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PHYTOPLANKTON WORKSHOP

Photosynthetic efficiency as a function of thermal stratification and phytoplankton size structure in an oligotrophic alpine lake

Christina Kaiblinger · Sonja Greisberger · Katrin Teubner · Martin T. Dokulil

Abstract Allometric relationships of phytoplankton communities were studied on the basis of a five-year data-set in a deep oligotrophic alpine lake in Austria. The seasonal phytoplankton succession in Mondsee is characterised by diatoms during winter mixing and a distinct metalimnetic population of *Planktothrix rubescens* during stratification in summer. The variation of phytoplankton photosynthetic efficiency between seasons was assessed using in situ carbon-uptake rates (5 years data) and Fast Repetition Rate Fluorometry (FRRF) (2 years data). The light-saturated, chlorophyll-specific rate of photosynthesis ($P^*_{\max}$), irradiance at the onset of saturation (E_k) and maximum light-utilisation efficiency (α^*) were determined for winter mixing and summer stratification. Fluorescence-based parameters as the functional absorption cross section of Photosystem II (σ_{PSII}) and the photochemical quantum yield (F_v/F_m) were additionally analysed in 2003 and 2004 to study the underlying physiological mechanisms for the variability in photosynthetic performance. Beyond their sensitivity to changing environmental conditions like thermal stratification, phytoplankton populations differ in their photosynthetic behaviour according to their size structure. Therefore Photosynthesis vs. Irradiance (P/E)-relationships were analysed in detail within a 1-year period from size fractionated cell counts, chlorophyll-*a* and carbon-uptake.

Keywords Primary productivity · $P^*_{\max}$ · E_k · Alpha · FRRF · Size classes

Introduction

Phytoplankton photosynthetic parameters in oligotrophic freshwaters are most commonly derived from in situ carbon-uptake rates. In order to provide an insight into the photosynthetic performance of phytoplankton assemblages in oligotrophic freshwaters, supplementary high resolution information on phytoplankton physiology can be obtained using Fast Repetition Rate Fluorometry (FRRF; Kolber et al., 1998), providing non-destructive, real time in situ estimates of

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Morphological plasticity of phytoplankton under different environmental constraints.

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photosynthetic parameters. Variations in photosynthetic efficiency are based upon mixing conditions which govern nutrient and light availability, and upon seasonal changes in species composition (Kaiblinger & Dokulil, 2005). However, phytoplankton size structure plays a major role for the physiological performance along the vertical light gradient. Small sized phytoplankton is proposed to have energetic advantages due to their surface/volume ratio (Raven, 1998), while large sized phytoplankton can have higher chlorophyll-specific productivity values (P^*) as shown by Legendre et al. (1993). Therefore size fractionated P/E (Photosynthesis/Irradiance) experiments are favourable to characterise the photosynthetic efficiency of phytoplankton assemblages.

In this study, data were analysed with respect to the differences in photosynthetic behaviour during mixed conditions, where phytoplankton is homogeneously distributed in the water column, and stratified conditions during summer, when a deep chlorophyll maximum (DCM), mainly composed of the cyanobacterium *Planktothrix rubescens*, occurs at a depth of 10–12 m in Mondsee. Concerning species that are confined to a certain season and depth like *P. rubescens*, the attempt was made to evaluate specific photosynthetic responses in terms of maximum chlorophyll-specific productivity ($P^*_{\max}$), maximum light-utilisation efficiency (α^*_{14C}) and Irradiance at the onset of saturation (E_k) from size fractionated C-uptake, chlorophyll-*a*, biovolume and light attenuation. In addition, fluorescence-based physiological parameters like the functional absorption cross section of Photosystem II (σ_{PSII}) and the photochemical quantum yield (F_v/F_m) were analysed in 2003 and 2004.

The working hypothesis was (1) to characterise the seasonal variation of the photosynthetic efficiency in phytoplankton, (2) to define the physiological response of specific phytoplankton species to changing environmental conditions, and (3) to determine P/E characteristics of the biggest size fraction (>11 µm).

Methods

The presented data were acquired in the years 1998–2000 and in 2003/2004 at fortnightly intervals in Mondsee, Austria. In situ photosynthetic rates of phytoplankton were estimated from carbon uptake applying the ^{14}C-technique after Steemann-Nielsen (1952). Light and dark glass-bottles were inoculated with 4 μC (=149 kBq) radioactive bicarbonate solution and horizontally suspended at in situ depth for 2 h from 1998 to 2000 and for 3 h in 2003/2004 respectively. In the laboratory, 4 ml of 2N Hydrochlorid acid was added to 50 ml of the samples and bubbled for 45 min (modified Acid bubbling method, ABM; Schindler et al. (1972)). From each light and dark bottle 10 ml sub-samples were transferred to scintillation vials and mixed with 10 ml of scintillation cocktail (Packard Ultima Gold). The ^{14}C content was measured as cpm in a Packard 1600 TR liquid scintillation counter, quench corrected and converted to dpm by internal efficiency. In the year 2000, size fractionated (<2 µm, 2–11 µm, <11 µm) experiments were carried out between April and December for the whole water-column (Greisberger, 2002). In the years 2003 and 2004, FRR-Fluorometry was applied in Mondsee. For details concerning instrument settings and calibration see Kaiblinger et al. (2005) and Kaiblinger & Dokulil (2005). The biophysical model of Kolber et al. (1998) was used to derive the initial fluorescence (F_0), the maximum fluorescence (F_m) and the functional absorption cross section of PSII (σ_{PSII}). The quantum efficiency of PSII was calculated from variable fluorescence ($F_v = F_m – F_0$) normalised to F_m, indicating the proportion of functional PSII reaction centres (Geider et al., 1993; Kolber & Falkowski, 1993). The vertical distribution of irradiance was measured as total available radiation with a LiCor 4π optical sensor and additionally with a precise 3 nm intervall spectroradiometer (RAMSES-SCC-VIS, TriOS) in 2003/2004. Chl-a concentration was determined following ISO 10620 (1992). After extraction with hot ethanol, Chl-a was determined from spectrometric measurements at 665 and 750 nm and corrected for phaeophytin using acidification according to Lorenzen (1967). Based on these data, Photosynthesis/Irradiance (P/E) relationships were derived using the tangent hyperbolic function after Jassby & Platt (1976):

$$P = P_{\max} * \tanh(\alpha^* E/P_{\max})$$

where $P_{\max}$ is the chlorophyll-specific maximum carbon uptake rate, α^* the maximum light-utilisation coefficient and E irradiance. In case when saturation was not reached, the sub-surface primary productivity was addressed as $P_{\max}$, α^* was subsequently calculated as the slope of the regression line. The parameters were log-transformed for normality and analysed for significant differences between seasons using a *t*-test.

Water temperature, pH, dissolved oxygen, specific conductivity and turbidity were measured with an automatic Yellow Springs 6502 profiler. 100 ml Phytoplankton-subsamples were fixed with Lugol's solution to determine abundance and biovolume after Utermöhl's sedimentation technique (Utermöhl, 1958).

Results

Winter mixing and the following stratification period were defined from temperature profiles and corresponding density differences. Stratification occurred from early May to mid October and was associated with surface water-temperatures between 14.1 and 25.8°C while mixing began end of October and lasted until mid of April of the following year (surface temperatures between 2.7 and 11.3°C). As expected, Chl-*a* was homogeneously distributed during the circulation period, while during stratification a DCM was observed in the thermocline. Microscopic determination of phytoplankton species and abundance indicated that the phytoplankton assemblage in the DCM was dominated by the filamentous cyanobacterium *P. rubescens* with up to 95% of the fresh weight biomass. The predominant taxa during the rest of the year were diatoms and small flagellates.

Seasonal analysis

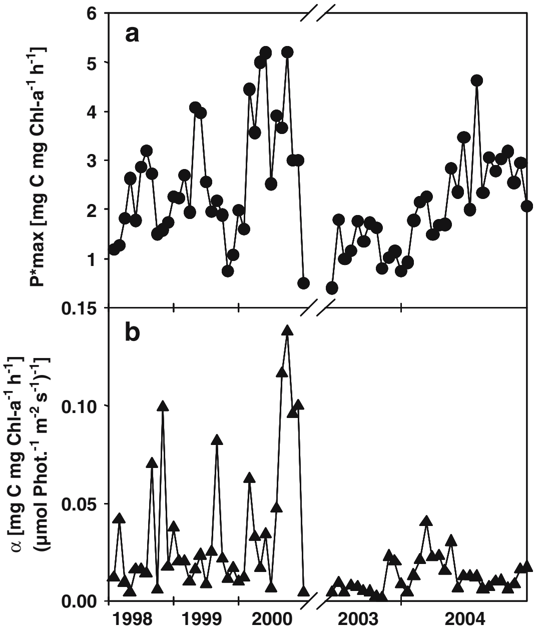

Fig. 1 Seasonal variability of $P^*_{\max}$ (**a**) and α^* (**b**) throughout the sampling period

Figure 1a shows the seasonal variation of the highest chlorophyll specific primary productivity ($P^*_{\max}$). $P^*_{\max}$ was in the range of 0.4–5.2 mgC (mg Chl-*a*)$^{-1}$ h^{-1}, highest in 2000 (average, 2.99 mgC (mg Chl-*a*)$^{-1}$ h^{-1}) and lowest in 2003 (1.19 mgC (mg Chl-*a*)$^{-1}$ h^{-1}). The seasonal variation of light utilisation efficiency α^* is given in Fig. 1b. The highest peak of α^* was measured in 2000 during winter and spring with maximum values between 0.06 and 0.14 mgC (mg Chl-*a*)$^{-1}$ h^{-1} (µmol phot. m^{-2} s^{-1})$^{-1}$. In the years 1998–2000, α^* was on seven occasions higher than 0.05 mgC (mg Chl-*a*)$^{-1}$ h^{-1} (µmol phot. m^{-2} s^{-1})$^{-1}$, while such peaks were missing in 2003 and 2004. $P_{\max}$ values during mixing periods and during summer stratified periods of the whole dataset (1998–2000 and 2003–2004) showed a significant seasonal pattern with highest chlorophyll specific primary productivity during summer stratification ($p < 0.001$, Fig. 2a). On the contrary, the maximum light-utilisation efficiency (α^*) was highest during winter and spring reaching maximum values between 0.06 and 0.14 mgC (mg Chl-*a*)$^{-1}$ h^{-1} (µmol phot. m^{-2} s^{-1})$^{-1}$. Light-utilisation efficiencies were calculated separately for 1998–2000 and 2003/2004 in a first step, but we decided to combine the whole dataset in a notched box-whisker plot, as there was no significant difference. α^* had a slightly higher median throughout the mixing period but

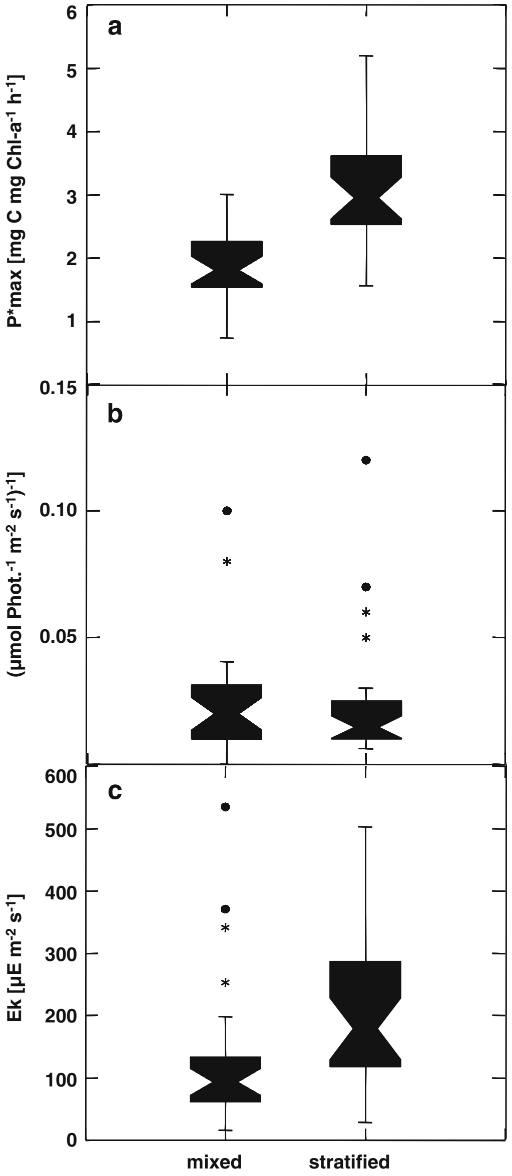

Fig. 2 Notched box-whisker plots of P^*_{max} (**a**), α^* (**b**) and E_k (**c**) for mixed and stratified conditions. The box contains 50% of the data, the outer limits of the notches are the 95% confidence limits of the median, indicated by the notch

there was no significant difference between seasons (Fig. 2b). The irradiance at the onset of saturation (E_k) is a derived parameter depending on P^*_{max} and α^*. The median E_k of 99 µmol phot. m^{-2} s^{-1} was significantly lower ($p < 0.005$) during mixed conditions than during stratification (median 180 µmol phot. m^{-2} s^{-1}) as indicated in Fig. 2c.

Physiological approach

Near the water-surface the quality of FRRF measurements was influenced by light intensity and did not provide reliable estimates. As a consequence, solely FRRF-measurements below 200 µmol Phot. m^{-2} s^{-1} were used to characterise physiological parameters. Under mixed conditions, when diatoms dominated the phytoplankton assemblage, the maximum quantum yield of photochemistry ($F_\mathrm{v}/F_\mathrm{m}$) varied from 0.49 to 0.60 (average 0.57, SD = 0.02) and showed a uniform distribution throughout the water-column. During stratification periods $F_\mathrm{v}/F_\mathrm{m}$ was generally lower (average 0.50, SD = 0.04) as presented in Fig. 3a. A characteristic vertical pattern was observed with quenched values near the surface, highest efficiencies towards the bottom of the mixed zone (6–8 m) and decreasing values further down the column corresponding to the light gradient.

The functional absorption cross section (σ_{PSII}) during mixed and stratified conditions is shown in Fig. 3b. σ_{PSII} varied from 195.4 to 366.2 (average 252.4 Å m^{-2}) between 6 and 15 m depth during mixed conditions and from 173.2 to 311.1 (average 221.9 Å m^{-2}) during stratification. As σ_{PSII} depends on the vertical mixing rate (Moore et al., 2003), the typical winter profile of σ_{PSII} showed a uniform distribution similar to $F_\mathrm{v}/F_\mathrm{m}$ and followed the vertical gradient of stratification in summer.

Size fractions

In 2000 a detailed study was undertaken to charakterise the contribution of picoplankton to primary production in Mondsee (Greisberger, 2002). The size fractionated data were analysed with respect to the photosynthetic efficiency of the separated size classes (<2 µm, 2–11 µm, >11 µm). The highest P^*_{max} (5.28 mgC (mg Chl-*a*)$^{-1}$ h^{-1}) was observed in the intermediate size-class (2–11 µm), which displayed at the same time the highest variability. In the smallest size fraction (<2 µm) P^*_{max} was between 1.8 and 2.3 mgC (mg Chl-*a*)$^{-1}$ h^{-1}, but the estimates were not significantly lower than the 2–11 µm size-fraction. P^*_{max} in the biggest size-fraction (>11 µm) was significantly lower than in the intermediate size-fraction and had the lowest median (1.85 mgC (mg Chl-*a*)$^{-1}$ h^{-1}), while no significant difference was observed in comparison to the smallest size fraction (Fig. 4a). The smallest size fraction had the highest light utilisation efficiency and the highest variability (0.001–0.17 mgC (mg Chl-*a*)$^{-1}$ h^{-1} (μmol phot. m^{-2} s^{-1})$^{-1}$, while the size fraction 2–11 μm had a maximum efficiency of 0.49 mgC (mg Chl-*a*)$^{-1}$ h^{-1} (μmol phot. m^{-2} s^{-1})$^{-1}$ and the lowest median (0.02 mgC (mg Chl-*a*)$^{-1}$ h^{-1} (μmol phot. m^{-2} s^{-1})$^{-1}$). The highest size fraction had the lowest α^* and the lowest variability but with 0.028 mgC (mg Chl-*a*)$^{-1}$ h^{-1} (μmol phot. m^{-2} s^{-1})$^{-1}$ a higher median than the intermediate size-class (Fig. 4b). The irradiance at the onset of saturation E_k displayed the highest variability in the smallest size fraction, reaching a maximum at 820 μmol phot. m^{-2} s^{-1}. The intermediate and the biggest size-classes showed very similar E_k-values in the range between 10 and 320 μmol phot. m^{-2} s^{-1} (Fig. 4c).

Discussion

On the basis of a five-year dataset, photosynthesis/irradiance responses of phytoplankton assemblages were evaluated for winter and summer populations. In 2003 and 2004, detailed information on the underlying physiological mechanisms of photosynthetic behaviour was obtained using FRRF, a technique which is rather novel to freshwaters (Kaiblinger & Dokulil, 2005). Size-fractionated data was available for a one-year period and offered the possibility to determine size-class dependent differences in photosynthetic behaviour.

Seasonal analysis

The seasonal phytoplankton succession in Mondsee was characterised by diatoms and small flagellates (Cryptophyceae and Chlorophyceae) during winter mixing and mass blooms of the filamentous cyanobacterium *Planktothrix rubescens* in summer and early autumn (Dokulil, 1987; Teubner et al., 2003). The difference between winter and summer phytoplankton populations in Mondsee is characterised by a slightly higher light utilisation efficiency in the winter-population, but significantly lower E_k and P^*_{max}. It is proposed that primary productivity is limited by light in spring and nutrients in summer (Diehl et al., 2002) The dominant diatom-species (e.g., *Aulacoseira* spp., *Asterionella* spp. and *Fragillaria* spp.) aggregate a higher amount of photoprotective pigments while they are continuously circulated through the water-column by convection currents in the mixing layers (e.g., Jørgensen, 1977; Harris, 1978). Willén (1991) reviewed that diatoms are good competitors at low light conditions (Hutchinson, 1957) with intermediate light saturation E_k between 190–240 μmol phot. m^{-2} s^{-1}. This statement is confirmed in our findings during the winter mixed period. As there was no significant difference in α^* observed here, E_k and P^*_{max} are temperature dependent.

Physiological approach

The importance of thermal stratification for the physiological state of phytoplankton assemblages is illustrated by the maximum quantum yields of photochemistry (F_v/F_m). Higher quantum yields of photochemistry (F_v/F_m) were observed under mixed conditions. The cellular pigmentation and pigment packaging increases during acclimation to low light conditions, which leads to a higher light utilisation efficiency (Bracher & Wiencke, 2000). During stratification, lower values of F_v/F_m indicate that there is a lower proportion of functional reaction centres (Kolber & Falkowski, 1993; Geider et al., 1993). Babin et al. (1996) reported lower photochemical quantum yields under nutrient limitation. Highest F_v/F_m (0.51) during summer occurred below the mixed zone between 6.5 and 10.5 m. Here, the density gradient enables phytoplankton to stay within moderate light intensities. In the metalimnion (10–12 m) where *P. rubescens* by far dominates the phytoplankton assemblage in summer, F_v/F_m was 0.39–0.44. These values most probably underestimate the efficiency of PSII because of alternative electron sinks: (1) thylakoids of cyanobacteria are also used for respiration, and (2) phycobilisomes can produce fluorescence (Kromkamp et al., 2001).

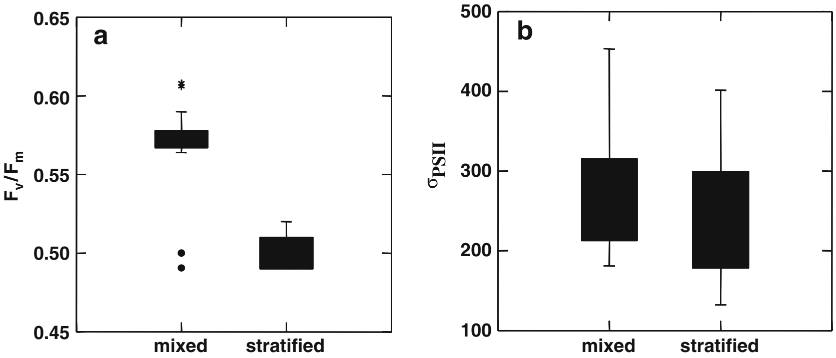

Fig. 3 Boxplots of the F_v/F_m (**a**) and σ_{PSII} (**b**) for mixed and stratified conditions illustrating the impact of thermal stratification on phytoplankton physiology

In contrast to the quantum yield of photochemistry, the functional absorption cross section σ_{PSII} was reduced during the mixed period. As Moore et al. (2003) pointed out, cells are moved faster through the vertical light gradient, than they can acclimate their photosynthetic apparatus. Therefore higher amount of photoprotective pigments are aggregated in the cells which lead to lower, uniformly depth-distributed σ_{PSII} (Koblizek et al., 2001). The low σ_{PSII} during the diatom dominated mixed period was consistent with taxon-specific data from Olson et al. (1996). Highest σ_{PSII} was observed at a depth around 7.5 m during stratification, declining to lower values down to 15 m depth. Uniformly low values were observed in the *Planktothrix* layer. Non-photochemical quenching can cause a reduction of σ_{PSII} up to 50% during a day (Falkowski et al., 1994), which explains the low values in the mixed zone in the upper 6 m during summer. Moreover, higher σ_{PSII} following nutrient limitation were reported by Berges et al. (1996).

Size fractions

Size fractionated primary productivity is commonly expressed as area-integrated total productivity of the euphotic zone (e.g. Happey-Wood, 1993; Weber & El-Sayed, 1987; Callieri & Stockner, 2002). Nixdorf (1985) and Desortová (1976) have found higher photosynthetic activity in small sized phytoplankton. However, P/E-relationships of size-fractionated phytoplankton data are scarce. FRRF was used by Cermeño et al. (2005) to assess the photosynthetic efficiency of size-fractionated phytoplankton. They found significantly higher P^*_{max} and F_v/F_m in the biggest size-fraction in summer. According to our results, the smallest size fraction, mainly composed of pico-cyanobacteria, had the highest and most variable α^* and E_k, and 50% of P^*_{max} was in a range between 1.9 and 3.1 mgC (mg Chl-*a*)$^{-1}$ h^{-1}. These findings indicate that picoplankton can acclimate very effectively to changing light conditions, reaching a median P^*_{max} of 2.85 mgC (mg Chl-*a*)$^{-1}$ h^{-1}. Han & Furuya (2000) found P^*_{max} in <3 μm size-fractions between 3.83 and 7.18 mgC (mg Ch l-*a*)$^{-1}$ h^{-1} in Tokyo Bay, but they did not investigate light utilisation efficiency. Putt & Prézelin (1985) observed α^* values between 0.01–0.06 mgC (mg Chl-*a*)$^{-1}$ h^{-1} (μmol phot. m^{-2} s^{-1})$^{-1}$ for cells in the size range 0.2–5 μm. The intermediate size-fraction is low-light acclimated with a maximum E_k of 440 μmol phot. m^{-2} s^{-1}, a less steep slope and high P^*_{max}, characteristics which Harris (1978) reviewed as typical for populations in cold, deep-mixed conditions. The biggest size fraction has similar E_k as the intermediate size-class, but a slope of 0.03 at maximum. This leads to a lower maximum productivity and indicates low-light adapted species. Pipp & Rott (1995) found low light acclimation and moderate maximum productivity for *Oscillatoria limosa*. As our data were not separated in winter and summer populations because size fractionated values from January to April 2000 were scarce, *Planktothrix rubescens* contributes to a large part, but not exclusively to this size class.

Conclusions

(1) Seasonal P/E-relationships in Mondsee 1998–2000 and 2003–2004 indicate that the

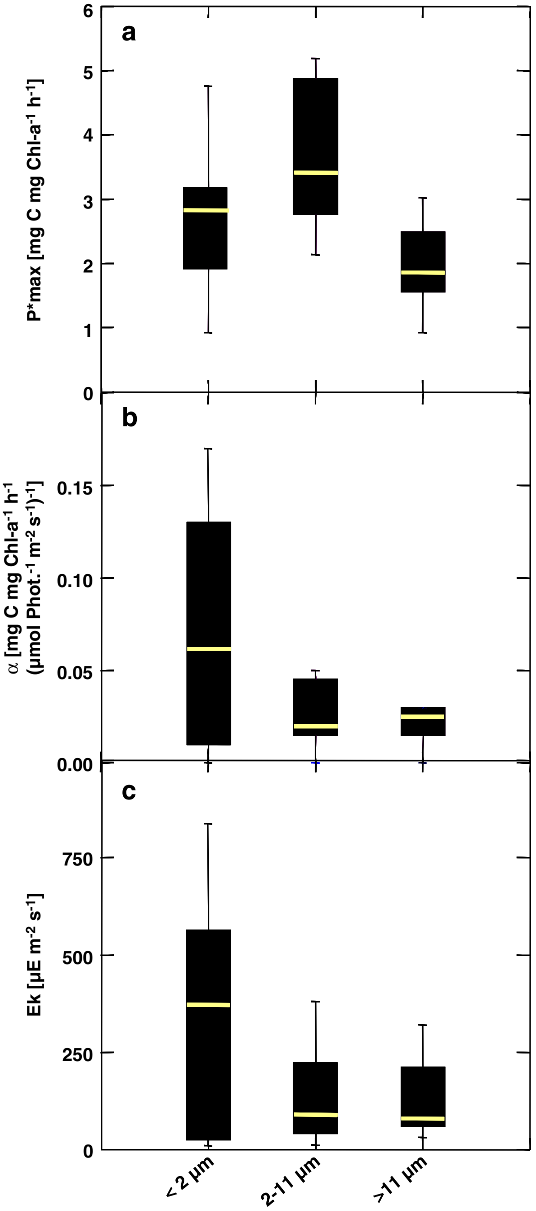

Fig. 4 Boxplots of $P^*_{\max}$ (**a**), α^* (**b**) and E_k (**c**) for the three size fractions <2 µm, 2–11 µm and >11 µm within a one year period. The median is indicated as white line

species assemblage in Mondsee is temperature dependent and warm acclimated.

(2) Throughout the mixed period in late autumn, winter, and spring, the short length of the day and the higher nutrient availability caused higher quantum yields of photochemistry (F_v/F_m), while the functional absorption cross section (σ_{PSII}) decreased because of photoprotective pigments.

(3) Although the size-class >11 µm was not exclusively composed of *P. rubescens*, α^* and $P^*_{\max}$ adequately describe the characteristics of this extremely shade adapted species which utilizes the green light spectrum in the metalimnion.

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