

Arch. Hydrobiol. Spec. Issues Advanc. Limnol. 48, p. 183–196, November 1996
Aquatic Microbial Ecology

Composition and distribution of phototrophic bacterioplankton in the deep communities of several central European lakes: The role of light quality

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with 8 figures and 1 table

Abstract: The vertical distribution of phototrophic bacterioplankton has been studied in the deep communities of several central European lakes during summer stratification. The highest concentrations of photosynthetic pigments were found in the metalimnion, where prokaryotes dominated. The different populations were vertically separated, with eukaryotic phytoplankton or cyanobacteria, Chromatiaceae and Chlorobiaceae occurring in three distinct successive layers. Light quality changes with depth resulted in the dominance of phototrophic species such as phycoerythrin-containing cyanobacteria and brown Chlorobiaceae, because their absorption ranges between 500 and 600 nm corresponded to the prevalent light spectra. Radiation niche complementarity allowed the coexistence of several species in different layers. Therefore, the composition and the stratification of these phototrophic deep communities was strongly determined by light quality.

Introduction

Seasonal stratification in lakes allows the development of well-established planktonic populations in the metalimnion, the most stable part of the water column. The metalimnion usually hosts a deep phototrophic community with a structure dominated by vertical gradients, which produce the physical segregation of water layers (REYNOLDS 1992). Variations of environmental parameters (i.e. light, nutrients, oxygen, sulfide) through these gradients determine the establishment of specific vertical niches in which competitive exclusion processes result in the dominance of different planktonic species or higher-level taxonomic groups. Anoxygenic phototrophic bacteria appear when the hypolimnion contains sulfide and reaches the photic zone. Therefore, a complex multi-layered community is usually developed in a vertical gradient generated between the upper warm, oxic, mixed layer and the deeper cold, anoxic, sulfide-rich layer. Different phototrophic populations occur within the gradient, according to their specific requirements and limitations (GUERRERO et al. 1987).

Spatial distribution of planktonic communities is primarily determined by vertical light attenuation, which imparts a strong verticality to the planktonic environment, particularly for the photoautotrophs (REYNOLDS 1992). In addition to decreasing light intensity, variations in its spectral distribution also modify light availability for photosynthesis at different depths (KIRK 1983, VILA & ABELLA 1994). Therefore, light quality must be considered as a selection factor in the competitive exclusion process. Concerning oxygenic phototrophs, maximum transmission ranges of the light spectrum may determine which group of species develop at the deep chlorophyll maxima, according to their pigment composition (CRAIG 1987). Light quality variations with depth have also been assigned to select between Chromatiaceae and Chlorobiaceae (PARKIN & BROCK 1980), or between differently pigmented groups of Chlorobiaceae (MONTESINOS et al. 1983, ABELLA & GARCIA-GIL 1988, PFENNIG 1989, VILA & ABELLA 1994).

Deep populations of phototrophic bacteria and phytoplankton were reported in several central European lakes from the early thirties (FINDENEGG 1935, RUTTNER 1937, VETTER 1937). Since then, studies on their species composition and distribution, ecology and relationship to anaerobiosis and the sulfur cycle have been conducted by different investigators (KUSEL-FETZMANN 1973, KOHLER et al. 1984, OVERMANN & TILZER 1989, EICHLER & PFENNIG 1990, ABELLA & GARCIA-GIL 1992).

The present work deals with deep phototrophic communities found in some lakes that we studied several times during recent years. The aim of this paper is to describe the composition and vertical distribution of phototrophic bacterioplankton in the deep communities of these lakes and to interpret their distribution in relation to light quality. The narrow width of the spectral band of light reaching the different layers has been analyzed and related to the dominant pigments of the phototrophic microorganisms present. Selective light absorption was primarily responsible for the coexistence of several phototrophic populations at different layers, adapted to different radiation niches.

Materials and methods

Lake studied (Fig. 1)

Rotsee is situated at Luzern (Switzerland) and was sampled in 1990 and 1991. Lake Cadagno is also located in Switzerland, in the Piora valley (Ticino), and was studied in 1993. Mittlerer Buchensee and Schleinsee are located in southern Germany, near Radolfzell and Langenargen, respectively. Both lakes were sampled in 1990, 1991 and 1993. Three Austrian lakes were also studied in 1993: Höllerersee and Krotensee, near Salzburg, and Längsee, near Klagenfurt (Kärnten). All these lakes were sampled only once in each year during the period of summer stratification.

Physical and chemical parameters

Physical and chemical parameters relevant for the characterization of the water column (conductivity, temperature, O₂ concentration, pH, Eh) were measured *in situ* using selective electrodes. Sulfide concentration

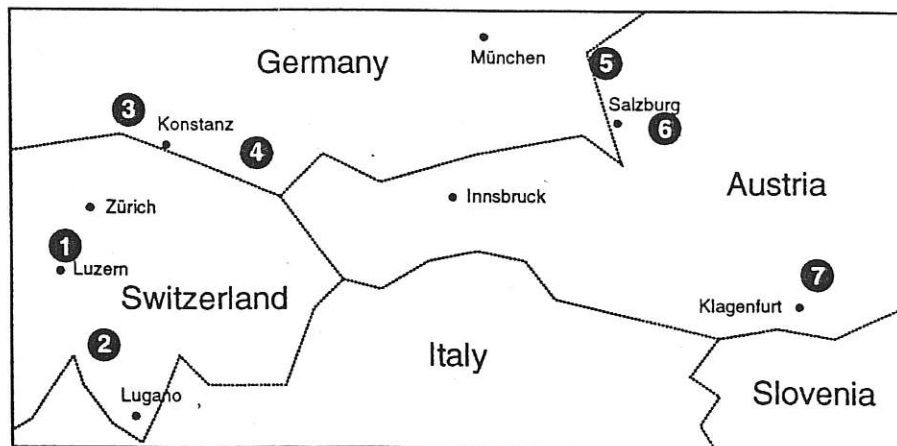


Fig. 1. Geographical location of the lakes studied: 1. Rotsee. 2. Lake Cadagno. 3. Buchensee. 4. Schleinsee. 5. Höllerersee. 6. Krotensee. 7. Längsee.

was determined in the laboratory following the Pachmayr method, as described by TRÜPER & SCHLEGEL (1964), from water samples fixed *in situ* with 1 M zinc acetate and 1 M NaOH.

Light measurements

Light measurements were performed throughout the water column in small depth intervals (0.25–1 m). Irradiance was measured with a battery-powered underwater spectroradiometer (LI-1800 UW; li-Cor, Inc., Lincoln, Nebr.) operated with a portable LCD terminal (LI-1800-01), connected by a 30 m underwater I/O cable (2218 UW-30). Downwelling irradiance spectra between 300 and 850 nm, at 2 nm intervals, were obtained around noon. Profiles were measured from the surface to the depth with the minimum light detectable for the spectroradiometer ($5 \times 10^{-4} \mu\text{E m}^{-2} \text{s}^{-1} \text{nm}^{-1}$). Data were transferred to a computer using a LI-1800 UW terminal interface, and integrated irradiance values for PAR and spectral bands were calculated.

Light absorption spectra between selected depths have been obtained from differential irradiance measurements, as the percentage of downwelling irradiance absorption between the shallowest and the greatest depths. These absorption data (% E_{abs}) have been calculated for each wavelength, taken at 2 nm intervals, as:

$$\%E_{\text{abs}} = 100 (E_i - E_j) \times (E_i)^{-1}$$

where E_i is the irradiance at the shallowest point of the range (i, j) and E_j is the irradiance at the deepest point. Spectra resulting from plotting % E_{abs} versus wavelength have been considered as *in situ*, *in vivo* absorption spectra and related to the different groups of photosynthetic pigment involved in light absorption.

Microorganisms

Water samples were collected using a special device designed for the study of steep gradients without mixing the microlayers, similar to the one described by JØRGENSEN et al. (1979), and stored in dark bottles. Population densities of phototrophic bacterioplankton and phytoplankton were estimated from concentrations of their photosynthetic pigments, bacteriochlorophylls (BChl) and chlorophyll (Chl *a*), respectively. Pigment concentrations were determined using a Milton Roy Spectronic 3000 Diode Array spectrophotometer after filtering and extracting the pigments in acetone (MONTESINOS et al. 1983). Some pigment extracts were stored and analyzed by HPLC, following the method by BORREGO & GARCIA-GIL (1994). Microbial groups and species were identified by pigment composition and optical microscopy.

Results and discussion

Distribution of phototrophic planktonic microorganisms

The metalimnion and the upper part of the hypolimnion held the densest phototrophic populations of the whole water column in all lakes studied, which is obvious from pigment profiles (Fig. 2). As a general feature, these deep phototrophic communities were composed of three different types of populations: phytoplankton (usually dominated by cyanobacteria), Chromatiaceae and Chlorobiaceae. The lakes varied (Table 1) with respect to their concentrations, the kind of dominant population, and the species composition.

the deep community in Schleinsee was dominated by eukaryotic phytoplankton species (a high diversity of Chlorophyceae, Bacillariophyceae, and Cryptophyceae) in June 1991. Algal populations were highly abundant in August 1993, but a dense Chromatiaceae plate was also obvious at 6 m depth. It was mainly composed of *Amoebobacter purpureus*, *Thiopedia rosea* and *Lamprocystis roseopersicina*. A population of *Lamprocystis roseopersicina* was dominant in Höllersee, too, causing the highest BChl *a* concentration at 10 m. Just above, a thin phycoerythrin-containing cyanobacterial population (*Oscillatoria rubescens*) was found.

In Längsee and Buchensee, similar Chromatiaceae plates developed: *Thiocystis violacea* and *Chromatium okenii* in Buchensee, *Lamprocystis roseopersicina* and also *Thiocystis violacea* in Längsee. They were placed below the phycoerythrin-containing cyanobacteria (Mainly

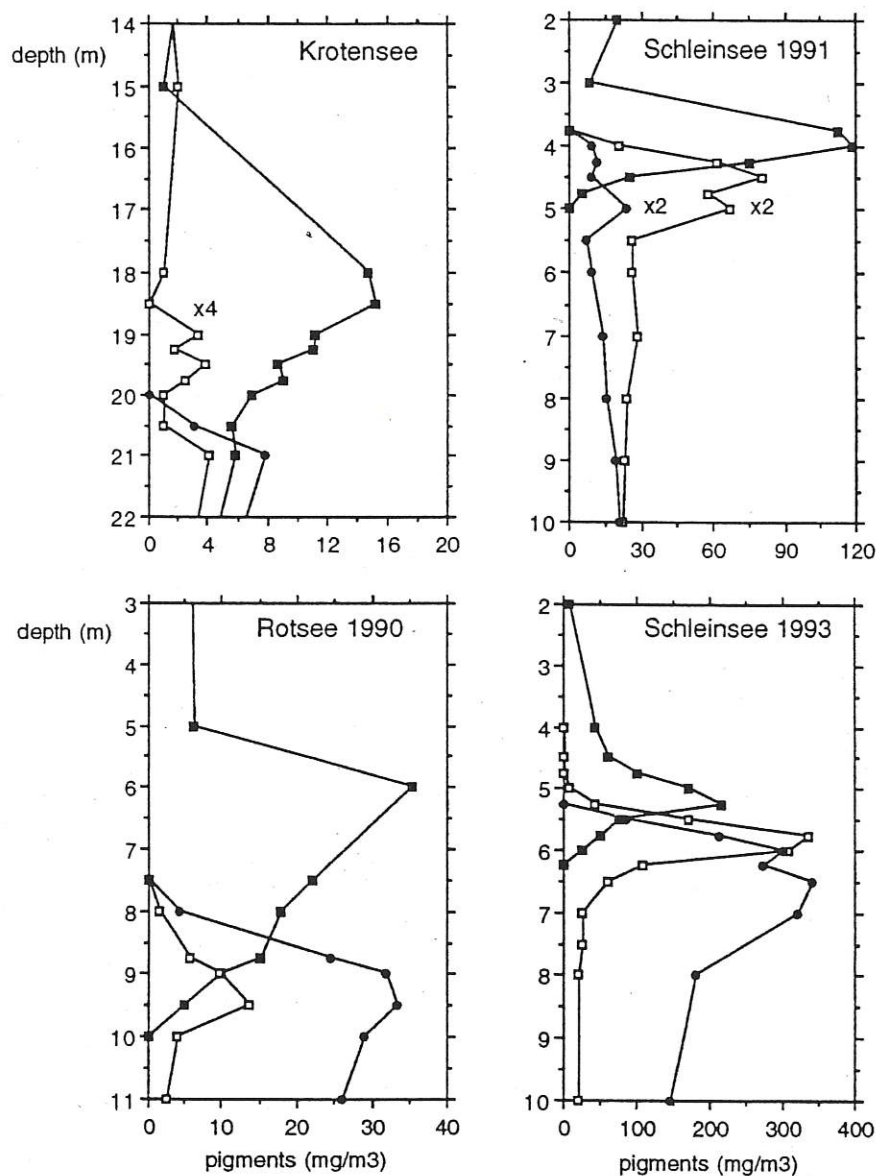


Fig. 2. Vertical distribution of deep phototrophic populations in the lakes studied on several selected occasions. Brown Chlorobiaceae, Chromatiaceae and both eukaryotic phytoplankton and cyanobacteria are represented by Bchl *e* (filled circles), Bchl *a* (empty squares), and Chl *a* (filled squares), respectively. The scale of some concentrations is enlarged (factors indicated).

Oscillatoria rubescens in both lakes), but reached lower Bchl *a* concentrations than in Schleensee and Höllersee. Lake Cadagno also contained both kinds of populations, cyanobacteria and Chromatiaceae (*Chromatium okenii*), but at greater depths (12–12.5 m).

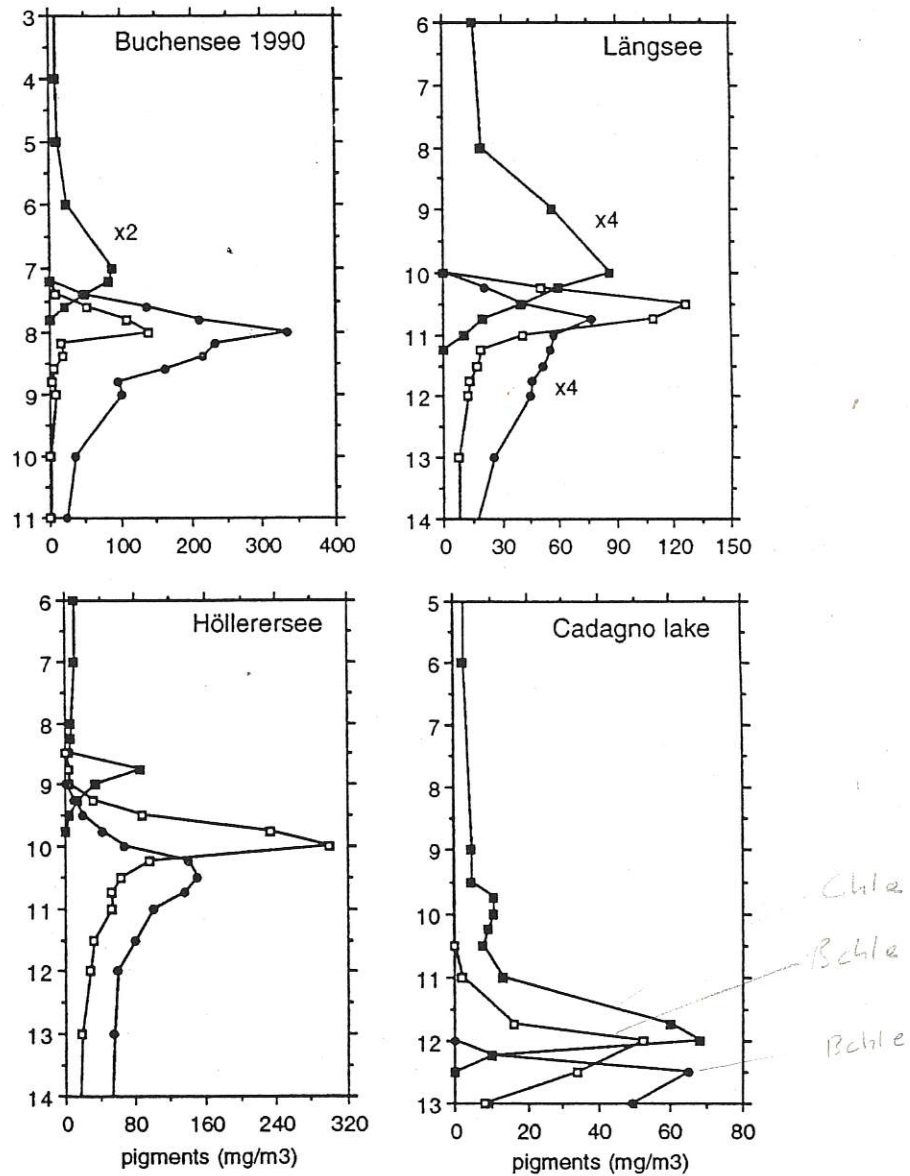


Fig. 2.

Rotsee and Krotensee communities were dominated by cyanobacterial plates characterized by phycoerythrin, with maxima at 6 and 18.5 m. The lowest Chl *a* and BChl concentrations were found in Krotensee, where cyanobacteria were represented by *Synechococcus* spp. Chromatiaceae were identified by optical microscopy, but they were almost undetectable spectrophotometrically.

Table 1. Dominant species and integrated pigment values for the whole water column (in $\text{mg} \times \text{m}^{-2}$) of Chl *a*, BChl *a* and BChl *e*, at the studied lakes and selected dates.

Lake	Date	Algae / cyanob.		Chromatiaceae		Chlorobiaceae	
		Chl <i>a</i>		BChl <i>a</i>		BChl <i>e</i>	
Buchensee	9/16th/1990	Or*	74	Tv, Co	75	Pp	393
Cadagno	9/4th/1993	cb.	97	Co	48	Pr	39
Höllerersee	8/26th/1993	Or	93	Lr	348	Pp	503
Krotensee	8/24th/1993	Sy	146	—	6	Pr	21
Längsee	8/30th/1993	Or	64	Tv, Lr	147	Pr	47
Rotsee	9/18th/1990	euk.	125	Tr	18	Pr	78
Schleinsee	6/20th/1991	euk.	161	Ap, Tr, Lr	52	Pr	111
Schleinsee	8/22th/1993	euk.	259	Lr	339	Pr	1002

*Species abbreviations: Or = *Oscillatoria rubescens*, cb. = undetermined cyanobacteria, Sy = *Synechococcus* sp., euk. = eukaryotic phytoplankton, Tv = *Thiocystis violacea*, Co = *Chromatium okenii*, Lr = *Lamprocystis roseopersicina*, Tr = *Thiopedia rosea*, Ap = *Amoebobacter purpureus*, Pp = *Pelodictyon phaeochlathratiforme*, Pr = "*Pelochromatium roseum*".

Chlorobiaceae populations were always present and represented by brown-pigmented species. *Pelodictyon phaeochlathratiforme* (OVERMANN & PFENNIG 1989) was found in Buchensee and Höllerersee, while "*Pelochromatium roseum*" consortia occurred in the other lakes. Brown-pigmented Chlorobiaceae reached their maximum BChl *e* concentration in Buchensee, where the *Pelodictyon phaeochlathratiforme* population overlapped the Chromatiaceae plate, but there also were dense *Pelodictyon* populations in Höllerersee and Schleinsee (August 1993).

Phototrophic microorganisms and their spectral fingerprints

Light absorption spectra between selected depths were related to the different phototrophic groups of microorganisms and helped in their identification, according to the *in vivo* absorption maxima and the spectral characteristics of photosynthetic pigments. Combinations of different pigments found in each spectrum establish the spectral properties of microorganisms responsible for light absorption between defined depths. In this study, they were especially useful to detect phycoerythrin-containing cyanobacterial populations, because it was not possible to discriminate them unequivocally from other Chl *a* containing populations by spectrophotometrical methods alone.

Fig. 3 shows some examples of different spectral ranges found in these lakes. At the Krotensee epilimnion, light absorption by photosynthetic pigments was very small, and thus the absorption spectrum was primarily affected by water and non-photosynthetic particles. Eukaryotic phytoplankton was easily identified in Schleinsee, between 4.5 and 5 m depth, while Chromatiaceae carotenoids dominated in the absorption spectrum between 5.5 and 6 m. Characteristic spectral fingerprints from Chromatiaceae also appeared in Lake Cadagno (11.5–12 m) and Höllerersee (10–10.5 m).

Krotensee (18–19 m), Buchensee (7–7.5 m) and Rotsee (7–8 m) showed the typical fingerprints of reddish cyanobacteria, characterized by the phycoerythrin absorption maximum at about 570 nm. In Längsee, a clear cyanobacterial spectral fingerprint (9–10 m) changed to a mixture of both cyanobacterial and Chromatiaceae absorption spectra at immediately greater depths (10–11 m).

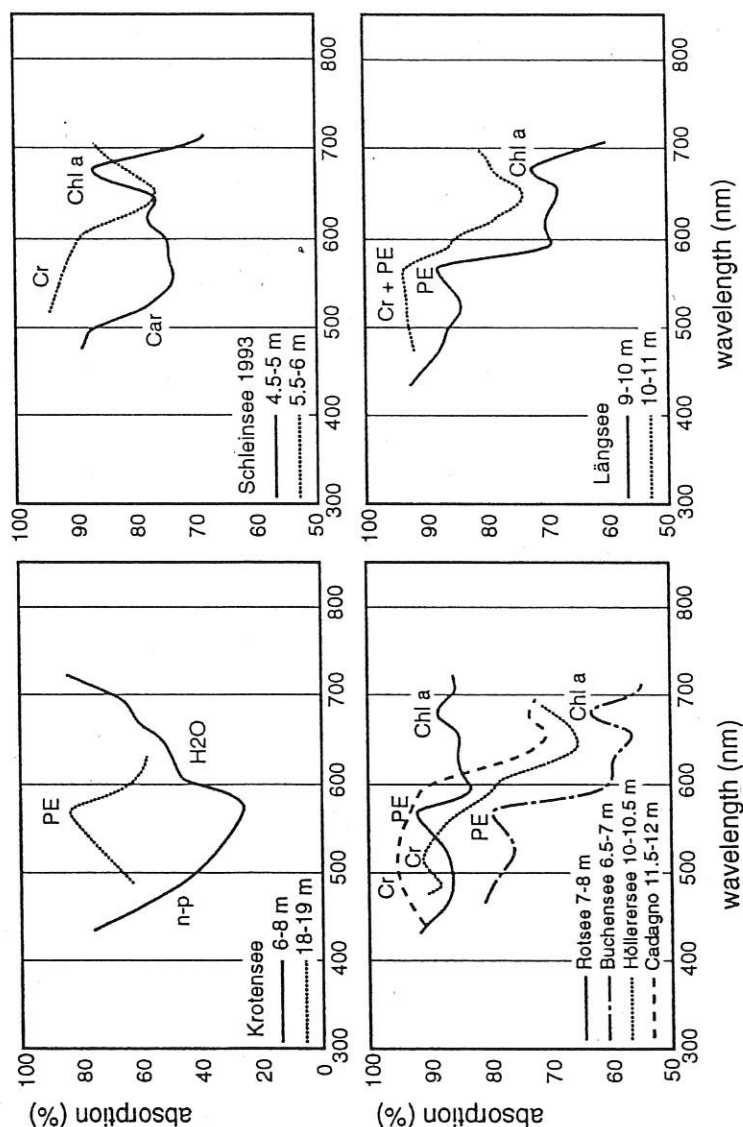


Fig. 3. Spectral absorption characteristics from *in situ* spectroradiometric analyses of different populations found in the studied lakes. They correspond to eukaryotic algae (Car + Chl *a*), phycoerythrin-containing cyanobacterial (PE + Chl *a*), and Chromatiaceae (Cr). In Krotensee, no photosynthetic pigments could be detected, and light absorption was mainly due to water and non-phototrophic organisms and particles. PE = phycoerythrin; Car = algal carotenoids; Cr = Chromatiaceae carotenoids; n-p = non-phototrophic elements.

Legend: ?

Light spectral distributions

Downwelling irradiance spectra obtained at different depths of these lakes are presented in Fig. 4, where some selected spectra representing the main changes in light climate are shown. The highest variations with depth are attributed to the absorption of long wavelengths (> 700 nm) by water and were mainly recorded at shallower layers, as known from previous studies conducted in some Spanish karstic lakes (VILA & ABELLA 1993). Differences among profiles were related to photosynthetic absorption by planktonic microorganisms.

In Krotensee, the water column was almost completely clear down to 18 m, resulting in a succession of light spectra scarcely affected by photosynthetic absorption of light. Maximum

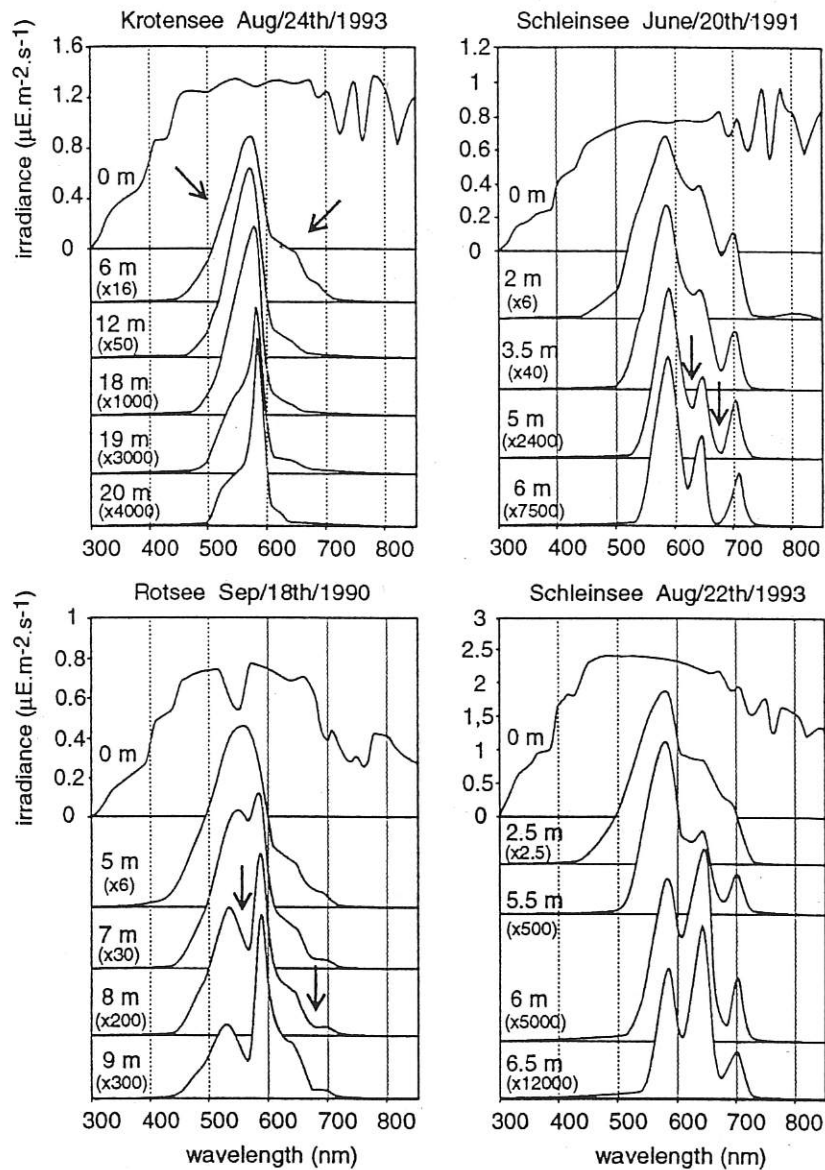


Fig. 4. Spectral composition of light at different depth in the lakes studied (dates are indicated in Table 1). Downwelling irradiance ($\mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) reaching each depth is represented on the Y-axis and wavelength on the X-axis. Magnifying factors for the vertical scale of each depth in respect to the surface spectra are indicated in parentheses. Some absorption characteristics that can be directly identified from these spectra are represented by arrows, corresponding to water and non-phototrophic organisms and particles (Krotensee), eukaryotic phytoplankton and phycocyanin-containing cyanobacteria (Schleinsee 1991), phycoerythrin-containing cyanobacteria (Rotsee, as well as Buchensee and Längsee) and Chromatiaceae (Cadagno, as in Schleinsee 1993 and Höllerersee).

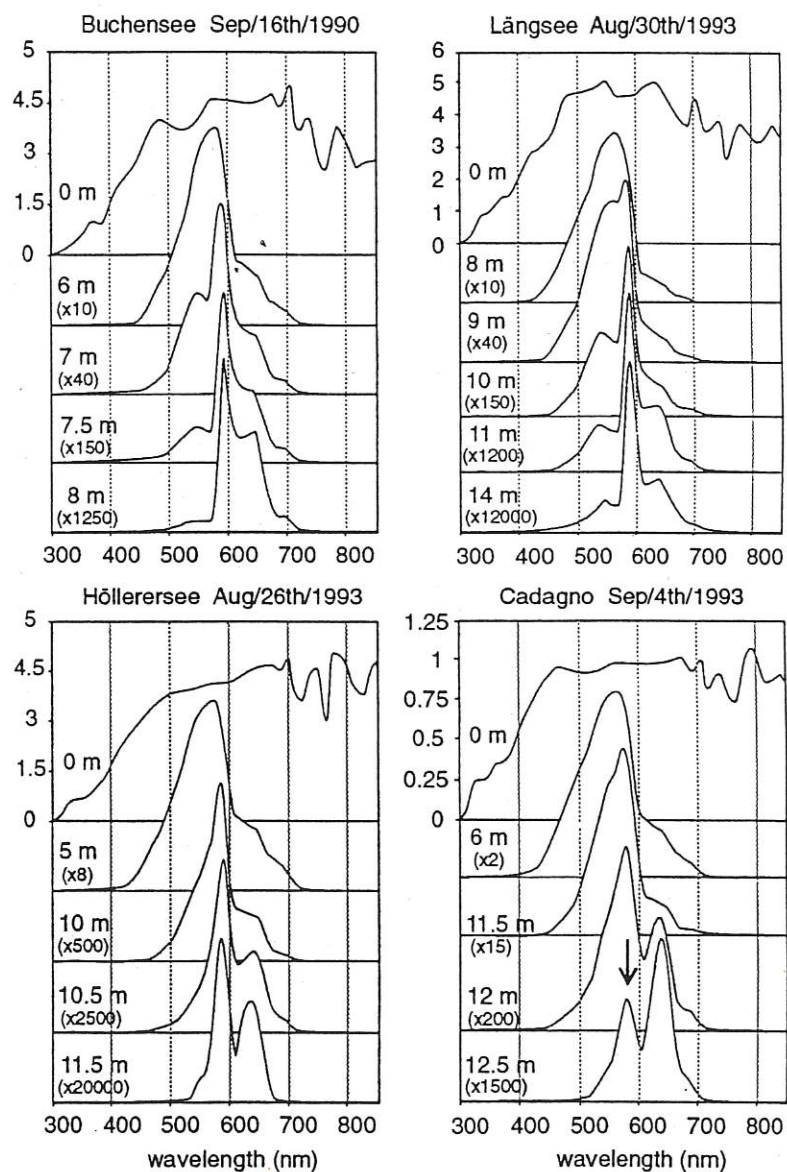


Fig. 4.

irradiance remained through the whole profile in a relatively wide range (a light window) with its maximum between 570 and 580 nm. Below 18 m, this window was narrower in coincidence with a deep population of phycoerythrin-containing cyanobacteria. In contrast, Schleinsee light spectra from June 1991 showed the absorption by a dense phytoplankton population, between 3.5 and 6 m, with both minimum irradiance wavelengths at 620 and 680 nm, corresponding to phycocyanin and Chl *a*, respectively.

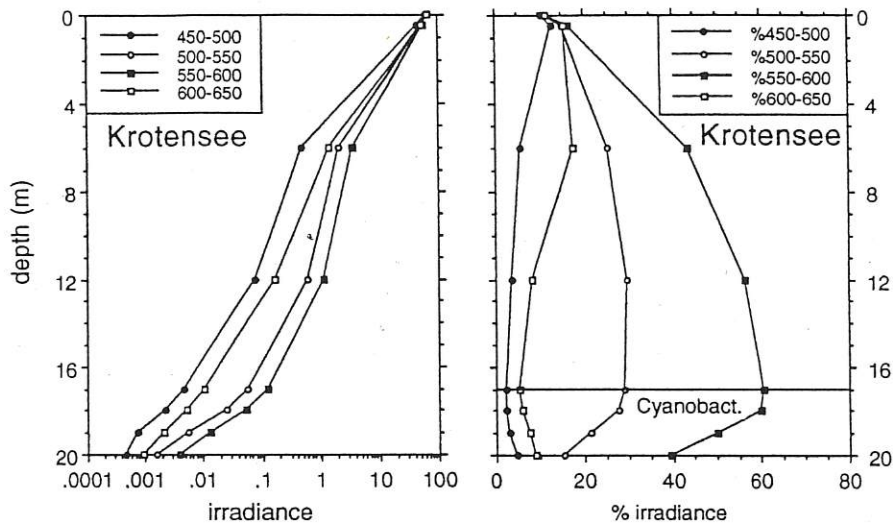


Fig. 5. Left: Light extinction profiles of the deepest-penetrating 50 nm-width wavebands in Krotensee. Right: Light percentage of each waveband in respect to the whole irradiance measured at each depth (300–850 nm) in Krotensee, showing the progressive enrichment in 550–600 nm with increasing depth.

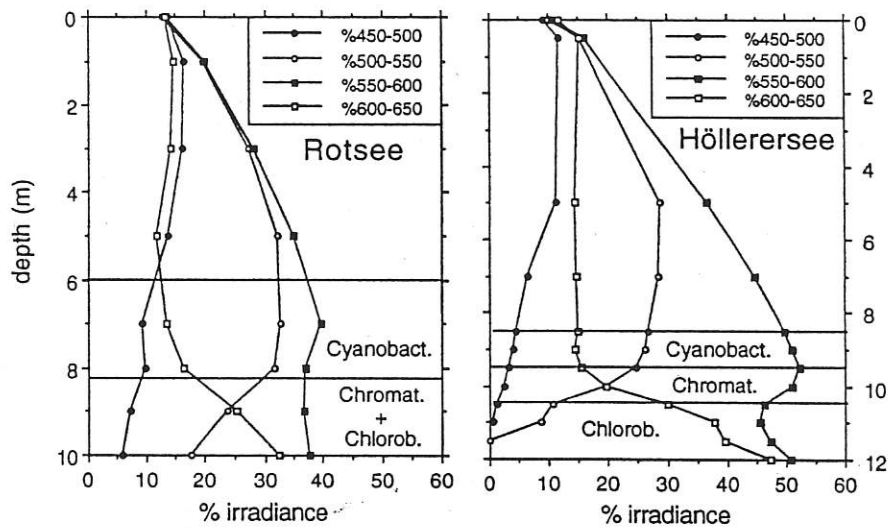


Fig. 6. Light percentage of deepest-penetrating 50 nm-width wavebands, in respect to total irradiance measured at each depth (300–850 nm), in Rotsee (left) and Höllersee (right). Deep phototrophic populations are indicated, in order to denote their absorption wavebands and the effects on relative light enrichment.

Deep light spectra in Buchensee, Längsee and Rotsee reflected the photosynthetic absorption by cyanobacterial populations. The minimal irradiance found at 570 nm resulted from the light absorption by phycoerythrin. Consequently, the irradiance maximum narrowed and shift-

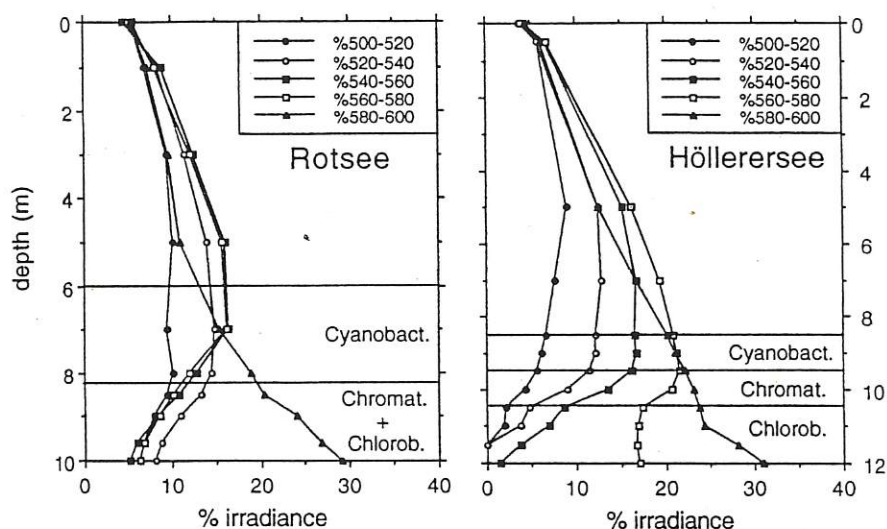
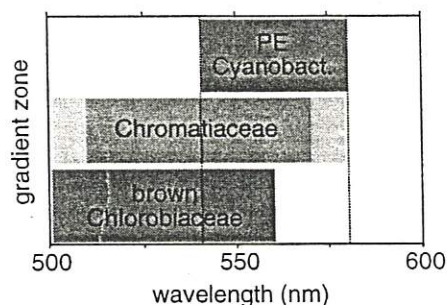


Fig. 7. Light percentage of 20 nm-width wavebands between 500 and 600 nm, in respect to total irradiance measured at each depth (300–850 nm), in Rotsee (left) and Höllerersee (right). Deep phototrophic populations are indicated as in Fig. 6.

Fig. 8. Conceptual model for the photosynthetic use of light between 500 and 600 nm in deep gradient zones. Because phycoerythrin-containing cyanobacteria reduce available light for both Chromatiaceae and Chlorobiaceae in the PE absorption range, these anoxygenic bacteria are forced to exploit the remaining radiation niches. However, a light window is still left over at wavelengths > 580 nm that is not used for anoxygenic photosynthesis.



ed to 580–590 nm. Higher densities of the cyanobacterial population in Rotsee affected the light spectra more intensely than in Längsee and Buchensee.

Spectra from Schleinsee (in August 1993), Höllerersee and Lake Cadagno showed an irradiance minimum between 600 and 610 nm, that could not be attributed to any pigment matching these wavelengths. Instead, it was caused by a wider absorption range from the lowest wavelengths up to 610–620 nm and related to the Chromatiaceae carotenoids (VILA & ABELLA 1993, 1994). Two irradiance maxima were thus found: the characteristic irradiance maximum at 570–580 nm, and a Chromatiaceae-dependent maximum between 630 and 640 nm. Dominance of the former or the latter depends on the balance between water absorption at longer wavelengths and Chromatiaceae light removal at shorter. Highly eutrophic Schleinsee also showed a minimal irradiance waveband at 670–680 nm, related to Chl *a*, while in Höllerersee the light spectrum was quenched below 600 nm by a deep phycoerythrin-rich cyanobacterial population.

Pigment selection by light quality

Pigment compositions of different populations found in the deep communities of these central European lakes were related to the spectral distribution of light. Most lakes contained reddish cyanobacteria, Chromatiaceae and brown Chlorobiaceae, all of them with photosynthetic pigments (phycoerythrin, okenone, isorenieratene) absorbing mainly at the central part of the spectrum (500–600 nm). With increasing depth, relative light enrichment in these central wavelengths became more distinct, especially between 550 and 600 nm (Fig. 5). Phycoerythrin-containing cyanobacteria were only absent at shallow depths (Schleensee), where light spectra were wider and less rich in these wavelengths (Fig. 4).

In contrast to green-coloured species, which are known to be dominant at shallower depths (MONTESINOS et al. 1983, VILA & ABELLA 1994), brown Chlorobiaceae were present in all lakes. Phototrophic microorganisms occurring in deep layers showed high concentrations of phycobilins and carotenoids which confer a better adaptation to the light available at these depths. Benthic photoautotrophs developed a high diversity of BChl to exploit near-infrared radiation (PIERSON et al. 1990), in a similar manner as planktonic species from shallow depths.

Radiation niche complementarity and coexistence of differently pigmented groups of phototrophic microorganisms

At the upper layer of deep communities, cyanobacteria fit best to the prevailing light, since the phycoerythrin absorption peak (570–580 nm) matched the ranges of maximum irradiance. Shaded phototrophic populations placed beneath were forced to use the remaining light. Thus, both Chromatiaceae and Chlorobiaceae absorbed wavelengths shorter than 550 nm. Fig. 6 shows the vertical profiles of the spectral ranges penetrating deepest in two lakes, which were dominated by cyanobacteria (Rotsee) and Chromatiaceae (Höllersee), respectively. Both lakes held brown Chlorobiaceae at the deeper layers of the multilayered community. The cyanobacterial population ceased relative enrichment within the 550–600 nm waveband, Chromatiaceae produced a decrease of both 500–550 and 550–600 wavebands, and Chlorobiaceae only affected light between 500 and 550 nm. As a result, the 600–650 nm waveband was progressively enriched through the gradient zone in all water columns, since it is not used by these phototrophic microorganisms.

A more accurate analysis of light absorption between 500 and 600 nm is provided in Fig. 7, allowing a precise elimination (Fig. 8) of the radiation niches. Cyanobacteria utilize light between 540 and 580 nm, Chromatiaceae increase light absorption between 500 and 580 nm, and brown Chlorobiaceae are specialized in wavelengths shorter than 560 nm. Wider absorption range of Chromatiaceae can be related to the high light requirements for their metabolic processes (VAN GEMERDEN 1980, VELDHUIS & VAN GEMERDEN 1986) and the possibility to utilize the phycoerythrin absorption range in the absence of reddish Cyanobacteria. Radiation niche complementarity between cyanobacteria and Chlorobiaceae is almost perfect. However, a small increase in the enrichment of Chlorobiaceae absorption ranges was found in Rotsee under the cyanobacterial layer. Spectral segregation of photosynthetic light removal enhances coexistence of different populations in these multi-layered structures (LINDHOLM 1992). However, Chlorobiaceae can be impaired by Chromatiaceae, because of the wide absorption range of the latter. A 580–600 nm waveband is favoured by all populations, as well as longer wavelengths (Fig. 6), and constitutes a light window that is left available at greater depths. It usually reaches the maximum penetration beneath deep communities, and it is not used for anoxygenic photosynthesis at these depths by any known microorganism. Future studies should focus on the dynamic aspects of selection, analyzing the relations between light quality and community composition in the context of seasonal succession.

Acknowledgements: Buchensee, Schleinsee and Rotsee were studied in 1990 with the participation of I.V. Pibernat and J.B. Figueras. X. Vila and C.M. Borrego were the recipients of doctoral scholarships from the Spanish Ministry of Education and Science, respectively from 1991 and 1992. Financial support for the studies conducted in 1993 was provided by the Spanish Ministry of Education and Science and the Austrian Academic Exchange Service, through the HU92-012B cooperation project. Acknowledgements are also due to the Institute of Limnology in Mondsee for all facilities offered during this part of the work and to the anonymous reviewers for their significant contributions to the improvement of this paper.

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