

WHOLE LAKE PRIMARY PRODUCTION ASSESSMENT BY BIO-OPTICAL MODELLING

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Abstract

A hypertrophic lake in Leipzig has been analyzed with respect to the basic limnological parameters, nutrients and phytoplankton community dynamic in the course of the year 2002. A bio-optical model was developed to assess the daily primary production based on the spectrally resolved surface irradiance, the light climate in the euphotic zone of the water column, the quantification of the light absorption by the phytoplankton and its photosynthetic efficiency measured with the help of *in-vivo* Chl *a*-fluorescence. Summing up the modeled primary production per day for the whole vegetation period it turned out that the productivity was no limited by the nutrients but by the light only. This is the first report that an adopted bio-optical modeling can be used to assess the annual primary production of a whole freshwater lake.

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Key words: bio-optical modeling, fluorescence, lake remediation measure, phytoplankton, primary production

INTRODUCTION

In the last four decades numerous German lakes had to be redeveloped due to eutrophication. Scharf *et al.* (1984) have described a broad variety of methods to increase water quality and biological diversity in eutrophicated lakes. Most strategies to reduce the nutrient content are based on techniques to export nutrients or to bind them irreversibly in the sediment. From the results of lake remediation actions it can be stated that the most successful and sustainable restoration measures are observed after nutrient export and prevention of new input. The restoration of the Eifelmaare (Germany), where Thienemann did his basic studies to start up modern limnology, is an excellent example for this hypothesis (Scharf 1984). However, in many cases it is not possible to reduce the nutrient input because nutrient sources are diffuse or the influx cannot be eliminated within short term. To prevent nutrient based eutrophication process phytoplankton primary production has to be reduced by artificial measures, *e.g.* turbulence (Oskam 1978). Destratification by a bubble plume prevents the development of anoxigenated hypo- or epilimnion and phytoplankton is shifted from the euphotic to the aphotic zone of the water column. This results in light limitation of the phytoplankton productivity (Reynolds *et al.* 1984, Steinberg 1983, Steinberg, Zimmermann 1988). However, in practice this method often failed (Steinberg, Tille-Backhaus 1990). One reason is the resuspension of phosphorus from the sediment by the air stream, which leads to a recycling of nutrients during the clear water stage in summer. This leads to fast oscillations of phytoplankton blooms (Bürge 1992). Even if intermittent destratification techni-

ques are applied it cannot be prevented that in the euphotic zone a short circuit of nutrients will be established which is responsible for high primary production throughout the vegetation period (Steinberg, Gruhl 1992). Therefore, the efficiency of a lake remediation measure by light limitation is still a matter of debate.

The crucial question of this strategy is whether the primary production can really be lowered by destratification. This question can only be answered by direct measurements of primary production. It is noteworthy that such a measuring technique is not really available yet. The radiocarbon technique, although tested and widely used, does not give reliable results in turbulent systems. The physiological situation for the phytoplankton enclosed in a fixed bottle with drastically changing ratios of CO₂/O₂ is far from the natural condition. Dynamic incubations reduce the problem to a certain extent but it is still highly speculative if the result from a few dynamic incubations can be extrapolated to assess the primary production of a whole lake during a whole vegetation period. Therefore, bio-optical models have been designed to overcome this problem. One can download the excel-sheets from the internet (Walsby 1997) to calculate the daily primary production. Although this is a very helpful and straightforward leading tool, one has to remind that the model is adopted either to the open sea or deep oligotrophic lakes. In eutrophic and phytoplankton-rich waters the light climate is strongly influenced by the absorption of the particulate matter and, therefore, a spectrally resolved model is required.

In this paper we report a study of the Lake Auensee in Leipzig (Germany), which is hypertrophic and whose phytoplankton primary production is not limited by nutrients at all.

In this lake, a recent sediment withdrawal measurement failed, since extracted nutrient contents were replaced by nutrient-rich seepage water within few weeks (Lewandowski *et al.* 2002). We have tested a newly developed bio-optical model, which calculates the phytoplankton primary production on measurable input-parameters.

MATERIAL AND METHODS

Field size description, sampling and chemical parameters

The Lake Auensee (56°927' N, 45°223' E) located in Leipzig (Germany), covers an area of 11.935 ha with a volume of 464,000 m³, a mean depth of 3–4 m, a maximal depth of 7 m and a hydraulic retention time of 1.8 years.

Samples were collected biweekly from April to October 2002, at a fixed point in the western part of the lake from surface to 3 m depth in 1 m steps.

Dissolved oxygen was measured at intervals of 0.5 m from the surface to the bottom of the lake using a WTW sensor (EOT 196 - OXI 196).

The Institute of Meteorology Leipzig measured global solar radiation. The underwater light field from surface to 1 m in 0.1 m steps was estimated from PAR determination using a spherical sensor (Zemoko, Kouderkerke, The Netherlands) in combination with a data-display (LI-250, LICOR, Lincoln, USA). Consequently, the euphotic zone (depth of the 1% light level) was calculated as:

$$z_{eu} = \frac{4.6}{k} \quad (1)$$

The vertical background attenuation coefficient was derived from:

$$k = \frac{LN(I_1) - LN(I_2)}{z_2 - z_1} \quad (2)$$

where I is the light intensity at depth z [m].

Secchi depth was measured with a white disk (20 cm diameter).

Water samples for the determination of phosphorus and nitrogen contents were taken with a 1 L Ruttner sampler (Dangelat, Berlin, Germany) at the surface, in 1 m and in 3 m of the water column. Nitrogen analyses were performed according to DIN EN ISO 10304-D19, whereas phosphorus analyses were performed according to DIN 38405-D11.

Water samples for Chl a -determination and for HPLC measurements were collected at the surface and 1 m, 2 m and 3 m below the water surface. The samples were fixed on a filter (GF 6, Schleicher & Schuell, Ø 50 mm) by vacuum filtration in dim light. Chl a -determination was done according to DIN 38 412 T 16.

Quantitative HPLC analysis was performed using a Waters Chromatography System (Waters Chromatography Division, Millipore GmbH, Eschborn, Germany) the system contained a Waters 600-MS pump with a system controller, a Waters 996 photodiode array detector and a Waters 717 auto sampler. The separation of the pigments was realized with a

reversed phase column (ET 250/4, Nucleosil 300-5 C₁₈; Macherey-Nagel, Düren Germany). The HPLC-aided pigment analysis of freshwater phytoplankton was described previously (Wilhelm *et al.* 1995).

Modeling of primary production of phytoplankton

Phytoplankton primary production (PP) during the vegetation period was calculated for the water column from surface to 3.4 m depth based on the following equation 3 (Gilbert *et al.* 2000a):

$$PP = \phi \cdot Q_{phar} \cdot 0.125 \cdot 3600 \quad (3)$$

PP: primary production [$\mu\text{mol O}_2 \text{ m}^{-2} \text{ h}^{-1}$]

ϕ : quantum yield

Q_{phar} : photosynthetically absorbed radiation [$\mu\text{mol m}^{-2} \text{ s}^{-1}$]

0.125: This factor includes the assumption that the absorbed PAR of PS II is 0.5 and that four electrons needed to evolution one oxygen molecule

3600: This factor converts time units from seconds to hours

The calculation of PP is based on the underwater radiation field (Q_{par}), derived on the basis of equation 4:

$$Q_{par}(z) = \int_{400nm}^{700nm} Q_0(\lambda, z) \cdot e^{(-a^*(\lambda, z)[Chl a] + k(\lambda, z)) \Delta z} d\lambda \quad (4)$$

$Q_{par}(z)$: photosynthetically available radiation [$\mu\text{mol m}^{-2} \text{ s}^{-1}$]

Q_0 : irradiance at the water surface [$\mu\text{mol m}^{-2} \text{ s}^{-1}$]

k : vertical background attenuation coefficient

Q_{par} was calculated in 0.1 m steps for whole water column. Q_{phar} describes the sorbed photosynthetically radiation by phytoplankton. On the basis of Chl a -specific absorption spectra (a^*) and the sun light spectra Q_{phar} was calculated for each depth from surface down to 3.4 m depth according to Gilbert *et al.* (2000a)

$$Q_{phar} = \int_{400nm}^{700nm} Q(\lambda) - Q(\lambda) \cdot e^{(-a^*(\lambda) [Chl a] \cdot d)} d\lambda \quad (5)$$

Q_{phar} : photosynthetically absorbed radiation [$\mu\text{mol m}^{-2} \text{ s}^{-1}$]

Q : photosynthetically active radiation [$\mu\text{mol m}^{-2} \text{ s}^{-1}$]

a^* : chlorophyll a -specific *in vivo* absorption coefficient at wavelength λ [$\text{m}^2 \text{ mg}^{-1}$ (Chl a)]

[Chl a]: chlorophyll a -concentration [mg (Chl a) m^{-3}]

d : layer depth [m]

The absorption spectra of natural samples were measured from 400 to 750 nm using a ZEISS M500 spectrophotometer. The chlorophyll a -specific absorption coefficients a^* [$\text{m}^2 \text{ mg}^{-1}$ Chl a] were calculated as:

$$a^*(\lambda) = E(\lambda) \cdot 2.303 / (d \cdot [Chl a]) \quad (6)$$

$E(\lambda)$: extinction at wavelength λ

- 2.303: conversion factor from decimal to natural logarithm
- d : optical path length [m]
- [Chl a]: chlorophyll a -concentration in [$\text{mg} \text{ (Chl } a) \text{ m}^{-3}$]

Photosynthesis-Irradiance (P-I) curves were measured by fluorescence (Schreiber *et al.* 1995) using a Xe-PAM fluorometer (Walz Effeltrich, Germany). The PI-parameters α (initial slope), I_k (characteristic irradiance) and P_m (maximum rate of photosynthesis) were calculated from the PI-curves according to the dynamic model of Eilers and Peeters (1988).

The photosynthetic quantum yield of freshwater phytoplankton samples at any given depth z [m] were calculated as:

$$\varphi(z) = \frac{\Phi_m \cdot (I_k \cdot a^* [\text{Chl } a])}{(I_k \cdot a^* [\text{Chl } a] + Q_{phar})} \quad (7)$$

- $\varphi(z)$: quantum yield at depth z [m]
- Φ_m : maximal quantum yield at depth z [m]
- I_k : value transition point at onset of light saturate dphotosynthesis
- a^* : chlorophyll a -specific *in vivo* absorption coefficient [$\text{m}^2 \text{ mg}^{-1} \text{ (Chl } a)$]
- Q_{phar} : photosynthetically absorbed radiation [$\mu\text{mol m}^{-2} \text{ s}^{-1}$]

RESULTS

Fig. 1 shows the Secchi-disk transparency and the surface chlorophyll a -concentrations during the vegetation period in 2002. Although biweekly sampling may not document all changes in such a productive lake, the data give clear evidence that the Secchi-disk transparency is closely correlated with the Chl a -content. This indicates that water transparency is mainly reduced by the phytoplankton density and not by other particulate matter. The mean Secchi depth was generally low (0.8 m), except in June 2002, when the trans-

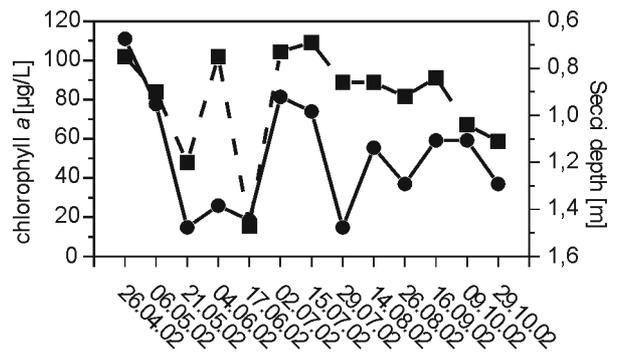


Fig. 1. Seasonal variation in Secchi depth (full squares) and chlorophyll a -concentration (full circles) in Lake Auensee (2002).

parency increased up to 1.5 m. Therefore, the euphotic zone is restricted to the upper 1.8 m. Chl a -concentrations vary during vegetation season between 20 and 100 $\mu\text{g L}^{-1}$. Maximum values were detected in spring (110 $\mu\text{g L}^{-1}$), at the beginning of summer (78 $\mu\text{g L}^{-1}$) and autumn (58 $\mu\text{g L}^{-1}$). It has to be emphasized that the Chl a -concentration in 1 m, 2 m and 3 m was similar to the surface concentration. If the chlorophyll a -concentrations of the surface layer (see Fig. 1) are added up, then chlorophyll a -concentrations per area ranged between 300-400 mg m^{-2} . These parameters confirm the hypertrophic state of Lake Auensee.

The noon time oxygen saturation at different depth during the vegetation period is shown in Fig. 2. The surface layer (0-1 m) showed large oscillations due to photosynthetic oxygen release and respiration losses, depending on variations in the daily solar irradiation and phytoplankton biomass. Below the euphotic zone the oxygen concentration decreased dramatically to zero. The sediment was anoxic from the beginning of the year until the autumn over turn.

The hypertrophic situation is furthermore confirmed by the nutrient concentrations given in Fig. 3. The nitrate concentrations ranged between 1.9 and 4 mg L^{-1} with the maximum values detected in the upper water layer during early

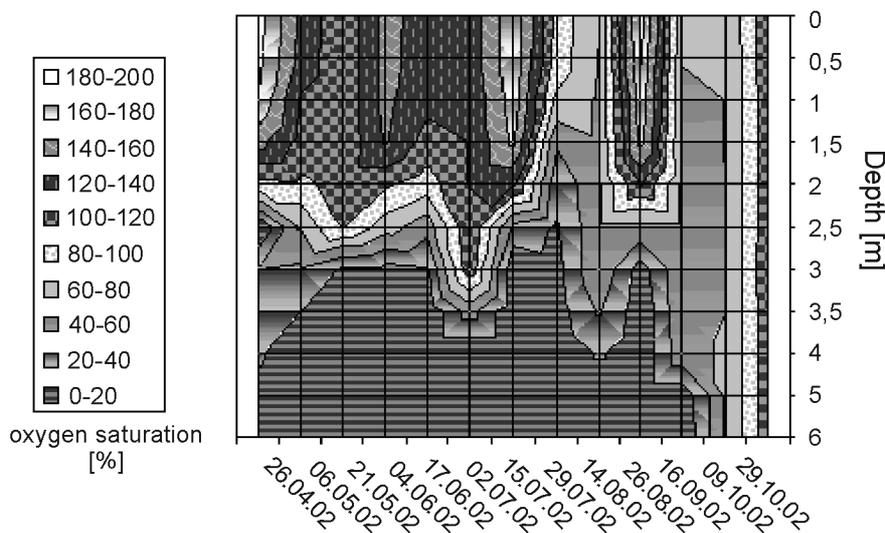


Fig. 2. Oxygen saturation [%] at different depth in Lake Auensee (2002). Note that the sediment is oxygen-free throughout the whole period (dark horizontal stripes) whereas the upper layers are oxygen saturated due to photosynthesis.

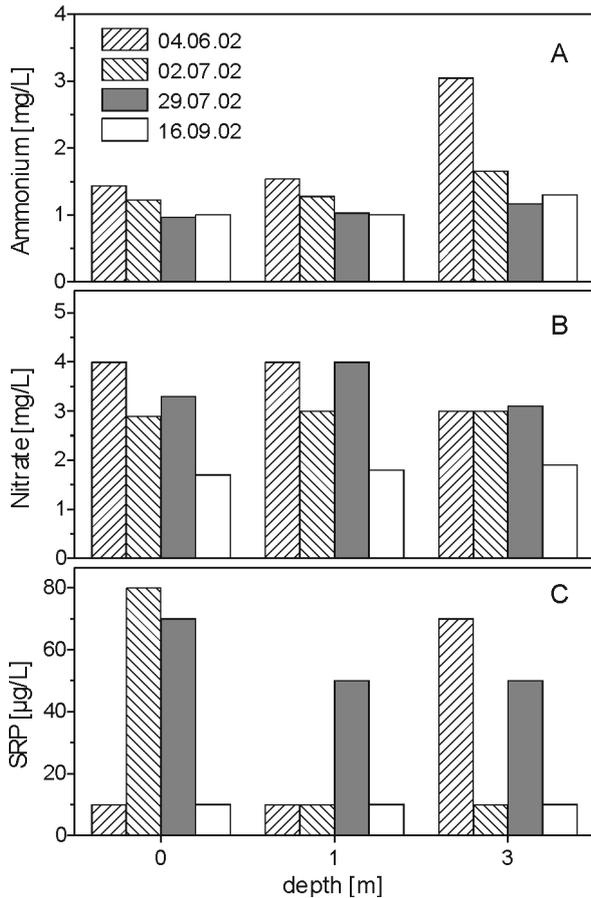


Fig. 3. Seasonal variation in the concentrations of nitrate (A), ammonium (B), and soluble reactive phosphorus (A) at three different depths in Lake Auensee (2002).

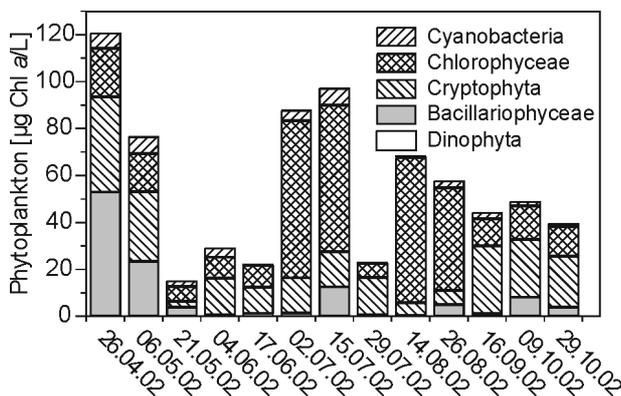


Fig. 4. Changes in phytoplankton composition in the surface water layer in Lake Auensee (2002) analysed by means of HPLC-aided pigment analysis.

summer. Ammonium concentrations were found between 1 and 2 mg L^{-1} in the euphotic part of the water column, reaching 6–12 mg L^{-1} close to the surface (data not shown).

A similar distribution was detected for soluble reactive phosphorus (SRP) concentrations. In the euphotic zone 10 and 80 $\mu\text{g L}^{-1}$ SRP were detected even in July ($>70 \mu\text{g L}^{-1}$). Due to the anoxic conditions in the sediment, phosphorus release and nutrient seepage water increased from summer to autumn.

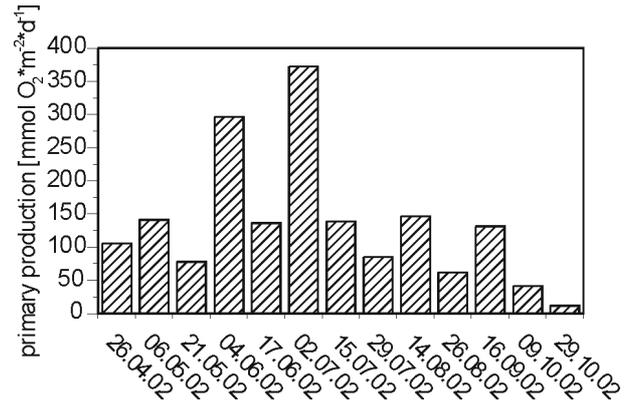


Fig. 5. Daily primary production in Lake Auensee measured by means of bio-optical modelling (for details see Materials and Methods) at different days in 2002.

The phytoplankton dynamic is characterized by fast changes in community structure as shown in Fig. 4. Based on HPLC analyzed pigment data the phytoplankton community starts in spring with a dominance of Bacillariophyceae, followed by Chlorophyceae in summer and by Cryptophyceae in autumn 2002. Between the phytoplankton biomass peaks, species of Cryptophyceae and Chlorophyceae were major constituents of the community. In May and at the beginning of June, mats of *Cladophora* sp. were observed as well as scums of *Microcystis aeruginosa*. The fast changes between different phytoplankton communities are a consequence of high growth rates of and and competition between the phytoplankton species.

The P-I curves of native phytoplankton samples were measured and integrated in a bio-optical model to calculate the absolute PP. Fig. 5 shows the estimated daily PP for 13 days in 2002. The daily PP ranged between 70 and 380 $\text{mmol O}_2 \text{m}^{-2} \text{d}^{-1}$. The observed differences between measurements are due to changes in the present phytoplankton biomass, the daily radiation or changes in the photosynthetic performance. The daily oxygen production was converted into biomass assuming that the ratio of C:O is equal and the phytoplankton biomass consists of $\text{C}_{106}\text{H}_{180}\text{O}_{45}\text{N}_{16}\text{P}_1$. The daily oxygen production was equivalent to 1–8 $\text{g biomass m}^{-2} \text{day}^{-1}$. The results of the daily PP during the year can be used to assess the annual PP, if the solar irradiation and temperature are taken into account. Based on these data the annual primary production between 500 and 600 $\text{g biomass m}^{-2} \text{a}^{-1}$ was estimated for Lake Auensee.

DISCUSSION

The fast changes between “clear water stages” and blooms in summer indicate a short circuit of the nutrients as well as strong grazing pressure. The half saturation constant for ammonium uptake was found to be between 0.1 and 29 μM ammonium (Kohl, Nicklisch 1988) whereas in Lake Auensee the ammonium concentration drops never below 70 μM . Therefore, photosynthetic electrons can be used without relevant losses for carbon assimilation. Taking the nitrate availability into account it is obvious that the phytoplankton growth is not limited by nitrate or by phosphate. The half

saturation constant for phosphate uptake is 0.6 μM for *Scenedesmus* sp. and *Asterionella formosa* (Gotham, Rhee 1981) and twice as much for the cyanobacteria *Anabaena flos-aquae* and *Microcystis aeruginosa*. However, the SRP was found to be about 1 μM throughout the summer. Therefore, we conclude that the phytoplankton growth is determined only by the efficiency of photosynthesis in Lake Auensee. Under this condition, the bio-optical model to estimate primary production is based on light absorption and photosynthetic quantum yields. It has been shown that fluorescence based electron transport rates are equivalent to oxygen production rates if both are referred to the number of absorbed quanta (Gilbert *et al.* 2000b). Comparing the results with outdoor algal mass cultures can validate the modeled phytoplankton PP. Söder (1981) used *Scenedesmus* outdoor cultures which has a similar yearly solar irradiance and energy budget. He found a maximal daily primary production of 11 g biomass $\text{m}^{-2} \text{day}^{-1}$. This value is close to the maximum of 8 g biomass $\text{m}^{-2} \text{day}^{-1}$ found in lake Auensee. In summary, the result from the bio-optical modeling is in good agreement with the values of algal biomass production in ponds. Therefore, the model presented here is a method to measure true primary production. Additionally, it can be confirmed that phytoplankton PP of lake Ausensee is not nutrient limited. Concluding, problems in measuring primary production by bottle exposure techniques will not any longer limit water quality surveillance.

Our model has an important additional advantage. The so-called Phyto-PAM (Walz, Effeltrich, Germany) allows measuring the photosynthetic quantum yields selectively for diatoms, green algae, and cyanobacteria as reported by Jakob *et al.* (subm.). Together with this information and the knowledge of the relative contribution of the major algal taxa to total chlorophyll calculated by HPLC-pigment fingerprinting (Wilhelm *et al.* 1995) or via flow-cytometry (Becker *et al.* 2002), it is easy to determine the contribution of the major algal taxa to total primary production. This taxon-resolved information is a solid basis for improved short-term water quality prediction and will contribute to our understanding of plankton communities.

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