

Comparison of spectral and broad-band models for computing photosynthetically absorbed radiation in turbid waters

Helgi Arst¹⁾, Ants Erm²⁾, Kersti Kangro³⁾, Tiina Nõges³⁾ and Peeter Nõges³⁾

¹⁾ Estonian Marine Institute, University of Tartu, Mäealuse 10A, 12618 Tallinn, Estonia

²⁾ Marine Systems Institute, Tallinn University of Technology, Akadeemia tee 21B, 12618, Tallinn, Estonia

³⁾ Institute of Zoology and Botany, Võrtsjärv Limnological Station, Estonian Agricultural University, 61101 Rannu, Estonia

Received 4 Oct. 2004, accepted 2 Aug. 2005 (Editor in charge of this article: Timo Huttula)

Arst, H., Erm, A., Kangro, K., Nõges, T. & Nõges, P. 2006: Comparison of spectral and broad-band models for computing photosynthetically absorbed radiation in turbid waters. *Boreal Env. Res.* 11: 55–65.

A comparison of values of photosynthetically absorbed radiation calculated with spectral and broad-band models was performed. Special attention was paid to turbid lake waters (Secchi depth ranging from 0.3 to 3 m). Ten measurement series of bio-optical characteristics were carried out in June and August 2003 at three Estonian lakes, Peipsi, Võrtsjärv and Harku. Photosynthetically absorbed radiation was calculated from measured quantum irradiance and a radiation model. The results obtained showed that in case of moderately clear waters (Secchi depth about 3 m) it is especially important to use a correct spectral model, as the errors of the broad-band model can be more than 40%–50%. For very turbid waters these errors usually do not exceed 20%. In our measurement results there was a rather remarkable variability of the bio-optical characteristics of the lakes. The relationships between depth-averaged assimilation number and primary production and between depth-integrated primary production and chlorophyll concentration could be described by polynomial functions with intercept = 0.

Introduction

Under the term primary production, P , we understand the production of autotrophic organisms which transform inorganic carbon and nutrients into living matter. The first step is photosynthesis which can be defined as the formation of carbon skeletons from inorganic precursors by utilizing radiant energy. The second step is biosynthesis where carbon skeletons serve as building-blocks for formation of all cellular components (Tilzer 1987). In photosynthesis, both photochemical and enzymatical processes take part. The rates

of photochemical processes depend on the light quanta absorbed by the photosynthetic pigments, and therefore both on the concentrations of these pigments and on the illumination intensity. Furthermore, the rates of enzymatical processes depend both on the concentration of the enzymes active in photosynthesis and temperature (Steeermann-Nielsen 1974).

There are several studies with the purpose of estimating primary production based on light intensity and the abundance of phytoplankton pigments (Bannister 1974, Platt and Jassby 1976, Morel 1978, Platt 1986, Tilzer 1987, Platt and

Sathyendranath 1988, Morel and Berthon 1989, Sathyendranath and Platt 1989, Sathyendranath *et al.* 1989, Smith *et al.* 1989, Schofield *et al.* 1990, Platt *et al.* 1991, Berthon and Morel 1992, Kyewalyanga *et al.* 1992, Woźniak *et al.* 1995, Kirk 1996, Sosik 1996, Siegel *et al.* 2001). Most often the water-column integrated primary production was determined from daily mean averages of photosynthetically available radiation. There are also publications where algorithms for estimating primary production are developed using remote sensing data (Platt 1986, Morel and Berthon 1989, Sathyendranath *et al.* 1989, Platt *et al.* 1991, Berthon and Morel 1992, Woźniak *et al.* 1995). When the objective of a study is to determine the daily variation of vertical profiles of primary production, it is important that the respective models have to be based on spectral data of underwater scalar quantum irradiance. However, often these data were missing and the fraction of radiant energy absorbed by algae at different depths was determined only approximately, mostly relying on the data on incident integral irradiance and absorption coefficient of light, averaged over photosynthetically-active region, PAR (400–700 nm). Note also that sometimes only underwater planar irradiance ($E_{d,PAR}$) is measured, but for primary production models we need quantum irradiance (q_{PAR}). However, converting the PAR irradiance at different depths from planar irradiance ($W\ m^{-2}$) into quantum irradiance ($\mu mol\ m^{-2}\ s^{-1}$), may bring about notable errors (Jerlov 1976, Reinart *et al.* 1998). The “air” value of $q_{PAR}/E_{d,PAR}$ is usually estimated to be $4.6\ \mu mol\ W^{-1}\ s^{-1}$ (Morel and Smith 1974). Jerlov (1976) showed that when we use this “air” value for all depths in the water, we get the relative errors, which are maximal for Jerlov’s oceanic water types I and II (e.g. for depth of 20 m they are 14%–16%). In oceanic waters absolute values of $q_{PAR}/E_{d,PAR}$ are smaller than 4.6. For waters characterized by low transparency, on the contrary, $q_{PAR}/E_{d,PAR}$ exceeds 4.6, and corresponding errors quickly increase with the depth. In estimations of Reinart *et al.* (1998) for six Estonian and Finnish lakes the average value of this error in the layer 1–3 m varied from 9% to 24% (Secchi disk depth was within the limits 0.4–2.4 m). Note that maximal errors were observed in lakes with high concentration of yellow substance.

The importance of the “spectral approach” in the primary production models was under special attention in Platt and Sathyendranath (1988), who proposed that spectral values of available light multiplied by respective spectral values of absorption coefficients of algae had to be integrated over the region of 400–700 nm. While in earlier publications the terms “incident illumination”, “light intensity”, “radiant energy” and/or “available light” were used, in the primary production model described by Smith *et al.* (1989) the need of spectral quantum irradiance was claimed. In this model, the photosynthetically absorbed radiation was computed from vertical distribution of spectral quantum irradiance and pigment-specific absorption coefficients spectra. The “spectral approach” for calculating the photosynthetically absorbed quantum irradiance was also used by Schofield *et al.* (1990). In Kyewalyanga *et al.* (1992) a comparison between primary production values measured *in situ* and calculated from spectral and broad-band models in the North Atlantic Ocean was made. However, only in a few publications (e.g. Kirk 1996, Sosik 1996) is it clearly stated that due to the fact that the algal cells are illuminated from all directions, primary production calculations have to be performed using the spectral data of scalar quantum irradiance.

As is known, parametrizing of primary production models is a rather complicated problem, as their parameters depend on the type of water body, biological activity of water (varies in time) and on the total effect of biological, hydrophysical and radiative characteristics at different depths (Bannister 1974, Morel 1978, Kiefer and Mitchell 1983, Morel and Berthon 1989, Smith *et al.* 1989, Kiefer and Gullen 1990, Morel and Ahn 1990, Berthon and Morel 1992, Kirk 1996, Sosik 1996, Nöges and Nöges 1998). We started to investigate the possibilities to elaborate a primary production model, that uses the spectral values of underwater scalar quantum irradiance and chlorophyll concentration as initial parameters. The first data series were collected in the summer of 2003. Our results allow a comparison of photosynthetically absorbed radiation obtained by a spectral to those obtained by broad-band models, for waters of moderate and low transparency. Consequently, errors caused by using a

broad-band model can be estimated. On the basis of our data also the relationships between different bio-optical characteristics can be determined and the vertical profiles of quantum yield can be calculated. However, the database obtained during our measurements in 2003 is yet insufficient for creating and final parametrizing a primary production model.

Material and methods

According to Smith *et al.* (1989) primary production $P(z)$ ($\text{mg C m}^{-3} \text{ h}^{-1}$) at depth z can principally be described with the following simple equation:

$$P(z) = M \times F(z) \times Q_{\text{PAR}}^*(z), \quad (1)$$

where M is the factor for converting moles of carbon to milligrams of carbon, equalling 12 000, $F(z)$ is the quantum yield of carbon fixation (mol C Einst^{-1}) at depth z , $Q_{\text{PAR}}^*(z)$ is photosynthetically absorbed radiation (in $\text{Einst m}^{-3} \text{ h}^{-1}$) at depth z . The index “PAR” denotes the photosynthetically-active region of the spectrum (400–700 nm):

$$Q_{\text{PAR}}^*(z) = \int_{400}^{700} q_0(\lambda, z) \left[\sum_1^n a'_i(\lambda) C_i(z) \right] d\lambda \quad (2)$$

Here $q_0(\lambda, z)$ is the scalar quantum irradiance at wavelength λ and depth z ($\text{Einst m}^{-2} \text{ nm}^{-1} \text{ h}^{-1}$), $a'_i(\lambda)$ are the pigment-specific absorption coefficients for the major absorbing pigment groups, and $C_i(z)$ is the pigment concentration at depth z . In case of only one algal species, or if using the $a'_{\text{ph}}(\lambda)$ spectrum, obtained as an average for some typical species combinations (e.g. $a'_{\text{ph}}(\lambda)$ determined by formulae presented by Bricaud *et al.* (1995) or Strömbeck and Pierson (2001)) Eq. 2 can be simplified:

$$Q_{\text{PAR}}^*(z) = \int_{400}^{700} q_0(\lambda, z) a'_{\text{ph}}(\lambda) C_{\text{chl}}(z) d\lambda \quad (3)$$

where C_{chl} is the concentration of chlorophyll *a*.

As stated before, because of the lack of the spectral data, primary production models are often built on integral values of incident irradiance and the vertical profile of irradiance is calculated using absorption coefficient of phytoplankton averaged over the PAR region, $a_{\text{ph,PAR}}$.

In this case:

$$Q_{\text{PAR}}^*(z) \approx q_{0,\text{PAR}}(z) a_{\text{ph,PAR}}(z) \quad (4)$$

where

$$q_{0,\text{PAR}}(z) = \int_{400}^{700} q_0(\lambda, z) d\lambda \quad (5)$$

and

$$a_{\text{ph,PAR}} = \frac{\int_{400}^{700} a_{\text{ph}}(\lambda) d\lambda}{\int_{400}^{700} d\lambda} \quad (6)$$

Let us call the model based on Eq. 3 a “spectral model”, and that based on Eqs. 4–6, a “broad-band model”. Of course, applying Eq. 4 (instead of Eq. 3) infers some errors, which should be estimated. Kyewalyanga *et al.* (1992) carried out these kind of estimations in 1990 during a spring bloom in the North Atlantic Ocean. They compared the results of primary production *in situ* measurements with those obtained by model calculations (a broad-band model and three versions of spectral models). In a 10-day period the percentage error in computed primary production was 0.6%–19.5% for spectral models 1 and 3, 12.6%–29.9% for spectral model 2, and 60%–69.8% for the broad-band model.

Returning to Eq. 1, the theoretical upper limit of $F = F_{\text{max}}$ is equal to 1 mole CO_2 reduced per 8 moles of quanta harvested by the phytoplankton pigments, hence $0.125 \text{ mol C Einst}^{-1}$ (Smith *et al.* 1989). Actually, the value of F is always smaller as a result of the influence of several factors, part of which are still poorly physically formalised (Smith *et al.* 1989). In this situation, investigators either continue *in situ* measurements of quantum yield or apply some simple estimates. In some cases, F can be modelled using some empirical relationships (Smith *et al.* 1989). As already noted, the theoretical limit of F_{max} is $0.125 \text{ mol C Einst}^{-1}$, but in bio-optical models, the apparent F_{max} is often treated as a constant ranging from 0.06 (Berthon and Morel 1992) to $0.1 \text{ mol C Einst}^{-1}$ (Smith *et al.* 1989). Rather often the value 0.08 is used (Tilzer 1987, Nöges and Nöges 1998). In our study, relying on the values of measured $P(z)$ and calculated Q_{PAR}^* , we can estimate the vertical profiles of $F(z)$ (Eqs. 1 and 3).

In open oceans phytoplankton is a strongly-dominating optically-active substance in water and the values of underwater irradiance are formed under the influence of absorption properties of phytoplankton and water itself. However, in coastal and inland waters also the other optically-active substances (suspended particles and dissolved organic matter) significantly absorb and scatter the light. The concentration of phytoplankton is usually much higher than in oceans, and Secchi disk transparency in turbid lakes can be more than 30 times lower than in open oceans. Thus, in addition to the studies by Kyewalyanga *et al.* (1992) for an ocean, the estimation of errors caused by applying the broad-band model for turbid waters is of interest. As the first step of these studies, we calculated the errors in the values of photosynthetically absorbed radiation for lake waters, Q_{PAR}^* , by comparing the results obtained from Eqs. 3 and 4.

The study areas were three Estonian lakes: Peipsi, Võrtsjärv and Harku. Trophic type and main morphometric data of these lakes are shown in Table 1. In 2003 we performed six field trips, three in June and three in August (i.e. two to each lake). Measurement series were planned twice a day (about 11:00–13:00 and 15:00–17:00), but due to rain at Peipsi only one series was performed both in June and August. The following characteristics were measured:

From water samples in the laboratory:

- Concentration of chlorophyll *a* (C_{chl} , mg m⁻³),
- Difference $c^*(\lambda) = c(\lambda) - c_d(\lambda)$, where $c(\lambda)$ is the beam attenuation coefficient for natural water, and $c_d(\lambda)$ is that for distilled water (spectral values with the step of 10 nm in the range of 400–700 nm). We call it “spectrometric” attenuation coefficient, measured in m⁻¹ (Arst 2003).

Field measurements:

- Water transparency by Secchi disk (z_{SD} , m).
- Incident plane quantum irradiance ($q_{\text{PAR,air}}$) in the photosynthetically-active region (400–700 nm), in micromol m⁻² s⁻¹.
- Underwater downwelling plane quantum irradiance ($q_{\text{PAR}}(z)$) in the same region (micromol m⁻² s⁻¹).
- Underwater downwelling scalar quantum irradiance ($q_{0,\text{PAR}}(z)$) in the same region (micromol m⁻² s⁻¹).
- Primary production at different depths ($P(z)$, mg C m⁻³ h⁻¹).

We determined the concentration of chlorophyll *a* by filtering the water samples through Whatman GF/C glass microfibre filters (pore size ~1.2 μm, diameter 47 mm; Whatman International Ltd., Mainstone, U.K.) extracting the pigments with hot ethanol (90%, 75 °C) and measuring the absorption at the wavelengths of 665 and 750 nm. Then the value of C_{chl} was calculated according to the Lorenzen (1967) method. For determination of the $c^*(\lambda)$ spectra from water samples we used a Hitachi U1000 spectrophotometer.

We measured the incident irradiance, $q_{\text{PAR,air}}$, and underwater downwelling plane irradiance, $q_{\text{PAR}}(z)$, by means of two quantum sensors (LI-192 SA), and for measurement of the underwater scalar irradiance, $q_{0,\text{PAR}}(z)$, we used a quantum sensor (LI-193 SA). Both instruments were manufactured by LI-COR Corporation (Lincoln, Nebraska, USA) and measure the quantum irradiance in the PAR region of spectrum. The sensitivity of the sensors is 4 μA per 1000 μmol s⁻¹ m⁻¹ and 7 μA per 1000 μmol s⁻¹ m⁻¹, respectively. These sensors have almost ideal quantum response between 400 and 700 nm and they are calibrated in μmol m⁻² s⁻¹ with uncertainty of ±5%. For recording of

Table 1. Trophic type and main morphometric data of the lakes under investigation. Typical variation of Secchi depth (z_{SD}) in summer is also shown.

| Lake | Trophic type | Area (km ²) | Average depth (m) | Maximum depth (m) | z_{SD} (m) |
|-----------|----------------|-------------------------|-------------------|-------------------|---------------------|
| Peipsi | meso/eutrophic | 2611 | 8.3 | 12.9 | 0.9–4.0 |
| Võrtsjärv | eutrophic | 270 | 2.8 | 6.0 | 0.3–1.6 |
| Harku | hypertrophic | 1.64 | 2 | 2.5 | 0.1–1.0 |

the measurements we applied a LI-COR Datalogger LI-1400. The sensors LI-193 SA and LI-193 SA were fastened to a frame, allowing measurements of q and q_0 at the same depth, and, step by step, to estimate their vertical profile as well as the respective ratio q_0/q . During the measurement procedure we lowered the instruments into the water and then brought them back to the surface (recording was done in both directions).

Because we measured only integral (in PAR region) values of quantum irradiance, but in Eq. 3 its spectral distribution is needed, we applied additionally model calculations. Firstly, using the model by Bird and Riordan (1986), from the measurement of $q_{\text{PAR,air}}$ the values of $q_{\Delta\lambda,\text{air}}$ were calculated for 30 narrow spectral intervals between 400 and 700 nm, each bandwidth $\Delta\lambda$ being 10 nm. The fact that the contribution of each wavelength interval in PAR region for quantum irradiance and plane irradiance is different, was thereby taken into account. Then we used a radiation model, which allows the computation of the spectra of $q(\Delta\lambda, z)$ on the basis of $q_{\Delta\lambda,\text{air}}$ and the spectra of $c^*(\Delta\lambda)$. The full description of this model is presented in Arst *et al.* (2002) and Arst (2003). Note that we cannot derive the spectral distribution of $q_0(\lambda, z)$ from the measured $q_{0,\text{PAR}}(z)$ values, because the contribution of each spectral interval changes with depth and is unknown. Instead of $q_0(\lambda, z)$ the $q(\Delta\lambda, z)$ spectra obtained from the model were used in Eq. 3, but afterwards the values of Q_{PAR}^* were corrected using the ratios $q_{0,\text{PAR}}/q_{\text{PAR}}$ determined from our *in situ* measurements. Additionally, for estimating the reliability of our model calculations, we integrated the spectra of $q(\Delta\lambda, z)$ from 400 to 700 nm and compared the results with the values of $q_{\text{PAR}}(z)$ measured *in situ*, using a LI-192 SA sensor.

We estimated primary production, $P(z)$, *in situ* using $^{14}\text{CO}_2$ assimilation technique (Steehan-Nielsen 1952). Depth integrated lake water was poured into 24 ml glass scintillation vials, 50 μl of sterile $\text{NaH}^{14}\text{CO}_3$ (VKI, Denmark) solution (1.7 μCi per vial) was added to achieve final activity 0.07 $\mu\text{Ci ml}^{-1}$. The vials were incubated for 2 hours at six depths in a lake. After incubation 6 ml of water from each sample was poured into a clean glass scintillation vial and acidified (pH < 2) by adding 150 μl of 0.5N HCl. Inorganic ^{14}C was assumed to be removed during

24 hours (Niemi *et al.* 1983, Hilmer and Bate 1989, Lignell 1992). Next, 5 ml subsamples were poured into new plastic vials. The radioactivity of water was measured by a LSC RackBeta 1211 counter (Wallac, Finland) using external standardization for DPM calculations. Scintillation cocktail Optiphase 'HiSafe 3' (Wallac, Finland) was applied. Primary production of different fractions was calculated according to the standard formula (Nielsen & Bresta 1984). Non-photosynthetic carbon fixation was measured in dark vials and subtracted from light assimilation.

For determining the values of $Q_{\text{PAR}}^*(z)$ we calculated the spectra of a_{ph} using the formula by Bricaud *et al.* (1995):

$$a_{\text{ph}}(\lambda) = a'_{\text{ph}}(\lambda)C_{\text{chl}}, \quad (7)$$

where the specific absorption coefficient $a_{\text{ph}}^*(\lambda)$ is calculated taking into account the "package effect" (Bricaud *et al.* 1995, Kirk 1996):

$$a'_{\text{ph}}(\lambda) = A(\lambda)C_{\text{chl}}^{-B(\lambda)} \quad (8)$$

Here A and B are positive, wavelength-dependent parameters (they are tabulated in the paper by Bricaud *et al.* 1995).

Note that the coefficients A and B were obtained by Bricaud *et al.* on the basis of analysing more than 800 phytoplankton absorption spectra, mainly describing the oceanic waters. Strömbeck and Pierson (2001) estimated A and B using measurement data in Swedish lakes. However, in comparison with our three Estonian lakes the Swedish lakes were considerably more transparent. Our test computations of $a'_{\text{ph}}(\lambda)$ by Strömbeck and Pierson gave at some wavelengths slightly higher, at some wavelengths slightly lower values in comparison with those by Bricaud *et al.* For the reason that Bricaud's results are widely used, we decided to perform our computations firstly on the basis of Bricaud's formula, but in the future to carry out our own investigations allowing estimates of A and B for turbid lakes.

Results

For demonstrating the numerical values of our results we chose some characteristics, which are

presented in Tables 2 and 3. Because our lakes are non-stratified (in our data the vertical variation of chlorophyll *a* did not exceed 15%), only the depth-averaged values of Chl*a* concentrations are shown. Values of c_{PAR}^* were calculated from the spectra of $c^*(\Delta\lambda)$ (measured from water samples in laboratory) as average over 400–700 nm. In turbid waters this characteristic is more suitable for describing the water transparency than Secchi disk (Arst 2003). Note that averaged values of $q_{\text{PAR,air}}$ were obtained from repeated, but discrete measurements performed during each 2-hour incubation. In condition of variable cloudiness obviously the continuous recording of $q_{\text{PAR,air}}$ is needed, and some errors in the results can appear (e.g. it is possible for Vörtsjärv in August 2003). The integral values of primary production (P_{int}) were calculated for the layer from the surface to the deepest point, where $P(z)$ was measured. It means that the primary production below

this depth was not taken into account. For this reason the values of P_{int} in the lakes Harku and Vörtsjärv are a little bit underestimated (by our approximate estimations the respective errors vary between 5% and 13%). Given data on C_{chl} and $P(z)$ it is possible to compute the values of chlorophyll-specific primary production (assimilation number, AN, $\text{mgC m}^{-3} \text{h}^{-1} \text{mg Chl}a^{-1}$) as their ratio. The maximal values of AN and P are also shown in Table 3, as well as the depth where they were observed (this depth is the same for AN_{max} and P_{max}).

As an example of our *in situ* measurement results the depth variation of the plane and scalar quantum irradiance measured in Peipsi on 11 June 2003 are shown in Fig. 1. The respective vertical profile of scalar quantum irradiance calculated by our model is also presented. Because of the cloudiness (7Ci/3Cu) the incident irradiance varied during the measurements (25 minutes) and the values of underwater irradiance were corrected taking this fact into account. Note, that just below the surface the accuracy of q_{PAR} and $q_{0,\text{PAR}}$ is probably to some extent lower than that in deeper layers, because the measurement results can be influenced by roughness of the water surface (during the measurement procedure there can be moments when the sensor is partly in the air). Some scattering of the measurement results in the layer of 0.25–2.5 m was obviously caused by wave-undulation, creating fluctuations of irradiance (solar “flashes”) in the upper layer of a water body. As we can see in the

Table 2. Values of C_{chl} (mg m^{-3}), c_{PAR}^* (m^{-1}) (both averaged over depth), $K_{\text{d,PAR}}$ (averaged over 2–4 series of Li-192 SA measurements, m^{-1}) and Secchi disk depth, z_{SD} (m), measured in the summer of 2003.

| Lake | Date | C_{chl} | c_{PAR}^* | $K_{\text{d,PAR}}$ | z_{SD} |
|-----------|--------------|------------------|--------------------|--------------------|-----------------|
| Peipsi | 11.VI.2003 | 9 | 1.4 | 0.67 | 2.75 |
| Peipsi | 20.VIII.2003 | 36 | 6.4 | 2.1 | 1 |
| Vörtsjärv | 12.VI.2003 | 44 | 12.1 | 2.5 | 0.5 |
| Vörtsjärv | 19.VIII.2003 | 59 | 13.3 | 2.3 | 0.5 |
| Harku | 10.VI.2003 | 54 | 13.2 | 3.4 | 0.5 |
| Harku | 18.VIII.2003 | 107 | 22.8 | 4.5 | 0.3 |

Table 3. Some results of measurements performed in summer 2003: incident irradiance, $q_{\text{PAR,air}}$ ($\mu\text{mol m}^{-2} \text{s}^{-1}$) (approximate average value during 2 hours of primary production measurements), integrated over depth primary production P_{int} ($\text{mgC m}^{-2} \text{h}^{-1}$), maximum primary production, P_{max} ($\text{mgC m}^{-3} \text{h}^{-1}$), maximum of assimilation number, AN_{max} ($\text{mgC mg Chl}a^{-1} \text{h}^{-1}$) (the depth of AN_{max} (m) is shown together with AN_{max} in parenthesis).

| Lake | Date | Time | Clouds | $q_{\text{PAR,air}}$ | AN_{max} | P_{int} | P_{max} |
|-----------|--------------|-------------|---------|----------------------|--------------------------|------------------|------------------|
| Peipsi | 11.VI.2003 | 11:00–13:00 | 7Ci/3Cu | 1555 | 1.0 (3) | 46 | 9.1 |
| Peipsi | 20.VIII.2003 | 12:00–14:00 | 10Sc,St | 300 | 3.2 (0) | 64 | 117 |
| Vörtsjärv | 12.VI.2003 | 10:45–12:45 | 10Sc,St | 310 | 1.5 (0) | 51 | 66 |
| Vörtsjärv | 12.VI.2003 | 14:50–16:50 | Clear | 1767 | 2.7 (0.5) | 91 | 119 |
| Vörtsjärv | 19.VIII.2003 | 11:35–13:35 | 1Cu | 1765 | 2.3 (0.5) | 148 | 137 |
| Vörtsjärv | 19.VIII.2003 | 14:30–16:30 | 5Cu | 1200 | 1.4 (0.5) | 86 | 81 |
| Harku | 10.VI.2003 | 11:30–13:30 | 9Cu | 675 | 1.8 (0.5) | 107 | 96 |
| Harku | 10.VI.2003 | 15:20–17:20 | 5Ci/1Cu | 1275 | 1.9 (0.25) | 94 | 100 |
| Harku* | 18.VIII.2003 | 11:40–13:40 | – | – | 3.9 (0.4) | 322 | 413 |
| Harku | 18.VIII.2003 | 15:30–17:30 | 8As/3Cu | 781 | 4.1 (0.4) | 296 | 442 |

* The value of q_{air} is missing due to technical failure of measurements.

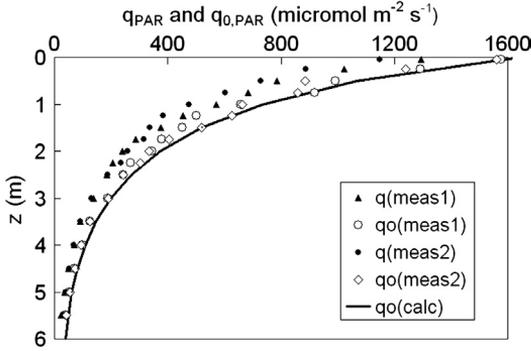


Fig. 1. Depth variation of plane ($q_{\text{PAR}}(z)$) and scalar ($q_{0,\text{PAR}}(z)$) quantum irradiances in Lake Peipsi on 11 June 2003, measured by sensors LI 192 SA and LI 193 SA, respectively. The vertical profile of $q_{0,\text{PAR}}(z)$ obtained from model calculations is also shown.

case shown in Fig. 1, the coincidence between measured and calculated values of $q_{0,\text{PAR}}$ was very good.

An important part of our study is the quantitative estimation of the errors of the primary production “broad-band” model in lake waters. This can be made comparing the values of $Q_{\text{PAR}}^*(z)$ obtained by Eqs. 3 and 4 (the errors in $P(z)$ are similar to the errors in $Q_{\text{PAR}}^*(z)$). The vertical variation of these errors is also of interest showing the reliability of the “broad-band” model at different depths. Let us denote the values of photosynthetically absorbed radiation respectively $Q_{\text{PAR,sp}}^*$ and $Q_{\text{PAR,bb}}^*$ (shortened from the words “spectral” and “broad-band”). Our results show that $Q_{\text{PAR,bb}}^*$ always exceeds $Q_{\text{PAR,sp}}^*$ and the ratio $Q_{\text{PAR,bb}}^*/Q_{\text{PAR,sp}}^*$ increases with increasing depth. Because we assume that $Q_{\text{PAR,sp}}^*$ (obtained from Eq. 3) is truthful, the relative error (RE) was determined as follows:

$$\text{RE} = \frac{Q_{\text{PAR,bb}}^* - Q_{\text{PAR,sp}}^*}{Q_{\text{PAR,sp}}^*} \quad (9)$$

The depth variation of RE is shown in Fig. 2. Note that because of the uncertainties of Q_{PAR}^* just below the surface ($z = 0$), the corresponding results were left out from correlation analysis. The maximal values of RE and its most intensive growth with depth were observed in Peipsi in June (moderately clear water). In this case RE at the depth of 5 m is already 40% and seems to

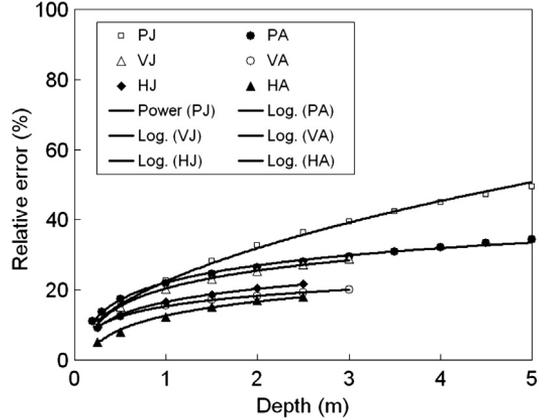


Fig. 2. Relative errors (RE) determined by Eq. 9 at different depths and in different lakes: PJ and PA are for Lake Peipsi in June and August respectively, VJ and VA are the same for Vörtsjärv, HJ and HA the same for Lake Harku. The type of regression formula is also shown for each case.

grow with depth. However, in very turbid lakes RE did not exceed 20% and beginning from the depth of about 2 m it increased only very slightly with depth. As we can see in Fig. 2, below the depth of about 0.2 m the depth dependence of RE was well described either by power or logarithmic functions. Note that for Peipsi in June the power law was much better, for Harku in August the logarithmic regression was preferable, for the other cases the power as well as the logarithmic functions were practically equally suitable. The coefficients of regression formulas and determination coefficients are shown in Table 4. The values of correlation coefficients are extremely high and $p < 0.005$, but there are only 6–12 points for each curve. Note that by our estimations the regression formulas obtained for

Table 4. Regression formulas describing the relative error RE (Eq. 9) as a function of depth (z) (formulas are reliable only below the depth of 0.2 m). The respective values of R^2 are also shown.

| Lake | Month | Regression equation | R^2 |
|-----------|--------|--------------------------------|-------|
| Peipsi | June | $\text{RE} = 22.4z^{0.51}$ | 0.998 |
| Peipsi | August | $\text{RE} = 7.1\ln(z) + 22.1$ | 0.996 |
| Vörtsjärv | June | $\text{RE} = 7.3\ln(z) + 20.4$ | 0.998 |
| Vörtsjärv | August | $\text{RE} = 4.3\ln(z) + 15.3$ | 0.999 |
| Harku | June | $\text{RE} = 5.4\ln(z) + 16.6$ | 0.999 |
| Harku | August | $\text{RE} = 5.8\ln(z) + 12.7$ | 0.992 |

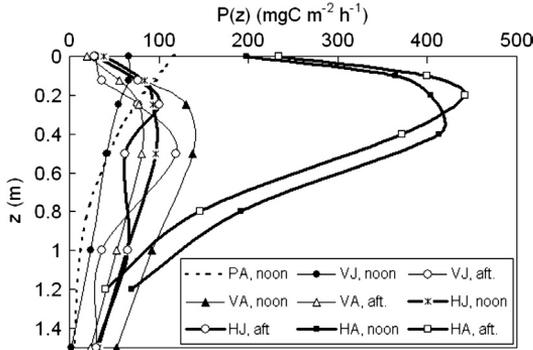


Fig. 3. Vertical profiles of primary production $P(z)$ measured in Estonian lakes in summer 2003 (the denotations are the same as in Fig. 2).

the depths $z > 0.2$ m are not suitable in the layer of 0–0.15 m, giving unreliable results.

The results shown in Fig. 2 and Table 4 were obtained using phytoplankton absorption coefficients calculated by the formula of Bricaud *et al.* (1995). We repeated the calculations using the coefficients obtained for Eq. 8 by Strömbeck and Pierson (2001), and also on the basis of data on eight different phytoplankton species, taking respective absorption spectra from Ahn *et al.* (1992). The corresponding relative errors were similar to those in the case of Bricaud's formula, and depended only slightly on the different species. The species investigated by Ahn *et al.* (1992) have not been observed in Estonian lakes.

Vertical profiles of primary production measured in this study are shown in Fig. 3. The curve for Peipsi in June is left out from the figure, because up to 1.5 m $P(z)$ is below $6 \text{ mg C m}^{-3} \text{ h}^{-1}$ and its maximum ($9.1 \text{ mg C m}^{-3} \text{ h}^{-1}$) is placed at the depth of 3 m. Naturally, the values of primary production depend on the amount of phytoplankton in the water. Figure 4 demonstrates the correlation of P_{int} and C_{chl} . Note that despite the small number of points, p was below 0.0002. The polynomial function (with intercept = 0) produced a most suitable regression curve. Our results allowed us to assume that the depth where $P = P_{\text{max}}$ depends on the value of incident irradiance and probably also on the transparency of water. Correlation analysis gave us the following relationship

$$z(P_{\text{max}}) = 0.00068q_{\text{PAR,air}}z_{\text{SD}} \quad (10)$$

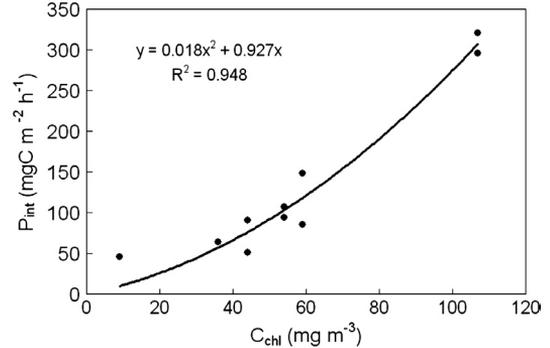


Fig. 4. Relationship between integral values of primary production (P_{int}) and chlorophyll a concentration (C_{chl}).

where $z(P_{\text{max}})$ and z_{SD} are in m, $q_{\text{PAR,air}}$ is in $\mu\text{mol m}^{-2} \text{ s}^{-1}$, $R^2 = 0.979$, p was below 0.000 000 2. However, taking into account that only one case (Peipsi, June) had the value $z(P_{\text{max}}) = 3$ m, but for all other cases $z(P_{\text{max}})$ varied between 0.01 and 0.5 m, the correlation results can be strongly influenced by this one value. When excluding the point “Peipsi, June”, the correlation of $z(P_{\text{max}})$ and $q_{\text{PAR,air}}z_{\text{SD}}$ gave us $z(P_{\text{max}}) = 0.0006q_{\text{PAR,air}}z_{\text{SD}}$, but the value of R^2 was only 0.697.

As in all cases there was only a slight variation of C_{chl} with depth, we calculated $\text{AN}(z)$ using the depth-averaged values of C_{chl} . This leads to similar shapes of the profiles of $\text{AN}(z)$ and $P(z)$. However, the regression line between their depth-averaged values, P_{av} vs. AN_{av} , is not linear (Fig. 5).

An example of the vertical profiles of $P(z)$ (measured) and $F(z)$ (calculated on the basis of Eq. 1) is presented in Fig. 6. Our calculations showed that for very turbid lakes (Võrtsjärv in August and Harku in both months) $F(z)$ can exceed its widely used maximum value, $0.08 \text{ mol C Einst}^{-1}$. It happened at the maximal depth of primary production measurements. Note that in all profiles of $F(z)$ the “weakest points” are (1) at the surface, because the uncertainty of $Q_{\text{PAR}}^*(z = 0)$, and (2) at the depths where $P(z)$ and/or $Q_{\text{PAR}}^*(z)$ have very small values (their ratio can be with big relative errors).

Discussion

Our results showed that when comparing the lakes in June and August there are remarkable

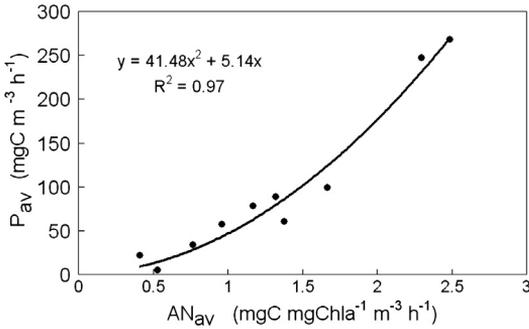


Fig. 5. Relationship between depth-averaged values of primary production (P_{av}) and respective assimilation number (AN_{av}) (the layer where the averaging is made is shown in Table 3).

differences for Peipsi and Harku, but Vörtsjärv is almost the same in both months. Extremely high values of C_{chl} , P_{max} and P_{int} were observed in Harku in August. In most cases vertical maximum of $P(z)$ was not located at the surface but in the layer between $0.5z_{SD}$ and z_{SD} , reflecting the inhibition of photosynthesis by surplus light intensity in surface water layer. The cases where P_{max} is at the surface (Peipsi in August and Vörtsjärv in June at noon) were caused by low values of $q_{PAR,air}$ because of overcast sky.

In general, the vertical profiles of $q_{0,PAR}$ measured *in situ* and calculated by the model agree either very well (example in Fig. 1), or rather well. Note, that the disagreement between the measured and calculated $q_{0,PAR}$ does not influence the results of comparing the “broad-band” and “spectral” models, because the values of underwater quantum irradiance are the same for both versions.

Comparison of the values of $Q_{PAR}^*(z)$ calculated from Eqs. 3 and 4 showed that for very turbid waters the relative errors of the “broad-band” model usually did not exceed 10%–20%, growing rather slowly with depth. However, in Peipsi in June (moderately transparent) these errors rather remarkably increased with depth, reaching 40% at the depth of 5 m. These results are in good correspondence with the estimations of Kyewalyanga *et al.* (1992) in the North Atlantic Ocean, where the percentage errors in computed production for the broad-band model were 60%–69.8%, but for different kind of spectral models they were mostly below 20%.

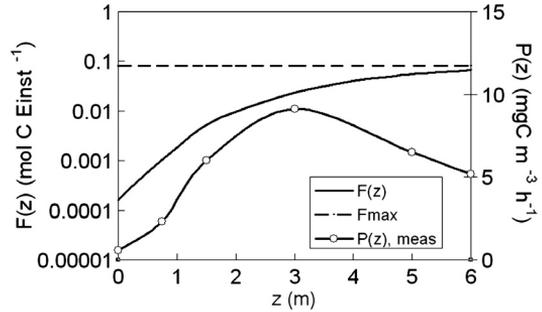


Fig. 6. Vertical profile of quantum yield $F(z)$ and primary production $P(z)$ in Lake Peipsi in June 2003. The maximum value $F_{max} = 0.08 \text{ mol C Einst}^{-1}$ is also shown in the figure.

Consequently, the correct “spectral” version is important to use not only in clear oceanic waters, but also in much less transparent lake waters (remember that Secchi disk depth for Peipsi in June was only 2.75 m).

Looking at the vertical profiles of primary production we have to pay attention to the extremely high values of P_{max} and P_{int} in Harku in August 2003 (Fig. 3). Obviously, it is not exceptional, because the very intensive phytoplankton blooms in late summer (C_{chl} exceeding sometimes even 400 mg m^{-3}) we observed also in years 1999–2001 (Arst 2003). Unfortunately, we have no older data about primary production in Harku.

Our data set showed that AN_{av} is related to P_{av} and that P_{int} depends rather strongly on C_{chl} . It occurred that both relationships can be described by polynomial functions with intercept = 0 (Figs. 4 and 5). The statistical reliability of the formulas obtained is high, but probably for final estimation of the coefficients the regression formulae should be determined relying on a larger data set.

The results of calculating the profiles of quantum yield gave realistic shapes of $F(z)$. However, as already noted before, in some cases in very turbid lakes the maximal values of $F(z)$ exceed its generally used value, $0.08 \text{ mol C Einst}^{-1}$. There can be several reasons: (1) the errors in the characteristics used for calculations of $F(z)$; (2) the coefficients of Bricaud’s formula are not suitable for very turbid lakes; (3) a hypothesis, that for extremely turbid lakes F_{max} can be more than $0.08 \text{ mol C Einst}^{-1}$ (e.g. about $0.1 \text{ mol C Einst}^{-1}$,

the limit of which was considered as a commonly accepted value in Smith *et al.* (1989)). The values of $F(z)$ allow estimation also of the errors appearing when instead of $q_0(\lambda, z)$ the values of $q(\lambda, z)$ are used in Eq. 3 (note that $q(\lambda, z)$ is always smaller than $q_0(\lambda, z)$). In this case the values of the quantum yield are higher and the result $F_{\max} > 0.08 \text{ mol C Einst}^{-1}$ is more possible. Consequently, for obtaining reliable results in primary production calculation models, the scalar irradiance data has to be used.

Conclusions

Our results show that when applying the primary production models for very turbid waters, the relative errors of the “broad-band” model usually did not exceed 10%–20%, growing rather slowly with depth. In moderately transparent Peipsi (in June 2003) these errors grew rather remarkably with depth reaching 40% at the depth of 5 m. Thus, it is important to use the correct “spectral” version not only in clear oceanic waters (Kyewalyanga *et al.* 1992), but also in much less transparent lake waters.

From 10 measurement series only one case corresponded to moderately turbid lakes: Peipsi in June 2003 ($z_{\text{SD}} = 2.75 \text{ m}$). All other cases described turbid or very turbid waters (z_{SD} ranged from 1 to 0.3 m). Altogether, we got a rather remarkable variability of the bio-optical characteristics: the values of C_{chl} were from 9 to 107 mg m^{-3} , $K_{\text{d,PAR}}$ from 0.67 to 5.5 m^{-1} , P_{int} from 46 to 322 $\text{mgC m}^{-2} \text{ h}^{-1}$ and P_{max} from 9 to 442 $\text{mgC m}^{-3} \text{ h}^{-1}$.

The relationships P_{int} vs. C_{chl} and P_{av} vs. AN_{av} can be described by polynomial functions with intercept = 0. Correlation analysis gave us a strong relationship also between $z(P_{\text{max}})$ and $q_{\text{PAR,inc}} z_{\text{SD}}$. The statistical reliability of the formulae obtained is high, but a final regression formula should probably be determined relying on a larger data set.

Our results from calculating the profiles of quantum yield showed that in most cases the measured $P(z)$ and calculated (on the basis of Bricaud’s formula) $Q^*_{\text{PAR}}(z)$ give rather realistic shapes of $F(z)$. In some very turbid lakes the maximal values of $F(z)$ exceeded its widely used

value, 0.08 mol C Einst^{-1} . There can be different reasons, but the most probable explanation is that the coefficients of Bricaud’s formula (Bricaud *et al.* 1995) are not suitable for very turbid lakes.

The values of quantum yield help us to estimate the additional errors appearing when in primary production models not using scalar quantum irradiance, $q_0(\lambda, z)$, but plane quantum irradiance, $q(\lambda, z)$. This induces the increase of the quantum yield and the possibility that $F_{\max} > 0.08 \text{ mol C Einst}^{-1}$ is higher. Consequently, for obtaining reliable results in primary production calculation models, the scalar irradiance data has to be used.

Acknowledgements: The authors are indebted to the Estonian Science Foundation (grant 5594) for financial support to this investigation. We should also like to thank M.Sc. Liis Sipelgas for performing the calculations based on the absorption spectra of different algal species and Dr. Ilmar Tõnno for the aid in field works and for phytoplankton analyses.

References

- Ahn Y.H., Bricaud A. & Morel A. 1992. Light backscattering efficiency and related properties of some phytoplankters. *Deep-Sea Res.* 39: 1835–1855.
- Arst H. 2003. *Optical properties and remote sensing of multi-componental water bodies*, Springer, Praxis-Publishing, Chichester, U.K.
- Arst H., Erm A., Reinart A., Sipelgas L. & 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. *Nordic Hydrology* 33(2): 207–226.
- Bannister T.T. 1974. Production equations in terms of chlorophyll concentration, quantum yield, and upper limit to production. *Limnol. Oceanogr.* 19: 1–12.
- Berthon J.-F. & Morel A. 1992. Validation of spectral light-photosynthesis model and use of the model in conjunction with remotely sensed pigment observations. *Limnol. Oceanogr.* 37(4): 781–796.
- Bird R.E. & Riordan C. 1986. Simple solar spectral model for direct and diffuse irradiance on horizontal and tilted planes at the earth’s surface for cloudless atmospheres. *J. Climate Appl. Meteorol.* 25: 87–97.
- Bricaud A., Babin M., Morel A. & Claustre H. 1995. Variability in the chlorophyll-specific absorption coefficients of natural phytoplankton: Analysis and parametrization. *J. Geoph. Res.* 100(C7): 13321–13332.
- Hilmer T. & Bate G.C. 1989. Filter types, filtration and post-filtration treatment in phytoplankton production studies. *J. Plankton Res.* 11: 49–63.
- Jerlov N.G. 1976. *Marine optics*, Elsevier Oceanography Series 5, Elsevier, Amsterdam–Oxford–New York.

- Kiefer D.A. & Cullen J.J. 1990. Phytoplankton growth and light absorption as regulated by light, temperature and nutrients. *Polar Res.* 10: 163–172.
- Kiefer D.A. & Mitchell B.G. 1983. A simple steady state description of phytoplankton growth based on absorption cross section and quantum efficiency. *Limnol. Oceanogr.* 28: 770–776.
- Kirk J.T.O. 1996. *Light and photosynthesis in aquatic ecosystems*, Cambridge University Press.
- Kywalyanga M., Platt T. & Sathyendranath S. 1992. Ocean primary production calculated by spectral and broadband models. *Marine Ecology Progr. Ser.* 85: 171–185.
- Lignell R. 1992. Problems in filtration fractionation of ^{14}C primary productivity samples. *Limnol. Oceanogr.* 37: 172–178.
- Lorenzen C.J. 1967. Determination of chlorophyll and phaeopigments; spectrophotometric equations. *Limnol. Oceanogr.* 12: 343–346.
- Morel A. 1978. Available, usable and stored radiant energy in relation to marine photosynthesis. *Deep-Sea Res.* 25: 673–688.
- Morel A. & Ahn Y.H. 1990. Optical efficiency factor of free living marine bacteria: Influence of bacterioplankton upon the optical properties and particulate organic carbon in the ocean waters. *J. Marine Res.* 48: 145–175.
- Morel A. & Berthon J.-F. 1989. Surface pigments, algal biomass, and potential production of the euphotic layer: Relationships reinvestigated in view of remote-sensing applications. *Limnol. Oceanogr.* 34: 1545–1562.
- Morel A. & Smith R.C. 1974. Relation between total quanta and total energy for aquatic photosynthesis. *Limnol. Oceanogr.* 19: 591–599.
- Nielsen G.A.E. & Bresta A.M. 1984. Guidelines for measurements of phytoplankton primary production. *Baltic Mar. Biol. Publ.* 1: 1–23.
- Niemi M., Kuparinen J., Uusi-Rauva A. & Korhonen K. 1983. Preparation of algal samples for liquid scintillation counting. *Hydrobiologia* 106: 149–159.
- Nöges P. & Nöges T. 1998. Advantages and limitations of optical methods in the estimation of the primary production of lakes. *Report Ser. Geophysics* 38: 59–67.
- Platt T. 1986. Primary production of the ocean water column as a function of surface light intensity: algorithms for remote sensing. *Deep-Sea Res.* 33: 149–163.
- Platt T. & Jassby A.D. 1976. The relationship between photosynthesis and light for natural assemblages of coastal marine phytoplankton. *J. Phycology* 12: 421–430.
- Platt T. & Sathyendranath S. 1988. Oceanic primary production: Estimation by remote sensing at local and regional scales. *Science* 241: 1613–1620.
- Platt T., Caverhill C.M. & Sathyendranath S. 1991. Basin scale estimates of oceanic primary production by remote sensing: the North Atlantic. *J. Geophys. Res.* 96: 15147–15159.
- Reinart A., Arst H., Nöges P. & Nöges T. 1998. Underwater light field in the PAR region of the spectrum in some Estonian and Finnish lakes in 1995–96. *Report Ser. Geophysics* 38: 23–32.
- Sathyendranath S. & Platt T. 1989. Computation of aquatic primary production: extended formalism to include effect of angular and spectral distribution of light. *Limnol. Oceanogr.* 34: 188–198.
- Sathyendranath S., Platt T., Caverhill C.M., Warnock R.E. & Lewis M.R. 1989. Remote sensing of oceanic primary production: computations using a spectral model. *Deep-Sea Res.* 36: 431–453.
- Schofield O., Bidigare R.R. & Prezelin B.B. 1990. Spectral photosynthesis, quantum yield and blue-green light enhancement of productivity rates in the diatom *Chaetoceros gracile* and the prymnesiophyte *Emiliana huxleyi*. *Marine Ecol. Progr. Ser.* 64: 175–186.
- Siegel D.A., Westberry T.K., O'Brien M.C., Nelson N.B., Michaels A.F., Morrison J.R., Scott A., Caporelli E.A., Sorensen J.C., Maritorena S., Garver S.A., Brody E.A., Ubante J. & Hammer M.A. 2001. Bio-optical modeling of primary production on regional scales: the Bermuda BioOptics project. *Deep-Sea Res.* II 48: 1865–1896.
- Smith R.C., Prezelin B.B., Bidigare R.R. & Baker K.S. 1989. Bio-optical modeling of photosynthetic production in coastal waters. *Limnol. Oceanogr.* 34: 1524–1544.
- Sosik H.M. 1996. Bio-optical modelling of primary production: consequences of variability in quantum yield and specific absorption. *Marine Ecol. Progr. Ser.* 143: 225–238.
- Steeman-Nielsen E. 1952. The use of radioactive carbon (^{14}C) for measuring primary production in the sea. *Journal du Conseil. Conseil Permanent International pour l'Exploration de la Mer* 18: 117–140.
- Steeman-Nielsen E. 1974. Light and primary production. In: Jerlov N.G. & Steeman-Nielsen E. (eds.), *Optical aspects of oceanography*, Academic Press, London-New York, pp. 361–388.
- Strömbeck N. & Pierson D.S. 2001. The effects of variability in the inherent optical properties on estimations of chlorophyll *a* by remote sensing in Swedish freshwaters. *Sci. Total Environ.* 268: 123–137.
- Tilzer M.M. 1989. The productivity of phytoplankton and its control by resource availability. In: Kumar H.D. (ed.), *Phycotalk*, Bavaras Hindi University, Varanasi, Rastogi and Co. Meerut, pp. 1–40.
- Woźniak B., Dera J., Semowski S., Hapter R., Ostrowska M. & Kaczmarek S. 1995. Algorithm for estimating primary production in the Baltic by remote sensing. *Studia i materiały oceanologiczne* 68: 91–123.