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The effects of diel changes in photosynthetic coefficients and depth of *Planktothrix rubescens* on the daily integral of photosynthesis in Lake Zürich

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ABSTRACT

In late summer and autumn, before the vertical circulation reaches the thermocline, the phytoplankton population of Lake Zürich is dominated by the red-coloured filamentous cyanobacterium *Planktothrix rubescens*, which stratifies in the metalimnion at depths close to the photosynthetic compensation point. The filament volume concentration reached a maximum of 12 $cm^3\ m^{-3}$; the depth of the maximum varied from 10.5 to 12.5 m. Changes in the depth distribution were attributed to a combination of (1) seiche movements, which raised or lowered the thermocline by up to 2 m over 36 h, and (2) flotation by the buoyant filaments relative to the isotherms, by up 0.4 m d^{-1}. These changes caused a 2-fold change in insolation at the *Planktothrix* peak. Estimates were made of the daily integral of photosynthetic O_2-production, $\Sigma\Sigma(NP)$, by the population of *P. rubescens* over a period of four cloudless days. The estimates were calculated from measurements of surface irradiance (at 5-min intervals), vertical light attenuation, temperature, filament volume concentration and the photosynthesis/irradiance (*P/I*) curves of filaments concentrated from the metalimnion. Despite the similar, high insolation on each of the four days, the calculated values of $\Sigma\Sigma(NP)$ varied from 9 to 53 mmol $m^{-2}\ d^{-1}$, owing to the changing depth distribution of the filaments. Measurements of *P/I* curves of lakewater samples incubated at a depth of 11 m showed changes in the photosynthetic coefficients during the day. These also generated large changes in calculated values of $\Sigma\Sigma(NP)$. The computer spreadsheet used to calculate $\Sigma\Sigma(NP)$ was modified to incorporate time-based changes in the photosynthetic coefficients and vertical distribution of the organism. These refinements provide a more accurate description of photosynthesis by the deep-living *P. rubescens*, which adjusts its position by buoyancy regulation to exploit the light field in the metalimnion, where it outcompetes other phytoplankton.

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Introduction

Rates of photosynthesis by phytoplankton organisms respond directly to changes in irradiance and temperature. Measurements of these responses have been used to calculate the potential photosynthesis at different depths and different times of day in lakes in order to estimate the daily productivity by phytoplankton populations. A standard procedure in the calculation of daily integrals of photosynthesis is to determine, usually in the laboratory, the relationship between photosynthesis (*P*) and irradiance (*I*). Coefficients are then calculated that describe this relationship (the *P* vs. *I* curve) and these are used to calculate the potential *P* from measurements of *I* at different depths and times. Inherent in these calculations is the assumption that the *P/I* relationship remains constant.

The capacity of phytoplankton for photosynthesis will vary over the daily cycle due to endogenous and exogenous factors. Unicellular algae (Sweeney, 1987) and cyanobacteria (Golden et al., 1997) exhibit endogenous circadian rhythms in physiological processes and in the expression of genes that encode proteins involved in photosynthesis (Ishiura et al., 1998). Exposure to high irradiances during the daytime can also cause a decrease in photosynthetic capacity (Kirk, 1994), one of the factors implicated in the 'hysteresis' effect (Schanz and Dubinsky, 1988), which generates asymmetry between photosynthetic rates under identical irradiance levels in the morning and afternoon.

We have investigated possible changes in the photosynthetic capacity of *Planktothrix rubescens* (Anagnostidis & Komàrek, nov. comb.) in Lake Zürich, Switzerland. During the summer a population of this red-pigmented filamentous cyanobacterium develops at depths between 8 to 15 m in the metalimnion of this lake (Thomas and Märki, 1949; Walsby, Avery and Schanz, 1998). The photon irradiance at these depths is typically less than 1% of the surface irradiance, often regarded as the minimum required to sustain net photosynthesis (Talling, 1957). Recent studies, however, have shown that isolates of *P. rubescens* from Lake Zürich are capable of positive net photosynthesis and growth at irradiances as low as 2 μmol m^{-2} s^{-1}, equivalent to 0.13 % of the surface irradiance at noon, when grown in a 12h:12h light-dark cycle (Bright and Walsby, 2000).

From the photosynthetic coefficients of *P. rubescens*, Micheletti, Schanz and Walsby (1998) calculated that the daily integral of photosynthesis of the population in the top 20 m of the water column in Lake Zürich had a negative value on only 5 of the 136 days between July and November. Bright and Walsby (2000) determined the relationship between growth rate and irradiance of a Lake Zürich strain of *P. rubescens* and similarly concluded from their culture experiments that the population remained productive on most days, though there were periods when the calculated production was insufficient to account for the observed increase in the population.

The calculations on the daily integral of photosynthesis performed by Micheletti et al. (1998) used the average coefficients calculated from *P/I* measurements made at only one period of the day. Moreover, no information was available on possible changes in the vertical distribution of the organism. We describe here an investigation of changes in the photosynthetic coefficients of the metalimnetic *Planktothrix* population during the day and the consequences this has for calculations of

the daily integral of photosynthesis by this population. The study also indicates that, because the metalimnetic population is located close to the photosynthetic compensation point, calculations of its potential photosynthesis are very sensitive to changes in its vertical distribution, which occur through migration and seiche movements within the lake.

The general limnology of Lake Zürich and the specific conditions during our investigations are described in Bossard et al. (this issue). Characteristic features of seasonal cycles and primary production by *Planktothrix rubescens* in Lake Zürich have been described by Walsby et al. (2001). Entrainment experiments simulating photoacclimation of *Planktothrix rubescens* were performed simultaneously with this study by Kromkamp et al. (this issue).

Materials and methods

Lakewater sampling

Samples were collected from the middle of Lake Zürich at a position (47º19.3′N, 8º34′E) between Bendlikon/Kilchberg on the south-west side and Kusen/Küsnacht on the north-east side. Samples were collected with a 5-l Friedinger bottle at depths of 0, 5, 10, 15, 20, and 40 m and at closer intervals near the thermocline (8 to 12.5 m, see below). A preliminary estimate of the depth of the *Planktothrix* maximum was obtained by filtering 200 ml samples of these lake water samples through glass fibre filters (GF 92, Schleicher and Schuell, Dassel, Germany) on the boat and noting the degree of purple-red coloration of the filter. Further samples were then taken for measurement in the laboratory.

Uniform water samples were obtained by combining four successive 5-l samples from a depth of 11 m in 50-l carboys covered in black polyethylene. The samples were mixed by several transfers between two carbuoys. Transparent 1.5-l polycarbonate bottles were filled with this lakewater and then suspended from a buoyed boom at an anchorage 100 m from the shore at Goldbach/Küsnacht (47º19.1′N, 8º34.4′E), where the lake bottom shelved steeply. The bottles were shaded from sunlight by black cloth during handling and transfer to the laboratory.

Simultaneous measurements of temperature, O_2 concentration and photon irradiance were made at 1-m depth (z) intervals: water temperature (Θ_z) was measured with a TTM 72 thermistor thermometer (Züllig AG, Rheineck, Switzerland), O_2 concentration (O_z) with an OXY 196 oxygen electrode (WTW, Weilheim, Germany), and PAR (I_z) with a LI-192 SB underwater quantum meter (LI-Cor, Lincoln, Nebraska). PAR immediately under the water surface (I_0) was also measured. The vertical light attenuation coefficient (attenuance) between adjacent depth intervals (z and z+1m) was calculated as $K_d = \ln(I_z/I_{z+1m})/(1\ m)$; for purposes of comparison with *Planktothrix* concentration, this was assumed to be the attenuance midway between the adjacent depths (at z+0.5 m).

Filament concentration in lakewater samples

Samples of 50 to 500 ml were filtered through nitrocellulose membrane filters (Schleicher and Schuell) of 8-μm pore size. The concentration of *Planktothrix* filament length was determined by epifluorescence microscopy and computer image analysis (Walsby and Avery, 1996). The biovolume was calculated by multiplying the length by the mean cross-sectional area of the filament, 25 μm^2 (Walsby, Avery and Schanz, 1998); filament biovolume concentration ($cm^3\ m^{-3}$) was calculated from the filter area analysed and volume of water filtered. Chlorophyll *a* concentrations were measured by filtering 200-ml samples through GF 6 filters (Schleicher and Schuell), which were stored at –30°C. The chlorophyll was extracted at room temperature by grinding the filter in 90% acetone. After 15 min the extract was clarified by filtration; the chlorophyll *a* concentration was determined by fluorimetry with excitation at 430 nm and emission measured at 668 nm (Schanz, 1982).

For determination of *P/I* curves, *Planktothrix* filaments were concentrated by filtering 2 l of lake water through a nitrocellulose filter (pore size 8 μm) under gravity, without application of vacuum. The wet filter was washed with about 10 ml of lake water and the *Planktothrix* filaments floated off. The samples were made up to 20 ml in the chamber of the apparatus described below (giving a concentration factor of 100-fold). Microscopy revealed that the filaments remained intact during this procedure.

Generation of P/I curves

Measurements of the rate of photosynthetic O_2 production were made with an apparatus similar to that described by Dubinsky et al. (1987). The O_2 electrode chamber (a cylinder of diameter 30 mm, length 28 mm, volume 20 cm^3) also accommodated a port for the fiberoptics of a PAM fluorometer (Walz GmbH, Effeltrich, Germany) for measurement of variable chlorophyll fluorescence (Kromkamp et al, this issue). The rate of O_2 production per unit volume of *Planktothrix* suspension ($\mu mol\ ml^{-1}\ h^{-1}$) was determined with an O_2 electrode (Yellow Springs, Model 5331) calibrated in water samples equilibrated with air (100% O_2 saturation) and containing sodium sulfite (0% saturation). Measurements were made for 3-min intervals during illumination by a beam of light from a slide projector, attenuated by neutral density filters (Balzers) to 10 different irradiances (see below). The *P/I* curve obtained was described by the exponential equation,

$$P = P_m\,(1 - \exp\,(-\alpha I/P_m)) + R + \beta I \qquad (1)$$

in which P_m is the light-saturated rate of oxygen production, R is the rate in the dark (a negative value), α is the initial slope of the *P/I* curve at low irradiance and β the slope (negative when there is inhibition) at high irradiance. The values of the coefficients P_m, α and β were determined by the least squares method, using the Solver software in Excel Sheet 1 of Integral.xls, described by Walsby (1997). From the filament biovolume concentration in these suspensions ($cm^3\ ml^{-1}$) the biovolume related rates of O_2 production were calculated ($\mu mol\ ml^{-1}\ h^{-1}/(cm^3\ ml^{-1})$ =

μmol cm^{-3} h^{-1}). The rate of respiratory O_2 uptake was measured in the dark. This rate includes the residual rate of consumption by the electrode, which was measured and subtracted.

Measurements of photon irradiance: cross-calibration of instruments

Measurements of PAR photon irradiance (wavelengths 400–700 nm, in units of μmol m^{-2} s^{-1}) were made with three instruments, each with a flat cosine sensor.

a) Photosynthesis chamber. The photon irradiance in the chamber was determined from measurements with a Macam quantum sensor type SD 101 QW placed against the back face of the rear window. For each series of *P/I* curves, measurements were made of the photon irradiance with water (I_w) and then with the concentrated *Planktothrix* sample (I_c) in the chamber. With the optical arrangement used, the irradiance immediately behind the front face of the chamber was found to be $1.41I_w = I_a$. The mean irradiance in the chamber was then calculated as $I_m = (I_a - I_c)/[\ln(I_a/I_c)]$.

b) Continuously recording sensor. Continuous recordings of the ambient light field were made with a LI-Cor (Lincoln, Nebraska) Quantum Sensor type LI-190SB on the roof of the Lindt & Sprüngli chocolate factory (47°19.1′N, 8°33.2′E) adjacent to the Limnology Station at Kilchberg and 100 m from the lake shore. The mean values over 5-min intervals were recorded with a data logger (LI-Cor, model LI-1000) and transferred to Excel spreadsheets.

c) Portable sensor. The measurements obtained with the sensors described were compared by calibration against the measurements obtained with a Macam SD226 COS Sensor used with a portable radiometer model Q203 PAR. The ratio of readings made with the Quantum Sensor (a) and this portable sensor (c) was (a/c) = 0.8618. The ratio of readings made with recording sensor (b) and this portable sensor was (b/c) = 0.8356. Therefore, the ratio of a/b = 1.0314 (i.e., a difference of about 3 %).

Phytoplankton counts

For the enumeration of phytoplankton, samples were fixed by adding concentrated neutralized Lugol's solution and stored in a refrigerator at 4°C. The sediment was later resuspended and transferred to a 1-ml Kolkwitz chamber; after sedimentation for 10 min, the species were enumerated and the total cell volume of each species determined using the procedure of Bleiker and Schanz (1989). The City of Zürich Water Supply provided data on phytoplankton abundance, using the Utermöhl technique, in samples taken at a depth of 10 m on 8 September 1999.

Buoyancy state of the filaments

A sample of lake water was mixed and pipetted onto a microscope slide that had a gap of 2 mm between the coverslip and slide. After 30 min, the numbers of filaments floating in the plane of the underside of the coverslip and those settled onto the plane of the slide were counted (Walsby and Booker, 1980).

Results

1) Continuous recordings of irradiance and windspeed

Measurements of irradiance at the water surface form the basis of the calculation of the daily integral of photosynthesis. Recordings of irradiance over the 4 d of the study are compared with the sine curve of solar irradiance for the geographical location in Figure 1. The irradiance was plotted against Local Solar Time (sun at its zenith at noon) calculated from the longitude correction as (1–8.567°/15° h^{-1}) = 0.429 h for Central European Time, and 1.429 h for Central European Summer Time (i.e. 12.00 h Local Solar Time is at 13.429 h CEST). Values for a cloudless sky at the latitude of Kilchberg (Fig. 1) were calculated from the sine equation of Kirk

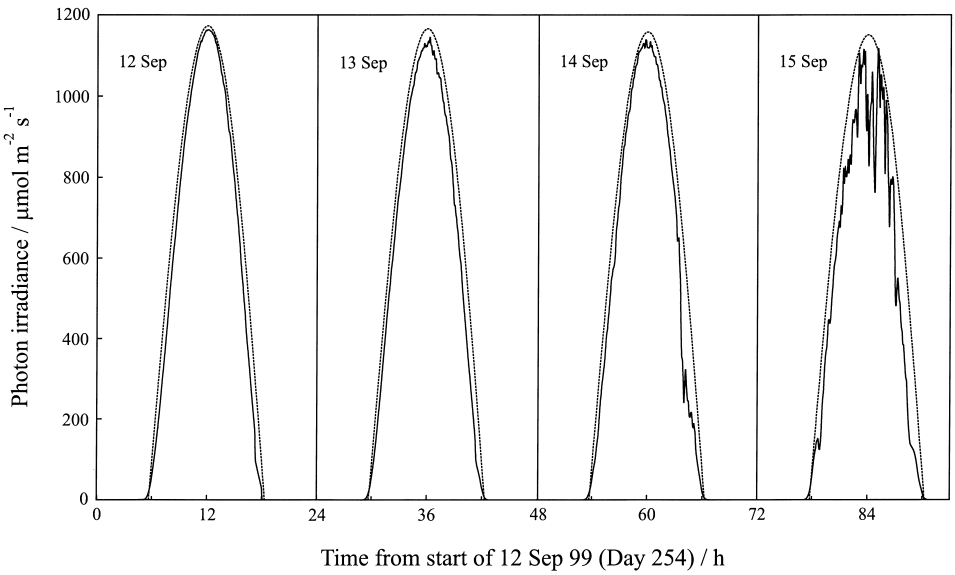

Figure 1. Measurements of photon irradiance (—) at 5-min intervals over the four days 12–15 September 1999. The sine curve (- - -) is the theoretical maximum value for the date and latitude, standardized to the highest measured value for the first day. The time is Local Solar Time (sun at its zenith at noon)

(1994), using the procedures described by Walsby (1997). The measured curves for the first three days demonstrate the nearly cloudless days; the curves are slightly attenuated near dawn and (more so) at dusk owing to the occlusion of the sensor by the hills bordering Lake Zürich. Corrections for reflection losses at the water surface were made by using the spreadsheet Integral.xls (Walsby, 1997). The corrections incorporate the roughening effect of windspeed (hourly averages) obtained from the Swiss Meteorological Institute (not shown). The average daily loss by reflection from the water surface over the 4 days was calculated to be 5.7%.

2) Vertical distributions of PAR and attenuance

The underwater irradiance field was calculated from the ratio of I_z/I_0, where I_z is the irradiance at depth z and I_0 is the irradiance immediately under the water surface. The high surface irradiance and transparency of the epilimnion during the study period permitted irradiance to be measured down to depths of 15-19 m at solar noon each day. Graphs of $\ln(I_0/I_z)$ versus depth indicated a uniform light attenuation throughout the epilimnion but an increased attenuance in the metalimnetic layers (Fig. 2), evidently due to light absorption by the *Planktothrix* layer (see below). The conventional euphotic depth, at which $I_z = 0.01\ I_0$ (Talling, 1957), was between 10–12 m.

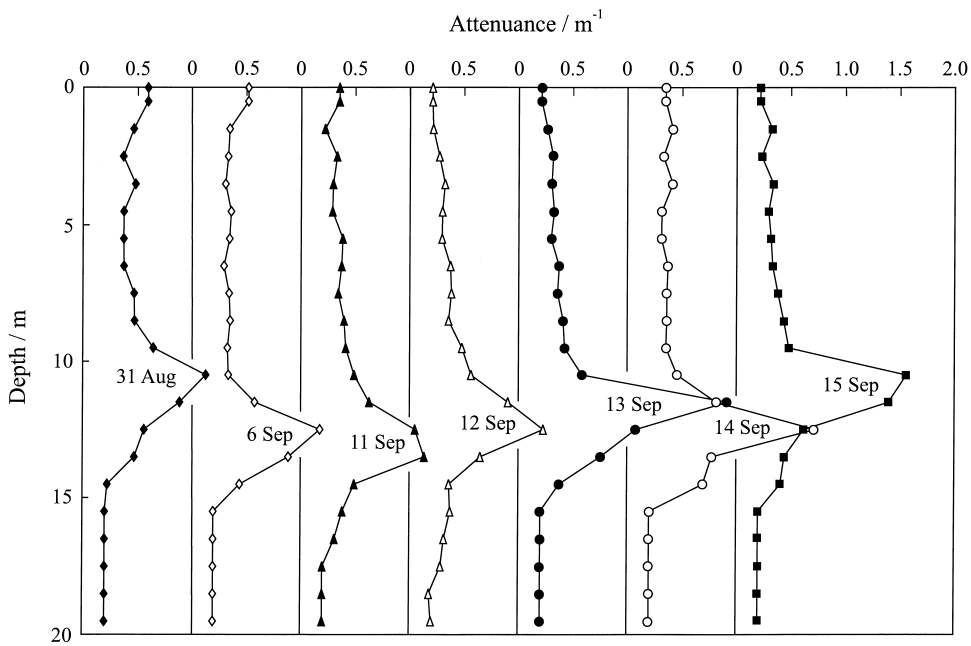

Figure 2. Changes in attenuance, K_d, with depth (z) on the seven sampling dates. The values of K_d are plotted at depths midway between depths of I_z measurements

3) Vertical distributions of Planktothrix *and proportion of total phytoplankton*

a) Phytoplankton

In the water sample taken by the City of Zürich Water Supply from a depth of 10 m over the deepest point in Lake Zürich (middle of the lake between Oberrieden and Herrliberg) on 8 September 1999, nearly 30 species of microalgae were enumerated. Of the total cell volume (10.4 $cm^3\ m^{-3}$), *P. rubescens* (9.3 $cm^3\ m^{-3}$) accounted for 89.7%, diatom species 5.4%, flagellates 4.5%, and other microalgae 0.5%. Microscopic examination (at ×200 magnification) of the filter-concentrated metalimnetic water sample used in measurements of *P/I* curves revealed small diatoms, such as *Stephanodiscus hantzschii*; the colonial diatoms *Fragilaria crotonensis, Tabellaria fenestrata,* and *Asterionella formosa*; the colonial chrysophyte *Dinobryon divergens*; the dinoflagellate *Ceratium hirundinella*; and small amounts of flagellates (*Rhodomonas* sp. and *Cryptomonas* sp., <30 µm in diameter). Together they contributed from 2.1 to 6.2% to the total biovolume; *P. rubescens*, determined separately by image analysis, formed the remainder of the biovolume.

b) Vertical distribution of Planktothrix

Measurements of the filament volume concentration of the *P. rubescens* population by image analysis showed that the depth of the peak concentration varied from 10-12.5 m on different days. The concentration at the peak exceeded that at adjacent sampling depths several fold, indicating that the population was sharply stratified (Fig. 3). This suggested that the actual peak of the population occurred at a depth between sampling depths and that it contained a higher filament concentration than that reported. We investigated the possibility of using light attenuation as a measure of *Planktothrix* concentration because measurements of K_d had been made at closer (1-m) intervals (Fig. 2) and K_d appeared to be correlated with the *Planktothrix* concentration (N).

4) Estimation of Planktothrix *biomass distribution from the attenuation coefficient*

Comparisons were made of the relationship between the attenuance (K_d) and *Planktothrix* filament concentration (N) from six pairs of measurements made at identical depths within the metalimnetic layer on 31 August (Day 242), 6 September (Day 248) and 12 September 1999 (Day 254). For these six pairs of values there was a linear relationship (Fig. 4); regression analysis indicated that

$$K_d = (0.0892\ N/cm^3\ m^{-3} + 0.375)\ m^{-1} \quad (2)$$

with $R^2 = 0.977$ ($N = 6$, $P < 0.001$). In the top 0-8 m of the epilimnion, where the attenuation was constant (Fig. 4) and *P. rubescens* was absent, the mean value of K_d on the 7 sampling days was $0.35 \pm 0.05\ m^{-1}$, i.e., within the range of the intercept in eqn (2). This is evidently the background attenuance (K_w) of the lake water, the dissolved yellow substances and suspended matter. The attenuation coefficient over the PAR waveband by Lake Zürich water and its nonchlorophyll-related components (K_w) has been estimated by Schanz (1985) to be $0.238\ m^{-1}$, with a 95%-confi-

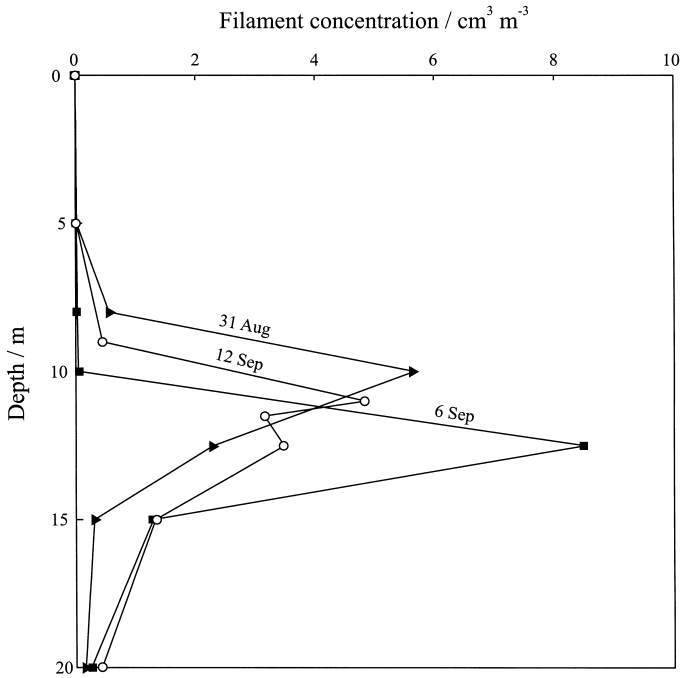

Figure 3. The vertical distribution of filament volume concentration of *Planktothrix rubescens* in Lake Zurich on 31 August, and 6 and 12 September 1999

dence interval of 0.080 to 0.395 m^{-1}; the values are highest in August and September when calcite precipitation occurs (Schanz, 1994). The intercept of 0.375 m^{-1} (eqn 2) is therefore within this range of K_w. From the attenuance above that attributable to K_w, the filament concentration can therefore be estimated as

$$N = [(K_d - K_w)/0.0892\ m^{-1}]\ cm^3\ m^{-3} = 11.2[(K_d - K_w)/m^{-1}]\ cm^3\ m^{-3}. \quad (3)$$

A fairly similar value can be calculated from the measurements made with a horizontal beam transmissometer by Walsby, Utkilen and Johnsen (1983) on suspensions of *P. rubescens* (red coloured *Oscillatoria agardhii*) in Lake Gjersjøen, Norway. A filament length concentration of 100 m l^{-1} (equivalent in Lake Zürich to a filament volume concentration of 2.5 $cm^3\ m^{-3}$) produced an increase in beam attenuance of $\Delta K_b = 0.31\ m^{-1}$; equating this to the increase in K_d, the relationship was therefore

$$N = (2.5\ cm^3\ m^{-3})\,(\Delta K_b/0.31\ m^{-1}) = 8.1\,[(K_d\text{-}K_w)/m^{-1}]\ cm^3\ m^{-3}. \quad (4)$$

The small difference may be attributed to differences, in the *Planktothrix* populations of the two lakes, of filament width or gas vesicle content, both of which are bound to affect the optical-section and thereby the N/K_d relationship (Dubinsky, 1992; Schanz, Senn and Dubinsky, 1997).

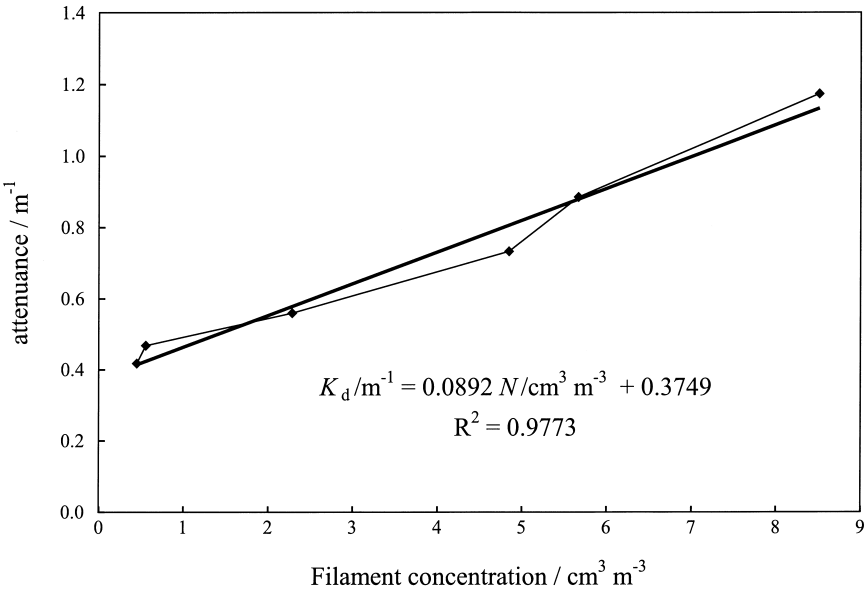

Figure 4. Comparison of the attenuance (K_d) and *Planktothrix* filament volume concentration (N) in the metalimnetic layers on Days 242 and 248

On 14 September 1999, measurements were made by J. H. Morrow of the irradiance at 4-cm depth intervals with an underwater spectroradiometer (Biospherical Instruments Inc., San Diego). The depth profile of the 560 nm wavelength, very close to the 555-nm absorption maximum of phycoerythrin in *P. rubescens*, revealed a steep change in attenuance at depths between 10 and 13 m. In principle, this sort of measurement would provide better information on the location of the *P. rubescens* population; it is not possible to determine the concentration profile here because no simultaneous measurements were made on filament distribution.

5) Water movements and temperature

While *Planktothrix* filaments will regulate their buoyancy in response to the vertical gradient of irradiance, they will float or sink relative to a thermally-stabilised water mass that is itself subject to movement by wind-induced seiches in the lake. Figure 5 shows that the peak of light attenuance, which indicates the peak of the *Planktothrix* population, moved from a depth of 10.5 m (above the 14°C isotherm) on Day 242 to 13.5 m (at the 11°C isotherm) on Day 253. Over this period the depth of the 11°C isotherm changed little and it is therefore concluded that there had been a downward movement of the *Planktothrix* population relative to the water mass. Over the following period, Day 253–257, the attenuance peak returned to the original depth of 10.5 m and again moved above the 14°C isotherm; it is noted, however, that this upward movement was superimposed on vertical fluctuations of up to

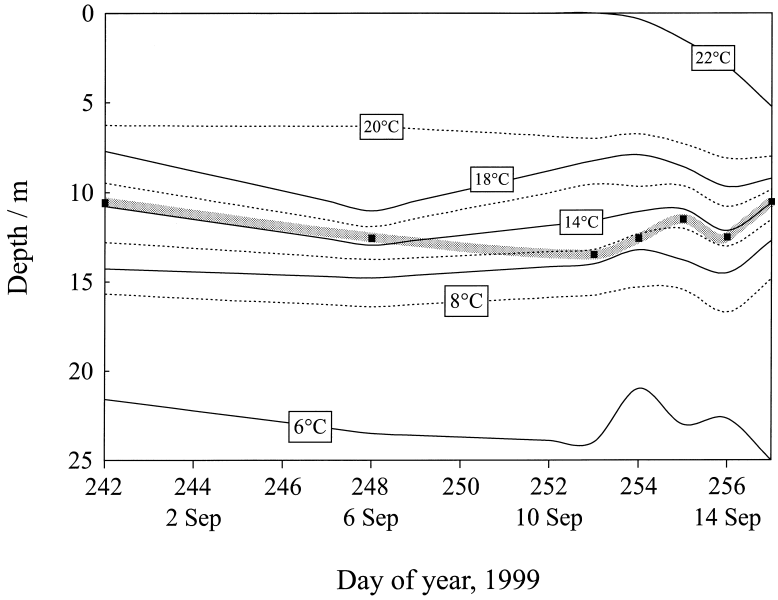

Figure 5. Changes in depths of isotherms at intervals of 2°C over the period 31 August to 15 September 1999. The depth of the peak attenuance is indicated by the the symbols (n) at the 7 sampling dates and the linking grey band

1.8 m by the isotherms, indicative of seiche movements. The movements of the peak of the filament population from the 11°C isotherm and then back to the 14°C isotherm over the last four days is equivalent to a depth change of 1.7 m relative to the water mass (mean value from 5 days) and indicates an average floating velocity of 0.4 m d^{-1}. Movements due to seiches and sinking or floating will affect the irradiance reaching the depth of the population peak; in turn, the irradiance change will affect the photosynthetic production and will feed back onto the buoyancy response.

6) Changes in P/I curves

P/I measurements were made on samples taken from the 11-m peak and from samples incubated in bottles at 11 m for 0, 2, 4, 6 and 25 h. The P/I curve for the first of these lakewater samples is shown in Figure 6 and changes in the photosynthetic coefficients are shown in Table 1. The results indicate a rise in α during the day; by the following morning, however, the value of α had returned to that of the previous morning. The value of P_m also increased during the day. Analysis of the data by non-linear regression using Sigmaplot 5 for Windows showed that both α and P_m were significantly lower in the early morning samples (10.30 on 12 September) than in the mid-afternoon (14.30 h sample, $p < 0.05$). The other major change was in the rate of respiratory oxygen uptake ($-R$), which doubled during the day. The measured values of R in the filtered lakewater sample contain an unknown contribution from

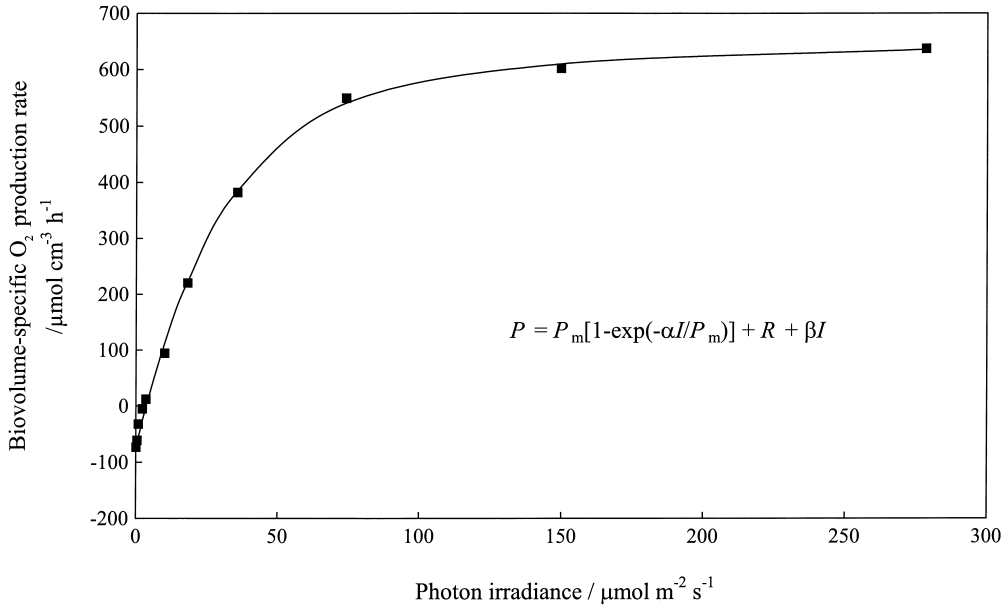

Figure 6. Measurements of photosynthetic O_2-production rate per biovolume of *Planktothrix* sp. concentrated from the lakewater sample from 11 m at 9.07 h Local Solar Time on 12 September 1999 (n). The line is calculated from equation (1) (shown in the figure) using the values of the coefficients P_m, R, α and β shown in column 2 of Table 1

Table 1. Changes in the photosynthetic coefficients (P_m, R, α and β) of *P. rubescens*, measured at a temperature Θ', in a water sample from a depth of 11 m taken at 10:30 h on 12 September and incubated in bottles at a depth of 11 m for 2 to 25 h. The values at midnight (§) are calculated by linear interpolation. For photosynthetic coefficients, see Fig. 6; R = measured respiration, R_s = respiration calculated as –0.110 P_m

In situ incubation time /h	0	2	4	6	§	25	Mean*
Date	12 Sep	12 Sep	12 Sep	12 Sep	12 Sep	13 Sep	
CEST of sampling /h min	10:30	12:30	14:30	16:30		11:30	
Solar time of sampling /h	9.07	11.07	13.07	15.07	24.00	10.07	
α/µmol cm^{-3} h^{-1} (µmol m^{-2} s^{-1})$^{-1}$	21.2	29.3	32.3	28.2	24.7	22.5	26.7
β/µmol cm^{-3} h^{-1} (µmol m^{-2} s^{-1})$^{-1}$	0.159	0.948	0.608	0.745	0.449	0.152	0.522
P_m /µmol cm^{-3} h^{-1}	664	579	702	682	673	754	676
R/µmol cm^{-3} h^{-1}	–73	–112	–134	–161	–116	–111	–118
R_s/µmol cm^{-3} h^{-1}	–73	–64	–77	–75	–74	–83	–74
Θ'/ ºC	15.5	15.5	15.5	15.5	15.5	15.5	15.5

* The mean values are calculated from the values of the measured samples only, not including the interpolated value at midnight.

zooplankton and other microorganisms collected on the filter and the contribution of the *Planktothrix* filaments cannot therefore be determined with certainty. In some of the following calculations a standardized value, R_s, is used, taken to be $-0.110\ P_m$, which is the ratio found in the first sample in Table 1 and is within the range of ratios found in laboratory cultures of Lake Zürich strains of *P. rubescens* (Bright and Walsby, 2000).

7) Daily integral of photosynthesis

Calculations have been made of the daily integral of photosynthesis from data gathered on the 12-15 September on the vertical distribution of *P. rubescens*, vertical light attenuation, vertical temperature profile and 5-min irradiance measurements throughout these days, using a version of the Integral.xls spreadsheets of Walsby (1997). The results are shown in Table 2. The calculations are all based on *P/I* curves made on Day 254 (12 Sep, see Table 1). We first comment on the different calculations used for estimating the daily integral on Day 254 and then on changes that occurred over the three subsequent days.

a) Different calculations for Day 254

If the photosynthetic rate is calculated with the coefficients obtained from the first *P/I* curve, the value obtained for daily integral of photosynthetic O_2 production for Day 254 is 16.3 mmol m^{-2} (Table 2, row 5). Similar calculations made with the raw data from the subsequent curves (obtained from samples incubated in bottles for 2, 4 and 6 h) all generate negative values, however, because of the proportionately larger values of R (not shown). If the calculation is made with the mean value of each

Table 2. Measurements of the *Planktothrix* population and daily insolation, with estimates of the daily integral of photosynthesis (in units of mmol m^{-2}) on four successive days calculated with different versions of the Integral.xls spreadsheet, using values of the photosynthetic coefficients (P_m, R, α and β) given in Table 1

Row	Day of year: Date		254 12 Sep	255 13 Sep	256 14 Sep	257 15 Sep
	Planktothrix population:	Depth range/m				
1	Areal biovolume, ΣN/cm^3 m^{-2}	0–25	29.9	41.1	37.2	39.4
2	Median depth of *Planktothrix*/m	0–25	11.7	11.2	12.0	10.5
3	Modal depth of *Planktothrix*/m	0–25	12.5	11.5	12.5	10.5
4	Insolation below surface/mol m^{-2} d^{-1}		29.2	28.3	27.6	25.0
	Photosynthetic integrals, $\Sigma\Sigma$(NP)/mmol m^{-2}, calculated using:					
5	Coefficients for the first sample	0–20	16.3	33.3	–1.2	35.9
6	Day-averaged coefficients, with R	0–20	0.02	14.5	–25.0	14.3
7	Day-averaged coefficients, with R_s	0–20	26.8	48.3	8.6	52.7
8	Coefficients interpolated, with R_s	0–20	27.3	48.6	9.4	53.1
9	Coefficients interpolated, with R_s	0–25	25.9	47.2	8.0	51.7

of the four coefficients in Table 1, the daily integral also has a value of only 0.02 mmol m^{-2}, because of the dominating effect of the high value of -R (Table 2, row 6).

As discussed above, because of the unknown contributions of other organisms to the measured rate of respiration, a better estimate of the compensation point of the *P. rubescens* population may be obtained by calculating a standardized value of the respiration rate from the ratio of R/P_m. When R is replaced by R_s, calculated as $-0.110P_m$ (equivalent to that for the first sample described in section (6) above), the value of the integral $\Sigma\Sigma(NP)$ is calculated to be 26.8 mmol m^{-2} (Table 2, row 7). This higher value reflects the increase in α, and to a lesser extent that of P_m, during the day.

These calculations were repeated using a spreadsheet in which the measured values of each of the coefficients (α, β, P_m and R) used in calculation of P were inserted in four columns to the left of the main integration table at the sampling times (Local Solar Time, given in Table 1) and the values at other times were calculated by linear interpolation. This more detailed calculation produced only small changes in the value of the double integral, e.g., from 26.8 to 27.3 mmol m^{-2} on Day 254, using the standardized value, R_s (Table 2, row 8). Photosynthetic integrals were also calculated for the population down to a depth of 25 m, the depth limit of data collection; the values were slightly lower (25.9 mmol m^{-2}; Table 2, row 9), reflecting the respiratory losses in small amounts of *P. rubescens* below the compensation point.

The changes in photosynthesis (NP_{zt}) calculated for different depths and times on Day 254, using the interpolated values of α, β, and P_m and R_s, are shown in Fig. 7a. Integration throughout the day gives the integral $\Sigma(NP)_z$ for each depth, z; integration of these depth integrals gives the double integral, $\Sigma\Sigma(NP)$ for all depths and times (i.e., equal to the total net primary productivity of the filaments, in the entire water column under 1 m^2 of surface in the course of 24 h). These are the values shown in Table 2, row 9. Figs. 7b, c and d show the results of similar calculations for Day 255 to Day 257.

b) Differences on the successive days, Day 254-257

Whichever method was used, the calculations indicate large differences between the daily integrals of photosynthesis of the four days. The daily integrals were inversely related to the mean depth of the population: the lowest value occurred on Day 256, when the median depth of the population was 12.0 m and the highest on Day 257, when the median depth was only 10.5 m. The depth changes have a profound effect on the productivity of the population; the causes of the change in depth distribution are discussed below.

The cumulative primary production over the four-day period was calculated as the running sum of the integral $\Sigma(NP)_t$ over 0-20 m at each successive 30-min interval (Fig. 8). It is seen that over the first 24 h the calculated photosynthetic gains exceed the respiratory losses of the whole population. Over the second day there is a greater net gain, but on the third day, when the population peak is moved down, there is little net increase. The greatest gain is made on the last day when the population has again moved upwards.

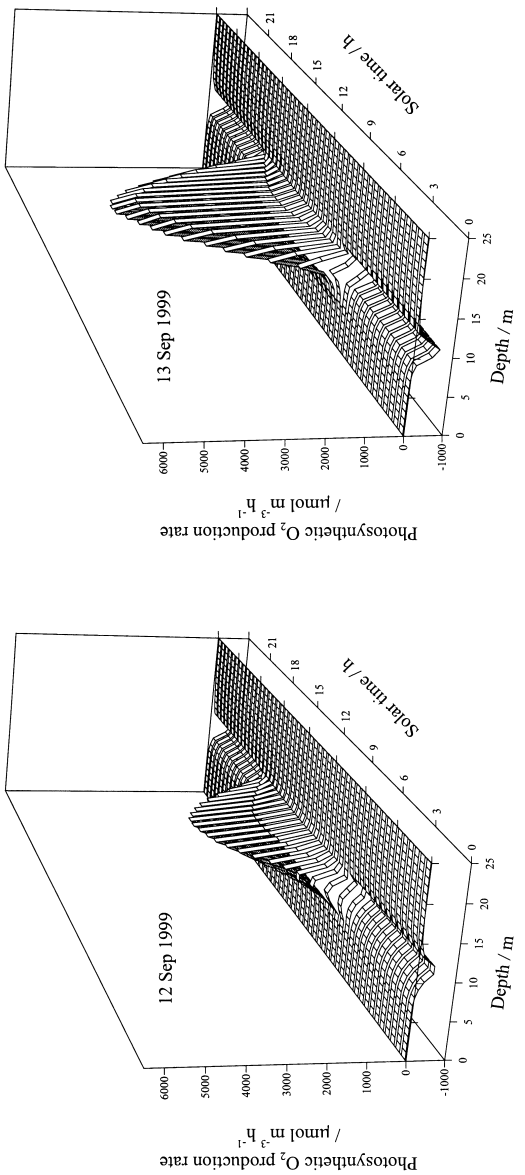

Figure 7. Rates of photosynthetic O_2-production at different depths and times on (a) Day 254; (b) 255; (c) 256; (d) 257

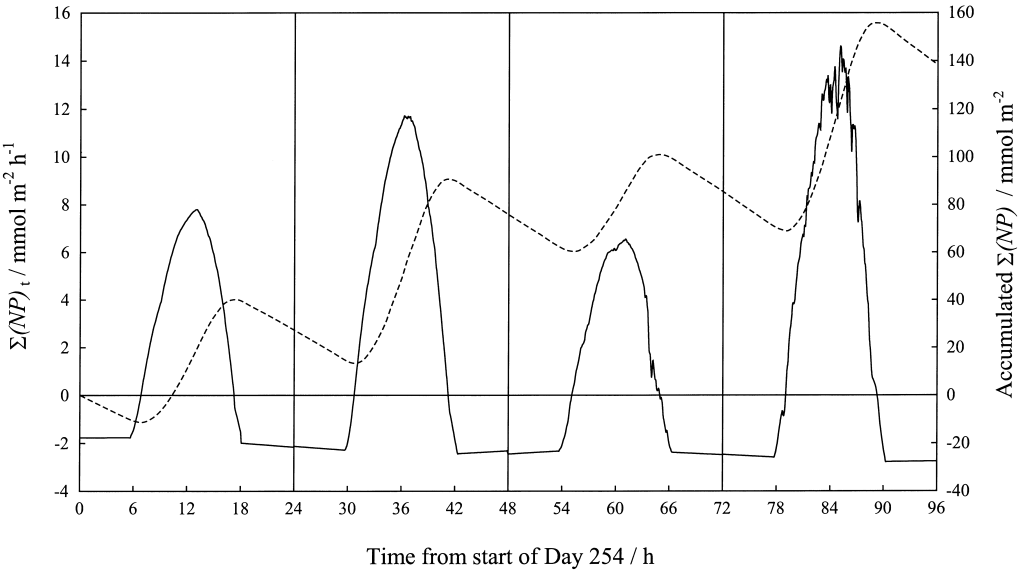

Figure 8. Integrals of photosynthesis from 0 – 20 m through the water column: (—) the integral $\Sigma(NP)_t$ at each successive time, t; (- - -) the cumulative integral $\Sigma(NP)$ calculated at 5-min intervals over the period 12 to 15 September 1999

Table 3. Changes in buoyancy of filaments floating in lakewater samples collected at different times and in samples suspended in bottles at different depths. The samples were those collected directly from a depth of 11 m or in 11-m samples suspended in bottles for 7.3 h at the depths shown

Date	Time /h:min	Depth /m	Sample	Total number	Number floating	Number sinking	% Floating
14-Sep-99	16:00	11.0	water	191	146	45	76
15-Sep-99	09:40	11.0	water	300	251	49	84
	17:00	11.0	bottle	251	194	57	77
	17:00	8.4	bottle	285	116	169	41
	17:00	3.0	bottle	189	57	132	30

8) Buoyancy of the filaments in the metalimnion

A sample of lake water examined at 16:00 h on 14 September 1999 contained freely suspended filaments. Counting filaments in the microscope chamber revealed that most were positively buoyant: 76% floating, 16% sinking (Table 3). In another sample taken at 09:40 h the following morning 84% were floating. This slightly higher value suggests a buoyancy increase occurred during the hours of darkness.

Samples of lakewater collected from a depth of 11 m were placed in polycarbonate bottles suspended at depths of 11.0 m, 8.4 m and 3.0 m from 09:50 h until

16:45 h, when they were brought to the laboratory for enumeration, completed within the next 2 h. In the 11-m bottle the filaments were evenly and separately suspended. In the 8.4-m bottle filaments had aggregated into small chords; they were dispersed by admitting an airspace in the bottle and gently rotating it end over end. In the 3-m bottle the filaments were in more tightly tangled bundles, which could be dispersed only partially by shaking. Only separate filaments were counted in the microscope slide. In the bottle suspended at 11 m filament buoyancy had decreased only slightly; in the 8.4-m bottle, more than half the filaments were sinking; in the 3.0-m bottle the majority had lost buoyancy (Table 3).

Discussion

Comparisons are first made with previous measurements on Lake Zürich. The *Planktothrix* filament biovolume, integrated from the surface to 25 m, was about 40 cm^3 per m^2 of lake surface compared to about 60 $cm^3\ m^{-2}$ at the autumnal maximum in both 1993 and 1994 but only 9 $cm^3\ m^{-2}$ in 1995. The peak concentration, however, was greater in the present period, 12 $cm^3\ m^{-3}$ compared with 6 $cm^3\ m^{-3}$ in 1993-4 and 3 $cm^3\ m^{-3}$ in 1995 (Walsby et al., 1998; Micheletti et al., 1998). Each summer the population of *P. rubescens* develops from a remnant of the spring population, which is mainly restricted to the metalimnion during the period of strong thermal stratification. In autumn, the temperature of the surface water layers decreases and the epilimnion becomes mixed down to the top of the *Planktothrix* layer. An increasing proportion of the population then becomes entrained in the surface mixed layer. In 1995, surface entrainment began at the end of August and stimulated primary production by exposing the filaments to higher insolation. Higher temperatures in 1999, however, delayed mixing and *P. rubescens* was still restricted to the stable metalimnion in mid September.

In 1995, the daily integrals of photosynthesis ranged from close to zero on days of low insolation in August, after the *Planktothrix* population had moved to its greatest median depth of 15 m; the highest values, 100 mmol m^{-2}, occurred on the brightest days after partial entrainment in the epilimnion (Micheletti et al., 1998). The lowest values here, however, occurred on days that received nearly the maximum insolation for the time of year and are explained by changes in the depth distribution of the *Planktothrix* population. We discuss below attempts to refine our estimates of the daily integral of photosynthesis by including effects of changing photosynthetic coefficients and vertical distribution in our calculations.

1) Effect of changes in photosynthetic coefficients

The results in Table 2 illustrate the sensitivity of the calculations to changes in measured values of the photosynthetic coefficients, and the dominating influence of R for populations near the compensation point. When R is standardized (to R_s), changes in the other coefficients, and especially in α and P_m, can result in a two-fold change in the daily integral, $\Sigma\Sigma(NP)$. In the most detailed calculation of $\Sigma\Sigma(NP)$ applied here, corrections were applied for the values of the photosynthetic coeffi-

cients as they changed during the day. Comparison of the result of this more complex calculation with a calculation based on coefficients equal in each case to the arithmetic mean of the 5 measurements made, revealed little difference (compare results in Rows 8 and 7 in Table 2). Larger differences would be generated, however, if an increase in α coincided with a decrease in irradiance.

The interpretation of the commonly observed increase in α under low irradiances is complicated: α is the product of ϕ_{max} (the quantum yield), which increases upon photoacclimation to low irradiance, and of a* (the in vivo, chlorophyll *a*-specific, optical cross-section), which decreases under such conditions (Berner et al., 1989; for definitions and discussion, see Dubinsky, 1992). Overall, α increases under low irradiance, since the response of ϕ_{max} is steeper than that of a* (Dubinsky, Falkowski and Wyman, 1986). An additional photosynthetic coefficient sensitive to photoacclimation is the light-saturated rate of photosynthesis, P_m, which increases linearly with the quantity and activity of Rubisco per photosynthetic unit (Fisher, Minaard and Dubinsky, 1989).

Our observations on photosynthesis over the diel time scale can be related to the seasonal changes by *P. rubescens* in Lake Zürich. In the stable, stratified water column *P. rubescens* should optimise its depth by regulating carbohydrate accumulation, through photosynthesis, or by regulating gas vesicle formation (Utkilen et al., 1985b). The *Planktothrix* cells will photoacclimate by changing pigment content, and perhaps pigment ratios, in response to the average irradiance and spectral composition at the depth of the layer (though Bright (1999) found only small changes in pigments of *P. rubescens* strain BC 9316 when transferred from red to green light). These conditions may change as the *Planktothrix* layer develops. While an increase in cellular chlorophyll will decrease a* due to internal shading (Berner et al., 1989, Dubinsky, 1992), an increase in concentration of other pigments relative to chlorophyll will increase a*. In the course of photoacclimation, the quantum yield, ϕ_{max}, increases as the irradiance decreases and P_m decreases as Rubisco levels fall in response to the decrease in photosynthetic electron flow. The value of α will also be affected by the organism's position in the underwater light field. These changes can be described in terms of the light-saturation coefficient, I_k (the ratio of P_m to α). As these coefficients are adjusted to the ambient light, they determine the rate of gross photosynthesis along the diel course of insolation. Respiratory losses, however, are also related to photoacclimation and increase significantly at high irradiance (Falkowski, Dubinsky and Wyman, 1985). The changes we observed in the course of the day are typical of the 'hysteresis effect'; we incorporated these changes in the evaluation of the daily photosynthetic integral.

The changes in the photosynthetic coefficients calculated here are based on single *P/I* curves made at intervals over a 25-h period; because the manipulations took more than 1 h to perform, it was not possible to replicate the measurements. Further investigations, however, with cultures of *P. rubescens* strain BC 9316 from Lake Zürich, have shown a consistent increase in both α and P_m at the start of the daily light period (I. Vaughan, P. A. Davis and A. E. Walsby, unpublished).

2) Effect of changes in depth distribution

By the end of the 1999 summer, *Planktothrix* had reached such a concentration that it became the principal determinant of light penetration. On Day 242 (31 August) the relative irradiance at 11.5 m, the median depth of the *Planktothrix* layer, was $0.0021 I_0$, only slightly above the compensation point for this organism; the relative irradiance at 14 m, near the bottom of the *Planktothrix* layer, was only $0.00049\ I_0$, below the compensation point. In the absence of the *Planktothrix* layer, the equivalent irradiances would have occurred at greater depths: extrapolation of the light attenuation curve in the surface layers (where $K_d = 0.39\ m^{-1}$) gives $0.0021\ I_0$ at 14.9 m and $0.00049\ I_0$ at 18.7 m. Clearly, as the population develops, the surrounding gradient of irradiance will steepen and the effect of buoyancy regulation will be to confine it to a narrower depth range. Moreover, small depth changes will result in large changes in insolation and consequently in primary production by the population.

The combination of the steep light gradient and the low irradiance in the metalimnion makes primary production very sensitive to changes in the vertical distribution of the organism. There are two factors that affect this vertical distribution: seiche movements by the lake water and buoyancy regulation by the filaments of *P. rubescens*.

a) Seiche movements

Walsby, Utkilen and Johnsen (1983) showed that while the position of a metalimnetic population of *Planktothrix* sp. in Lake Gjersjøen, Norway, was confined to the 16.5°C isotherm, its depth oscillated over a range of 1.5 m owing to seiche movements. Seiches, internal gravity waves, occur after wind moves surface water to the leeward end of a lake, depressing the thermocline there. When the wind abates, the surface water returns and the thermocline oscillates about a node with a periodicity, T, that is affected by the length of the lake, and by the densities and depths of water in the hypolimnion and epilimnion (Horne and Goldman, 1994) . Horn, Mortimer and Schwab (1986) described such movements in Lake Zürich based on the Talweg track (a smoothed curve following the deepest contours of the channel), which is 30 km long (28 km along the interface). Changes in the Talweg direction along the basin and the varied topography of surrounding land impose a marked variability and nonuniformity on the distribution of windstress at the surface and subsequent responses of the water masses. The overall response is a combination of several internal seiche modes; the first dominant mode has period of 44 h, which would explain the depth changes of the thermocline over the 4-d period (Fig. 5). Weaker signals come from second, 24 h, and third, 17 h, modes.

During the study period, the seiche caused no change in the thickness of *Planktothrix* layer between 10 and 14°C isotherms, but the depth of the more transparent epilimnion changed by as much as 2 m (Fig. 5). The relative irradiance at the top of the *Planktothrix* layer therefore changed by a factor of $\exp(K_d 2\ m)$, equal to 0.45 when $K_d = 0.4\ m^{-1}$. This must have had a large effect on the rate of photosynthesis by the light-limited *Planktothrix* population, (compare Figs. 7a and 7b). $\Sigma\Sigma(NP)$ will clearly be affected by whether the *Planktothrix* layer is raised up during the day time or the night time. Naturally, elevation of the population in one part of the lake

is compensated by depression in another part; it does not follow, however, that the seiche effect can therefore be neglected, because the changes of photosynthesis with irradiance, and irradiance with depth are both non-linear. Modelling is required to determine the overall outcome for the lake.

b) Filament buoyancy movements

Planktothrix spp. perform buoyancy regulation, increasing their buoyancy in low irradiance and losing buoyancy in high irradiance (Utkilen et al., 1985a). By this means they regulate their position on a vertically decreasing light gradient and stratify in the metalimnion of lakes (Walsby and Klemer, 1974; Walsby et al., 1983). Filaments there gain buoyancy at night and slowly float up; in the day they lose buoyancy and slowly sink. Kromkamp and Walsby (1990) measured the rates of buoyant density change in a red-coloured strain of *Planktothrix (Oscillatoria)* sp. at different irradiances, and they modelled its stratification. Buoyancy and vertical movements change in response to the daily changes in light, but the phase is delayed by the response time. Owing to their small size, filaments move at less than 10 μm s^{-1} (0.86 m d^{-1}); the amplitude of their vertical movement may be less than 0.10 m d^{-1}, considerably less than the amplitude of the seiche. For a population at equilibrium there would be equal proportions of floating and sinking filaments averaged over the day but more sinking in the afternoon (Kromkamp & Walsby, 1990). The preponderance of floating filaments observed in Lake Zürich at the end of the afternoon indicates that the population was floating up on Day 257. This corroborates the evidence from the upward movement of the population peak relative to the isotherms over Days 253–257.

The positive buoyancy of the *P. rubescens* filaments suggests that, in the period immediately before Day 254, they had experienced a decrease in light dose. There are several possible causes for this. (1) Quantitative modelling shows that, even under constant insolation, the mean depth of a population oscillates over a period of several days as filaments overshoot or undershoot a particular depth on successive days (Kromkamp and Walsby, 1990). (2) There will be a seasonal decrease in light dose as the autumnal equinox approaches. Micheletti et al. (1998) showed the *Planktothrix* population peak gradually moved up from its maximum depth of 15 m in early August to 9 m in October. (3) Additional decreases in light dose might occur locally at the sampling point owing to seiche movements, as discussed above. (4) There will be increased light absorption by the growing population. This might not itself affect the uppermost depth of the *Planktothrix* layer (as long as the attenuance in the epilimnion remains constant), but it would affect the depth distribution within the layer; the interactions are complex and require investigation by modelling.

Conclusions

Because *P. rubescens* stratifies at a depth so close to its integrated euphotic depth (Walsby, 1997) calculations of its photosynthetic production are very sensitive to changes in its depth distribution. It is important to obtain an accurate description of this distribution. First, the depth of sampling should be determined with a pressure

transducer rather than from the length of the sampling wire, because of uncertainties in the wire angle. Secondly, samples should be taken at close intervals through the population peak (a recording fluorimeter or transmissometer would give a continuous record of the depth distribution). Thirdly, the effects of seiche movements and their interaction with the periodicity of the natural light cycle should be investigated.

Changes in the photosynthetic coefficients also have a profound affect on the calculated production. The modifications made to the integrating spreadsheet described here provide a means of incorporating measurements from several *P/I* curves into calculations of the daily integral of photosynthesis.

A further factor, not considered above, is the changing spectral distribution with depth. In Lake Zürich there is a proportional enrichment in the green waveband with increasing depth (Schanz, 1986). *P. rubescens* strain BC 9316 absorbs strongly in green wavelengths and has a higher photosynthetic efficiency in green light than in white light (Bright, 1999). In the metalimnion of the lake, *P. rubescens* will have a higher value of α than that measured under white light; this will affect its competitive advantage over green algae. By growing in the metalimnion *P. rubescens* may also intercept nutrients as they diffuse up from the hypolimnion. Together, these factors enable the cyanobacterium gradually to produce the largest population of photoautotrophs in the lake: Micheletti et al. (1998) showed that, at a similar period in 1995, *P. rubescens* accounted for 85% of the chlorophyll in the lake.

It is paradoxical that the largest population should be produced by phytoplankton with the lowest growth rate: *P. rubescens* has a growth rate of only 0.4 d^{-1} when cultured in continuous light and only 0.12 to 0.19 d^{-1} on a light-dark cycle (Foy, 1980; Meffert, 1971; Zimmermann, 1969; Bright and Walsby, 2000). By regulating its buoyancy with gas vesicles, *P. rubescens* not only minimizes losses by sedimentation but also maintains its position at a depth where it is not outcompeted by other phytoplankton. The mechanism of buoyancy regulation is interlocked with photosynthetic production (Oliver, 1994; Walsby, 1994); as long as the water column remains thermally stratified, the mechanism should maintain the organism above its compensation depth but prevent it from straying into depths where photosynthesis is strongly light-saturated or inhibited. Studies with several planktonic cyanobacteria indicate that the irradiance required for buoyancy loss is lower when nutrients are limiting (Klemer, 1978; Klemer, Feuillade and Feuillade, 1982; Konopka, Kromkamp and Mur, 1987). This may explain why *P. rubescens* in Lake Zürich positions itself so far down the vertical light gradient.

In a completely stable water column a stratifying organism might become perfectly acclimated to the diel cycle of irradiance. The population of *P. rubescens* in Lake Zürich, however, must contend with seiches, which, like other destabilising movements, take place on time scales too short to allow for the full photoacclimation (Fisher et al., 1996). Inevitably, the photosynthetic performance of the organism will fall below its potential value for the depth to which it had previously acclimated. In the present study, seiche-generated displacements and diel changes in photosynthetic coefficients were shown to have a significant effect on overall primary productivity.

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