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Primary production of phytoplankton in a strongly stratified temperate lake

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Abstract

Lake Verevi (12.6 ha, maximum depth 11.0 m, mean depth 3.6 m) is a strongly eutrophic and stratified lake. *Planktothrix agardhii* is the most characteristic phytoplankton species in summer and autumn, while photosynthesizing sulphur bacteria can occur massively in the metalimnion. Primary production (PP) and chlorophyll *a* concentration (Chl *a*) were seasonally studied in 1991, 1993, 2000, and 2001. Vertical distribution of PP was rather complex, having usually two peaks, one at or near the surface (0–1 m), and another deeper (at 3–7 m) in the metalimnion. The values of dark fixation of CO_2 in the metalimnion were in most cases higher than those in the upper water layer. Considering the average daily PP 896 mg C m^{-2} and yearly PP 162 mg C m^{-2}, Secchi depth 2.34 m, and epilimnetic concentrations of chlorophyll *a* (19.6 mg m^{-3}), total nitrogen and total phosphorus (TP, 52 mg m^{-3}) in 2000, L. Verevi is a eutrophic lake of a 'good' status. Considering the total amounts of nutrients stored in the hypolimnion, the average potential concentrations in the whole water column could achieve 1885 mg m^{-3} of TN and 170 mg m^{-3} of TP reflecting hypertrophic conditions and a 'bad' status. Improvement of the epilimnetic water quality from the 1990s to the 2000s may have resulted from incomplete spring mixing and might not reflect the real improvement. A decreased nutrient concentration in the epilimnion has supported the establishment of a 'clear epilimnion state' allowing light to penetrate into the nutrient-rich metalimnion and sustaining a high production of cyanobacteria and phototrophic sulphur bacteria.

Introduction

Primary production (PP) of photoautotrophic organisms, first of all phytoplankton, is a process that depends on and influences many biotic and abiotic mechanisms representing a major synthesis of organic matter in aquatic systems. It initiates food chains and forms a basis of the ecological pyramid. Uncertainties in PP will influence all other calculations of productivity, for example zooplankton and fish. PP also forms the most relevant basis for the classification of lakes into different trophic categories (Hakason & Boulion, 2002).

Photosynthesis is often low at the lake surface, due to inhibition by ultraviolet light, with a peak at some depth below. This peak is set at light saturation (I_k); its size and position depend on the light-saturated rate of photosynthesis per unit of biomass (P_{max}) and the total biomass (B, usually expressed as chlorophyll *a*) of the photosynthetic cells present. I_k is often low for cyanobacteria and higher for green algae. The P_{max} value tends to increase with temperature, almost doubling for every 10 °C. Photosynthesis-depth curves for stratified and non-stratified lakes are similar if primary production is expressed as per unit biomass of phytoplankton (Moss, 1998).

The rate of photosynthesis is mostly limited by the energy source (light), inorganic substrate (CO_2, H_2S for sulphur bacteria) and inorganic nutrients

(N, P, Si). In stratified lakes, light is sufficiently available in the epilimnion while the deep hypolimnion is often rich in nutrients (N, P). If surface light intensity is adequate, most phytoplankton species inhabit the fraction of the water column with the optimal light conditions. Because wind mixes the uppermost water layer, the phytoplankton is usually exposed to light intensity equal to the average light intensity of the mixing zone. During the period of stratification, the epilimnetic phytoplankton is usually nutrient-limited while low-light-adapted species (e.g. genera *Limnothrix* and *Planktothrix*) can develop pronounced maxima in the metalimnion as long as the light intensity does not drop below the compensation point for those species. Photosynthetic bacteria can develop below the phytoplankton zone in lakes with an anaerobic hypolimnion and a buildup of H_2S, as long as light penetrates into the H_2S zone (for more detailed discussion see Lampert & Sommer, 1997).

Lake Verevi (12.6 ha, maximum depth 11.0 m, mean depth 3.6 m) is a strongly eutrophic and stratified lake situated in Elva, a small summer-resort town (population 7000) in South Estonia. The situation of the lake has been observed since the 1950s, based on occasional sampling as well as some periods of seasonal measurements including water chemistry, species composition, and biomass of hydrobionts. The results of previous investigations were published in a book in Estonian (Timm, 1991). In the 1980s, *Planktothrix agardhii* (Gomont) Anagn. & Kom. was reported to be the most characteristic phytoplankton species in L. Verevi in summer and autumn. Phytoplankton biomass in summer were about 20 gWW m^{-3} and could exceed 50 gWW m^{-3} in autumn, and also under the transparent ice in February (Laugaste, 1991). In 1995–1997 an extremely pronounced seasonally changing biological stratification was found in Lake Verevi. In June, the surface layer was dominated by two filamentous cyanophytes, *Aphanizomenon flos-aquae* and *Planktothrix agardhii* together with small flagellates. At a depth of 5–6 m *Cryptomonas* sp. was a codominant to *P. agardhii*. A mass occurrence of photosynthesizing purple sulphur bacterium *Thiopedia rosea*, an obligate anaerobe, gave evidence of oxygen depletion at 5–6 m. In August, the epilimnion was inhabited by small flagellates, *A. flos-aquae* formed a dense layer in the upper part of the metalimnion, while a maximum of *P. agardhii* together with *Thiopedia rosea* was located deeper in the anoxic layers. In September, when the turbulent mixing extended to a depth of 5 m, both cyanophyte species occurred in the epilimnion. At that time green sulphur bacteria *Pelodictyon luteolum* peaked in the anoxic layer (Nõges & Nõges, 1998a).

The present paper deals with vertical distribution and diurnal, seasonal and interannual dynamics of primary production and related indices in Lake Verevi with the aim to:

1. quantify the annual rate of primary productivity; study the patterns of vertical distribution of primary production and their relationship to the physical stratification of the water column as well as to the amount of phototrophic plankton, light conditions, and nutrient regime;
2. study the seasonal dynamics of primary production, the interannual variation and relationship with the meteorological conditions and physico-chemical stratification;
3. evaluate the present ecological status of the lake.

Material and methods

Primary production in L. Verevi was measured during the period of 1991–2001 by ^{14}C-technique (Steeman-Nielsen, 1952) and *in situ* exposition. Frequency of the measurements varied on a large scale (Table 1). In 1991, 1993 and 1995–1997 measurements of particulated PP were made with $NaH^{14}CO_3$ (Izotop, St. Petersburg), final activity of 0.08 μCi ml^{-1}. The metalimnion was defined as the layer in which the temperature gradient was ≥1.5 °C m^{-1} (Nõges & Nõges, 1998a). The water from the epi- and metalimnion was poured into 24 ml glass scintillation vials. When handling the anaerobic water from the metalimnion, special attention was paid to maintaining the anaerobic and low light conditions – the vials were kept in a dark box, the tube from the water sampler was placed on the bottom of the vial and the water was allowed to overflow slowly from the vial for some seconds. The vials were incubated for 2 h at midday (usually from 11 a.m. to 1 p.m.) in the lake, at the same depths where the water was taken from