In situ measurements and model calculations of primary production in turbid waters

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ABSTRACT: Data on the productivity of aquatic ecosystems helps to understand the food web relationships and functioning of these ecosystems. A semi-empirical model for calculating the phytoplankton primary production in turbid waters was elaborated. In situ measurements of the necessary bio-optical parameters were collected in 3 turbid Estonian lakes from 2003 to 2005. Secchi depth, chlorophyll a, and integrated primary production ranged from 0.1 to 3 m, 4.2 to 389 mg m⁻³, and 17 to 435 mg C m⁻² h⁻¹, respectively. Two model versions (spectral and integral) were developed for calculating the vertical profiles of primary production, $P(z)$. The basic equation described $P(z)$ as a function of photosynthetically absorbed radiation and quantum yield of carbon fixation. The main difference between the models resides in the data on underwater irradiance. We also derived a new algorithm for calculating the vertical profiles of the quantum yield. According to the statistical parameters the preferable model is the spectral model, but the integral model can also be recommended. The quality of the integral model was increased by changing the coefficients in the quantum yield algorithm, by which we compensated for the errors in photosynthetically absorbed radiation in this model. We conclude that the spectral and integral models perform well in computing primary production in turbid lakes. Both models allowed estimation of the primary production profiles and integrated production of the water column, as well as the daily dynamics and daily and monthly totals.

KEY WORDS: Limnology · Marine optics · Bio-optical parameters of lakes · Primary production

INTRODUCTION

The main aim of productivity measurements in aquatic ecosystems is to better understand 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 measure either the rate of oxygen release or carbon dioxide uptake by plants. In the latter case, the radioactive $^{14}$C method is used. Both methods measure the instantaneous rate of photosynthesis during short (1 to 2 h) exposures.

Water bodies differ in their ability to bind carbon: the differences can be attributed mainly to differences in productivity. Because of changing light conditions, planktonic photosynthesis has a pronounced daily 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 and integrated. Bio-optical model calculations could provide an alternative to this time-consuming $^{14}$C method. Modeling is especially important in turbid waters of high productivity, where the abrupt light gradient may cause large errors if traditional field methods are applied.


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Several studies estimate primary production from light intensity and abundance of phytoplankton pigments (e.g. Bannister 1974, Platt & Jassby 1976, Morel 1978, Schindler 1978, Tilzer 1984, 1989, Platt 1986, Fee et al. 1987, Platt & Sathyendranath 1988, Morel & Berthon 1989, Sathyendranath & Platt 1989, Sathyendranath et al. 1989, Smith et al. 1989, Schofield et al. 1990, Platt et al. 1991, Berthon & Morel 1992, Kyewalyanga et al. 1992, Woznyak et al. 1992, 1995, Kirk 1996, Sosik 1996, Siegel et al. 2001), but in some studies the nutrient parameters were also used. Often the water-column-integrated primary production was determined from daily mean averages of photosynthetically active radiation (PAR). Widely used are the methods where the dependence of photosynthesis on available light is expressed by an equation consisting of 2 parameters: (1) the initial slope \( \alpha \) \[ \text{mg C (mg chl a)}^{-1} \text{h}^{-1} \] and (2) the assimilation number \( \beta \) \[ \text{mg C (mg chl a)}^{-1} \text{h}^{-1} \] (Platt et al. 1977, Sathyendranath et al. 1989). In these models the data on vertical profiles of PAR \( \text{Ein} \text{s} \text{t} \text{m}^{-2} \text{s}^{-1} \) are also needed. This is a rather complicated approach and gives results on the basis of radiation integrated over the PAR region.


Our purpose was to elaborate a simple model for estimating the vertical profiles of primary production (as well as their values integrated over the water column) that needs as its initial data a few parameters measured in situ: the vertical profiles of spectral (or integral) underwater quantum irradiance and chlorophyll a (chl a) concentration. In case of the first version (spectral model), we advanced on previous approaches by using both spectral data of underwater quantum irradiance and absorption coefficients of phytoplankton. Our second version (integral model) broadens the applicability of our approach due to the fact that it exploits the easily obtained PAR irradiance data. With these models we are able to reproduce \( ^{13} \text{C} \) estimates of primary productivity while improving the temporal resolution of productivity.

**MATERIALS AND METHODS**

**Measurements and study sites.** In order to build our models, we obtained numerous in situ primary production profiles and corresponding solar irradiances (incident and underwater), as well as chl a values from 3 shallow, turbid lakes in Estonia. From 2003 to 2005, these measurements were performed repeatedly in 3 Estonian lakes: Lake Peipsi, Lake Võrtsjärv, and Lake Harku. All of these lakes are quite shallow and turbid (Table 1), and similar to other turbid lakes throughout the world (Kirk 1981, Dekker & Peters 1993, Lindell et al. 1999, Herlevi 2002, Arst 2003). Sampling was conducted on 14 d in Lake Peipsi, on 14 d in Lake Võrtsjärv, and on 8 d in Lake Harku. Measurements were taken twice daily (about 11:00 to 13:00 and 15:00 to 17:00 h), except when unfavorable weather or logistic problems occurred. Altogether, 53 field and laboratory measurement series were completed in June and August, 2003, and in several months from April to September, 2004 to 2005.

Primary production \( P(z) \) \( \text{mg C m}^{-3} \text{h}^{-1} \) was estimated in situ at 6 different depths in the lake using the \( ^{14} \text{CO}_2 \) assimilation technique (Steeman Nielsen 1952) and a 2 h incubation around midday (the choice of the depths of incubation bottles depended on the transparency of the water). After incubation, the water was acidified \( \text{pH} < 2 \) with 0.5 N HCl to remove the remaining inorganic \( ^{14} \text{C} \) (Niemi et al. 1983, Hilmer & Bate 1989, Lignell 1992), then sample radioactivity was measured in an LSC RackBeta 1211 counter (Wallac) using external standardization for DPM (disintegrations min \(^{-1}\) ) calculations and Optiphase ‘HiSafe 3’ scintillation cocktail (Wallac). \( P(z) \) was calculated by the

<table>
<thead>
<tr>
<th>Lake</th>
<th>Trophic type</th>
<th>Area (km(^2))</th>
<th>Average depth (m)</th>
<th>Maximum depth (m)</th>
<th>( z_{SD} ) (m)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Peipsi</td>
<td>Meso/eutrophic</td>
<td>2611</td>
<td>8.3</td>
<td>12.9</td>
<td>0.9–3.0</td>
</tr>
<tr>
<td>Võrtsjärv</td>
<td>Eutrophic</td>
<td>270</td>
<td>2.8</td>
<td>6.0</td>
<td>0.3–1.6</td>
</tr>
<tr>
<td>Harku</td>
<td>Hypertrophic</td>
<td>1.64</td>
<td>2</td>
<td>2.5</td>
<td>0.1–1.0</td>
</tr>
</tbody>
</table>
standard formula (Nielsen & Bresta 1984). Non-photosynthetic carbon fixation was measured in dark vials and subtracted from the light assimilation. Integrated values of primary production, \( P_{\text{int}} \), were calculated by integrating \( P(z) \) over depth.

Incident planar quantum irradiance \( q_{\text{PAR}}(z = 0) \) (\( \mu \text{mol m}^{-2} \text{s}^{-1} \)) was measured above the water every 2 min throughout the 2 h incubation of the \( P(z) \) bottles. For these measurements, we used a LI-192 SA quantum sensor (LI-COR Corporation SA) in the photosynthetically active region (PAR: 400 to 700 nm).

Underwater downwelling planar and scalar quantum PAR irradiances, \( q_{\text{PAR}}(z) \) (quantum sensor LI-192 SA) and \( q_{\text{DPAR}}(z) \) (quantum sensor LI-193 SA), respectively, were determined at several depths \( z \), giving 2 to 4 vertical profiles of irradiance during each 2 h period. The choice of depths depended on the transparency of the water. From the profiles of \( q_{\text{PAR}}(z) \), we calculated the depth-averaged diffuse attenuation coefficient of PAR, \( K_{\text{d,PAR}} \), using a semi-logarithmic plotting of \( q_{\text{PAR}}(z) \) versus depth; \( K_{\text{d,PAR}} \) was equal to the slope of the least-square regression line through these points.

Relative transparency of water was measured by a Secchi disk \( (\varepsilon_{\text{SD}}, \text{m}) \) and concentrations of chl \( a \) (\( C_{\text{chl}} \), in \( \text{mg m}^{-3} \)) were calculated by the Lorenzen (1967) method.

Spectra of the light attenuation coefficient in filtered and unfiltered water samples in the wavelength range of 350 to 700 nm were obtained using a Hitachi U1000 laboratory spectrophotometer. On the basis of these results, we derived the spectral values of the diffuse attenuation coefficient, \( K_{\text{d,PAR}} \), integrated primary production \( (P_{\text{int}}) \), and the depth-averaged diffuse attenuation coefficient of photosynthetically active radiation \( K_{\text{d,PAR}} \). The parameters \( C_{\text{chl}} \), \( q_{\text{PAR}}(z = 0) \) and \( K_{\text{d,PAR}} \) are in \( \text{mg m}^{-3} \), \( \mu \text{mol m}^{-2} \text{s}^{-1} \), and \( \text{m}^{-1} \), respectively.

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 at depth (Figs. 1 & 2). There can be some exceptions, however: in low illumination, the maximum of the \( P(z) \) curve is located at or near the surface [Fig. 1 for Lake Peipsi (13 July 2004), where \( C_{\text{chl}} \) = 19, \( q_{\text{PAR}}(z = 0) \) = 320, and \( K_{\text{d,PAR}} \) = 2.6; Lake Võrtsjärv on the afternoon of 14 June 2005, where \( C_{\text{chl}} \) = 42, \( q_{\text{PAR}}(z = 0) \) = 1000, and \( K_{\text{d,PAR}} \) = 7.8; Lake Harku on the afternoon of 17 May 2004, where \( C_{\text{chl}} \) = 62, \( q_{\text{PAR}}(z = 0) \) = 1000, and \( K_{\text{d,PAR}} \) = 2.7. The parameters \( C_{\text{chl}} \), \( q_{\text{PAR}}(z = 0) \) and \( K_{\text{d,PAR}} \) are in \( \text{mg m}^{-3} \), \( \mu \text{mol m}^{-2} \text{s}^{-1} \), and \( \text{m}^{-1} \), respectively.

Basic equations of the model. Our purpose was to compile a primary production model that applies the spectral values of underwater quantum irradiance and chl \( a \) concentration as initial parameters. The general approach was similar to that of Smith et al. (1989), where \( P(z) \) was described by the following simple equation:

\[
P(z) = \Psi Q_{\text{PAR}}(z) F_{\text{PAR}}(z)
\]

where \( P(z) \) is in milligrams of carbon per cubic meter per hour, \( \Psi \) is the factor 12 000 for converting moles of carbon to milligrams of carbon, \( Q_{\text{PAR}}(z) \) is the photosynthetically absorbed radia-

![Fig. 1. Vertical profiles of primary production measured in situ \( P(z, \text{meas}) \), from 2003 to 2005: Lake Peipsi at noon on 11 June 2003, where chl \( a \) concentration (\( C_{\text{chl}} \)) = 9, the incident planar quantum irradiance \( q_{\text{PAR}}(z = 0) \) = 1810, and the depth-averaged diffuse attenuation coefficient of photosynthetically active radiation \( K_{\text{d,PAR}} \) = 0.74; Lake Peipsi at noon on 13 July 2004, where \( C_{\text{chl}} \) = 19, \( q_{\text{PAR}}(z = 0) \) = 320, and \( K_{\text{d,PAR}} \) = 2.6; Lake Võrtsjärv at noon on 23 April 2004, where \( C_{\text{chl}} \) = 28, \( q_{\text{PAR}}(z = 0) \) = 1030, and \( K_{\text{d,PAR}} \) = 1.6; Lake Võrtsjärv on the afternoon of 14 June 2005, where \( C_{\text{chl}} \) = 42, \( q_{\text{PAR}}(z = 0) \) = 1000, and \( K_{\text{d,PAR}} \) = 2.2; Lake Harku on the afternoon of 17 May 2004, where \( C_{\text{chl}} \) = 62, \( q_{\text{PAR}}(z = 0) \) = 1000, and \( K_{\text{d,PAR}} \) = 2.7. The parameters \( C_{\text{chl}} \), \( q_{\text{PAR}}(z = 0) \) and \( K_{\text{d,PAR}} \) are in \( \text{mg m}^{-3} \), \( \mu \text{mol m}^{-2} \text{s}^{-1} \), and \( \text{m}^{-1} \), respectively.
where the specific absorption coefficient \( a'_{\text{ph}}(\lambda) \) is calculated taking into account the ‘package effect’ (Morel & Bricaud 1981, Bricaud et al. 1995, Kirk 1996). A and B are positive, wavelength-dependent parameters, as tabulated in Bricaud et al. (1995). Their study used 815 spectra of living phytoplankton in different regions of the world ocean and covered a \( C_{\text{chl}} \) range from 0.25 to 25 mg m\(^{-3}\). Although widely used, the parameters A and B in Bricaud et al. (1995) may not be reliable for eutrophic lake waters with high \( C_{\text{chl}} \). However, we could not find any publications with the spectra of A and B for very turbid lakes. Thus, we used Bricaud’s data and hoped that, through the process of quantifying, we could elaborate a proper model for estimating phytoplankton production profiles in lakes.

The values of \( q(\lambda, z) \) can be determined from either underwater measurements using a spectrophotometer, or corresponding values of \( q(\lambda, z = 0) \) and the spectral diffuse attenuation coefficient \( K_d(\lambda) \). Although \( K_d(\lambda) \) can also depend on depth, the 3 lakes sampled were not stratified, and we used the following formula (Derra 1992, Kirk 1996, Arst 2003):

\[
q(\lambda, z) = (1 - r) q(\lambda, z = 0) \exp[-K_d(\lambda)z] \tag{4}
\]

where \( r \) is the mean value solar radiation (\( r \approx 0.06 \)) reflected from water surface.

Determination of \( Q_{\text{PAR}}(z) \) from Eqs. (2) to (4) provides a spectral model for computing \( P(z) \).

When spectral data are lacking, a primary production model can be built using integral values of incident irradiance and underwater irradiance, averaged over PAR waveband absorption coefficients of phytoplankton, \( a_{\text{ph,PAR}} \) as follows:

\[
Q_{\text{PAR}}(z) = q_{\text{PAR}}(z) a_{\text{ph,PAR}} \tag{5}
\]

\[
q_{\text{PAR}}(z) = \int_{400}^{700} q(\lambda, z) d\lambda \tag{6}
\]

\[
a_{\text{ph,PAR}} = \int_{400}^{700} a'_{\text{ph}} C_{\text{chl}}(\lambda) d\lambda \tag{7}
\]

Note that although Eq. (4) describes the attenuation of spectral irradiance, a similar exponential law is also widely used to calculate the values of integral underwater irradiance, \( q_{\text{PAR}}(z) \):

\[
q_{\text{PAR}}(z) = q_{\text{PAR}}(z = -0) \exp(-K_{d,PAR}z) \tag{8}
\]

where \( q_{\text{PAR}}(z = -0) = (1 - r) q_{\text{PAR}}(z = 0) \). The reliability of this approach for ice-free water bodies was estimated in Arst et al. (2000).

Eqs. (5) to (8) together with Eq. (1) are the basic equations of an integral (or broad-band) model.
Because the algal cells are illuminated from all directions, primary production calculations should be performed using scalar quantum irradiance \( q_{\lambda}(\lambda,z) \) and \( q_{0,\text{PAR}}(z) \) data, not underwater planar quantum irradiance \( q(\lambda,z) \) or \( q_{\text{PAR}}(z) \) \( \text{(Kirk 1996; Sosik 1996)} \); therefore, in the spectral model, the photosynthetically absorbed radiation [using a new denotation, \( Q_{\text{PAR}}(z) \)] should be computed by the following equation:

\[
Q_{\text{PAR}}^*(z) = \int_{0}^{790} q_{0}(\lambda,z) a_{\lambda}^* \rho(\lambda) C_{\text{chl}} d\lambda
\]  

\( (9) \)

In the integral model, \( Q_{\text{PAR}}^*(z) \) should be computed by the following equation:

\[
Q_{\text{PAR}}^*(z) = q_{0,\text{PAR}}(z) a_{\text{PAR},\text{PAR}}(z)
\]  

\( (10) \)

Consequently, instead of Eq. (1), we now have the following equation:

\[
P(z) = \Psi Q_{\text{PAR}}^*(z) F_{\text{PAR}}(z)
\]  

\( (11) \)

In this equation, \( Q_{\text{PAR}}^*(z) \) is determined from scalar quantum irradiance.

### RESULTS AND DISCUSSION

**Correction for derivation of \( Q_{\text{PAR}}^*(z) \) from the values of \( q_{\text{PAR}}(z) \)**

We had no spectral data on \( q_{\lambda}(\lambda,z) \); consequently, we could not determine \( Q_{\text{PAR}}^*(z) \) directly using Eq. (9). We hypothesized that \( Q_{\text{PAR}}(z) \) can be estimated from \( Q_{\text{PAR}}(z) \) using a correction, \( C(z) \) as follows:

\[
Q_{\text{PAR}}^*(z) = C(z) Q_{\text{PAR}}(z)
\]  

\( (12) \)

where \( Q_{\text{PAR}}(z) \) should be calculated by Eq. (2). We assumed that this correction could be estimated from measured \( q_{\text{PAR}}(z) \) using a correction, \( C(z) \) as follows:

\[
C(z) = \frac{q_{0,\text{PAR}}(z)}{q_{\text{PAR}}(z)}
\]  

\( (13) \)

The relationship \( \frac{q_{0,\text{PAR}}(z)}{q_{\text{PAR}}(z)} \) is known to depend on the angular structure of the underwater light field, on the incident solar irradiance, on the solar zenith angle, and on the absorption and scattering properties of the aquatic environment. In the upper layer of an ice-free water body, the ratio \( q_{0,\text{PAR}}/q_{\text{PAR}} \) generally increases with depth, with the numerical values usually remaining between 1.1 and 2.5 \( \text{(Reinart 2000)} \). In clear-water lakes at deeper layers, the asymptotic state of the angular structure of light is reached, but that was not observed in the shallow turbid Estonian lakes. The ratio \( q_{0,\text{PAR}}/q_{\text{PAR}} \) we measured near the surface was between 1.3 and 1.8, increasing with increasing turbidity of the water. This ratio reached about 1.7 at 5 m depth in Lake Peipsi, about 2.2 at 2.5 m in Lake Võrtsjärv, and about 3.5 at 1 m in Lake Harku. These values of \( q_{0,\text{PAR}}/q_{\text{PAR}} \) show that the use of planar irradiance without a correction coefficient instead of scalar irradiance should be avoided in bio-optical models.

For our model, we needed a generalized algorithm of \( C(z) \) that allowed calculation of values for each depth. We assumed that \( C(z) \) is a function of \( C_{\text{chl}} \) and the diffuse attenuation coefficient of light, \( K_{\text{d,PAR}} \). We performed a regression analysis on measured \( \text{in situ} \) \( C_{\text{chl}} \), \( K_{\text{d,PAR}} \), and the respective \( q_{\text{PAR}}(z) \) and \( q_{0,\text{PAR}}(z) \) values, and found that the best regression curve for the parameter \( C(z) \) was an exponent. We found that rather good results can be obtained when we suppose that the first coefficient of this exponent depends only on \( K_{\text{d,PAR}} \), and the second coefficient, only on \( C_{\text{chl}} \). The regression analysis gave the following results:

\[
C(z, C_{\text{chl}}, K_{\text{d,PAR}}) = C_{\text{chl}} \exp(C_{\text{chl}})
\]  

\( (14) \)

\[
C_1 = 1.32 K_{\text{d,PAR}}^{0.113} R^2 = 0.692, p < 0.0001
\]  

\( (15) \)

\[
C_2 = 0.0023 C_{\text{chl}} + 0.016; R^2 = 0.819, p < 0.0001
\]  

\( (16) \)

Here, \( q_{\text{PAR}}(z) \) and \( q_{0,\text{PAR}}(z) \) were in \( \text{μmol m}^{-2} \text{s}^{-1} \), \( C_{\text{chl}} \) was in \( \text{mg m}^{-3} \) and \( K_{\text{d,PAR}} \) was in \( \text{m}^{-1} \).

The reliability of Eqs. (14) to (16) needs confirmation. For this we compared measured and calculated \( q_{0,\text{PAR}}(z) \). We computed 107 vertical profiles (1651 individual measurements) of \( q_{0,\text{PAR}}(z) \) from Eqs. (13) to (16), using respective \( q_{\text{PAR}}(z) \), \( C_{\text{chl}} \), and \( K_{\text{d,PAR}} \), which all were measured \( \text{in situ} \). We excluded data from depths of <10 cm because undulation of the spherical sensor made readings unreliable. The following regression formula was obtained:

\[
q_{0,\text{PAR}}(\text{meas},z) = -0.23 + 1.002 q_{\text{PAR}}(\text{calc},z)
\]  

\( (17) \)

where \( N = 1651, R^2 = 0.984, SE = 43 \) \( \text{μmol m}^{-2} \text{s}^{-1} \), \( p < 0.000001 \), and mean absolute error and mean absolute relative error were 0.4 \( \text{μmol m}^{-2} \text{s}^{-1} \) and 12.6%, respectively (Fig. 3). These estimates show that Eqs. (14) to (16) provide reliable values of \( q_{0,\text{PAR}}(z) \). Consequently, we first must determine \( Q_{\text{PAR}}(z) \) from the spectral or integral method, and then use Eqs. (12) to (16) to calculate the respective \( Q_{\text{PAR}}^*(z) \).

**Algorithm to determine the quantum yield**

Our purpose was to derive an algorithm of quantum yield that was based on the same initial data as the algorithm for photosynthetically absorbed radiation. Smith et al. \( \text{(1989)} \) proposed the following equation:

\[
F(z) = \frac{F_{\text{max}} k_p}{k_p + q_{\text{PAR}}(z)}
\]  

\( (18) \)
where \( F_{\text{max}} \) and \( k_F \) were treated as the constants, \( F_{\text{max}} = 0.08 \text{ mol C Einst}^{-1} \) and \( k_F = 10 \text{ Einst m}^{-2} \text{ d}^{-1} \). Taking into account Eq. (8) we arrive at the following equation:

\[
(19)
\]

Because our in situ data were per hour, and we could not use \( k_F \) in \( \text{Einst m}^{-2} \text{ d}^{-1} \), we performed a mathematical analysis in order to estimate the suitability of Eq. (18). The integral model of primary production was most straightforward, according to Eqs. (1), (5), (8), and (19), as follows:

\[
(20)
\]

The parameters \( \Psi \), \( a_{\text{ph,PAR}} \), \( q_{\text{PAR}}(z = -0) \), \( F_{\text{max}} \), and \( k_F \) do not depend on depth, and their product can be considered to be a constant (\( H \)). Thus, Eq. (20) becomes:

\[
(21)
\]

Because \( \Psi \), \( a_{\text{ph,PAR}} \), \( q_{\text{PAR}}(z = -0) \), \( F_{\text{max}} \), \( k_F \), and \( K_{d,\text{PAR}} \) are positive values, the vertical profile of primary production, as determined by Eq. (21), always shows decreasing of \( P(z) \) with increasing depth. Consequently, when using Eq. (18) (from Smith et al. 1989), we can never obtain the typical profiles of \( P(z) \) with a maximum at some depth (like the measured profiles in Figs. 1 & 2).

Thus, we needed a new algorithm for computation of quantum yield. We tested (by using a fitting method) different modifications of Eq. (18). Our purpose was to find an algorithm for \( F_{\text{PAR}}(z) \) that is capable of giving shapes of primary production profiles similar to those measured in situ. The best results gave the following modification:

\[
F_{\text{PAR}}(z) = \frac{F_{\text{max}}}{[1 + Mq_{\text{PAR}}(z)]^n}
\]

where \( F_{\text{max}} = 0.08 \text{ mol C Einst}^{-1} \) and \( M \) and \( n \) are the parameters that can depend on incident irradiance as well as on the bio-optical characteristics of the water body. Some examples of testing the ability of Eq. (22) to give the typically observed shapes of primary production profiles are shown in Fig. 4, the corresponding vertical profiles of quantum yield are in Fig. 5. In these calculations we used some realistic values of \( q_{\text{PAR}}(z = 0) \) (Einst m\(^{-2}\) h\(^{-1}\)), \( K_{d,\text{PAR}} \) (m\(^{-1}\)), and \( C_{\text{chl}} \) (mg m\(^{-3}\)), and the parameters \( M \) and \( n \) were taken provisionally to be constants. Because the unit μmol
m−2 s−1 is more commonly used than as Einst m−2 h−1, in these figures \( q_{\text{PAR}}(z=0) \) is given in \( \mu \text{mol m}^{-2} \text{s}^{-1} \).

Only in the case of low illumination is the maximum of primary production \( P_{\text{max}} \) located at the surface; e.g. \( q_{\text{PAR}}(z=0) = 200 \ \mu \text{mol m}^{-2} \text{s}^{-1} \) in Fig. 4. As \( q_{\text{PAR}}(z=0) \) increases, \( P_{\text{max}} \) moves towards greater depths.

In order to determine which way the coefficients \( n \) and \( M \) (Eq. 22) influenced the vertical profile of primary production, we calculated \( P(z) \) for different \( n \) and \( M \), taking \( q_{\text{PAR}}(z=0) = 1400 \ \mu \text{mol m}^{-2} \text{s}^{-1} \), \( C_{\text{chla}} = 50 \ \text{mg m}^{-3} \), and \( K_{d,\text{PAR}} = 2.5 \ \text{m}^{-1} \). The \( P(z) \) profile depended on the variations of \( n \) and \( M \) until some depth, but there was almost no influence of \( n \) and \( M \) in deeper layers (Fig. 6).

**Quantification of a primary production model**

**Determination of \( q(\lambda, z) \) and \( Q_{\text{PAR}}(z) \) from in situ data**

As shown, determination of \( Q_{\text{PAR}}(z) \) requires the values of \( q(\lambda, z) \) or corresponding \( q(\lambda, \text{incident}) \) and \( K_d(\lambda, z) \) (Eqs. 2 & 4), which can be provided with an underwater spectrophotometer. We had only the spectra of the beam attenuation coefficient \( c(\lambda) \), measured from water samples using the laboratory spectrophotometer U1000 (Hitachi). Thus, we had to calculate the values of \( q(\lambda, z) \) indirectly. In order to accomplish this, first, during the 2 h incubation period of \( P(z) \), we recorded the incident \( q_{\text{PAR}} \) using the PAR waveband sensor LI-192 SA, and computed its hourly average value. Then, by use of a model for spectral distribution of downwelling solar irradiance by Bird & Riordan (1986) \((E_{\lambda b} \text{ in W m}^{-2})\), we found the contributions, \( W(\Delta \lambda) \), of narrow (10 nm) wavebands in the PAR region for a given solar zenith angle. After, we converted these results into Einst m−2 h−1 (Dera 1992, Arst 2003), we could compute the necessary values of \( q(\lambda_{\Delta \lambda}, z = 0) \). For determination of the spectral diffuse attenuation coefficients \( K_d(\Delta \lambda) \) for intervals \( \Delta \lambda \), we used the spectra of \( c(\lambda) \), measured from corresponding water samples in the laboratory, and the model described in Arst et al. (1997, 2002) and Arst (2003).

The vertical profiles of downwelling planar quantum irradiance were calculated as follows:

\[
q(\Delta \lambda, z) = W(\Delta \lambda)(1 - r)q_{\text{PAR}}(z = 0) \exp(-K_d(\Delta \lambda)z) \tag{23}
\]

where \( W(\Delta \lambda) \) is a weighting coefficient (the contribution of each narrow interval in the PAR quantum irradiance), \( r = 0.06 \), \( K_d(\Delta \lambda) \) is the diffuse attenuation coefficient of light in the interval \( \Delta \lambda \), and \( q_{\text{PAR}}(z = 0) \) is the incident radiation on the water surface averaged hourly during the incubation period of the \( P(z) \) bottles. Then, \( q_{\text{PAR}}(z) \) is the sum over the waveband 400 to 700 nm, as in the following equation:

\[
q_{\text{PAR}}(z) = \sum_{\Delta \lambda} q(\Delta \lambda, z) \Delta \lambda \tag{24}
\]

We estimated the depth-averaged diffuse attenuation coefficient, \( K_{d,\text{PAR}} \), from vertical profiles of \( q_{\text{PAR}}(z) \) calculated using Eq. (24). Similarly, we were able to determine \( K_{d,\text{PAR}} \) from our measured in situ \( q_{\text{PAR}}(z) \) profiles. Thus, we could compare the model values of \( K_{d,\text{PAR}} \) with those obtained from in situ measurements.

We can estimate the relative differences (RE) between \( q_{\text{PAR}}(z) \) values comparing the results by integral and spectral models, \( q_{\text{PAR}}(\text{int}) \) and \( q_{\text{PAR}}(\text{sp}) \), respectively, from the following formula:

\[
\text{RE} = \frac{2|q_{\text{PAR}}(\text{int}) - q_{\text{PAR}}(\text{sp})|}{[q_{\text{PAR}}(\text{int}) + q_{\text{PAR}}(\text{sp})]} \tag{25}
\]

The values of RE at different depths were calculated for 38 irradiance profiles in all lakes. At the surface \( \text{RE} = 0 \), then it increased with depth to some maximum value, after which it decreased, even reaching zero when \( q_{\text{PAR}} \) was very small at depth. In some cases the maximum of RE was 40 to 50% and mostly it exceeded 15%. The maximum RE was usually observed near the depth of \( P_{\text{max}} \). These results agree with those in Arst et al. (2006).

The specific spectral absorption coefficient, \( a'_{\text{ph}}(\lambda) \), was calculated from Eq. (3) using the intervals \( \Delta \lambda \) and averaging the coefficients \( A \) and \( B \) over these intervals, in place of \( \lambda \). After that, \( Q_{\text{PAR}}(z) \) was calculated from Eq. (2) using a sum over the PAR range instead of the integral, and, finally, we calculated \( Q_{\text{PAR}}^*(z) \) by correcting the values of \( Q_{\text{PAR}}(z) \) according to Eq. (12) so that:

\[
Q_{\text{PAR}}^*(z) = C(z) \sum_{\Delta \lambda} q(\Delta \lambda, z)a'_{\text{ph}}(\Delta \lambda)\Delta \lambda \tag{26}
\]
where the sum was taken over 30 intervals, each of 10 nm width, in the region from 400 to 700 nm. The correction coefficient $C(z)$ was calculated from Eqs. (13) to (16).

Quantification of the algorithm for quantum yield

We applied Eq. (22) to all 53 in situ measurements of $P(z)$ in order to determine the values of $M$ and $n$ that gave the best agreement between the measured and calculated profiles of $P(z)$. Both models, spectral and integral, were considered. In the case of the integral model, the first step should be the comparison of photosynthetically absorbed radiation obtained using spectral and integral versions of the model, $Q'_{\text{PAR}}(z, \text{sp})$ and $Q'_{\text{PAR}}(z, \text{int})$. It was made for 223 individual pairs of results at the depths from 0.1 to 6 m, while $C_{\text{chl}}$ varied from 4 to 79 mg m$^{-3}$ (Fig. 7). We left out the cases at the surface, because both $Q'_{\text{PAR}}(z = -0, \text{sp})$ and $Q'_{\text{PAR}}(z = -0, \text{int})$ are determined on the basis of the same values, $q(z = -0)$, and differences are very small. The differences between $Q'_{\text{PAR}}(z = -0, \text{sp})$ and $Q'_{\text{PAR}}(z = -0, \text{int})$ are notable (Fig. 7); this leads to the conclusion that for the integral model we cannot use in Eq. (22) the same $n$ and $M$ that are suitable for the spectral model. Thus, for the integral model we need new values of $n$ and $M$, which differ from those in the spectral model and are capable of balancing the errors in $Q'_{\text{PAR}}(z)$ of the integral model. It is necessary to explain the mechanism of this ‘compensation’. Primary production is calculated as a product of 2 parameters, $Q'_{\text{PAR}}(z)$ and $F_{\text{PAR}}(z)$ (Eq. 11). So, when $Q'_{\text{PAR}}(z)$ has systematic errors for some reason, we have to change $F_{\text{PAR}}(z)$ so that the product $Q'_{\text{PAR}}(z)F_{\text{PAR}}(z)$ has reliable values. For instance, when $Q'_{\text{PAR}}(z)$ is too small, we have to enlarge $F_{\text{PAR}}(z)$ or vice versa. The change of $F_{\text{PAR}}(z)$ is possible when changing the parameters $M$ and $n$ in Eq. (22). Despite the fact that in deeper layers, $P(z)$ is nearly independent of $M$ and $n$, the ‘compensation method’ markedly improved the results from the integral model.

According to our estimations, a constant value of $n = 3$ was suitable for the spectral model, and $n = 2$, for the integral model. However, the coefficient $M$ varied in each individual case. Use of these ‘individual’ values of $M$ usually gave very good agreement between measured and calculated profiles of $P(z)$. For practical use of our models, we have to quantify the parameter $M$. We assumed that $M$ is a function of incident irradiance and bio-optical parameters. Tests of different versions (using regression analysis) led us to conclude that our dataset needed to be divided into 3 groups according to chl a content. In ‘Group 1’, $C_{\text{chl}}$ was from 4 to 35 mg m$^{-3}$; in ‘Group 2’, it was from 35 to 100 mg m$^{-3}$; and in ‘Group 3’, $C_{\text{chl}}$ was >100 mg m$^{-3}$.

In the case of the spectral model, the variations of ‘individual’ $M$ were from 0.25 to 1.1 (Group 1), from 0.33 to 0.78 (Group 2), and from 0.14 to 0.23 (Group 3). The corresponding variations for the integral model were from 0.45 to 2.2 (Group 1), from 0.65 to 1.5 (Group 2), and from 0.25 to 0.65 (Group 3). Applying the multiple regression analysis, we got suitable equations for $M$ with both models, but only for Groups 1 and 2. These multiple regression equations and respective statistical parameters are presented in Table 3. The determination coefficients in Table 3 vary from 0.67 to 0.88. It can be supposed that in the case of a larger database, $R^2$ will be higher and the equations for the parameter $M$ can be, to some extent, different.

In conditions of very high chlorophyll content (Group 3), no good regression between $M$ and the water properties was found; however, a constant value of $M = 0.18$ (spectral model) and $M = 0.35$ (integral model) gave more or less satisfactory results ($N = 12$). Remember that the suitability of the spectra of A and B in Eq. (3) for very high $C_{\text{chl}}$ was not proved.

Comparison of measured and calculated primary production

The vertical profiles of measured, $P_{(\text{meas})}$, and calculated primary production, $P_{(\text{calc})}$, according to the spectral model are compared in Fig. 8a,b. Although some cases exist when $P_{(\text{meas})}$ differed markedly from $P_{(\text{calc})}$, most of the measured and calculated vertical profiles of primary production were similar. It was surprising, that even for very high $C_{\text{chl}}$ we found the cases in which the profiles of $P_{(\text{meas})}$ were close to those obtained by the spectral model (Fig. 8b). Because of
possible errors in the measurements of the initial data (incident irradiance, \(C_{chl}\), \(K_d\) and \(P_{(meas)}\), it seems that our spectral model performed well in computing primary production in turbid lakes. The main difficulty of using the spectral model is the need for spectral data on \(q(\lambda, z = 0)\) and \(K_d(\lambda, z)\). Even so, when no underwater spectrometer is available, the spectral data can be derived from laboratory measurements and a special model for calculation of \(K_d(\lambda, z)\).

The regression of \(P_{(meas)}\) versus \(P_{(calc)}\) for both spectral and integral models (Group 1 and 2 together, \(C_{chl}\) from 4 to 79 mg m\(^{-3}\)) is illustrated in Fig. 9. We left Group 3 out of our statistical analysis due to the uncertainty of \(A\) and \(B\) spectra for very high \(C_{chl}\) in Eq. (3) (Bricaud et al. 1995). The results show (Fig. 9) that the spectral model gives the best coincidence between \(P_{(meas)}\) versus \(P_{(calc)}\), but the integral model (when used with modified parameters \(n\) and \(M\) from Table 3) is not significantly worse.

The statistical characteristics of the regression \(P_{(meas)}\) versus \(P_{(calc)}\) are presented in Table 4. From these data we can conclude that our spectral model for computation of primary production in turbid lakes is good, but the integral model is also acceptable.

In addition to the vertical profiles of \(P(z)\), we estimated the respective integral values, \(P_{int}\), that were calculated by integration of \(P(z)\) over depth. These results can only be considered as approximations for 2 reasons. First, sometimes the first bottle was located 5 to 10 cm below the surface, not just under it, and, at the maximum depth of measurements, \(P(z)\) was not zero, but had some small value. Second, \(P_{int}\) was calculated using the trapezoidal rule, which somewhat understi-

### Table 3. Regression formulae for the parameter \(M\) (in Eq. 22) for the spectral and integral models of primary production. In these formulae \(q_{PAR}(z = 0)\) is in Einst m\(^{-2}\) h\(^{-1}\), \(C_{chl}\) in mg m\(^{-3}\), and \(K_{d,PAR}\) in m\(^{-1}\). N: number of measurement series.

<table>
<thead>
<tr>
<th>Model</th>
<th>Group</th>
<th>(M)</th>
<th>(R^2)</th>
<th>SE</th>
<th>(p)</th>
<th>(N)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Spectral</td>
<td>1</td>
<td>0.97 – 0.0036(q_{PAR}(z = 0)) – 0.067(K_{d,PAR}^{2.5})</td>
<td>0.831</td>
<td>0.11</td>
<td>&lt;0.0001</td>
<td>15</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>0.80 – 0.0077(q_{PAR}(z = 0)) – 0.00066(C_{chl})</td>
<td>0.713</td>
<td>0.07</td>
<td>&lt;0.0001</td>
<td>26</td>
</tr>
<tr>
<td>Integral</td>
<td>1</td>
<td>1.99 + 0.028(q_{PAR}(z = 0)) – 0.154(K_{d,PAR}^{2.5})</td>
<td>0.883</td>
<td>0.22</td>
<td>&lt;0.0001</td>
<td>15</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>1.58 – 0.138(q_{PAR}(z = 0)) – 0.0025(C_{chl})</td>
<td>0.669</td>
<td>0.15</td>
<td>&lt;0.0001</td>
<td>26</td>
</tr>
</tbody>
</table>

Fig. 8. Comparison of measured and calculated (using spectral model) primary production \(P(z)\): (a) Lake Peipsi—13 July 2004, where \(C_{chl} = 15.5, q_{PAR}(z = 0) = 300,\) and \(K_{d,PAR} = 2.6\); 17 August 2005, where \(C_{chl} = 33, q_{PAR}(z = 0) = 1062,\) and \(K_{d,PAR} = 1.6\); Lake Vörtsjärv—14 September 2004, where \(C_{chl} = 79, q_{PAR}(z = 0) = 1300,\) and \(K_{d,PAR} = 2.5\); 22 September 2005, where \(C_{chl} = 67, q_{PAR}(z = 0) = 783,\) and \(K_{d,PAR} = 2.6\); (b) results obtained for Lake Harku: 12 July 2004, where \(C_{chl} = 124, q_{PAR}(z = 0) = 1308,\) and \(K_{d,PAR} = 6.3\); 16 June 2005, where \(C_{chl} = 260, q_{PAR}(z = 0) = 1160,\) and \(K_{d,PAR} = 6.5\); 16 August 2005, where \(C_{chl} = 333, q_{PAR}(z = 0) = 990,\) and \(K_{d,PAR} = 7.7;\) 18 October 2004, where \(C_{chl} = 160, q_{PAR}(z = 0) = 82,\) and \(K_{d,PAR} = 3.4.\) The parameters \(C_{chl}, q_{PAR}(z = 0),\) and \(K_{d,PAR}\) are in mg m\(^{-3}\), \(\mu\)mol m\(^{-2}\) s\(^{-1}\), and m\(^{-1}\), respectively.

Fig. 9. Comparison of measured and calculated values of primary production, \(P(z)\), for spectral and integral models (Groups 1 and 2 together).
mated $P_{\text{int}}$ in comparison with real values; nevertheless, $P_{\text{int(\text{meas})}}$ and $P_{\text{int(\text{calc})}}$ were calculated similarly and should be comparable.

The regressions of $P_{\text{int(\text{meas})}}$ versus $P_{\text{int(\text{calc})}}$ for Groups 1 and 2 together (Fig. 10) showed that, in most cases, the differences between measured and calculated $P_{\text{int}}$ were rather small. The statistical characteristics of these regressions are presented in Table 5.

Our results showed that of the 2 primary production models, the best was the spectral model; however, the integral model, which needs only data on integral scalar irradiance in the PAR region, but not on the scalar irradiance spectra, can also be recommended.

Due to the large number of equations it is rational to include a small table helping to separate the instructions for the spectral model from those for the integral model (Table 6).

### CONCLUSIONS

We elaborated 2 versions (spectral and integral) of a semi-empirical model for calculation of the vertical profiles of primary production in lakes. Quantification of these models was for conditions in the ranges of 4.2 to 389 mg m$^{-3}$ for chl $a$ concentration (separately for 3 groups by $C_{\text{chl}}$) and 0.1 to 3 m for Secchi depth. However, due to doubt that the parameter $a_{\text{ph} (\lambda)}$ obtained (according to the data of Bricaud et al. 1995) can be unreliable for very high $C_{\text{chl}}$, we left these cases out of the statistical analysis and confined ourselves to the maximum value of $C_{\text{chl}} = 79$ mg m$^{-3}$.

For calculations of primary production, the spectral model needs \textit{in situ} measured data on chlorophyll content in the water and the spectra (in PAR region) of incident quantum irradiance on the water surface and the corresponding spectra of the diffuse attenuation coefficient of underwater irradiance. The only parameters that are necessary from the literature are the coefficients in the formula for determining the spectra of the absorption coefficient of phytoplankton (e.g. from Bricaud et al. 1995). The integral model also requires the data on chlorophyll, but, from the point of view of radiation characteristics, it is simpler: only \textit{in situ} measured integral values of incident quantum irradiance on the water surface and the corresponding spectra of the diffuse attenuation coefficient of underwater irradiance.

In both models, using regression analysis, a parameterization of Eq. (22) was performed. The results, described in Table 3, are valid at the present stage of the study. It can be supposed that in the case of a larger database, the parameters $M$ and $n$ in Eq. (22) can, to some extent, be different. However, due to good coincidence of measured and cal-

### Table 4. Statistical parameters of the regressions $P(\text{meas})$ versus $P(\text{calc})$ for spectral and integral models (Groups 1 and 2 together). AE: mean absolute error; N: number of points. SE and AE both in mg C m$^{-2}$ h$^{-1}$

<table>
<thead>
<tr>
<th>Model</th>
<th>$R^2_{\text{adj}}$</th>
<th>SE</th>
<th>Regression</th>
<th>p</th>
<th>AE</th>
<th>N</th>
</tr>
</thead>
<tbody>
<tr>
<td>Spectral</td>
<td>0.919</td>
<td>11.0</td>
<td>$y = 0.988x + 0.31$</td>
<td>&lt;0.000001</td>
<td>0.2</td>
<td>241</td>
</tr>
<tr>
<td>Integral</td>
<td>0.856</td>
<td>14.7</td>
<td>$y = 0.957x - 0.87$</td>
<td>&lt;0.000001</td>
<td>2.8</td>
<td>241</td>
</tr>
</tbody>
</table>

### Table 5. Statistical parameters of the regressions $P_{\text{int(\text{meas})}}$ versus $P_{\text{int(\text{calc})}}$ for spectral and integral models (Groups 1 and 2 together). AE: mean absolute error; N: number of points. SE and AE both in mg C m$^{-3}$ h$^{-1}$

<table>
<thead>
<tr>
<th>Model</th>
<th>$R^2_{\text{adj}}$</th>
<th>SE</th>
<th>Regression</th>
<th>p</th>
<th>AE</th>
<th>N</th>
</tr>
</thead>
<tbody>
<tr>
<td>Spectral</td>
<td>0.955</td>
<td>12.0</td>
<td>$y = x + 1.0$</td>
<td>&lt;0.000001</td>
<td>0.2</td>
<td>41</td>
</tr>
<tr>
<td>Integral</td>
<td>0.925</td>
<td>15.5</td>
<td>$y = 0.989x - 6.8$</td>
<td>&lt;0.000001</td>
<td>-7.9</td>
<td>41</td>
</tr>
</tbody>
</table>

### Table 6. Formulas and parameters for calculating the primary production in lakes for spectral and integral models. Note that in the fifth column an equation for determining $a_{\text{ph} (\lambda)}$ is given for the spectral model, but one determining $a_{\text{ph,PAR}}$ is given for the integral model

<table>
<thead>
<tr>
<th>Model</th>
<th>$P(z)$</th>
<th>$Q_{\text{PAR}}(z)$</th>
<th>$Q_{\text{PAR}}^*(z)$</th>
<th>$a_{\text{ph}}$</th>
<th>$F_{\text{PAR}}(z)$</th>
<th>$n$</th>
<th>$M$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Spectral</td>
<td>Eq. 11</td>
<td>Eq. 2</td>
<td>Eq. 12</td>
<td>Eq. 3</td>
<td>Eq. 22</td>
<td>3</td>
<td>see Table 3</td>
</tr>
<tr>
<td>Integral</td>
<td>Eq. 11</td>
<td>Eq. 5</td>
<td>Eq. 12</td>
<td>Eq. 7</td>
<td>Eq. 22</td>
<td>2</td>
<td>see Table 3</td>
</tr>
</tbody>
</table>
calculated $P(z)$, we can conclude that the present form of Eq. (22) works well.

According to statistical parameters, the preferable model is the spectral model, but the integral model can also be recommended. Both models can be successfully used for estimation of the integrated primary production over the water column. We assume that the models elaborated in the present study can also be used for estimation of primary production profiles in turbid coastal and marginal sea waters.

An important result is the new form of the algorithm for calculation of the vertical profiles of the quantum yield of carbon fixation (Eq. 22). This algorithm was first quantified for the spectral model from in situ data from 3 Estonian lakes. The integral model, in which $Q_{\text{PAR}}(z)$ was less reliable than that for the spectral model, was improved by changing the coefficients $M$ and/or $n$ in Eq. (22).

Both models allow estimation, not only of the primary production profiles and water-column-integrated production, but also of their daily dynamics and daily and monthly totals. The idea is based on the fact that only incident irradiance varies noticeably, and often irregularly, during a day, but the other initial parameters of the model change slowly over time. Thus, for estimation of the temporal dynamics of primary production in a lake, daily data are needed on incoming PAR irradiance combined with episodic measurements of chl a concentration and the diffuse attenuation coefficient in the water.

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