Article

Phytoplankton dynamics in a shallow lake dominated by common water milfoil

Kerstin Häggqvist[1*] and Tore Lindholm[2]

[1] *Åbo Akademi University, Department of Biosciences/Biochemistry, Artillerigatan 6A, 20520, Åbo, Finland*
[2] *Åbo Akademi University, Department of Biosciences/Environmental and Marine Biology, Artillerigatan 6A, 20520 Åbo, Finland*
* *Corresponding author email: kerstin.haggqvist@abo.fi*

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Abstract

Phytoplankton temporal fluctuation and vertical distribution were studied by seasonal and close interval siphon sampling (May-Sep) in a shallow lake dominated by common water milfoil (*Myriophyllum sibiricum*). Factors potentially regulating phytoplankton primary production were investigated *in situ* in 2 enrichment bioassays. The results suggest that the macrophyte vegetation provided an unfavourable habitat for large colonial chlorophytes. Small species, mainly cryptophytes but also small chlorophytes and cyanobacteria, characterised the summer phytoplankton. Phytoplankton abundance as well as primary production were considerable and remained in the mesotrophic range. The total nitrogen to total phosphorus ratio during the growth season, and the enrichment bioassays, showed that phosphorus was a significant regulator of primary production. Small-celled species had competitive advantages in the dense vegetation, and the canopy structure created by dense stands of common water milfoil allowed phytoplankton growth. Hence, although the macrophytes altered the physical and chemical conditions in the lake, coexistence of small-celled algae and macrophytes was possible.

Key words: high pH, limiting factor, microstratification, *Myriophyllum sibiricum*, phytoplankton, shallow lake

Introduction

Changes in steady states have been documented in an array of different ecosystems, where a shift from one stable state to another takes place as the ecosystem passes its boundary of resilience (Scheffer et al. 2001, Folke et al. 2004). Stable states in eutrophic, shallow lakes were among the first described examples of the phenomenon (Carpenter et al. 1985, Scheffer et al. 1993). These lakes may have clear water dominated by macrophytes, or turbid water dominated by phytoplankton (Moss 1990, Scheffer 1990, Scheffer et al. 1993, Janse 1997). The processes involved in the regime shifts are far from straightforward; the various feedback mechanisms interact, and the extent to which they control the stable states is often lake specific (Mulderij et al. 2007, Scheffer and van Nes 2007, Sayer et al. 2010).

The alternating phytoplankton–macrophyte regimes of shallow, eutrophic lakes are well studied (Scheffer et al. 2001, Scheffer and van Nes 2007). Phytoplankton population and abundance in lakes without macrophytes are different from those in lakes with macrophytes (Moss 1990, Jasser 1995). The underlying mechanisms or combination of mechanisms for such a response are hard to determine due to the complex macrophyte–phytoplankton interactions (Søndergaard and Moss 1998, Sayer et al. 2010). Free-floating macrophytes are able to effectively reduce phytoplankton biomass and species diversity, but the phytoplankton response depends on the periodicity and extent of macrophyte dominance (O'Farrell et al. 2009). Macrophyte dominance in shallow oxbow lakes significantly influences phytoplankton species structure but does not automatically result in clear water (Krasznai et al. 2010). Schriver et al. (1995) pointed out the

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influence of zooplankton on phytoplankton in dense macrophyte vegetation but noted the presence of other structuring factors as well. Thus, the habitat created by macrophytes depends on their composition, coverage, growth form, and seasonal dynamics, with subsequent diverse responses among the phytoplankton, at times leading to neither strictly clear nor strictly turbid water states in shallow lakes (O'Farrell et al. 2009, Krasznai et al. 2010, Sayer et al. 2010).

In this study we explored the phytoplankton in a shallow lake dominated by dense stands of common water milfoil (*Myriophyllum sibiricum*). Although the macrophytes covered nearly the whole lake area (Lindholm et al. 2008), the growth form of *Myriophyllum* spp. does not strongly diminish the subsurface light (Mulderij et al. 2007). Phytoplankton dynamics were investigated by seasonal sampling (May-Sep). Using close interval sampling we studied the minute vertical distribution of the phytoplankton in the dense vegetation. In addition, we considered factors potentially regulating phytoplankton primary production in 2 enrichment bioassays *in situ*.

Study site

Lake Österträsk (60°21′15.0588″N, 20°0′2.819″E, Åland, southwest Finland; Fig. 1) is a shallow lake characterised by dense growth of common water milfoil (*Myriophyllum sibiricum*) since the beginning of the 1990s (Lindholm and Hägg 2001). High summer pH values, as high as pH >10, and clear water are other features of the shallow lake (Lindholm and Hägg 2001, Lindholm et al. 2008). Lake mean depth is about 2 m, maximum depth <4 m, and the surface area is 25 ha (Lindholm et al. 2008). The 3.5 km^2 catchment area consists of rocks, moraine, coniferous

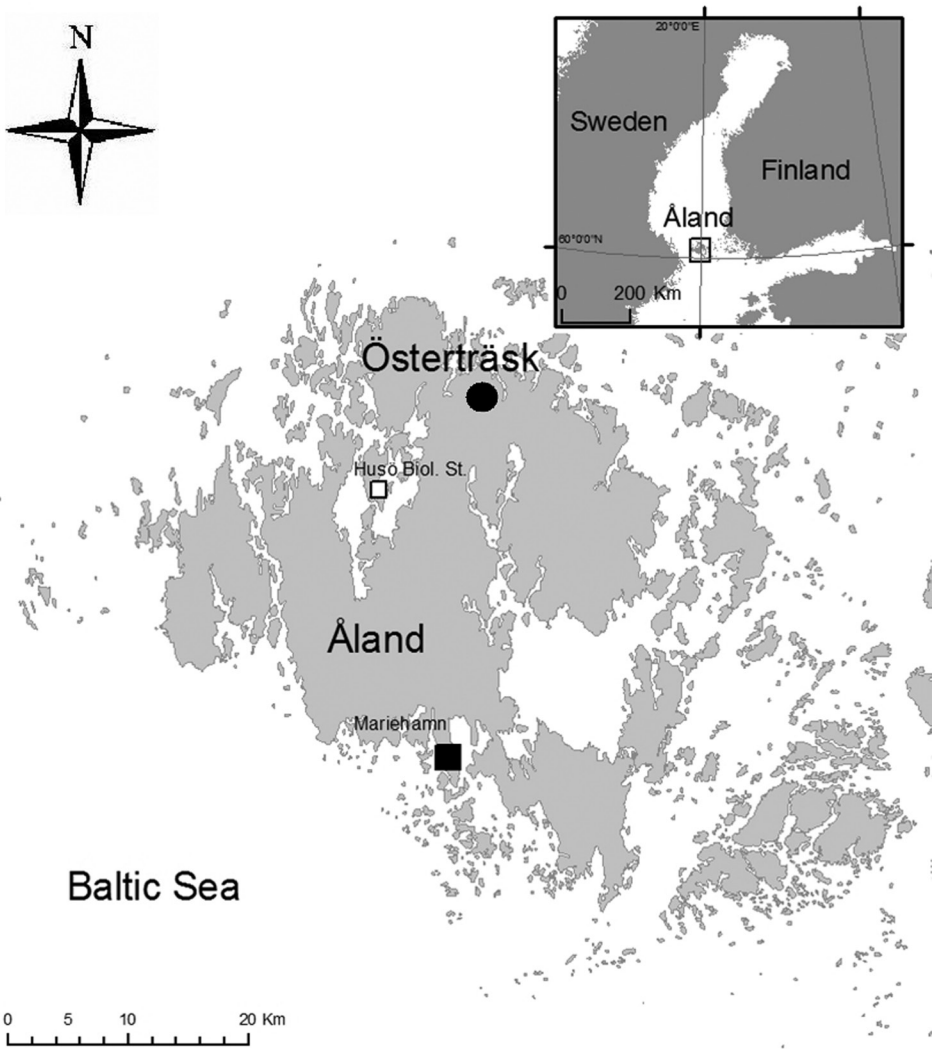

Fig. 1. Study area.

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forests, and some fields (Lindholm et al. 2008). In the 1940s the lake was described as oligotrophic, and no common water milfoil was reported (Cedercreutz 1947). In the late 1970s moderate eutrophication was observed (Storberg 1980). At the time of our study, average surface concentration of total nitrogen was 250–600 μg L^{-1}, and total phosphorus 20–28 μg L^{-1} (Lindholm et al. 2008). With the exception of local common reed (*Phragmites australis*) and green filamentous algae along the shoreline, common water milfoil dominated the whole lake from late July (Lindholm et al. 2008). The summer of 2006 was dry, and in Österträsk the water level gradually sank, reaching a value of −55 cm in late August.

Methods

During May–September 2006 water samples were taken once or twice a month (Limnos water sampler, 2 L) at the centre of the lake at every 0.5 m depth down to 3.5 m. Secchi depth, temperature, and light (LI 188B radiometer) were measured at every sampling. The samples were analysed for pH, dissolved oxygen (DO), chlorophyll *a* (Chl-*a*), total nitrogen (TN) and total phosphorus (TP). Phytoplankton primary production (PP) was measured with the ^{14}C-method (Vollenweider 1969). Light and dark bottles (50 mL) were incubated *in situ* for 1.5 h and the ^{14}C-filters (Whatman NC 45) analysed (Wallac 1410 Liquid Scintillation Counter) as in Lindholm et al. (2001). Water pH was analysed in the laboratory with a Metrohm 691 pH meter. DO was measured according to the Winkler method; TN and TP were determined according to Koroleff (1983a, 1983b). For Chl-*a*, water samples of 450 mL or 500 mL were filtered (Whatman GF/C filters). The filters were deep-frozen and later homogenised, extracted in 90% acetone for 3 h, centrifuged, and analysed spectrophotometrically (SFS 1983). Phytoplankton samples were preserved with acidic Lugol's solution (0.5 mL/100 mL sample; Willén 1962). Preserved phytoplankton samples were quantified (Utermöhl 1958) in 10 mL sedimentation chambers by counting individual cells or colonies at 400× magnification in an inverted microscope (Nikon Eclipse TE 200). Generally 100 individuals of the most common species were counted in 4–6 diagonals. Sparsely occurring species >40 μm were counted at 200× magnification on the whole chamber area.

Microstratification in the macrophyte vegetation was studied 5 times during June–September by siphon sampling (Lindholm 1979) at a fixed station ~2 m deep. Water was sampled at eleven depths (0.5, 1.0, 1.5, 1.6, 1.7, 1.8, 1.9, 2.0, 2.1, 2.2, and 2.3 m). Sinking water level and increasing macrophyte vegetation at the bottom hindered the sampling at 2.1–2.3 m in July–August. The samples were analysed for pH, DO, and Chl-*a*. Secchi depth, temperature, and light were also measured. Quantification of the dominating phytoplankton species was done for every depth as described.

Factors potentially regulating phytoplankton PP were studied in 2 enrichment bioassays *in situ* (Lindholm 1978), the first 11–15 June and the second 27–31 July. The response of surface phytoplankton to addition of bottom water, iron (Fe), phosphorus and nitrogen (N + P), and phosphorus (P) was tested. Polyethylene bags (double folded, thickness 0.05 mm) were filled with lake water (9 L) and hung *in situ* on a rack. Nutrient doses (1 mL) were added to the bags once, and the order of the treatments was random. Five replicates of each treatment, as well as 5 controls (in all 25 bags) were incubated for 5 days. The nutrient doses (Table 1) simulated a doubling of ambient surface water concentrations (Table 2). Filtered (Sartorius fibreglass filters) hypoxic bottom water was added once as 5% doses; the concentration was arbitrarily determined because the bioassays were of a preliminary character. To assure the solubility of the iron dose, EDTA was added (Fe:EDTA, 1:1.5; Coale 1991). Samples for phytoplankton PP were taken on day 1, 3, and 5 in the June bioassay, on day 1 and 3 in the July bioassay, and measured *in situ* with the ^{14}C-method (Vollenweider 1969). The bottles were incubated on a horizontal rack at 0.2 m. Phytoplankton samples were taken on day 5 and quantified as described.

Table 1. Compounds and final concentrations of the added components in both enrichment bioassays.

Treatment	Added Compound	Concentration (μg L^{-1})
Fe (chelated)	$FeSO_4 \times 7\ H_2O$	10
N + P	$KNO_3 + KH_2PO_4$	200 + 20
P	KH_2PO_4	20

Table 2. Initial lake surface (0.5 m) conditions during the June bioassay (10.6.2006) and July bioassay (26.7.2006), oxygen concentration (O_2), total nitrogen (TN), total phosphorus (TP) and chlorophyll *a* (Chl-*a*).

Parameter	June Bioassay	July Bioassay
Temperature (°C)	17	22
Light (μE s^{-1} m^{-2})	900	800
pH	8	10
O_2 (mg L^{-1})	10	11
TN (μg L^{-1})	600	550
TP (μg L^{-1})	30	20
Chl-*a* (μg L^{-1})	6	4

The bioassay data, or their transformations, did not meet the assumption of equal variances, and the adequate repeated measures ANOVA was not used in the statistical analyses. Instead, differences in phytoplankton PP were studied with GMAV5 (for Windows) one-factor analyses. Differences in phytoplankton PP between the bioassays were investigated with GMAV5 2-factor analyses. Because GMAV5 requires balanced experiments, analyses of phytoplankton PP on day 3 and 5 in the June bioassay were done with 4 replicates due to missing values (because of torn bags). Analyses of differences in phytoplankton PP between the 2 bioassays were also done with 4 replicates. Homogeneity of variances was tested with Cochran's C test. To further analyse treatment differences, pairwise *a posteriori* SNK-tests were used. Phytoplankton species abundance in the enrichment bioassays was investigated with PRIMER 6.1.6. nonparametric multivariate analyses (Clarke 1993). All species data were square root transformed before the analyses to balance differences between dominating and rare species. Differences in phytoplankton species abundance was tested with similarity analyses (one-way ANOSIM). Similarity percent breakdown procedures (SIMPER) were used to study which species contributed to the differences.

Results

The DO concentration varied between 6 and 13 mg L^{-1} at 0–2.0 m (Fig. 2). Siphon sampling showed no marked temperature gradient in the macrophyte vegetation (Fig. 3a and b), but revealed, contrary to the samples taken with the Limnos water sampler, bottom hypoxia in July and August (Fig. 3b). In August–September, DO supersaturation (120–150%) was measured down to ~1.5 m, indicating high photosynthetic activity of the dense vegetation. Water pH increased from ~8 in May–June to ~10 in August (Fig. 2); the rise in pH was measured at all depths throughout the sampling season. The Secchi depth was generally >2.5 m (Fig. 2); TN varied between 155 and 600 µg L^{-1} (excluding an isolated case of high values in early June when TN max. 1220 µg L^{-1} was measured); and TP concentration remained between 15 and 30 µg L^{-1} (Fig. 2). While the concentration of TN and TP decreased at the bottom in June (Fig. 3c), an opposite pattern was measured in August (Fig. 3d). The Chl-*a* concentration at 0–2 m was on average ~9 µg L^{-1} and the phytoplankton PP ~14 mg C m^{-3} h^{-1} (Fig. 4a). During the sampling season, phytoplankton PP (P_{max}), increased from 5 mg C m^{-3} h^{-1} in May to 26 mg C m^{-3} h^{-1} in early July, and decreased to 17 mg C m^{-3} h^{-1} in September. Phytoplankton PP generally occurred down to 3 m (Fig. 4b); P_{max} and peaks in Chl-*a* as well as phytoplankton abundance (Fig. 4c) were recorded at 0–1.6 m, the maximum rate of (the highest value in a vertical series) of phytoplankton PP indicating optimal light conditions in this depth interval. With the exception of September, the Chl-*a* concentrations remained >5 µg L^{-1} above and at 2 m. The light available at 1 m was between 40 and 70% of the light available just below the surface.

In May and early June (Fig. 5a) the chrysophytes *Dinobryon divergens* and *Mallomonas* spp. dominated the phytoplankton. In June, *D. divergens* dominated down to 2.1 m, whereas deeper *Cryptomonas rostratiformis* was abundant. By end of June, *C. rostratiformis* dominated down to 2.0 m. From July and onward the proportion of predominantly small celled cyanobacteria (e.g., *Snowella* spp.) and chlorophytes (e.g., *Monoraphidium minutum*, *Nephrocytium limneticum*, *Paulschulzia pseudovolvox*,

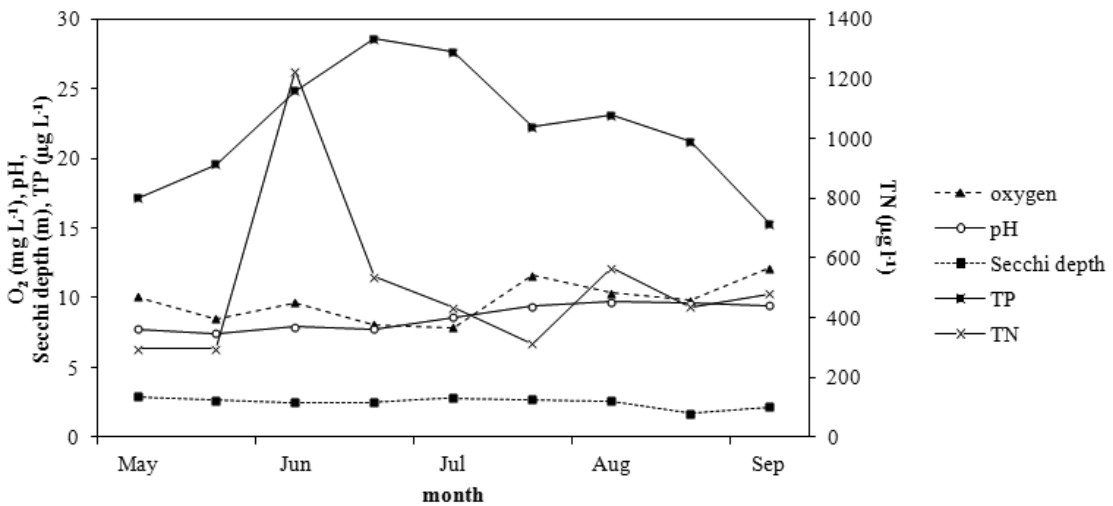

Fig. 2. Secchi depth, oxygen concentration (O_2), pH, total phosphorus (TP), and total nitrogen (TN) at 1.5 m.

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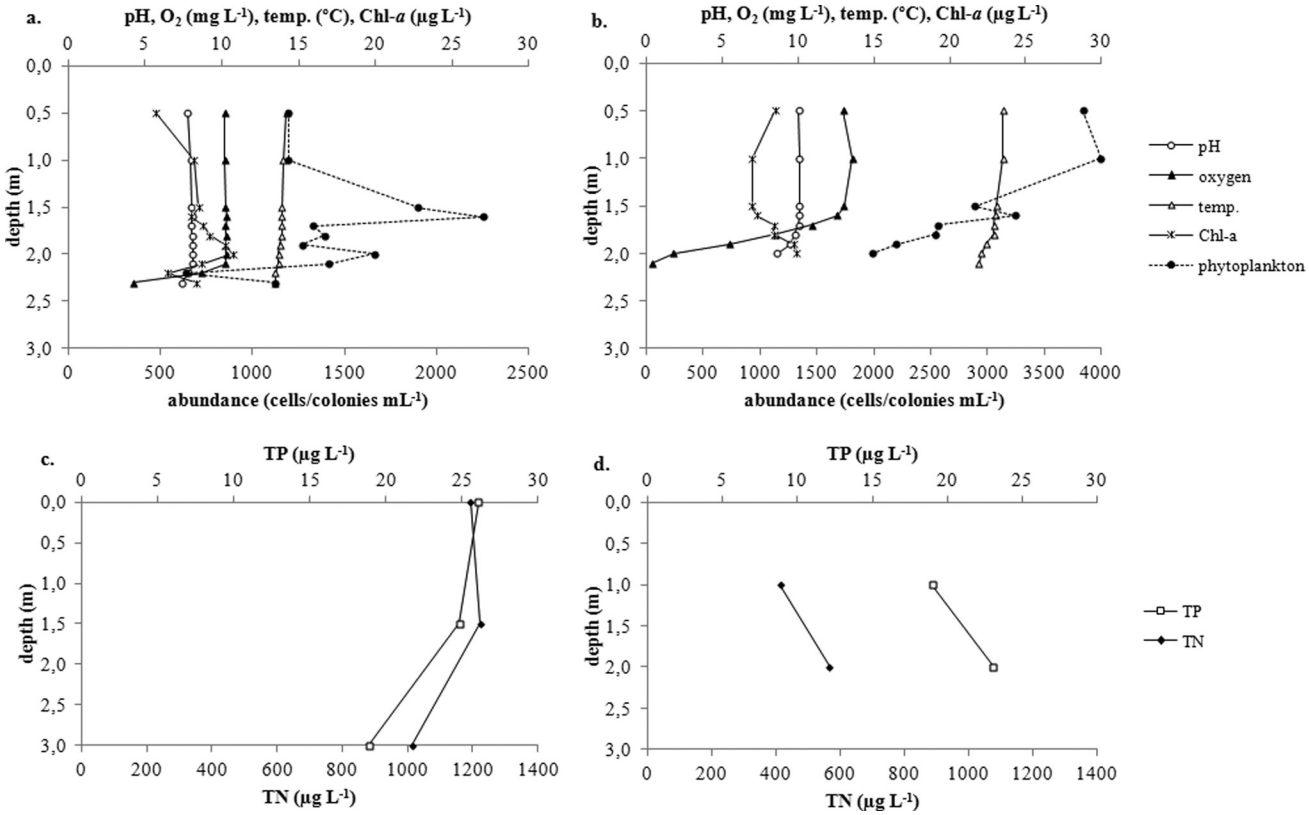

Fig. 3. Vertical profiles of pH, temperature (temp.), oxygen (O_2), chlorophyll *a* (Chl-*a*), and phytoplankton abundance in **a.** June and **b.** August. Vertical profiles of total nitrogen (TN) and total phosphorus (TP) in **c.** June and **d.** August. Total phytoplankton species number consists of individuals of which >65 cells/colonies were counted (with a theoretical confidence interval of ±25%).

P. tenera) increased (Fig. 5b–d). The 1.5–2.0 m depth interval was dominated by chlorophytes (e.g., *Monoraphidium minutum*) in July and *Snowella* spp. in August. In September an unidentified small colonial cyanobacterium (possibly *Aphanothece* sp.) dominated at every depth. Cryptophytes, especially small species (5–10 µm; *Rhodomonas*/*Plagioselmis* sp.), were abundant during the study period (Fig. 5a–d). In July and August they dominated at 0–1.5 m, but high cell densities were also observed deeper than 1.5 m.

In the June bioassay, phytoplankton PP was significantly higher in the N + P treatment on day 1 (one-factor analyses, $F_{4,20} = 26.4$, $p \leq 0.001$), day 3 (one-factor analyses, $F_{4,15} = 74.5$, $p \leq 0.001$), and day 5 (one-factor analyses, $F_{4,15} = 46.3$, $p \leq 0.001$; Fig. 6a). Phytoplankton species abundance in the N + P treatment was significantly different from the other treatments due to higher abundances of *Paulschulzia pseudovolvox* and *Micractinium pusillum* (attributing to 60% of the difference, SIMPER). In the July bioassay the phytoplankton PP in the N + P treatment, as well as the P treatment, were significantly higher on day 1 (one-factor analyses, $F_{4,20} = 10.0$, $p \leq 0.001$) and day 3 (one-factor analyses, $F_{4,20} = 1590$, $p \leq 0.001$; Fig. 6b). Phytoplankton species abundance in the N + P and the P treatments differed most due to higher abundance of *Paulschulzia pseudovolvox*, *P. tenera* and *Chlamydomonas* sp. (attributing to 55–65 % of the difference, SIMPER). A significant interaction between time of bioassay and phytoplankton PP was measured between the 2 bioassays (2-factor analyses, $F_{4,30} = 5.4$, $p \leq 0.01$). Phytoplankton PP in the N + P and in the P treatments was higher on day 3 in the July bioassay (Fig. 7). *Dinobryon divergens* and *Micractinium pusillum* were observed in the June bioassay, while *Monoraphidium minutum*, small flagellates, and *Paulschulzia tenera* were noted mainly in the July bioassay. Added bottom water or Fe did not induce a significant response in phytoplankton primary production (Fig. 6a and b, Fig. 7).

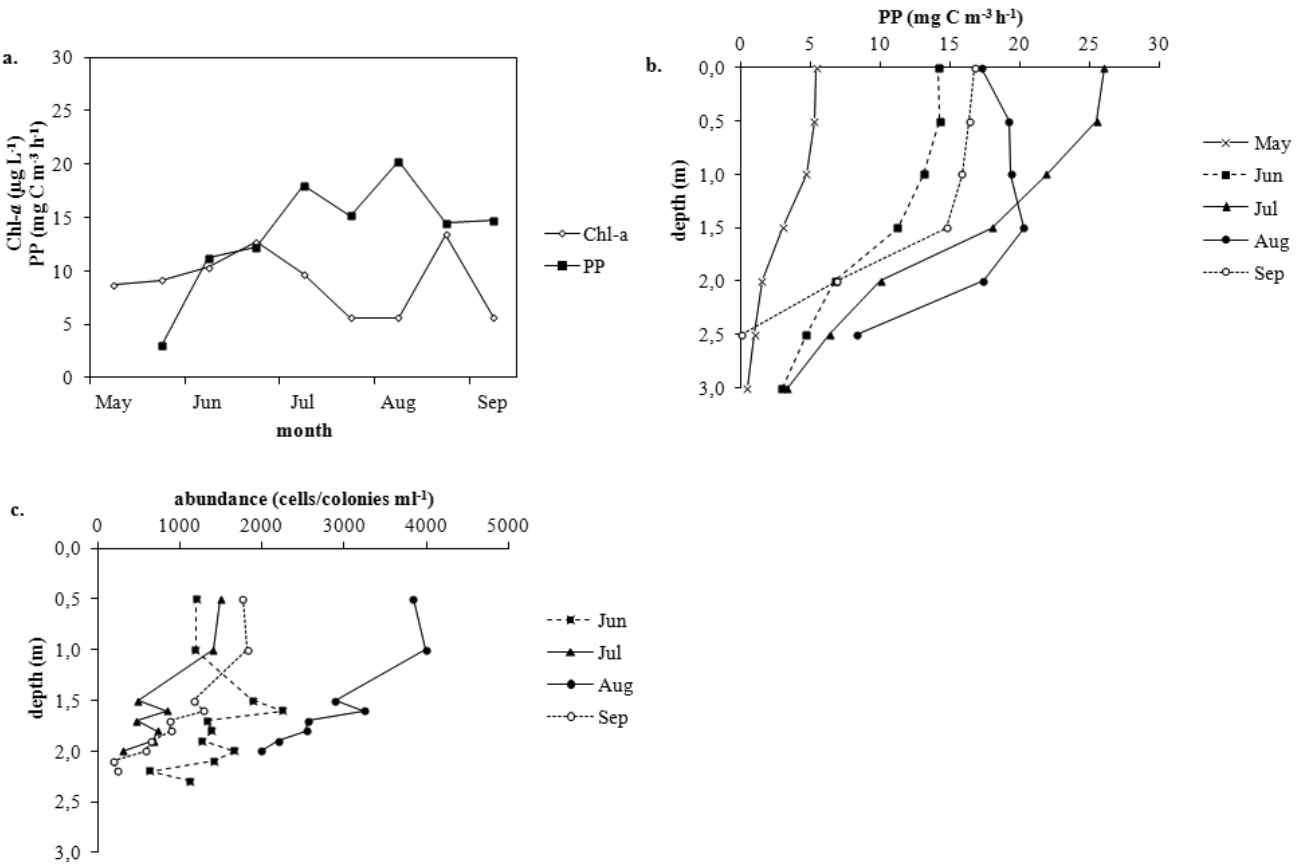

Fig. 4. a. Chlorophyll *a* (Chl-*a*) and phytoplankton primary production (PP) at 1.5 m. Vertical profiles of **b.** phytoplankton primary production (PP) and **c.** phytoplankton abundance. Total species number consists of individuals of which >65 cells/colonies were counted (with a theoretical confidence interval of ±25%).

Discussion

During the growth season in Österträsk, the phytoplankton abundance and primary production were considerable, both before and during maximum development of the macrophytes. Based on phytoplankton PP and concentration of Chl-*a*, TN, and TP, the lake was mesotrophic (criteria in Wetzel 2001, Reynolds 2006). The TN to TP ratio during May–September suggests that phosphorus was an important regulator of phytoplankton PP, as indicated by the enrichment bioassays. Also, the concentration of Chl-*a* and phytoplankton PP were within the range expected for the TP concentration of the water (criteria in Wetzel 2001). Oxygen depletion increased in August, and the dense macrophyte vegetation contributed to a considerable bottom accumulation of organic material. Dense macrophyte vegetation and decaying macrophytes may cause low bottom oxygen concentrations and increase the release of phosphorus (Søndergaard and Moss 1998, van Nes et al. 2007); thus, an internal loading of phosphorus is possible in Österträsk. Although poor bottom oxygen conditions in Österträsk created conditions for denitrification, which may significantly influence nitrogen availability in lakes with dense macrophyte vegetation (Reddy et al. 1989, Caffrey and Kemp 1992, Søndergaard and Moss 1998, Eriksson and Weisner 1999), the Chl-*a* concentration and phytoplankton PP were within the range expected for the measured TN concentration (criteria in Wetzel 2001). However, the vast amount of macrophytes showed that Österträsk was a productive lake with considerable amounts of nutrients bound to the macrophytes, which could underestimate the trophic categorization of the lake (Canfield et al. 1983).

The abundance of *Paulschulzia pseudovolvox*, *P. tenera*, and *Chlamydomonas* sp. significantly increased in our nitrogen and phosphorus enrichments, especially in the July bioassay. These species are characteristic of mesotrophic clear water lakes (Reynolds et al. 2002),

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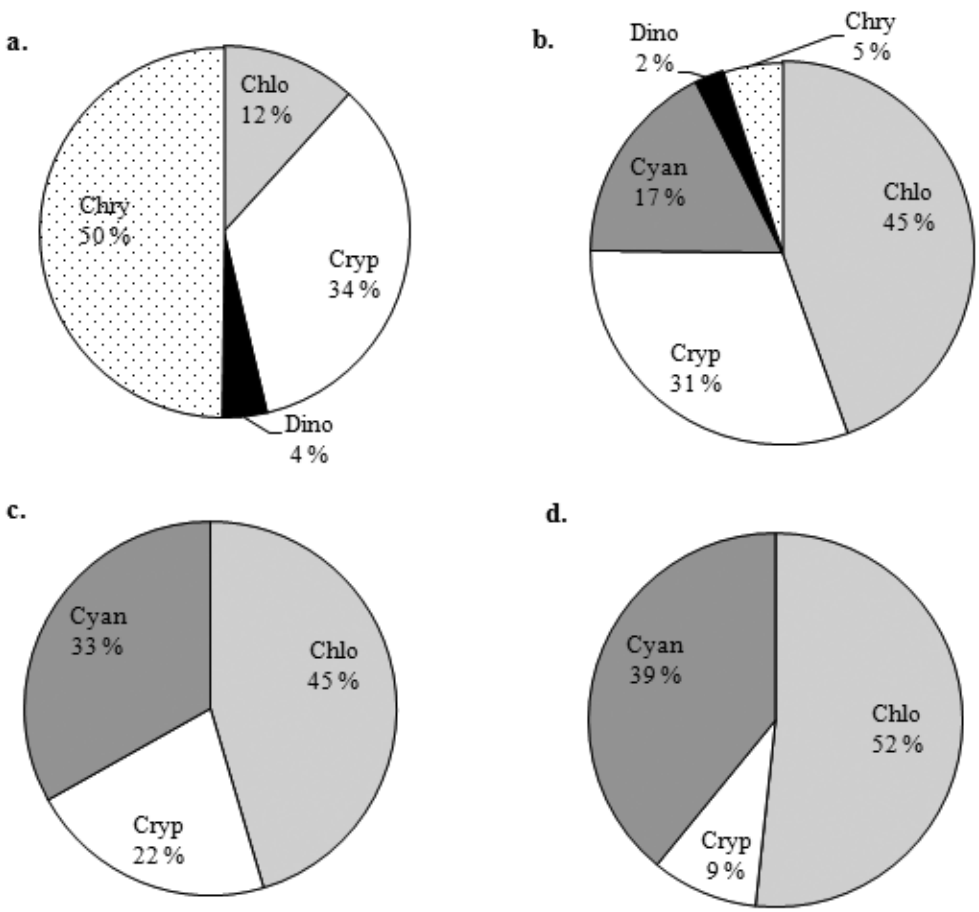

Fig. 5. The phytoplankton assemblage in **a.** June, **b.** July, **c.** August, and **d.** September. Total species number consists of individuals of which >65 cells/colonies were counted (with a theoretical confidence interval of ±25%). Chlo: Chlorophyta, Chry: Chrysophyta, Cryp: Cryptophyta, Cyan: Cyanobacteria and Dino: Dinoflagellata.

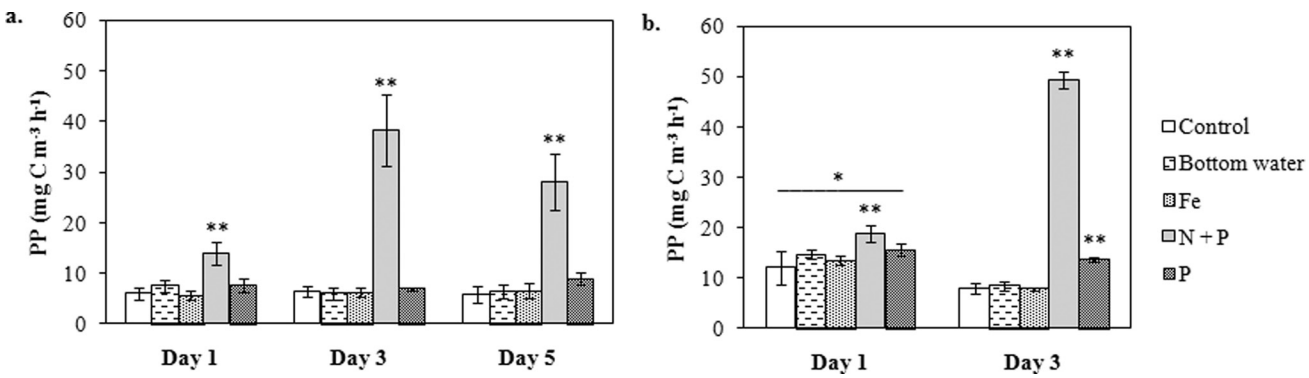

Fig. 6 a. Phytoplankton primary production (PP, mean value ± SD) in the June bioassay (11–15 June). **b.** Phytoplankton primary production (PP, mean value ± SD) in the July bioassay (27–31 July). Significant differences are shown with an asterisk (pairwise SNK-tests, * $p \leq 0.05$, ** $p \leq 0.01$). The line combines significantly different treatments.

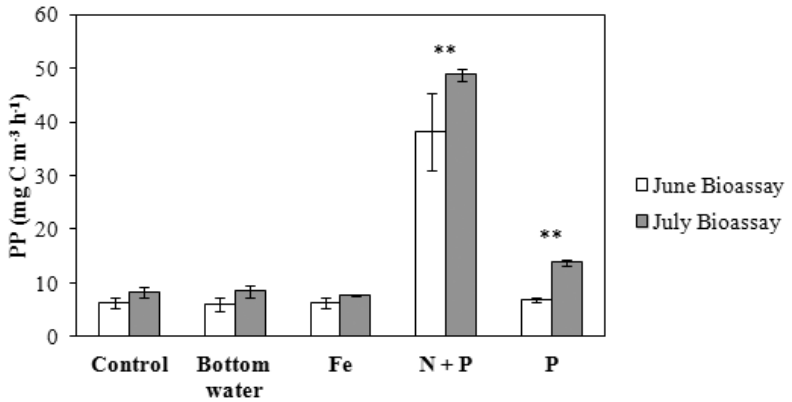

Fig. 7. Phytoplankton primary production (PP, mean value ± SD) on day 3 in the June and July bioassays. Significant differences are shown with an asterisk (pairwise SNK-tests ** $p \leq 0.01$).

suggesting that the small cryptophytes, chlorophytes, and cyanobacteria dominating the lake phytoplankton were better competitors among the macrophytes than the colonial chlorophytes. Furthermore, the colonial chlorophytes abundant in the nitrogen and phosphorus enrichments are sensitive to scarcity in carbon dioxide (CO_2) concentration (Reynolds et al. 2002), which was likely in Österträsk with a pH >9 from late July and onward. O'Farrell et al. (2009) noted a decrease in colonial chlorophytes during light limitation caused by free-floating plants. In Österträsk, the substantial phytoplankton PP down to at least 2.0 m during most of the growth season, point to strong light competitors among the phytoplankton. Small-celled phytoplankton have the physiological potential for effective nutrient and light acquirement (Raven 1998, O'Farrell et al. 2007, Litchman and Klausmeier 2008). Cryptophytes, present in the phytoplankton of Österträsk throughout the growth season in 2006, are often found in light-restricted environments (Gervais 1998, Barone and Naselli-Flores 2003). The phytoplankton PP in the deep part of the water column may also reflect the growth form of *Myriophyllum* spp., causing only intermediate shading effects (Mulderij et al. 2007).

A characteristic small-celled chlorophyte in Österträsk was *Monoraphidium minutum*, present in the phytoplankton from July to September and vertically evenly distributed throughout the period. Species of this genus are tolerant to stratified conditions but sensitive to nutrient limitation (Reynolds et al. 2002), reflected by their increase in the phosphorus and nitrogen enrichments in the July bioassay. The increase in cyanobacteria in July and August can partly be explained by their high temperature optima (Reynolds 2006). Cyanobacteria can also utilise low CO_2 concentrations under high pH (Shapiro 1997). Schriver et al. (1995) found that cyanobacteria increased as macrophyte vegetation increased, implying that they were able to persist in the quiescent environment due to their low sinking rates and resistance to nutrient limitation.

As in other shallow, macrophyte-dominated lakes (Schriver et al. 1995, Søndergaard and Moss 1998, Fonseca and Bicudo 2011), small and motile species characterised the phytoplankton in Österträsk. Small-celled phytoplankton may have competitive advantages in a macrophyte-dominated habitat. Because of their small size, and the flagella in some species, they can move comparatively effortlessly in a macrophyte jungle (Søndergaard and Moss 1998) and absorb nutrients in the heterogeneous environment (Sommer 1988). Phosphorus uptake by vertically moving cryptophytes has long been known (Salonen et al. 1984), and by exploiting nutrient rich layers, some cryptophytes reach a high growth rate (Ojala et al. 1996).

In conclusion, our results show that the dense vegetation of common water milfoil in Österträsk affected the phytoplankton without causing nutrient limitation. High pH, created by macrophyte photosynthesis (Lindholm et al. 2008), led to the early disappearance of chrysophytes sensitive to low CO_2 concentrations (Reynolds et al. 2002), but possibly also limited the appearance of large colonial chlorophytes. The concentration of TN and TP were adequate for mesotrophic conditions. Small celled cryptophytes, chlorophytes, and cyanobacteria prevailed in the dense vegetation and caused a vigorous phytoplankton PP, even among the macrophytes.

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