incoming irradiance. It depends on the solar zenith angle and cloudiness (clear sky, overcast, or variable cloudiness). This dependence was most evident in the daily variations of $P(z)$ and $P_{\rm int}$, but it is noticeable also in variations of $P_{\rm int}$(day) during a month. For instance, in L. Võrtsjärv under clear sky conditions on 12 May 2009 the value of $P_{\rm int}$(day) was 1903 mg C m^{-2} day^{-1}, but in the overcast conditions of 14 May 2009 it was less than half this value, 925 mg C m^{-2} day^{-1} ($C_{\rm chl}$ was respectively 35.2 and 34.8 mg m^{-3}). This dependence was considerably smaller for the monthly sums (Fig. 6). The increase of $P_{\rm int}$ during the summer in L. Peipsi was undoubtedly caused by the increase in the phytoplankton concentration from May to late summer (Figs 1 and 5).

We cannot conclude from the fact that the dependence of $P_{\rm int}$ on $C_{\rm chl}$ is noticeable in L. Peipsi but almost imperceptible in L. Võrtsjärv that R^2 is higher in clear-water lakes (the 4-month average of $C_{\rm chl}$ in L. Peipsi was noticeably smaller than that in L. Võrtsjärv). The determination coefficient R^2 of the regression $P_{\rm int}$ vs $C_{\rm chl}$ depends on the limits of the change in $C_{\rm chl}$ in the regression database (in the case of a small difference between maximum and minimum values of $C_{\rm chl}$ we will get lower R^2 compared with the case when $C_{\rm chl}$(min) and $C_{\rm chl}$(max) are widely separated). Figure 7 demonstrates this regression relying on the values of measured $P_{\rm int}$ (2-hour incubations at six depths in the water) obtained using the results of our episodic measurements of $P(z)$ in three lakes (Peipsi, Võrtsjärv, Harku) from 2003 to 2009 (altogether 78 results of $P_{\rm int}$). Lake Harku is a small hypertrophic lake in northern Estonia, described in (Arst et al., 2008c). In Fig. 7 the variability range of $C_{\rm chl}$ for L. Peipsi is from 2.8 to 36 mg m^{-3}, for L. Võrtsjärv it is from 17 to 82 mg m^{-3}, and for L. Harku from 46 to 335 mg m^{-3}. The determination coefficient of the regression shown in Fig. 7 is 0.754; the scatter of the points is mostly caused by different irradiances during the measurements of $P_{\rm int}$. Thus, the determination coefficient R^2 of the regression $P_{\rm int}$ vs $C_{\rm chl}$ was usually higher when we considered a group of lakes with very different $C_{\rm chl}$.

The values of $P(z,t)$ and $P_{\rm int}$ shown in the present study can be regarded as examples that demonstrate the efficiency of our primary production model, which only requires three initial parameters. It does not account for all factors influencing primary production (e.g. tempera-

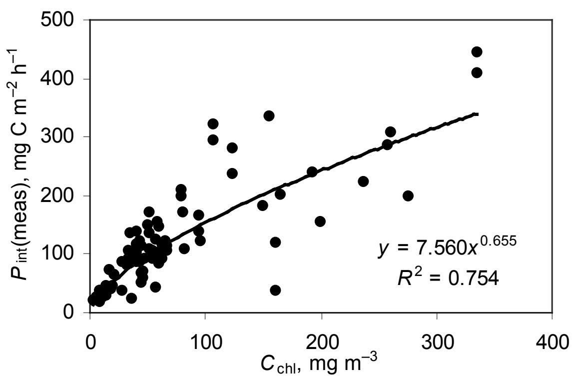

Fig. 7. Regression $P_{\rm int}$(meas) vs $C_{\rm chl}$ obtained from episodic measurements of $P(z)$ profiles in three lakes (Peipsi, Võrtsjärv, Harku) during ice-free periods in 2003–2009 (altogether 78 values of $P_{\rm int}$(meas)) (Kauer, 2012).

ture, nutrients, and turbulence), although some of these factors are considered indirectly (e.g. temperature through light and nutrients through chlorophyll). The results of the modelled $P(z)$ values were rather close to the measured ones (Arst et al., 2008a), which confirms the reliability of the model. Our model in its present form is rather specific to the lakes where it was calibrated, but still it is expected to work also on other turbid temperate lakes. The models with numerous initial parameters (our three parameters plus temperature, nutrients, and turbulence) are extremely difficult to quantify, and they need complicated in situ measurements. In some cases the whole data complex need not be available.

The results obtained (Figs 3–6) describe $P(z,t)$ and P_{int} in two eutrophic lakes during a relatively short period (123 days in four warm months) while data for the cold season are missing. This restricts comparison with our results. We did not find published data allowing us to draw detailed contour plots like Figs 3 and 4. In (Wetzel, 2001) the dependence of $P(z,t)$ on depth and time is presented as isolines for two lakes: oligotrophic Lake Lawrence and hypereutrophic Lake Wintergreen (both in Michigan). In that study the corresponding values of integrated areal primary production are also shown. In oligotrophic L. Lawrence the summer maximum of P_{int} was about 500 mg C m^{-2} day^{-1}, in mesotrophic/eutrophic L. Peipsi it was 1390 mg C m^{-2} day^{-1}; in hypereutrophic L. Wintergreen P_{int}(max) was about 2000 mg C m^{-2} day^{-1}, in eutrophic L. Võrtsjärv 2340 mg C m^{-2} day^{-1}. There are also some other studies giving monthly and yearly averages of P_{int}. In (Yoshida et al., 2003) the production by phytoplankton in the southern basin of the ultra-oligotrophic Lake Baikal (eastern Siberia, Russia) was measured by in situ methods during March–October in two consecutive years (1999 and 2000). As can be expected, the values of P_{int} were noticeably smaller than those for our lakes, with a maximum of 424 mg C m^{-2} day^{-1} in August. Joniak et al. (2003) describe results of measurements of primary production carried out in situ in 1992–1997 (every month and during the growing seasons every fortnight) in the Maltański Reservoir, Poland. The maximum areal photosynthesis (P_{int}) during the study period, 4700 mg C m^{-2} day^{-1}, was observed in July 1994. Nõges et al. (1993) reported some episodic measurements in summer 1991 in three Estonian lakes: Valgjärv (oligotrophic), Uljaste (semidystrophic), and Korijärv (highly eutrophic). The summer maximums of P_{int} in these lakes were 1051, 554, and 1325 mg C m^{-2} day^{-1}, respectively. Rather thorough investigations were carried out in Lake Kinneret, Israel (Berman and Pollingher, 1974; Berman, 1976; Yacobi et al., 1996; Yacobi, 2003, 2006). From 1990 to 2003 the water parameters of L. Kinneret were observed and monthly averages of P_{int} for that period were estimated. The average value of P_{int} in L. Kinneret was maximal in May, 2674 mg C m^{-2} day^{-1} (Yacobi, 2006). Lake Kinneret deserves attention due to the irregular vertical and horizontal distribution of C_{chl} and $K_{\text{d,PAR}}$ during phytoplankton blooms. According to Yacobi (2006), from March to June the value of $K_{\text{d,PAR}}$ for the 0–0.5 m layer can exceed that for the 1.5–6.5 m layer as much as four times. This large difference is connected with the vertical distribution of C_{chl}, which can show a strong and sharp maximum (even up to 600 mg m^{-3}) in some sublayers between 0 and 5 m (at different depths). From those data we can conclude that our primary production model elaborated for well-mixed lakes is not suitable for L. Kinneret.

The computation results obtained in the present study should be interpreted as approximations. The main sources of uncertainties are (a) the semi-empirical formulation of the model itself; (b) errors in the measurements of $q_{\text{PAR}}(z=0)$, C_{chl}, and $K_{\text{d,PAR}}$; (c) frequent interpolation of the values of C_{chl} and $K_{\text{d,PAR}}$. Some irregular profiles of $P(z,\text{meas})$ suggest uncertainties in the measurement results as well (Arst et al., 2008a, 2012). In shallow, well-mixed lakes in which C_{chl} and $K_{\text{d,PAR}}$ do not change vertically one cannot expect an irregular depth profile of $P(z,\text{meas})$.

The developed automated models for rapid estimates of phytoplankton primary production are a useful tool for filling the gaps in the measured primary production data and potentially extending the data series over periods for which other biological and chemical data are available. This helps to give a realistic estimation of the annual and interannual variability of primary production to be used in further ecosystem analyses. The integral version of our primary production model was applied by Nõges et al. (2011) for approximate estimation of the daily, monthly, and yearly sums of P_{int} in L. Võrtsjärv during 1982–2009.

Our models can be usable in the monitoring programmes of the well-mixed lakes. Regular data on primary production are necessary for the estimation and prediction of the ecological state of a lake. However, in this case the monitoring data have to contain all three input parameters needed for model calculations.

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REFERENCES

Arst, H. 2003. *Optical Properties and Remote Sensing of Multicomponental Water Bodies*. Springer & Praxis-Publishing, Chichester, UK.

Arst, H., Erm, A., Reinart, A., Sipelgas, L., and Herlevi, A. 2002. Calculating irradiance penetration into water bodies from the measured beam attenuation coefficient II: Application of improved model to different types of lakes. *Nord. Hydrol.*, **33**(2–3), 207–226.

Arst, H., Nõges, T., Nõges, P., and Paavel, B. 2008a. *In situ* measurements and model calculations of primary production in turbid waters. *Aquat. Biol.*, **3**, 19–30.

Arst, H., Erm, A., Herlevi, A., Kutser, T., Leppäranta, M., and Reinart, A. 2008b. Optical properties of boreal lake waters in Finland and Estonia. *Bor. Environ. Res.*, **13**, 133–158.

Arst, H., Nõges, T., Nõges, P., and Paavel, B. 2008c. Relations of phytoplankton in situ primary production, chlorophyll and underwater irradiance in turbid lakes. *Hydrobiologia*, **599**, 169–176.

Arst, H., Nõges, P., Nõges, T., Kauer, T., and Arst, G.-E. 2012. Quantification of a primary production model using two versions of the spectral distribution of the phytoplankton absorption coefficient. *Environ. Model. Assess.*, **17**, 431–440.

Berman, T. 1976. Light penetrance in Lake Kinneret. *Hydrobiologia*, **49**, 41–48.

Berman, T. and Pollingher, U. 1974. Annual and seasonal variations of phytoplankton, chlorophyll, and photosynthesis in Lake Kinneret. *Limnol. Oceanogr.*, **19**(1), 31–54.

Bricaud, A., Babin, M., Morel, A., and Claustre, H. 1995. Variability in the chlorophyll-specific absorption coefficients of natural phytoplankton: analysis and parametrization. *J. Geophys. Res.*, **100**(C7), 13321–13332.

Forget, M.-H., Sathyendranath, S., Platt, T., Pommier, J., Vis, C., Kyewalyanga, M., and Hudson, C. 2007. Extraction of photosynthesis–irradiance parameters from phytoplankton production data: demonstration in various aquatic systems. *J. Plankt. Res.*, **29**, 249–262.

Jaani, A. 2001. The location, size and general characterization of Lake Peipsi and its catchment area. In *Lake Peipsi. Meteorology, Hydrology, Hydrochemistry* (Nõges, T., ed.), pp. 10–17. Sulemees Publishers, Tartu.

Joniak, T., Gołdyn, R., and Kozak, A. 2003. The primary production of phytoplankton in the restored Maltañski Reservoir in Poland. *Hydrobiologia*, **506–509**, 311–316.

Kauer, T. 2012. *Estimation of the Underwater Light Field and Phytoplankton Primary Production in Different Estonian Lakes*. Tallinn University, Dissertations on Natural Sciences, 29. Tallinn University Press.

Kirk, J. T. O. 1994. *Light and Photosynthesis in Aquatic Ecosystems*. Cambridge University Press, Cambridge.

Kondratyev, K. Ya. 1965. *Radiation in the Atmosphere*. Academic Press, New York, London.

Laas, A., Nõges, P., Kõiv, T., and Nõges, T. 2012. High frequency metabolism study in a large and shallow temperate lake revealed seasonal switching between net autotrophy and net heterotrophy. *Hydrobiologia*, **694**, 57–74.

Lancelot, C. and Mathot, S. 1986. Biochemical fractionation of primary production by phytoplankton in Belgian coastal waters during short- and long-term incubations with ^{14}C-bicarbonate. *Mar. Biol.*, **86**, 219–226.

Lorenzen, C. J. 1967. Determination of chlorophyll and phaeopigments; spectrophotometric equations. *Limnol. Oceanogr.*, **12**(2), 343–346.

Mäemets, A. 1977. *Eesti NSV järved ja nende kaitse*. Valgus, Tallinn (in Estonian).

Møller Jensen, L. 1985. ^{14}C-labelling patterns of phytoplankton: specific activity of different product pools. *J. Plankt. Res.*, **7**, 643–652.

Morel, A. and Bricaud, A. 1981. Theoretical results concerning light absorption in a discrete medium, and application to specific absorption of phytoplankton. *Deep Sea Res.*, **28**, 1375–1393.

Nõges, T. and Kangro, K. 2005. Primary production of phytoplankton in a strongly stratified temperate lake. *Hydrobiologia*, **547**, 105–122.

Nõges, T. and Nõges, P. 1998. Primary production of Lake Võrtsjärv. *Limnologica*, **29**, 29–40.

Nõges, P. and Nõges, T. 2006. Indicators and criteria to assess ecological status of large shallow temperate polymictic lakes Peipsi (Estonia/Russia) and Võrtsjärv (Estonia). *Bor. Environ. Res.*, **11**, 67–80.

Nõges, P., Haberman, J., Tammert, H., Tuvikene, A., and Ott, I. 1993. Estimation of the state of three Estonian small lakes on the basis of bioproductivity. *Proc. Estonian Acad. Sci. Biol. Ecol.*, **3**, 65–84.

Nõges, T., Arst, H., Laas, A., Kauer, T., Nõges, P., and Toming, K. 2011. Reconstructed long-term series of phytoplankton primary production of a large shallow temperate lake: the basis to assess the carbon balance and its climate sensitivity. *Hydrobiologia*, **667**, 205–222.

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

Reinart, A. and Herlevi, A. 1999. Diffuse attenuation coefficient in some Estonian and Finnish lakes. *Proc. Estonian Acad. Sci. Biol. Ecol.*, **48**, 267–283.

Reinart, A. and Nõges, P. 2004. Light conditions in Lake Võrtsjärv. In *Lake Võrtsjärv* (Haberman, J., Pihu, E., and Raukas, A., eds), pp. 141–149. Estonian Encyclopaedia Publishers, Tallinn.

Robson, B. J. 2005. Representing the effects of diurnal variations in light on primary production on a seasonal time-scale. *Ecol. Model.*, **186**, 358–365.

Smith, R. C., Prezelin, B. B., Bidigare, R. R., and Baker, K. S. 1989. Bio-optical modeling of photosynthetic production in coastal waters. *Limnol. Oceanogr.*, **34**, 1524–1544.

Sosik, H. M. 1996. Bio-optical modelling of primary production: consequences of variability in quantum yield and specific absorption. *Mar. Ecol. Prog. Ser.*, **143**, 225–238.

Steeman Nielsen, E. 1952. The use of radioactive carbon (^{14}C) for measuring primary production in the sea. *J. Cons. Int. Explor. Mer*, **18**, 117–140.

Wetzel, R. G. 2001. *Limnology. Lake and River Ecosystems*. 3rd edn. Elsevier Academic Press, San Diego.

Yacobi, Y. Z. 2003. Seasonal variation in pigmentation of the dinoflagellate *Peridinium gatunense* (Dinophyceae) in

Lake Kinneret, Israel. *Freshwater Biol.*, **48**, 1850–1858.

Yacobi, Y. Z. 2006. Temporal and vertical variation of chlorophyll *a* concentration, phytoplankton photosynthetic activity and light attenuation in Lake Kinneret: possibilities and limitations for simulating by remote sensing. *J. Plankt. Res.*, **28**, 725–736.

Yacobi, Y. Z., Pollingher, U., Gonen, Y., Gerhardt, V., and Sukenik, A. 1996. HPLC analysis of phytoplankton pigments from Lake Kinneret with special reference to the bloom-forming dinoflagellate *Peridinium gatunense* (Dinophyceae) and chlorophyll degradation products. *J. Plankt. Res.*, **18**, 1781–1796.

Yoshida, T., Sekino, T., Genkai-Kato, M., Logacheva, N. P., Bondarenko, N. A., Kawabata, Z. et al. 2003. Seasonal dynamics of primary production in the pelagic zone of southern Lake Baikal. *Limnology*, **4**, 53–62.

Fütoplanktoni primaarproduktsiooni mudeli arendamine ja rakendamine kihistumata järvedes

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Fütoplanktoni primaarproduktsiooni tulemusena toodetud orgaanilise aine kogus näitab veekogu troofilist taset ja seeläbi ka vee kvaliteeti. Et hinnata järvede ökoloogilist seisundit ja prognoosida selle võimalikke muutusi, on kindlasti vajalikud andmed primaarproduktsiooni sesoonse ning pikaajalise muutlikkuse kohta. Primaarproduktsiooni *in situ* mõõtmised on aeganõudvad ja nende suuremahuline teostamine väga kallis. Mudelarvutused on siin heaks alternatiiviks. Käesoleva uurimuse eesmärgiks on: 1) edasi arendada meie poolt varem (Arst et al., 2008a) koostatud primaarproduktsiooni mudeleid, b) näidata nende mudelite praktilist rakendamist Eesti järvedel.

Automatiseeritud mudeli rakendamist primaarproduktsiooni profiilide päevase muutlikkuse kirjeldamiseks, samuti produktsiooni päeva- ja kuusummade arvutamist on näidatud Peipsil ning Võrtsjärvel 2009. aasta nelja kuu (mai–august) jooksul mõõdetud andmebaasi alusel. Üle veesamba integreeritud primaarproduktsiooni päevasummade muutlikkuse piirid olid Peipsil 100–1390 mg C m^{-2} $päev^{-1}$ ja Võrtsjärvel 780–2338 mg C m^{-2} $päev^{-1}$.