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The formation and dynamics of deep bacteriochlorophyll maximum in the temperate and partly meromictic Lake Verevi

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Abstract

Vertical distribution of phytoplankton and the formation of deep chlorophyll maximum (DCM) in the metalimnion of a small stratified and partly meromictic temperate lake was studied in 1999 and 2000. During summer DCM usually occurred on the borderline of H_2S and oxygen-containing waters. At the depths where the bacteriochlorophyll (Bchl) maxima were observed, the sulphide concentration was usually relatively low compared to the bottom layers, where its concentration reached as high as possible saturation level. In April 2000, DCM was formed at the depth of 3.5 m, and lowered thereafter slowly to 6.5 m by October. The concentration of Bchl *d* reached the highest values (over 1000 $\mu g\ l^{-1}$) just before the water column was mixed up in autumn. In December and April Bchl *d* was detectable only near the bottom of the lake. The concentration of chlorophyll *a* yielded by the spectrophotometric phaeopigment corrected method and by HPLC (high pressure liquid chromatography), fit rather well in the upper layers. In deeper water layers chlorophyll *a* concentration (Chl *a*) measured by spectrophotometry was overestimated about 47 times if compared to HPLC values because of the high Bchl *d* in that layer. In most cases vertical profiles of primary production (PP) did not coincide with the vertical distribution of the pigment content; the maximum values of PP were found in the epilimnion. In some cases PP had notably high values also at the depth of DCM. In the upper layers Chl *a* usually did not exceeded 20 $\mu g\ l^{-1}$ in spring and 10 $\mu g\ l^{-1}$ in summer. The moderately high Chl *a* in the epilimnion in spring was significantly reduced after the formation of thermocline most probably because of the establishment of the nutrient limitation in epilimnion. Decreasing Chl *a* concentration in the epilimnion led to increased water transparency and better light conditions for photosynthetic bacteria in metalimnion.

Introduction

Anoxygenic photosynthetic bacteria contain a single type of reaction centre with a pigment bacteriochlorophyll, which absorbs light of longer, less energy-rich wavelengths than plant chlorophylls (Brock et al., 1994). Green bacteria (Chlorobiaceae) and purple sulphur bacteria (Chromatiaceae) use elemental sulphur, sulphide, thiosulfate, or hydrogen gas as electrondonor, whereas the purple non-sulphur bacteria use electrons from hydrogen or organic substrates. All these bacteria require anaerobic conditions for photosynthetic activity and can grow at very low light intensities. They are present where light reaches anaerobic, sulphide-containing zones in lakes. In meromictic or stagnant holomictic lakes, a dense population of photosynthetic bacteria appears frequently in the contact layer between the oxidative and reductive zones (Takahashi & Ichi-

mura, 1970). By dominating in anoxic regions of the water column they influence primary production (PP), elemental cycling, and trophic interactions (Hurley & Watras, 1991). These bacteria keep growing during the season and show a characteristic pattern of vertical distribution (Takahashi & Ichimura, 1968).

The main factors determining the growth of photosynthetic sulphur bacteria in lakes are H_2S concentration and light conditions (Takahashi & Ichimura, 1970; Steenbergen & Korthals, 1982; Rodrigo et al., 2000). In many aquatic ecosystems, selective attenuation determines that only certain wavelengths of light reach the water layer containing sulphide. For purple and green sulphur bacteria that possess pigments with a specific absorption spectrum, light quality and intensity are key factors in determining which types of bacteria can develop in certain conditions (Parkin & Brock, 1980; Guerrero et al., 1985).

Pigment concentrations are used as indirect measures of photosynthetic biomass in planktonic community. Chlorophyll *a* is the most common measure of phytoplankton biomass while bacteriochlorophylls act as markers for phototrophic bacteria (Hurley & Watras, 1991).

The present paper studied the formation of deep chlorophyll maximum (DCM) in the metalimnion of a small stratified and partly meromictic temperate lake with the aim to quantify the extent of DCM and to find out the regularities and controlling factors of its development.

Description of the study site

Lake Verevi is a hypertrophic but partly meromictic lake with an area of 12.6 ha, maximum depth of 11.0 m, and mean depth of 3.6 m (for more details see Ott et al., present issue). During the summer period the thermocline and chemocline are well established (Figs. 1 and 2).

Materials and methods

Lake Verevi was investigated 15 times from April to December in 2000. On 7 September 1999, samples were taken for performing the HPLC (high pressure liquid chromatography) analysis. Samples were collected at the deepest area of the lake from eight different depth horizons (Table 1), chosen depending on the vertical profiles of temperature and oxygen. Water transparency was measured by a Secchi disc. The profiles of temperature and dissolved oxygen were measured vertically using an Aqua-Check Water Analyzer (USA). Nutrient analyses were performed using the photometric methods described by Grasshoff et al. (1983): soluble reactive phosphorus (SRP) was measured by the molybdate blue method using ascorbic acid as reductant; nitrates were reduced to nitrites by reduction with a cadmium column; in order to determine total nitrogen and total phosphorus, organic compounds were mineralized into nitrite and phosphate, using persulphate. The concentration of sulphide was determined by the methylene blue method described by Parkin & Brock (1980) using an HACH DR/2000 spectrophotometer (USA).

Chlorophyll *a* and Bchl *d* were determined spectrophotometrically using their maximum absorption wavelengths in 90% acetone, 662–665 nm and 654 nm respectively. Pigment samples were filtered on Whatman GF/F filters and extracted with 90% acetone by soaking the filters in the solvent for 4 h at room temperature. The extracts were vortexed and centrifuged for 10 min at 3000 rpm min^{-1}. The absorption of the extract was determined in the region of 430–800 nm by the scanning UV–VIS spectrophotometer Cecil-3000 (Great Britain). Chl *a* concentration was calculated by the equations of Jeffrey & Humphrey (1975) and Lorenzen (1967). For bacteriochlorophyll *d* the equation of Takahashi & Ichimura (1970) was used.

For HPLC analysis in September 1999, the filters were soaked in 1 ml methanol and extracts were sonicated before injection into the column. The analysis of photosynthetic pigments was performed with an HPLC system consisting of an HP 79852A solvent delivery system, coupled to an HP1100 variable-wavelength adsorbance detector. The separating column was a 25 cm long 0.5 cm ID 5 μm ODS-Hypersil column. The injection volume was 100 μl and the flow rate was 1 ml min^{-1}. The samples were injected via a Rheodyne 7125 dosator. Absorption was measured at the wavelength of 435 nm. The solvents and the gradient are described by Mantoura & Llewellyn