Deep living *Planktothrix rubescens* modulated by environmental constraints and climate forcing

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Abstract The cyanoprokaryote *Planktothrix rubescens* has been studied for over four decades in an alpine lake, Mondsee, Austria. We hypothesise that impacts of climate change can be distinguished from other environmental constraints controlling its population dynamics. During thermal stratification, *P. rubescens* formed a deep chlorophyll maximum in the metalimnion. Seasonal and diurnal depth distributions indicated that *Planktothrix* lived well below the euphotic zone, at low light levels and moderate temperatures. Photosynthetic parameters indicated a shade adapted population. The eutrophication and

rehabilitation periods of Mondsee were characterised by fluctuations controlled by phosphorus, with periods below the P-threshold associated with low biovolumes and relatively stable populations. Positive net changes of *Planktothrix* biovolume occurred during the spring–summer transition and in autumn. During summer, the population usually declined to an annual minimum. The standardised residuals of annual biovolumes responded positively to the climate signal of the Winter North Atlantic Oscillation and the timing of the onset of stratification. An inverse relationship existed between off-set and persistence of stratification. *P. rubescens* only benefits from climate warming early in the year, during late spring overturn and early summer. Longer periods of summer stratification did not favour biovolume development.

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Introduction

Most freshwater habitats in the world today are affected by eutrophication (Smith & Schindler, 2009), with the problem of nutrient enrichment now further exacerbated by the effects of climate change (Dokulil & Teubner, 2011). The underlying causes of eutrophication have long been recognised (Vollenweider, 1966) and even though there have

been great advances in understanding, it remains a particular problem because of algal blooms, scums and water quality issues (Schindler, 2006; Dodds & Cole, 2007). The deterioration in lake water quality is often associated with the excessive proliferation of cyanobacteria (Pearl & Ustach, 1982; Steinberg & Hartmann, 1988).

The most obvious nuisance is when there is a mass appearance of cyanobacteria in surface blooms. However, in deep lakes that stratify during summer, problems may be hidden in deeper water because some planktonic cyanobacteria thrive in the metalimnion where they build up deep chlorophyll maxima (DCM). This behaviour seems paradoxical because the epilimnion should be more attractive for autotrophic organisms (Davis et al., 2003). One of the best and most widespread examples of this behaviour is the cyanoprokaryote *Planktothrix rubescens* (de Candolle ex Gomont) Anagnostidis et Komárek (1988). This ‘paradoxical’ species is seen by others as an efficient ‘ecosystem engineer’ acting as a major organizing force (Padisák et al., 2010). Whatever the viewpoint, this species has a world-wide distribution in lakes of different sizes (Guiry & Guiry, 2011) but is of particular importance in deep, stratifying and eutrophic lakes. One adaptive advantage of *P. rubescens* is its ability to maintain populations even under declining or low phosphorus concentrations (Chorus et al., 2011, p. 84ff). Thriving mainly in the metalimnion, the species can become a nuisance because many strains can be toxic (Ostermaier & Kurmayer, 2010) and may transfer the toxin to higher trophic levels (Sotton et al., 2011). At higher nutrient levels, the species may even produce surface blooms (e.g. Almodóvar et al., 2004).

Planktothrix rubescens is one of the most studied organisms among the filamentous cyanoprokaryotes. This is because of its early seasonal appearance and the striking visual appearance of blooms. For example, it occurred frequently during the winter in Lac de Morat, Switzerland, during the nineteenth century. People at that time believed that the phenomenon was due to the reappearance of blood of Burgundy soldiers drowned during a battle in 1478. This myth triggered the German name ‘Burgunderblutalge’ (refer also to the red cock legend in Padisák et al., 2010). However, the cause of the red colouration was correctly identified by De Candolle (1825), who named the organism *Oscillatoria rubescens*.

The basionym of *P. rubescens* is, therefore, *Oscillatoria rubescens* D.C. ex Gomont 1892. (Skulberg & Skulberg, 1985; Anagnostidis & Komárek, 1988). It was first described as the purple or red-coloured form of planktonic *Oscillatoria* occurring in stratifying lakes, while the morphologically very similar taxon but blue-green form, *Oscillatoria agardhii*, was commonly described from polymictic, e.g. riverine and shallow lakes (shallow eutrophied ‘H₂S-*Oscillatoria* lakes’ described by Wundsch, 1940, see also *Oscillatoria agardhii/rubescens* Skulberg, 1977; Skulberg & Skulberg, 1985). Their different colouration relates to the presence of phycobilins, which are light harvesting pigments. The ‘blue-green’ phycocyanin is the only phycobilin occurring in *P. agardhii*, while *P. rubescens* also contains high concentrations of the ‘purple’ phycoerythrin, which gives it the characteristic colour. This different phycobilin pigment composition is seen as diacritical feature delineating strains of *P. agardhii* and *P. rubescens* according to phylogenetic analysis based on 16S rDNA sequences (Suda et al., 2002). Both *P. rubescens* and *P. agardhii*, contain oscillaxanthin. This carotenoid is not common in other taxa and was first isolated from *P. rubescens* (Karrer & Rutschmann, 1944; Goodwin, 1976; Rowan, 1989). The genus *Planktothrix* was described by Anagnostidis & Komárek (1988). The emended description of *P. rubescens* (D.C. ex Gomont) Anagnostidis et Komárek 1988 refers to the family Phormidiaceae. The main morphological features of *P. rubescens* include solitary trichomes or filaments that are able to move by gliding forwards and backwards (trembling), thylakoids arranged perpendicularly to the longitudinal side of cells, the even distribution of gas vesicles in the protoplast and the lack of false branching of trichomes (Fig. S1). Also, *P. rubescens* has cells where the length is slightly shorter than the width (Anagnostidis & Komárek, 1988; Komárek & Komárková, 2004). Toxic and non-toxic strains of *Planktothrix* have been found in European lakes including Mondsee (Kurmayer et al., 2011) but the proportions of genes encoding the synthesis of toxic peptides differed between populations from different lakes but did not vary seasonally within a lake.

In Austria, *P. rubescens* appeared shortly after it was first found in several Swiss lakes in the late nineteenth century (e.g. Bachmann, 1897) in a lake north of the Alps. In 1909 it invaded the Wörthersee in

Carinthia south of the Alpine ridge and further spread through the lake districts thereafter (Findenegg, 1973). The taxon appeared in Mondsee in fall 1968, when phosphorus concentrations increased (Findenegg, 1969). *Planktothrix*, however, occurred throughout the re-oligotrophication phase and almost disappeared when the lake became oligo-mesotrophic. It still maintains a very small population at present.

The aim of the present review is to assess the population dynamics of *P. rubescens* in Mondsee over 40 years, from 1969 to 2010, and to identify the environmental constraints responsible for its rise and fall in abundance. We hypothesise that the metalimnetic populations of *P. rubescens* have been affected by climate change, which is now modifying ecological conditions within the lake.

The Study site

Mondsee is an alpine oligo-mesotrophic lake situated in central Austria (47°50'N, 13°23'E) at 480 m above sea level. It has an area of 13.8 km², a mean depth of 37 m and a maximum depth of 68 m. The lake regularly stratifies during summer while ice coverage in winter is sporadic. Therefore, Mondsee switches between dimictic and monomictic mixing regimes. For more details on the lake's location, morphometry and hydrology refer to Dokulil & Skolaut (1986).

Methods

Data sources

The quantitative data for *P. rubescens* for the years 1969–1972 were extracted from Findenegg (1969, 1972, 1973), those for 1977–1980 from Schwarz (1979a, b, 1981) and Jagsch (1979), and for 2005–2010 from Schay & Wimmer (2010), Wolfram et al. (2010) and Mildner et al. (2010).

Annual average total phosphorus (TP) concentrations for 1969–1974 were inferred from *Planktothrix* biovolume (PB) using the regression equation $PB = 1.54 TP + 12.8$ ($r^2 = 0.42$, $n = 638$) and from palaeo-data as described in Dokulil & Teubner (2005). Average TP data for the years 1975–1981 and 2004–2006 were taken from Achleitner et al. (2007). Those for 2007–2010 come from Schay & Wimmer

(2010), Wolfram et al. (2010) and Mildner et al. (2010). All other data between 1982 and 2004 are original. All methods used in these studies were standard techniques, mostly cross-checked to allow comparison of data from different laboratories.

Depth distribution of *P. rubescens* for the years 1982–84 are biomass estimates while the years 2003/04 were deduced from measurements using delayed fluorescence (DF) excitation spectroscopy (Gerhardt & Bodemer, 1998).

Euphotic depth (z_{eu}) was defined as the depth where photosynthetic available radiation (PAR) is 1% of surface light intensity. In the absence of direct measurements this depth was calculated from Secchi-disk readings by a factor of three empirically determined for Mondsee. Mixing depth (z_{mix}) was taken as the depth of maximum density difference calculated from water temperature.

Long-term sampling

Over the 40-year sampling period different sampling depths and strategies were used. Samples from discrete depths were usually taken with a Ruttner sampler (prior to 1982) or later with a Schindler–Patalas trap. Integrated samples for the top 20 m were obtained with a Schröder sampler (Schröder, 1969). Sampling intervals ranged from weekly to monthly. In a few cases, the interval was biweekly or daily as, e.g. when photosynthetic characteristics were measured. Similarly, sampling depths also varied over time. Details on the ¹⁴C technique used for productivity estimates are given in Kaiblinger et al. (2007).

Diurnal sampling

High resolution measurements were performed during a stable thermal stratification period in mid-July 2002 for two diurnal cycles ('High moon' workshop). Samples for phytoplankton and lipophilic pigments were taken at 0.5, 1, 2, 3.5, 5.5, 7.5, 9.5, 12.5, 14.5, 18, 22 and 28 m at 3-h intervals. Methods of counting phytoplankton samples, analysis of chl-*a* and lipophilic pigments and related results are described in detail in Greisberger & Teubner (2007). Details of spectroscopic properties specifically used for analysing the concentrations of the carotenoid Oscillaxanthin are described in Goodwin (1976) and Rowan (1989). Hourly profiles of chlorophyll fluorescence

(Haardt-fluorimeter, Lincoln, USA), conductivity, oxygen and water temperature (YSI 6920 profiler) were measured at depth intervals of 0.25 m. Incoming PAR was continuously monitored over intervals of 10 min by using cosine corrected PAR sensor (LI 190). Under water light regime was measured with a scalar quantum sensor (LI 190 SB) connected to an integrating quantum meter (LI 188) made by LI-COR Inc, USA. The measurements were corrected for the immersion effect. Values of 1 and 0.1% surface light intensity were calculated from vertical attenuation coefficients. The maximum values of relative thermal resistance against mixing (RTRM; Vallentyne, 1957) were estimated from 0.25 m resolution profiles of water temperature and used to define the depth of thermocline (also defined here as z_{mix}).

Data treatment

The length of trichomes of *P. rubescens* at different depth was estimated by notched box-whisker plots using SYSTAT 10 (SPSS Inc.). Boxes were notched at the median; the length of the notches indicated 95% confidence intervals. Break points in time series were visualised by rescaled adjusted partial sums (RAPS) following Garbrecht & Fernandez (1994).

$$\sum_{t=1}^k \frac{Y_t - \bar{Y}}{S_Y} \quad (1)$$

with Y_t = value at time t , $\bar{Y}$ = mean of the series and S_Y = standard deviation of the mean. Schmidt stability was calculated according to Livingstone and Schanz (1994).

In situ net changes of PB were calculated from short time investigations (≤ 1 week) according to

$$\mu' = \frac{(\ln B_2 - \ln B_1)}{t_2 - t_1} \quad (2)$$

with B_2 and B_1 biovolumes at time t_2 and t_1 .

Long-term datasets of intra-annual biovolumes of *P. rubescens* were highly variable (coefficient of variation, CV = 0.96). Annual biovolumes of *P. rubescens* were hence standardised and linearly detrended to remove strong inter-annual variation prior to estimating climate response in the time series. These standardised residuals (SR) of *P. rubescens* were related to a climate signal, the Hurrell's station based North Atlantic Oscillation Index (NAO, Hurrell et al.,

2001). Monthly indices were taken from <http://www.cgd.ucar.edu/cas/jhurrell/indices.html>, accessed 7 September 2011. Standardised residuals of annual biovolumes of *P. rubescens* were further correlated with original data of dates of lake stratification (low CV which ranged from 0.02 to 0.11) and its detrended time series data. Pearson correlations coefficients are shown for the detrended lake stratification data in Fig. 9 (r_{SR}) and also for the original lake stratification data (r) in the text.

RTRM values for the long-term data set were calculated in depth intervals of 1 m. The on-set of thermal stratification was defined as the date, the Julian day, when maximum RTRM-value exceeded the threshold value of 9.5. Similarly, the off-set of stratification was defined by the Julian day when the maximum RTRM-value fell below 9.5 leading to unstable thermal conditions in the water column and finally autumnal overturn. The duration of summer stratification was the time span in Julian days between dates of on- and off-set.

Results

Long-term dynamics

After its first appearance in autumn 1968 (Findenegg, 1969), *P. rubescens* rapidly increased in biovolume and reached a first peak in 1971 in Mondsee (Fig. 1). No data exist for the bloom years 1973–1976, only indirect evidence from visual observations of surface appearance of the species (Fig. S2) and palaeolimnological records of the marker pigment oscillaxanthin in the sediments (Schultze, 1985; Dokulil & Teubner, 2005). Maximum observed biovolumes occurred in the years 1977–1979 ($4.4 \text{ mm}^3 \text{ L}^{-1}$ in 1979). As a consequence of restoration measures in the catchment, quantities of *Planktothrix* rapidly declined thereafter, reaching values below $0.002 \text{ mm}^3 \text{ L}^{-1}$ in 1998–2000. Beginning in 2001, biovolumes of *P. rubescens* increased again to values similar to the 1980s. The peak of $1.3 \text{ mm}^3 \text{ L}^{-1}$ in 2004 was followed by a rapid decline, leading to very low values from 2006 to 2010.

Annual average PB and TP concentrations strongly corresponded to each other during the period from 1969 to 2010 (Fig. 2), as is also indicated by the parallel progression of the RAPS in the lower panel. In the first phase, from 1969 to 1979, annual mean TP concentrations increased in the lake, peaking at $35 \mu\text{g L}^{-1}$ in 1978 (eutrophication phase), and *P. rubescens*

Fig. 1 Biovolume of *P. rubescens* as $10^6 \mu\text{m}^3 \text{L}^{-1}$ (equivalent to $\mu\text{g L}^{-1}$ biomass) in Mondsee for the years 1969–2010. For data sources refer to relevant paragraph in “Methods”

Fig. 2 Annual average total phosphorus (TP) and concentration of *P. rubescens* for 1969–2010 (A) and the readjusted partial sums (RAPS) of both variables (B)

proliferated. Both variables drastically declined then until TP concentrations dropped consistently below $10 \mu\text{g L}^{-1}$ and biovolumes below $0.1 \text{mm}^3 \text{L}^{-1}$ in 1990 (restoration phase). The next 10-year period, from 1990 to 2000, was characterised by low and further declining average biovolumes, reaching an annual minimum of $0.001 \text{mm}^3 \text{L}^{-1}$ in 1998 (stabilisation phase). Afterwards, *P. rubescens* mean biovolumes increased again, peaking at $0.4 \text{mm}^3 \text{L}^{-1}$ in 2003, followed by a drastic decline to values much below $0.01 \text{mm}^3 \text{L}^{-1}$ in very recent years.

Depth distribution

Depth distribution and formation of the metalimnetic maximum layer of *P. rubescens* is shown together with water temperature, z_{eu} and z_{mix} for the years 1982–1984 and 2003–2004 in Fig. 3. The formation of a *Planktothrix*-layer between 10 and 15(20) m began when the lake started to thermally stratify. Maximum biovolumes were associated with water temperatures of 6–16°C and at depths of greatest density difference. *P. rubescens* grew well at depths below z_{eu} , i.e. at light levels of less than 1% and below the mixing zone during the stratified period. Positive net change of biovolume (μ') averaged 0.099day^{-1} (0.002–0.446) were deduced from weekly observations. Positive net changes mainly occurred during late spring-early summer or in autumn. The layering was terminated usually when temperature stratification began to weaken and mixing depth increased. In the autumn of 1983, however, quite a large population remained in the epilimnion and managed to survive the winter, so it was able to proliferate throughout the water column at spring overturn.

The depth distribution of *P. rubescens* and related variables are further shown in detail for two diurnal cycles during summer stratification in Fig. 4. In addition, phytoplankton composition is shown for certain depths in Fig. 5 for these sampling dates. The density and the RTRM illustrate the usual separation with the epilimnion in the top 5–6 m, a thick metalimnetic layer from 6 to 13.5 m and the hypolimnion below during thermal stratification.

Fig. 3 Contour plot of water temperature ($^{\circ}\text{C}$) with euphotic depth (z_{eu} in m) as continuous line (A) and *P. rubescens* biomass in $\mu\text{g L}^{-1}$ with mixing depth (z_{mix} in m) for 1982–1984 (B). Contour plot of water temperature ($^{\circ}\text{C}$) with euphotic depth (z_{eu} in m) as continuous line (C) and *P. rubescens* biomass as chl-*a* equivalents ($\mu\text{g L}^{-1}$) from DF-spectrometry with mixing depth (z_{mix} in m) for 2003 and 2004 (D)

The biovolume of *P. rubescens* was negligible in the top 9 m, because it contributed less than 1% to total biovolume of phytoplankton (Figs. 4, 5). At a depth of 9.5 m, coinciding with the depth of the thermocline at 9.4 m (depth variation from 8 to 11 m), the biovolume of *P. rubescens* increased and contributed 9% to total phytoplankton (Fig. 5, left panel). This depth also related to a light availability of 1%, because the euphotic zone was deepest at 10.7 and 10.3 m, respectively, during these 2 days in July.

Fig. 4 Diurnal depth distribution of *P. rubescens* as contour plot (A) and mean verticals (B). All data are from Mondsee sampling on 23/24 July 2002. With exception of the biovolume of *P. rubescens* the depth resolution is 0.25 m. A Biovolume of *P. rubescens* is indicated by shaded areas: <0.4 (white), 0.5–1 (light gray), 1.1–1.5 (mid-gray), >1.6 (dark gray). Lines refer to the depth of 1% (euphotic depth) and 0.1% light availability, respectively, and mixing depth (thermocline as depth of maximum values of RTRM). B Profiles as averages of the two

Biovolumes of *P. rubescens* further increased below the thermocline at 12.5 and 14.5 m reaching 0.97 and 0.91 $\text{mm}^3 \text{L}^{-1}$, respectively, which was about 85% of total biovolume. The *Planktothrix* layer occupied a zone at and below the margin of the thermocline where light was available between 1 and 0.1% (Fig. 4A). In the main layer at 12.5 m, 0.1% light intensity lasted for at least several hours per day (11 h on sunny 23.7.2002, 5 h on cloudy 24.7.2002). Based on the hourly fluorescence profiles (resolution 0.25 m), the depth of the population maximum of *P. rubescens* was even slightly deeper between 13 and 13.5 m and hence very close to the boundary between meta- and hypolimnion (Fig. 4B). The gravity point of the *P. rubescens* population moved marginally downwards in the afternoon and slightly dispersed during morning and night (Fig. 4A). Enhanced oxygen

diurnal cycles: biovolume of *P. rubescens* (*P. rub.*), total chlorophyll-*a* of phytoplankton measured by fluorescence (chl-*a*), RTRM and density, conductivity (Cond) oxygen saturation ($\text{O}_2\%$). The mean maximum value of RTRM is 11 and refers to a depth resolution of 0.25 m (maximum RTRM value of 1-m depth interval is 43 (not shown) and hence above the threshold of 9.5 used as threshold for the onset of stratification in Mondsee, see “Methods”)

Fig. 5 Relative contribution of *P. rubescens* to total phytoplankton (left panel) and the composition of eukaryotic phytoplankton (right panel) at discrete depth of epilimnion (0.5, 1 and 2 m), metalimnion (9.5 m, 12.5 m) and hypolimnion (14.5 m). Data are averages from Mondsee sampling on 23/24 July 2002 (see method). *Chry* chrysophytes, *cDiat* centric diatoms, *pDiat* pennate diatoms, *Cryp* cryptophytes, *Din* dinoflagellates, *Plarub* *P. rubescens*, B_{phyto} biovolume of total phytoplankton, B_{Plarub} biovolume of *P. rubescens*

saturation was found from 7.5 to 11.5 m, which decreased slightly with depth and fell below 100% at 14 m (Fig. 4B).

The vertical distribution of phytoplankton other than *P. rubescens* was largely even (Fig. 5, right

panel). The biovolume other than *P. rubescens* was dominated by diatoms (38–47 %), while dinoflagellates and cryptophytes contributed, on average, 16–24% and 14–20%, respectively. Chrysophytes and cyanobacteria other than *P. rubescens* were of minor importance. The only remarkable change with depth was found among the centric and pennate diatoms, e.g. centric diatoms made up 45–46% of phytoplankton in the surface layer (excluding *P. rubescens*), while pennate diatoms were almost absent (<1%). In the deeper layers below the thermocline at 12.5 and 14.5 m, the centric diatoms decreased to 33–35% while the pennate diatoms increased to 5–10%. The pennate diatoms were composed mainly of the genera *Asterionella*, *Fragilaria* (including former *Synedra*), *Nitzschia* and *Tabellaria*.

A distinct vertical pattern can be further seen by comparing the trichome length of *P. rubescens* at two metalimnetic strata (Fig. 6A). Trichomes at 9.5 m depth were significantly shorter than those at 12.5 m ($p < 0.05$, Fig. 6B). The trichome length varied from 28 to 1090 μm (median, see Table 2). In general, the frequency of shorter trichomes was much higher than of longer trichomes.

During the diurnal cycle survey in Mondsee, *P. rubescens* was the only abundant cyanobacterium containing the carotenoid pigment oscillaxanthin (Goodwin, 1976; Rowan, 1989). This marker pigment was significantly correlated to the abundant biovolume of *P. rubescens* below 9.5 m (Fig. 7). The median ratio of oscillaxanthin per biovolume of *P. rubescens* was $5.74 \times 10^{-8} \mu\text{g} \mu\text{m}^{-3}$, that of oscillaxanthin per chl-*a* of *P. rubescens* $0.081 \mu\text{g} \mu\text{g}^{-1}$ (Table 2). When biovolume was $<0.025 \text{ mm}^3 \text{ L}^{-1}$ (samples from epilimnion) the spectroscopic signal of oscillaxanthin was under the detection limit applying a standard protocol aimed at analysing the many phytoplankton chlorophylls and carotenoids in a one analytical run.

Productivity

In July 1987 an in situ productivity ¹⁴C-experiment was performed in which *Planktothrix* was taken from the DCM and then distributed over z_{eu} , exposing it to the entire light gradient. Comparison was made to the total phytoplankton assemblage, which was taken conventionally at each depth. The photosynthetic parameters obtained from chl-specific carbon uptake

Fig. 6 Variation of length of trichomes of *P. rubescens* at sampling depth 9.5 (median length = 421 μm , $n = 552$) and 12.5 m (median length = 556 μm , $n = 1160$) in July 2002 in Mondsee. Variation is shown as frequency distribution (A) and as box-plot (B)

Fig. 7 Relationship between the biovolume of *P. rubescens* and its marker pigment oscillaxanthin at 9.5, 12.5 and 14.5 m depth. All data are from Mondsee sampling at 23/24 July 2002

versus light intensity (P – I curve) are summarised in Table 1.

Maximum rate of photosynthesis (P_{max}) of *Planktothrix* was lower and light harvesting efficiency at low light (α) was higher than that of total phytoplankton. As a result, light saturation (I_K) of photosynthetic rate was reached at lower light intensity for *P. rubescens*.

Further, photoinhibition at light intensities above 640 $\mu\text{mol PAR}$ was observed for *P. rubescens* while no inhibition was found for the total phytoplankton sample. All these parameters pointed to low light acclimation in *P. rubescens*.

Climate response

As the yield of *P. rubescens* was primarily linked to nutrient status (Fig. 8), annual average biovolumes of *P. rubescens* did not directly correspond to climate signals. To disentangle the phosphorus control and climate effects, all annual biovolumes of *P. rubescens* were converted to standardised residuals before testing correlations (SR biovolume of *P. rubescens*, see “Methods”). These residuals were significantly correlated with the large-scale climate phenomenon in February, the NAO_{Febr} ($r = 0.37$, $p < 0.05$, Fig. 9A). Statistical analysis with other months and periods of NAO did not reveal a significant response pattern of *P. rubescens* over the time-period from 1969 to 2004 and, therefore, is not shown. Physical lake mixing conditions, specifically the timing of on- and off-set of thermal stratification and the duration of summer

Table 1 Photosynthetic parameters deduced from ^{14}C -productivity versus light intensity (P – I curves) comparing *P. rubescens* and total phytoplankton

Photosynthetic parameter	<i>P. rubescens</i>	Total phytoplankton
P_{max} [$\text{mg C (mg chl-}a\text{)}^{-1} \text{ h}^{-1}$]	4.32	6.03
α [$\text{mg C (mg chl-}a\text{)}^{-1} \text{ h}^{-1} (\mu\text{mol photons m}^{-2} \text{ s}^{-1})^{-1}$]	0.024	0.019
E_K ($\mu\text{mol photons m}^{-2} \text{ s}^{-1}$)	180	317
E_I ($\mu\text{mol photons m}^{-2} \text{ s}^{-1}$)	630	n.a.
Photoinhibition (% P_{max})	40	0

P_{max} maximum chl-*a* specific productivity, α light efficiency, E_K light intensity at onset of saturation, E_I light intensity at inhibition

Fig. 8 Regression of *P. rubescens* (PR) annual average biomass versus TP concentration for 1969–1989 and for 1990–2010 (*inset*). The dashed lines are the 95% confident limits. The regression equation, explained variance and significance level is given in the main graph

stratification in Mondsee (Fig. 9B), were identified as factors which mediate the climate signal to biological response. This figure refers only to the years 1979 to 2003 because detailed depth profiles are lacking for the other years.

The on-set of stratification in Mondsee occurred on average in early May, on Julian day 122, and varied from day 85 to 143 in the year. The SR of biovolume of

P. rubescens were positively correlated with the timing of this on-set, the original data (r) and the detrended (r_{SR}) Julian days, respectively ($r = 0.39$ and $r_{SR} = 0.41, p < 0.05$). The breakdown of summer stratification occurred on average in early November, on Julian day 307, and varied from day 290 to 323. In contrast to the on-set of stratification, we found an inverse relationship between the SR of *P. rubescens* and the timing of breakdown of thermal stratification ($r = -0.43$ and $r_{SR} = -0.44, p < 0.05$). An even stronger inverse response was found in the case of the time-span of thermal stratification ($r = -0.52$ and $r_{SR} = -0.55, p < 0.01$). The thermal stability of the water column can be expressed by Schmidt's stability. Maximum values for Schmidt's stability increased slightly with years and responded to warming in Mondsee (not shown). SR of biovolume of *P. rubescens* were negatively related with values of the annual maximum of Schmidt's stability ($r = -0.50, r_{SR} = -0.42, p < 0.01$, not shown in figures).

Annual average long-term seasonality

The annual patterns of *P. rubescens* biovolume, total chlorophyll-*a* concentration of phytoplankton, the mixing and euphotic depth are shown as long-term averages for the years 1979–2003 in Fig. 10. During spring overturn early in the year, biovolumes of *P. rubescens* only slightly increased (Phase I). With the transition into thermal stratification (Phase II), the biovolume of *P. rubescens* increased to an initial

Fig. 9 Climate response of *P. rubescens*. The annual biovolumes of *P. rubescens* are displayed as standardised residuals (SR biovolume *P. rubescens*). **A** The response to the NAO-index in February (NAO_Febr), and **B** the Julian days of the on-set, breakdown and duration of thermal stratification. **A** relates to the

period 1969–1972, 1977–1980, 1982–2004 ($n = 30$), **B** for 1979–1980, 1982–1993 ($n = 25$). Pearson correlation coefficients for SR biovolume of *P. rubescens* versus residuals of the timing of stratification (r_{SR}) and 0.95 significance intervals are shown (* $p < 0.05$, ** $p < 0.01$)

Fig. 10 Annual pattern for biovolume of *P. rubescens*, total chlorophyll-*a* concentration of phytoplankton and the depth of mixing and euphotic zone shown as long-term averages ($n = 25$, 1977–1980, 1982–2003)

peak, while the total phytoplankton already formed the spring maximum, which was usually the main peak of the year in Mondsee. Immediately after the on-set of

thermal stratification, *P. rubescens* rapidly reached its maximum in the year, coinciding with the formation of the metalimnetic layer (Phase III). Total phytoplankton rapidly declined and water transparency increased during this clear-water phase. The annual average maximum of water transparency coincided, therefore, with the annual peak of *P. rubescens* biovolume, which occurred in the long-term average by mid to end of July (Julian day 173, median Julian day = 157, Table 2). In the following Phase IV, mainly characterised by a progressive deepening of the thermocline (see z_{mix} in Fig. 10), biovolume of *P. rubescens* rapidly decreased while total phytoplankton formed a summer high. By the end of summer, the decline of *P. rubescens* slowed down to an annual minimum by mid to end September (mean Julian day 272 in Phase V; median 248, Table 2). This was followed by a steep increase leading to a second, smaller peak by the end of mid-November, on Julian day 323 (transition Phase VI). Finally, with the start of the autumnal overturn (Phase VIII) both *P. rubescens* and total phytoplankton declined to winter values.

Table 2 Summary of main morphological and eco-physiological characteristics of *P. rubescens* in the alpine lake Mondsee for the thermal stratified period

Variable	Median (range)	<i>n</i>	Study period
Depth of <i>P. rubescens</i> layer (m)	12.5 (8–15)		1982–1984, 2000–2004
BV net change (μ' , d^{-1})	0.099 (0.002–0.446)		1982–1984, 2000–2004
Trichome length (μm)	500 (28–1090)	1,712	July 2002
Trichome width (μm)	5.3 (5.1–6.4)	40	July 2002
Oscillaxanthin/Biovol. ($\mu\text{g } \mu\text{m}^{-3}$)	5.74×10^{-8}	36	July 2002
Oscillaxanthin/chl- <i>a</i> ($\mu\text{g } \mu\text{g}^{-1}$)	0.082 (0.042–0.18)	36	July 2002
Chl- <i>a</i> at DCM ($\mu\text{g } \text{L}^{-1}$)	3.3 (0.4–32.1)	1,150	1977–2004
Light at DCM (% surface L.I.)	0.3 (0.1–1)		1982–1984, 2002
Water temperature at DCM [$^{\circ}\text{C}$]	11.3 (4.9–24.0)	1,039	1982–2004
$z_{\text{eu}}/z_{\text{mix}}$	0.31 (0.18–4.83)	289	1982–2004
pH	8.20 (7.70–8.20)	1,150	1982–2004
Conductivity ($\mu\text{S } \text{cm}^{-1}$)	305 (268–320)	1,150	1982–2004
Alkalinity (mval)	3.0 (2.6–3.1)	1,150	1982–2004
$\text{PO}_4\text{-P}$ (SRP, $\mu\text{g } \text{L}^{-1}$)	0.7 (<0.3–2.6)	201	1982–2004
Total phosphorus (TP, $\mu\text{g } \text{L}^{-1}$)	9.5 (4.0–28.1)	665	1982–2004
$\text{NH}_4\text{-N}$ ($\mu\text{g } \text{L}^{-1}$)	9.6 (0.0–61.9)	349	1982–2004
$\text{NO}_3\text{-N}$ ($\text{mg } \text{L}^{-1}$)	0.6 (0.2–1.1)	1,122	1982–2004
Total nitrogen (TN, $\text{mg } \text{L}^{-1}$)	0.62 (0.12–1.20)	404	1982–2004
P_{max} [$\text{mg C (mg chl-}a)^{-1} \text{ h}^{-1}$]	1.85 (0.9–3.0)	15	2000
α [P_{max} ($\mu\text{mol photons m}^{-2} \text{ s}^{-1})^{-1}$]	0.028 (0.003–0.031)	15	2000
E_K ($\mu\text{mol photons m}^{-2} \text{ s}^{-1}$)	79 (35–320)	15	2000
Timing annual peak (Julian day)	157 (91–195)	31	1969–1972, 1977–2004
Timing annual min (Julian day)	248 (198–301)	31	1969–1972, 1977–2004

Discussion

Long-term dynamics

Biovolume development of *P. rubescens* since 1969 can be characterised by a number of periods triggered by different events. The appearance and early success of *Planktothrix* must be attributed to high and increasing nutrient loading to the lake that originated from sewage effluents (Findenegg, 1969, 1973). Similar observations linking the appearance and expansion of *P. rubescens* to enhanced nutrient input have been made at several other sites (e.g. Edmondson et al., 1956). The beginning of sewage diversion in 1973 started a new era in which nutrient loads, particularly phosphorus, were reduced. Response of the lake was, however, delayed until 1979, when total phytoplankton biovolume began to decline until it reached a somewhat stable period of low values beginning in 1989 (Dokulil & Teubner, 2005). Such a reversal has been recognised in many other places (e.g. Schanz & Thomas, 1981).

The wax and wane of *P. rubescens* during these eutrophication and restoration periods was strongly controlled by phosphorus concentration ($r^2 = 0.89$, $p < 0.001$), as indicated in Fig. 8. The relation inserted in Fig. 8 shows that growth of *Planktothrix* was largely uncoupled from phosphorus for the last 20 years. Even the increase in biovolume in the years 2001–2006 (see Figs. 1, 2) was unrelated to TP and must have been triggered by factors other than P-load.

Analysis of biomass distribution versus a gradient of phosphorus concentration from several Austrian and Bavarian lakes revealed that *P. rubescens* proliferated under mesotrophic conditions (Teubner et al., 2004), opposing the general notion that the taxon is a ‘eutrophic’ species (see Table 1 in Ernst et al., 2009). Consequently, *P. rubescens* is one (among others) used to characterise mesotrophic to moderately eutrophic conditions when assessing the ecological status of lakes in the context of the Water Framework Directive (e.g. Wolfram et al., 2008).

Vertical niche separation

A number of plankton assemblages can form a DCM by aggregation or growth. Many types of deep living phytoplankton assemblages have been described from freshwater and marine systems (Cullen, 1982;

Reynolds, 1992; Adler et al., 2000) that respond differently to environmental gradients.

The DCM formation by *P. rubescens* during summer thermal stratification is commonly described for oxygenic metalimnetic layers at or below the euphotic zone. This behaviour is well documented and is usually regulated by buoyancy changes responding to alterations in the light climate (e.g. Konopka, 1982; Micheletti et al., 1998; Teubner et al., 2003; Walsby et al., 2004). The strong density gradient in the metalimnion additionally creates a strong buoyancy force that prevents mixing and hence avoids entrainment. The composition of these phytoplankton assemblages in deep layers, mainly *P. rubescens*, can persist throughout a season, building a steady state assemblage that differs from assemblages in the epilimnion (e.g. Teubner et al., 2003; Lake Ammersee).

The occasional appearance at the lake surface, as was observed during the eutrophication period in Mondsee, also is a common feature (see “Introduction” and Fig. S2) and has been explained by changes in buoyancy regulation induced by mixing at the end of the stratified season (Walsby et al., 2006). Entrainment during mixing, therefore, also explains persistent biovolumes throughout the water column in autumn and, depending on meteorological conditions, during winter as was observed in 1983 to 1984 in Mondsee (see Fig. 3). Moreover, the species is acclimated or even adapted to low light intensities and low water temperatures allowing winter survival (Holland & Walsby, 2008).

High-resolution profile measurements have shown that the metalimnion is a zone almost free from turbulences in lakes (Ford & Johnson, 1983; Etemad-Shahidi & Imberger, 2001; Yamazaki et al., 2010). In Mondsee, we found a narrow stratum of the maximum population of *P. rubescens* at 13–13.5 m within the metalimnion extending over 7–8 m. It supports the theory that trichomes can easily move within this low turbulence layer by physiological buoyancy regulation in response to vertical light gradients (Walsby et al., 1983; Walsby, 2005). Effects of internal waves, as observed by Cuypers et al. (2011), can be safely ruled out because of permanent calm weather during the 2 days of observation.

Planktothrix rubescens modulated their buoyancy in Mondsee to aggregate in the dim light layer from 1 to 0.1% light intensity, which is sufficient light to support net growth but does not damage or inhibit the

photosynthetic apparatus. The population maximum layer at 13–13.5 m seemed to be optimal for *P. rubescens*, even if it was close to the boundary layer between the metalimnion and the hypolimnion (at 14 m in mid-July). These findings were substantiated by photosynthesis–irradiance response curves in Mondsee. Analysing the 11 µm size fraction of phytoplankton assemblage, which was almost exclusively composed of *P. rubescens* for the year 2000 (Kaiblinger et al., 2007), observed photosynthetic parameters were similar to those measured in an in situ experiment in 1987 (see Table 1). All photosynthetic parameters (Table 2) describe a strongly shade acclimated species, which utilises the small amounts of light reaching the metalimnion. The main light-harvesting pigments in *P. rubescens* are phycocyanin and phycoerythrin. These phycobilins enable this cyanobacterium to use low light intensities but also the narrow, almost monochromatic wave band of light quality in these deep layers.

Another aspect of physiological adjustment to deep layers is heterotrophic growth stimulated by dim light as reported from amino acid uptake experiments in Lake Zürich by Zotina et al. (2003) and Walsby & Jüttner (2006). The dim-light uptake rate of certain amino acids was two- to ninefold higher than the dark-uptake rate in their studies. Further, E_K values for amino acid uptake were much lower than for photosynthesis. Both studies from Lake Zürich found that heterotrophy, stimulated by low light intensity, supplemented autotrophic growth of *P. rubescens* in the deep metalimnetic strata. *P. rubescens* might be able, therefore, to grow even if there was insufficient light available for autotrophic growth. During the diurnal study in July 2002 in Mondsee, the maximum population layer at 13–13.5 m was 3–4 m below both the euphotic depth and the thermocline. Moreover, trichome length of *P. rubescens* at 9.5 m was significantly shorter than at 12.5 m. This observation supports findings by Walsby (2005) that longer trichomes tend to respond faster than shorter ones and are even able to migrate to deeper strata on sunny days. All these diurnal patterns confirm the physiological adjustment of *P. rubescens* to deep strata conditions discussed before (see vertical pattern 1983–1984 above).

The marker pigment oscillaxanthin

Oscillaxanthin is found in some phytoplankton species, mainly in filamentous cyanobacteria as *P. rubescens*, but also, e.g. in *P. agardhii* and *Aphanizomenon*

spp. (Goodwin, 1976; Rowan, 1989; Rücker et al., 1995; Schlüter et al., 2004). This carotenoid has been commonly studied as a fossil pigment in sediments (e.g. Griffiths, 1978; Lami et al., 2000), while studies on plankton were more rare (Rücker et al., 1995; Schlüter et al., 2004; Greisberger & Teubner, 2007). Many pigments are ruled out as markers because they occur in numerous genera and even in several algal classes. In contrast, oscillaxanthin has an advantage because it is present in just a few species and of those, it is often possible to separate them by differences in their ecology. For example, *P. rubescens* and *P. agardhii* have different niches and, therefore, blooms in a lake usually consist of only one or the other. Our results confirm that this marker pigment can be used to infer biovolumes of *P. rubescens* when biomass is large. When biovolume contribution to total phytoplankton is low, the analytical techniques were at the detection limit, as has been described above for the epilimnetic samples with low biovolumes of *P. rubescens* in Mondsee. The median ratio of oscillaxanthin to chl-*a* calculated for *P. rubescens* from our field samples was twice as high as for cultures of *Aphanizomenon* and *Anabaena* grown under highlight conditions published in Schlüter et al. (2004).

Climate impact

How climate controls the lake's phenology and, therefore, affects the dynamics of *P. rubescens* was central to the analysis of the relationship between the NAO signal and ecosystem function. A positive NAO_{Febr} index relates to years of relative high insolation, high air temperature and low precipitation in the catchment of Mondsee. A negative NAO_{Febr} is associated with the opposite weather situation in the region (Dokulil et al., 2010; Nöges et al., 2010). We further show that an increase of hypolimnetic water temperatures by 0.1–0.2°C per decade was mediated by climate trends related to winter NAO signal (Dokulil et al., 2006). The response of *P. rubescens* to the winter climate signal is shown in Fig. 9. The annual biovolume development of *P. rubescens* increased during years of positive NAO_{Febr}, i.e. during years of warm winter–spring weather. The biovolumes were further dependent on the timing of the on- and off-set of the stratification and the time span between these two dates. The response of *P. rubescens* to stratification, however, did not show a general stimulation or

inhibitory effect but changed within a year, as described by direct and inverse correlation patterns in Fig. 9. The annual average pattern shown in Fig. 10 indicates that the response of *P. rubescens* is in general different from the total phytoplankton during periods other than overturn. This independent, or indirectly related, development can be explained by vertical niche separation of epilimnetic and metalimnetic assemblages. Although *P. rubescens* was vertically separated, the species only benefited from thermal stratification in the beginning of the year, during Phases II and III. A prolonged period of summer stratification later in the year, as a consequence of climate warming, however, was not an advantage for biovolume development. These intra-annual shifts between early year forcing and mid-summer–autumn weakening of *P. rubescens*, explain the significant positive but weak correlation between the annual biovolume of *P. rubescens* and the climate signal NAO_{Febr} .

The temporal coincidence of the annual peak of water transparency and the annual metalimnetic peak of *P. rubescens* in Mondsee is a common pattern described for the transition from spring to summer in other studies (e.g. Salmaso et al., 2003; Teubner et al., 2003; Talling et al., 2005). During this growth period, *P. rubescens* might not only benefit from sufficient light and nutrient availability for autotrophic growth but also from low light-stimulated uptake of organic compounds released to the metalimnion after the breakdown of the phytoplankton spring peak. Adenylate energy charge measurements in Mondsee by Jewson & Dokulil (1982) support the organic breakdown in the thermocline. In this context, a zone of low turbulence to some extent seems crucial for the growth of *P. rubescens* at depth. A metalimnion that extends over several metres, as shown in this study for Mondsee, allows *P. rubescens* to move easily by physiological buoyancy regulation between strata with light intensities around E_K sufficient for photosynthesis or, at even deeper strata, to light intensities below E_K , beneficial for amino acid uptake. In some lakes (e.g. Anneville et al., 2004), the development of *P. rubescens* early in the year is discussed in view of overwintering biovolume. In Mondsee, winter biovolumes of *P. rubescens* were sometimes higher than summer minima and were even enhanced in certain years, as discussed for the transition from 1983 to 1984.

Climate warming, however, benefits the growth of *P. rubescens* only during the spring-early summer transition but not later in the year. The decline of *P. rubescens* to an annual minimum in summer lasts over several weeks during thermal stratification (indicated as Phases IV and V in our long-term seasonality Fig. 10). This decline to the summer minimum is confirmed by a statistically strong but inverse relationship between the annual biovolume of *P. rubescens* and the duration of thermal stratification. Therefore, the lengthening of the period of thermal stratification by warming is not beneficial for *P. rubescens*. Other phytoplankton species, which are mixotrophic and motile might benefit even more from a longer stratification period in summer, because they can exploit nutrient patches not only in the deep layer but also near the surface. Flagellates of crypto-, chryso- and dinophyceans play an important role in deep alpine lakes (Dokulil, 1988; Fott et al., 1999; Sonntag et al., 2006; Tolotti et al., 2012) and can account for more than 40% of the phytoplankton taxa as recorded for mesotrophic alpine Ammersee (Teubner et al., 2003). In the case of the diurnal distribution pattern in Mondsee 2002, many photosynthetic flagellates were evenly distributed over depth and, therefore, behaved differently from *P. rubescens*, living almost exclusively in deeper layers.

Summary and conclusions

The main characteristics of *P. rubescens* and associated environmental variables observed over four decades in the alpine lake, Mondsee are summarised for the stratified period in Table 2. The ranges for chlorophyll-*a* and water temperature are, at first glance, surprisingly wide. Considering the various phases of ecosystem changes during the four decades of observation, these ranges are clear because they cover periods of eutrophication and years of extremes in water temperature like 2003. The variation and median of the light climate substantiate that *P. rubescens* lives substantially below the 1% light level and prefers situations when the euphotic depth is equal or less than the mixing zone. The median and ranges of the light climate, the $z_{\text{eu}}/z_{\text{mix}}$ ratio and the nutrients, particularly TP and TN fall well into values reported by Schreurs (1992) for Dutch lakes. The photosynthetic parameters obtained in 2000

(Kaiblinger et al., 2007) all indicate shade adaptation of *P. rubescens*. On average, the *Planktothrix* population peaks in May to June and reaches its minimum in August to September.

For deep living *Planktothrix rubescens* populations the following conclusions can be drawn:

- Preference for living under dim light (<1%) and cool water temperatures (5–12°C) at a depth of large density changes (metalimnion) and reduced turbulence.
- Life in or below the thermocline is aided by physiological acclimation of photosynthesis and buoyancy regulation.
- Survival during the stratified period is possible because of a potentially heterotrophic subsistence.
- Population dynamics during periods of lake eutrophication or rehabilitation are primarily controlled by phosphorus.
- Proliferation of *P. rubescens* is optimal at meso- to moderately eutrophic conditions.
- Benefits from climate warming are restricted to the winter signal transmitting weak climate forcing during late spring and early summer (transition period from vernal overturn to the on-set of thermal stratification). Longer periods of summer stratification showed no advantage for population development.
- The annual average long-term pattern indicates that population dynamics of *P. rubescens* are different from the development of total phytoplankton during the period of stratification.

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