

Resource ratios and phytoplankton species composition in a strongly stratified lake

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Abstract

The epilimnetic phytoplankton and its relations to nutrient content in Lake Verevi through the whole vegetation period in 2000 were studied. Lake Verevi (surface 12.6 ha, mean depth 3.6 m, maximum depth 11 m) is a hypertrophic hard-water lake, where the so-called spring meromixis occurs due to an extremely warm spring. Most dissolved nutrients in the epilimnion were low already in spring, and their concentrations were quite stable during the study period. The concentration of total silicon was very low in spring but increased rapidly in summer. Total phosphorus followed the pattern for stratified eutrophic lakes, and total nitrogen was quite high. The stoichiometric N:P ratio fluctuated between 25 and 81. The dynamics of phytoplankton biomass with a spring peak from April to May and a late summer peak from July to August is typical of Estonian eutrophic lakes. Green algae and chrysophytes occurred in the phytoplankton throughout the vegetation period. The spring peak was dominated by diatoms (*Synedra ulna* and *Synedra acus* var. *angustissima*) and the summer peak was caused by *Aphanizomenon klebahnii* and *Ceratium hirundinella*. The study showed that in physically stratified systems, the total concentration of limiting resources and plain physical factors (light and temperature) may be more important in the determination of phytoplankton dominants than different resource ratios. A combination of light and temperature optimum, along with nutrient utilization and transport capacity, effectively segregates phytoplankton species and can be used for the explanation of seasonal succession pattern.

Introduction

Our knowledge about the abiotic and biotic factors regulating the species composition of natural phytoplankton communities is still very sketchy. The mechanisms explaining the species dominance patterns in lakes during the vegetation period vary greatly and sometimes even show discrepancies. Among numerous hypotheses, the use of resource ratios, as predictor of microalgal species composition, is the most applicable in limnological practice. The resource–ratio hypothesis is the backbone in Tilman's mechanistic theory of com-

petition (Tilman, 1977, 1982), which uses simple graphical models to predict the steady state outcome of competition for two potentially limiting resources from single species physiological traits. Tilman's theory has been thoroughly tested by chemostat experiments in the laboratory with algae from unialgal strains and with natural phytoplankton communities (Sommer, 1989, 1993; Smith & Bennet, 1999). However, these arguments did not sound convincing to all limnologists, and some skepticism exists in the literature concerning the potential applicability of this equilibrium theory to real-world ecological systems (Reynolds,

1996, 1999). Although there is sample evidence to support a strong effect of the resource ratios on phytoplankton structure and functioning, some additional factors are clearly important, and these moderating factors may override other factors in some systems. For example, stratification, buoyancy regulation, light regime and grazing could potentially affect the phytoplankton biomass and species composition (Smith & Bennet, 1999).

The aim of the study was to describe the phytoplankton species composition and succession in the epilimnion of a strongly stratified lake, and clarify how the ratios of growth limiting resources or single abiotical factors determine biomasses of species in a community.

Materials and methods

Lake Verevi is a small and relatively deep lake situated in town Elva in South Estonia. Table 1 shows the main morphometric and limnological characteristics of this dimictic, strongly stratified hard-water lake. Additional morphometrical, hydrological and limnological data are presented by Ott et al. and Nõges & Kangro, in the present issue. Human activities in the watershed cause considerable input of domestic pollutants and Lake Verevi has changed from moderately eutrophic at the beginning of 20th century to a hypertrophic lake in the 1980s. The highly eutrophic phase persists still today.

The lake was sampled from April to October 2000 at the deepest point located in the broader part near the western shore. Physical data (transparency, temperature) was recorded weekly. The temperature profiles were measured vertically using the multiprobe Aqua-Check Water Analyzer (USA). Underwater light intensity was not measured. The availability of the light resource (light

index) was calculated indirectly from the Secchi-disc readings according to Sommer (1993):

$$LI = 2(SD/Z_{mix}) \times (D/24)$$

where LI is the light index, SD is Secchi depth (m), Z_{mix} is mixing depth, and D is day length (h). Mixing depth was defined as upper water layer in which the temperature gradient was $< 1.5^{\circ}\text{C m}^{-1}$.

Biological and chemical data were collected by a pre-planned programme (for details see Nõges & Solovjova, 2005) that covers densely mixing periods in spring and autumn and has longer intervals in the stagnation period. Water samples were taken at two depths, at 0.5 m (Layer 1) and in the middle of the epilimnion (Layer 2). The latter sampling depth differed from case to case depending on the evolution of the stratification. The phytoplankton and water samples were gathered using a special vacuum probe. A Masterflex pump (model N 7533-60) with an easy-load pump head (model 7518-12) was used for pumping water to the surface. A hose with inner Ø 8 mm was placed vertically into the water. The lower tip of the hose was closed and the water was sucked through a horizontal tube in order to obtain water from horizontal layers. The capacity of the complex device was approximately 2 l min^{-1} . For more details see Zingel & Ott (2000).

Chemical analyses were performed using the methods described by Grasshoff et al. (1982). Dissolved reactive phosphorus (SRP) was measured by the molybdate blue method using ascorbic acid as reductant. Nitrate and nitrite were determined by reduction with a cadmium column. In order to determine total nitrogen (TN) and total phosphorus (TP), organic compounds were mineralized into nitrite and phosphate, using persulphate. Standard photometric analysis was applied to complete each named estimation (Grasshoff et al., 1982). The silicon content was

Table 1. Morphological and limnological characteristics (epilimnion in summer during 1998–2000) of Lake Verevi, South Estonia

Morphometrical parameters		Limnological parameters min. . max	
Surface area (ha)	12.6	Secchi depth (m)	0.7 ... 4.2
Volume, 10^6 m^3	453.6	Tot P, $\mu\text{g l}^{-1}$	22 ... 153
Maximum depth (m)	11.0	Tot N, $\mu\text{g l}^{-1}$	670 ... 2450
Mean depth (m)	3.6	Chlorophyll <i>a</i> , $\mu\text{g l}^{-1}$	4 ... 110
Water exchange times per year	0.63	Silicon, mg l^{-1}	100 ... 8