SHORT COMMUNICATION

Do light quality and low nutrient concentration favour picocyanobacteria below the thermocline of the oligotrophic Lake Stechlin?

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Abstract. In May 1995, a short-term study on the vertical distribution of phytoplankton in the holomictic, oligotrophic Lake Stechlin revealed a deep chlorophyll maximum (DCM) due to an increase in phytoplankton biomass below the thermocline. The DCM was dominated by centric diatoms, which probably just passed those water layers while sinking to the sediment, and by picocyanobacteria. The DCM was situated well above the 1% level of photosynthetically active radiation, but received almost exclusively light of wavelengths between 500 and 600 nm. The dominant picocyanobacteria were pre-adapted to this environment by the possession of phycoerythrin. The competitive advantage of picocyanobacteria compared with other phycoerythrin-containing phototrophs was probably the most efficient nutrient uptake under low nutrient conditions as a consequence of the small size of picoplankton.

The ecology of algae in deep chlorophyll maxima (DCM) has been studied in freshwater ecosystems (Moll and Stoermer, 1982; Lindholm, 1992; Reynolds, 1992; Pedrós-Alió and Guerrero, 1993), as well as in marine ecosystems (Cullen, 1982; Revelante and Gilmartin, 1995). These studies revealed that the appearance of DCM requires a sufficiently low trophic state and that DCM were due to a higher chlorophyll:cell ratio, the accumulation of viable sinking cells, the accumulation of migrating flagellates or to *in situ* growth. In the oceans, almost all studies have dealt with oligotrophic systems (e.g. Furuya, 1990; Estrada *et al.*, 1993; McManus and Dawson, 1994), whereas DCM in oligotrophic lakes have only been studied in exceptional cases (Coon *et al.*, 1987; Kettle *et al.*, 1987; Jackson *et al.*, 1990; Shortreed and Stockner, 1990). The species composition of phytoplankton in the marine DCM studied so far was very diverse. Different species of prochlorophytes (e.g. Shimada *et al.*, 1993), diatoms (e.g. Revelante and Gilmartin, 1995), cryptomonads (e.g. Kamiya and Miyachi, 1984), chrysomonads (e.g. Kamiya and Miyachi, 1984), picoplanktic eukaryotes (e.g. Furuya, 1990) or picoplanktic prokaryotes (e.g. Karlson *et al.*, 1996) were observed. In the oligotrophic lakes, diatoms, green algae and cyanobacterial picoplankton dominated in the deep water layers (Coon *et al.*, 1987; Shortreed and Stockner, 1990). The present study tries to explain the species selection of phototrophs below the thermocline of the oligotrophic Lake Stechlin with the help of an analysis of light and nutrient conditions.

Lake Stechlin (surface area 4.3 km², mean depth 22.8 m, maximum depth 68 m) is a holomictic, dimictic hardwater lake in northeastern Germany (Casper and Koschel, 1995). The lake is oligotrophic (total phosphorus 16 µg l⁻¹, dissolved inorganic nitrogen 95 µg l⁻¹, chlorophyll a 1 µg l⁻¹; mean values from 1992–1994 given by Casper and Koschel, 1995). *In situ* measurements and sampling were carried out mainly in the northern basin, and also in two further basins from 17 to 19 May 1995.

Water temperature, pH and oxygen saturation were registered *in situ* with an H20 Multiparameter Water Quality Data Transmitter (Hydrolab). The underwater photon flux density (PFD) was characterized with LI 193 SB Spherical Quantum Sensors (LICOR) and with a LI-1800 UW Underwater Spectroradiometer (LICOR). The fluorescence of chlorophyll a and phycoerythrin (PE) was registered *in situ* with a 1301 Phy/Aut 2R/Chla/Mie Backscat-Fluorometer (Haardt). Water samples were collected by means of a Ruttner sampler. Concentrations of soluble reactive phosphorus (SRP), ammonium and nitrate were measured with the Perstorp Analytical system Tecator Fiastar 5010/5030 in filtrates of the subsamples (0.6 µm). Subsamples for the analysis of chlorophyll a were filtered (Whatman GF/F) and hot ethanol extraction of the filters, spectrophotometric determination of the extracts' absorption and calculations were performed according to DIN 38412-L16 in DEV (1985). The biomass of nanophytoplankton and microphytoplankton was determined in Lugol-fixed subsamples under a Zeiss Axiovert inverted microscope using Hamilton's (1990) computerized plankton counter. The enumeration of autotrophic picoplankton (APP) was based on the counting of autofluorescing cells (MacIsaac and Stockner, 1993); subsamples were concentrated on black membrane filters (pore size 0.45 µm; Schleicher & Schuell ME 25/31) and the filters were embedded in 30% glycerine and analysed with a Zeiss Axiovert epifluorescence microscope (green excitation: filter set 48 77 15; blue excitation: filter set 48 77 09). Cell dimensions were estimated by light and electron microscopy (J.Padisák *et al.*, submitted); a cell density of 1 g cm⁻³ was assumed.

A maximum of chlorophyll concentration coupled with a peak in PE concentration was detected between 12 and 18 m depth in the different basins of Lake Stechlin on all sampling days (Figure 1A and B). The maximum was mostly due to an increase in phytoplankton biomass (Figure 2A). The chlorophyll content of algal biomass increased only below the DCM (Figure 2B). Phytoplankton in Lake Stechlin were mainly composed of unicellular picocyanobacteria and centric diatoms, both groups showing a maximum of biomass in the DCM (Figure 2A). According to the method of Pick (1991), the picocyanobacteria were only comprised of cells containing PE as APP exclusively showed red fluorescence under green excitation and yellow fluorescence under blue excitation. Red or no fluorescence of APP under blue excitation was not observed.

Fig. 1. Vertical distribution of chlorophyll a concentration (**A**), phycoerythrin concentration (**B**), the ratio of phycoerythrin concentration to chlorophyll a concentration (**C**) and water temperature (**D**) on 3 days in different basins of Lake Stechlin [see the legend in (D)].

A: chlorophyll a (µg l^{-1})

B: phycoerythrin (µg l^{-1})

C: phycoerythrin/chlorophyll (%)

D: water temperature (°C)
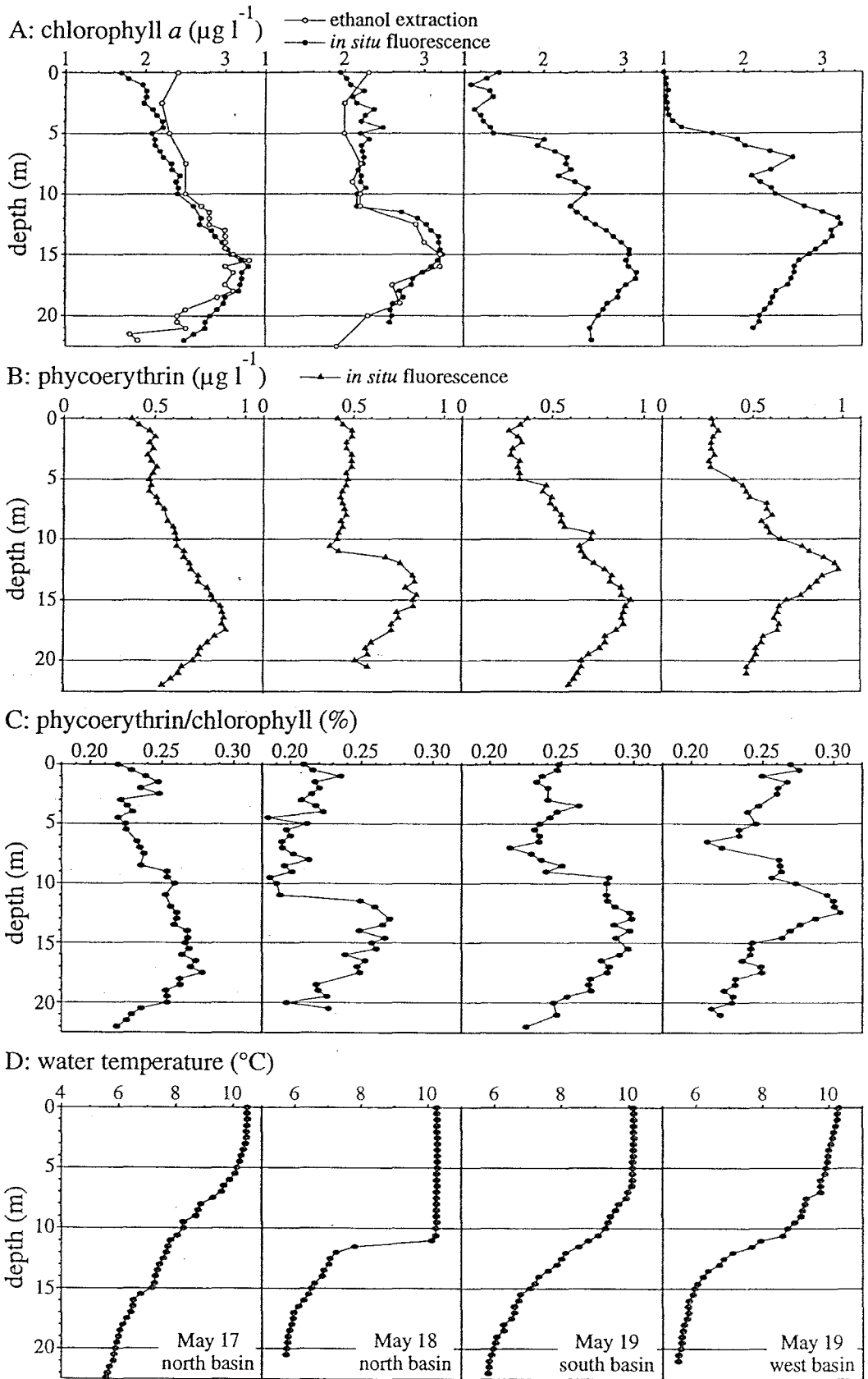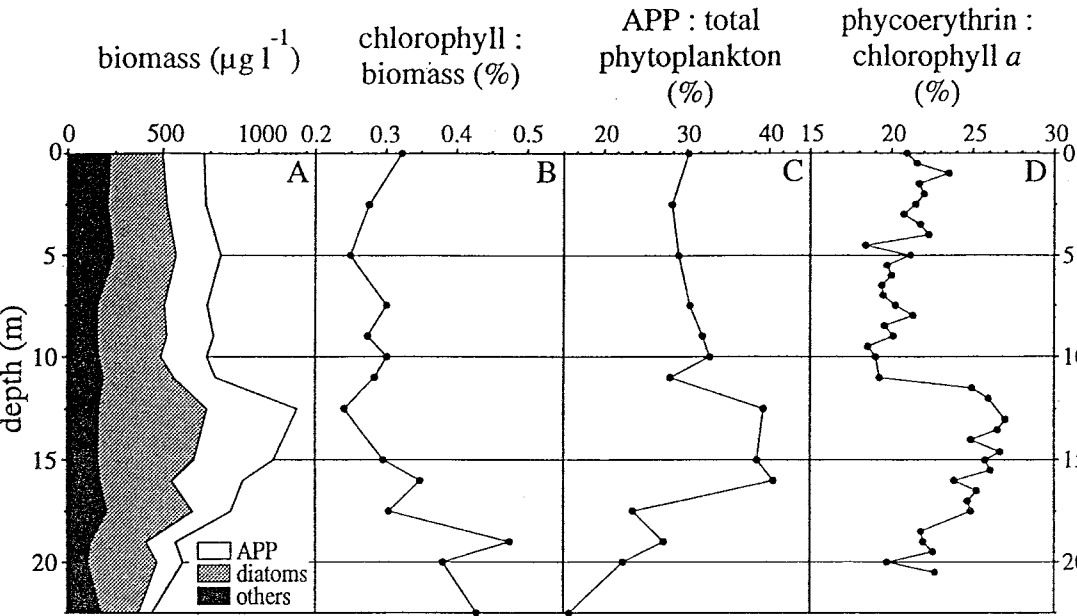
Fig. 2. Vertical distribution of different characteristics of phytoplankton in the northern basin of Lake Stechlin on 18 May. (**A**) Cumulative biomass of different groups of phytoplankton; (**B**) proportional chlorophyll content of phytoplankton biomass; (**C**) biomass of APP as a percentage of total phytoplankton biomass; (**D**) ratio of phycoerythrin concentration to chlorophyll *a* concentration.

The biomass of the rest of the phytoplankton (mainly chrysophytes and *Rhodomonas* sp.) decreased slightly as the depth increased (Figure 2A). The ratio of picocyanobacterial biomass to total phytoplankton biomass was largest in the DCM (Figure 2C), as was the ratio of PE to chlorophyll *a* (Figure 2D). This ratio showed the same pattern in the other basins and on the other days (Figure 1C), indicating that picocyanobacteria were important in the DCM throughout.

A gradient of temperature divided Lake Stechlin into two strata: between 0 and 25 m, temperature decreased from ~10 to 5.4°C (Figure 1D); between 25 and 50 m, temperature decreased from 5.4 to 5.0°C. The decline in temperature in the upper layers was rather smooth on 17 May due to low wind speed and high global radiation on the preceding days (Figures 1D and 3). In the night from 17 to 18 May, strong wind (Figure 3; maximum wind speed 14.9 m s^{-1}; German Weather Service, personal communication) mixed the upper 11 m, leading to a sharp thermocline (Figure 1D). As a result of lower wind speed and higher global radiation on the following day (Figure 3), the thermocline became less steep (Figure 1D). The DCM was not associated with a stratum of a distinct change in temperature or water density. Obviously, the maximum was situated at depths that were not included in the upper mixed layer even if strong winds prevailed (Figures 1A, 1D and 3).

The DCM was situated well above the lower boundary of the euphotic zone [1% of surface photosynthetically active radiation (PAR)]; on a sunny day, the algae in the DCM received a PAR of ~65 µE m^{-2} s^{-1}, whereas on a cloudy day only 3.6 µE m^{-2} s^{-1} were available around noon (Figures 3 and 4). There was a distinct change in the spectral composition of downwelling light as the depth
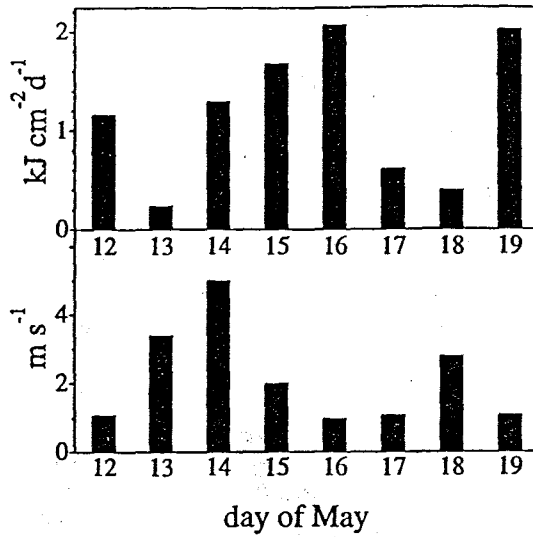
Fig. 3. Global radiation (**upper panel**) and wind speed (**lower panel**) at the shore of Lake Stechlin in May 1995 (German Weather Service, personal communication).

increased. At the level of the DCM, the PAR was mainly composed of wavelengths between 500 and 600 nm (maximum transmittance at 566 nm; Figure 5).

The concentrations of SRP and ammonium nitrogen were low (mean values for the upper 22 m: 1.1 µg P l⁻¹, 23 µg N l⁻¹) and did not show a distinct stratification
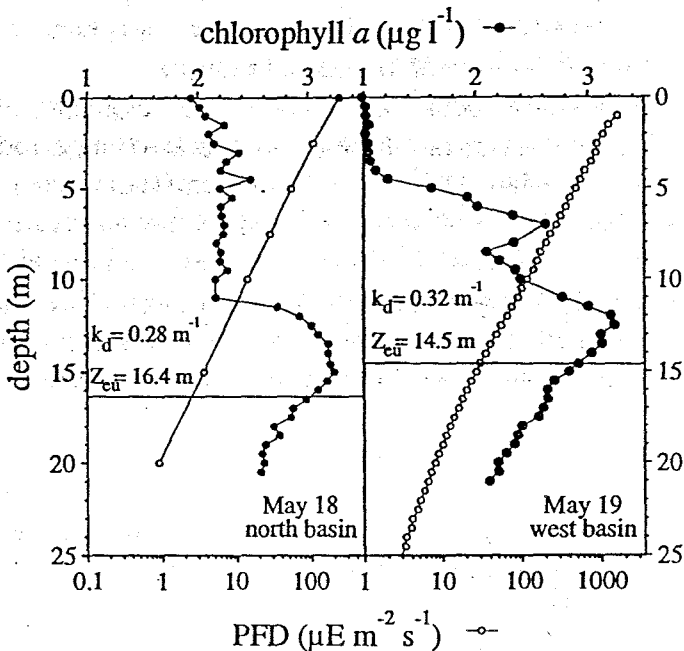

Fig. 4. Vertical distribution of chlorophyll a concentration and photon flux density (PFD) of photosynthetically active radiation on 2 days in different basins of Lake Stechlin. PFD data for 18 May represent mean values of a continuous measurement between 10:00 and 14:00 h, whereas PFD data for 19 May represent a single measurement at noon. The vertical attenuation coefficient (K_d) and euphotic depth (z_{eu}) are given; z_{eu} is marked with a horizontal line.
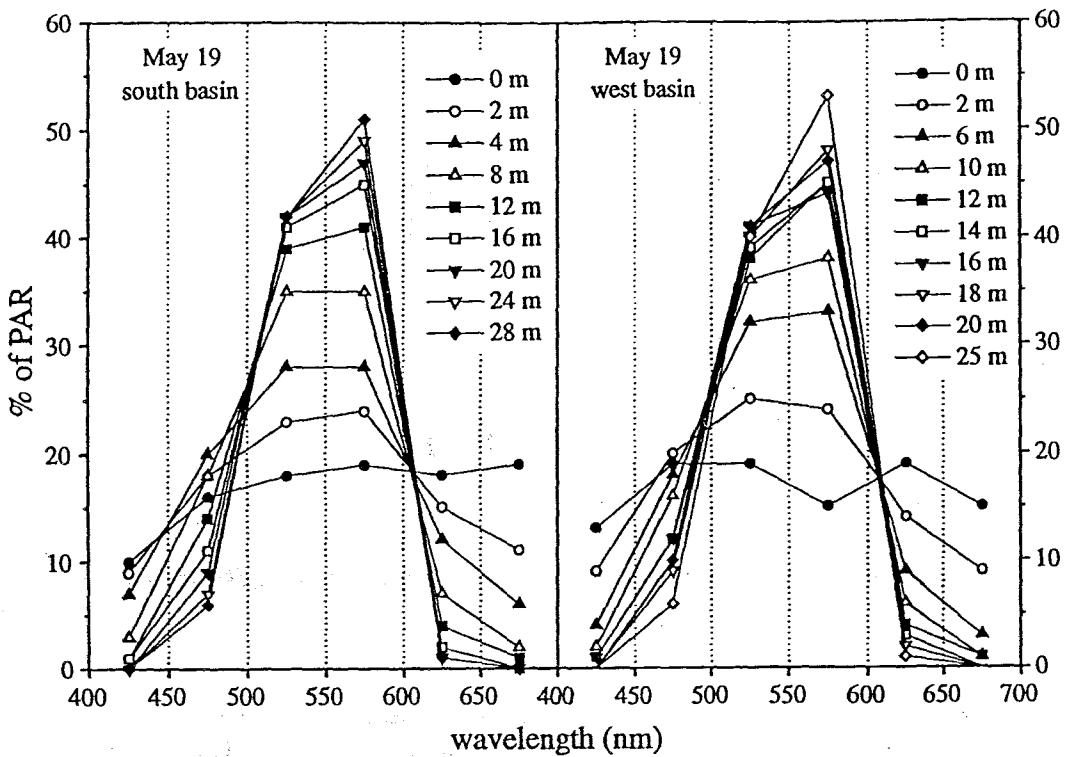
Fig. 5. Photon flux density in six wavelength ranges as a percentage of the total PFD of photosynthetically active radiation (PAR) at different depths of Lake Stechlin. Each point represents the sum of the PFD measured in 1 nm steps in a wavelength range of 50 nm.

pattern. The concentration of nitrate N increased as the depth increased (Figure 6). The oxygen concentration and the pH values were between 9.0 and 11.2 mg O_2 l^{-1}, and pH 7.98 and 8.17, between 0 and 50 m depth.

The results from the present study focus on 3 days at the beginning of the stratification period. They represent a typical phase of phytoplankton periodicity in Lake Stechlin. Scheffler and Padisák (1997) showed that centric diatoms dominated the phytoplankton in April/May 1994, sank to the hypolimnion in late May and remained at a low biomass for the rest of the year. Studies by J.Padisák *et al.* (submitted) revealed that a population maximum of picocyanobacteria in the upper hypolimnion was typical during the stratification period in Lake Stechlin in 1994 and 1995. The deep maximum of APP was seen as a sharp, well-defined layer in late spring and early summer, whereas in mid-May 1994/1995 a wider band of maximum APP abundance was observed (J.Padisák *et al.*, submitted; this study). It is very likely that picocyanobacteria lived and grew below the thermocline of Lake Stechlin since their deep maximum was observed over several months (J.Padisák *et al.*, submitted) and maintenance of deep populations by sedimentation of epilimnetic cells is unlikely because of the very low sinking rates of picoplankton (Takahashi and Bienfang, 1983).

With stable stratification, a new habitat developed below the thermocline that was characterized by the lack of turbulence and the restriction of PAR to wavelengths between 500 and 600 nm (Figure 5). This light climate is a consistent feature of Lake Stechlin (cf. Richter and Koschel, 1985). Only cryptophytes,
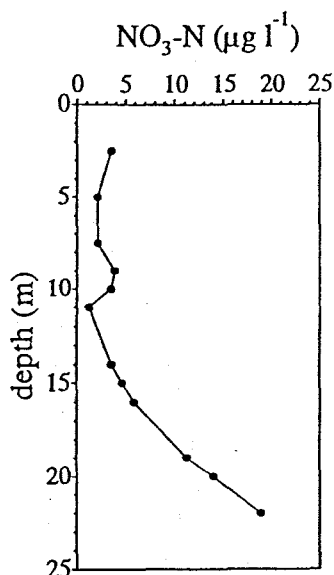
Fig. 6. Vertical distribution of the concentration of nitrate nitrogen on 18 May in the north basin of Lake Stechlin.

gas-vacuolated cyanobacteria or picocyanobacteria are able to cope with these conditions for a prolonged period because they avoid sinking losses by motility, buoyancy or smallness, and only they can possess PE. This pigment absorbs energy between 500 and 600 nm with highest efficiency (Kirk, 1994). Therefore, only species from these pre-adapted groups could benefit from the higher nitrate concentration below the thermocline. This benefit increased in the course of the summer because the hypolimnetic nitrate concentration increased (J.Padisák *et al.*, submitted). DCM associated with the top of the nutricline, but not necessarily with the thermocline, are well known from oligotrophic Lake Tahoe (Coon *et al.*, 1987) and oligotrophic Sproat Lake (Shortreed and Stockner, 1990). In marine systems, the 'typical tropical structure' of the eastern tropical Atlantic Ocean with a maximum of chlorophyll concentration near the nitracline has been recognized (reviewed by Cullen, 1982) and analogous situations have been found in other regions of low trophic state [e.g. the northwestern Mediterranean (Estrada *et al.*, 1993); the western tropical Atlantic Ocean and the Caribbean Sea (McManus and Dawson, 1994); the tropical and subtropical western Pacific Ocean (Furuya, 1990); the Skagerrak (Karlson *et al.*, 1996)].

It is very likely that the centric diatoms co-dominant in the DCM in May 1995 were just passing these water layers on their way down to the sediment (cf. Scheffler and Padisák, 1997). The factor positively selecting picocyanobacteria below the thermocline of Lake Stechlin was probably the low nutrient (especially SRP) concentration. Smaller cells have higher nutrient uptake capabilities than larger cells (Raven, 1986; Rai and Jacobsen, 1990; I.Nedoma *et al.*, submitted) so that APP has an advantage over larger filamentous cyanobacteria and crypto-phytes under conditions of nutrient limitation. This advantage can, however, be counteracted by higher nutrient leakage in picoplankton (Raven, 1986). Another advantage for APP is the ability to use very low PFD (which prevailed below the

thermocline in cloudy periods) more efficiently than larger eukaryotes or filamentous cyanobacteria because the photon absorption rate per unit cell volume increases with decreasing cell size (Raven, 1986; Glover et al., 1987).

Marine studies revealed that cyanobacterial autotrophic picoplankton were co-dominant in the DCM in some cases (e.g. Furuya, 1990; Karlson et al., 1996), but often of no importance (e.g. Furuya and Marumo, 1983; Estrada et al., 1993; McManus and Dawson, 1994; Revelante and Gilmartin, 1995). In lakes as well, there are only very few records of APP in DCM. In the oligotrophic lake Mittlerer Buchensee, picocyanobacteria containing PE could contribute >50% to the biomass of phototrophs containing chlorophyll in the DCM, but *Cryptomonas*, *Oscillatoria* and *Lyngbya* were important, too (Overmann and Tilzer, 1989). In oligo-mesotrophic Little Round Lake, *Synechococcus* containing phycocyanin or *Oscillatoria utermöhlii* dominated the DCM (Craig, 1987). Both Mittlerer Buchensee and Little Round Lake are meromictic, and their DCM were close to the anoxic monimolimnion (Craig, 1987; Overmann and Tilzer, 1989) so that direct comparison to holomictic, oligotrophic lakes like Lake Stechlin or to the ocean is not possible. In oligotrophic Sproat Lake, *Synechococcus* exhibited abundance maxima near the thermocline only in late summer or early fall (Shortreed and Stockner, 1990). The summer DCM of Sproat Lake was dominated by diatoms (Shortreed and Stockner, 1990) so that it is very likely that the light climate of Sproat Lake was different to that of Lake Stechlin. Pick and Agbeti (1991) showed metalimnetic APP maxima in four oligotrophic to mesotrophic lakes and explained them by low light preference of picocyanobacteria. Boraas et al. (1988) showed preliminary data on peaks of APP production in 5–15 m depth in the oligotrophic Lake Baikal. In a study that did not consider picocyanobacteria, Krienitz and Scheffler (1994) reported on a deep layer maximum dominated by green algae in 20 m depth of Lake Stechlin in July 1992. In most lakes of higher trophic status, filamentous cyanobacteria or cryptophytes, but never APP, dominated the DCM (Eberly, 1964; Ichimura et al., 1968, 1981; Finlay et al., 1991; Konopka et al., 1993; Pedrós-Alió and Guerrero, 1993; Gervais, 1997). Studies on the competitive ability of APP and surveys of the vertical distribution of APP in other oligotrophic lakes are necessary to prove the hypothesis that nutrient availability is important for species selection in the DCM of lakes. Since many cyanobacteria have a poor ability to utilize nitrate N (Blomquist et al., 1994; Présing et al., 1996), it has to be tested in the future whether deep-living picocyanobacteria can really use elevated hypolimnetic nitrate concentrations.

The importance of light quality for the species selection in marine DCM has been shown in culture experiments as well as in field observations. A marine *Synechococcus* clone rich in PE grew best and photosynthesized most efficiently in green light, whereas marine eukaryotic picoplankton clones did so in blue–violet light (Glover et al., 1986, 1987). Wood (1985) concluded from *in situ* experiments that due to their different photosynthetic apparatus, eukaryotic picoplankton are able to outcompete *Synechococcus* at extreme depths in the ocean where only blue and violet light penetrates. McManus and Dawson (1994)

reported on a marine DCM in which prochlorophytes dominated that had adapted to the blue–green light at the level of the DCM by a very high chlorophyll *b/a* ratio. Comparing 38 lakes, Pick (1991) showed that light attenuation was the most significant correlate of picocyanobacterial abundance and that the composition of the picocyanobacterial assemblage changed with increasing light attenuation. PE-rich APP dominated in the oligotrophic lakes, whereas APP containing phycocyanin and allophycocyanin were most abundant in the highly coloured lakes (Pick, 1991). Pick (1991) explained this difference by the change in spectral quality of underwater radiation with increasing trophic status of lakes, and by the different absorption properties of PE and phycocyanin. From these studies, it seems obvious that light quality is one of the major selective factors for phytoplankton species composition, especially in deep water strata or in highly coloured waters. Until today, however, there have been only very few studies that combined their analyses of vertical distribution of phytoplankton with a characterization of the underwater light climate in oceans (e.g. McManus and Dawson, 1994) or oligotrophic lakes (the present study).

The vertical structures of the oligotrophic ocean and of oligotrophic lakes in summer are analogous regarding the pattern of the vertical distribution of temperature, light energy, nutrients and phytoplankton biomass (a hypothesis that has to be verified by more detailed observations of the vertical distribution of phytoplankton in the lakes). On the other hand, the light climate and the pigment composition of the dominant phytoplankton species in the DCM differ from system to system. Basically, these differences do not exist between lakes and oceans, but between different oceanic regions and different types of lakes. To be able to understand the species selection in the DCM of lakes and oceans, more detailed investigations of the vertical distribution of phytoplankton species and their photosynthetic pigments in relation to light quality would be important. If these investigations show that picocyanobacteria are an important part of the deep-living autotrophs in systems with a light climate similar to Lake Stechlin, it will be interesting to compare the physiological adaptations of different marine and freshwater *Synechococcus* strains. As several clones of morphologically similar picocyanobacteria exist in lakes (Postius *et al.*, 1996), further studies are necessary to find out whether picocyanobacteria in freshwater DCM are spring populations surviving below the thermocline in summer (*sensu* Moll and Stoermer, 1982) or whether specially adapted clones live in the DCM.

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