ARTICLE SCIENTIA *gerundensis*, 14:57-69 (1988)

LAKE VECHTEN, SCHLEINSEE AND BUCHENSEE AS EXAMPLES OF WEST CENTRAL EUROPEAN HOLOMICTIC LAKES CONTAINING PHOTOTROPHIC BACTERIA

X. G. Riera, L. J. Garcia-Gil and C. A. Abella

Institut d'Ecologia Aquàtica. Estudi General de Girona (UAB). Hospital, 6. 17071-Girona.

RESUM

El present treball ha estat realitzat a tres llacs holomíctics de l'oest i del centre d'Europa en els quals han estat caracteritzats físico-químicament i biològicament. L'objectiu central de l'estudi ha estat analitzar l'ecologia microbiana de les poblacions de bacteris fototròfics presents a l'hipolímnion dels esmentats llacs. A partir d'aquí, s'han establert relacions entre la físico-química del llac i els grups de bacteris fototròfics presents per tal d'ajustar el màxim un model. Aquest és un model de predicció de l'aparició de determinades espècies o grups de bacteris fototròfics en funció, principalment, de paràmetres com la llum o la concentració de sulfhídric, el tipus de pigments i la presència de vacuoles de gas.

RESUMEN

El presente trabajo ha sido realizado en tres lagos holomícticos del oeste y centro de Europa. En el mismo, se les ha caracterizado físico-química y biológicamente. El objetivo central del estudio ha sido analizar la ecología microbiana de las poblaciones de bacterias fototróficas presentes en el hipolimnion de los mencionados lagos. A partir de aquí, se han establecido relaciones entre la físico-química del lago y los grupos de bacterias fototróficas presentes a fin de ajustar al máximo un modelo. Éste es un modelo de predicción de la aparición de determinadas especies o grupos de bacterias fototróficas en función, principalmente, de parámetros como la luz, la concentración de sulfhídrico, tipos de pigmentos y presencia de vacuolas de gas.

ABSTRACT

The present work has been done in three west central european holomictic lakes. They have been physico-chemically and biologically characterized. The central objective of this paper has been analyze the microbial ecology of the phototrophic bacteria populations that develop in the hypolimnion of these lakes. The relationship between different physico-chemical conditions and the main group of phototrophic bacteria that develops in each one has been checked in order to adjust a model. This model allows to predict the occurrence of determined species or groups of phototrophic bacteria as a function of, mainly, light and sulfide concentration, pigments and presence of gas vacuoles.

Key words: Buchensee, *Chloronema giganteum, Chloronema spiroideum,* holomixis, microbial ecology, *Pelodictyon «phaeoglomerans»,* phototrophic bacteria, Schleinsee, Vechten.

INTRODUCTION

Since the occurrence of phototrophic bacteria was described for the first time by Bavendamm (1924), a lot of references about their ecology have appeared. The presence of phototrophic bacteria in the studied lakes has already been noticed by Verdouw and Dekkers (1980) in lake Vechten (The Netherlands), Fitz (1986) in Buchensee and Vetter (1937) in Schleinsee (both in the Federal Republic of Germany).

Phototrophic bacteria develop in almost all aquatic environments with enough light (both intensity and quality) and sulphide (anaerobic conditions) (Pfenning, 1978). Some of these conditions occur in the freshwater holomictic lakes. These kind of lakes show a typical pattern of winter circulation causing the disappearance of phototrophic bacteria populations from the water by changing the anaerobic conditions of the hypolimnion into aerobic. However, and due to the thermal stratification in spring, the hypolimnion becomes anaerobic and the phototrophic bacteria recolonize it from the sediment. Hence, this work attempts to compare them in order to ascertain which are the main factors that allow them to grow under such conditions in the holomictic lakes mentioned above.

Riera (1987) and Abella & Garcia-Gil (1988) have developed a model which explains the selection of different species of phototrophic bacteria mainly through both light intensity and quality and sulfide concentration. Data obtained are compared to this model in order to check its accuracy.

MATERIAL AND METHODS

Samples were all taken at the site of maximal depth of every lake. Just after sampling, they were kept cold in the dark until analysis, performed within 48 hours.

Temperature, conductivity, dissolved oxygen and light intensity were mesured *in situ* using respectively, a digital display termistor Crison T-637, a S-C-T YSI 33 meter, a dissolved oxygen YSI 57 meter and a selenium photocell connected to a LCD HIOKI-meter.

The rest of the physico-chemical analyses were done in a field laboratory. Redox potential and pH were mesured by a platinum electrode Methrom AG 9100 and an Orion RX-Combination elctrode pH 9156, both connected to a pH/ISE meter Orion 720. Sulphide was mesured using a selective electrode Orion 94-16 and a double junction reference electrode Orion 90-02. Total iron was analysed by the thiocianate method modified from Vogel (1978).

Pigment analyses were done filtering 250 mL of sample through a Sartorius filter (0.45 μm of pore diameter) covered by a thin layer of $MgCo_3$. The cells remain in the magnesium carbonate layer and can be resuspended in 90 % acetone (Montesinos, 1982). The concentration of bacteriochlorophylls *a*, *d* and *e* in μg/L was calculated by the following formules (Gloe et al., 1975; Smith & Benítez, 1955; Takahashi & Ichimura, 1970):

Bchl $a = 25.2 \times (A_{775} - A_{830}) \times f$
Bchl $d = 10.2 \times (A_{654} - A_{830}) \times f$
Bchl $e = 25.2 \times (A_{650} - A_{830}) \times f$
being: $f = v/V.d$
V =filtered volume in liters.
v = extract volume in mililiters.
d = pathlenght of the used cuvette.

Total number was calculated by counting directly under microscope after staining with methylen blue. A 0.2 mL volume of water from different depths were deposited over a 1 cm^2 surface of a microscopic slide and heated until water evaporation. This method allows a direct sampling for total number in the field. Counting was done at 320× in a bright field Zeiss microscope.

RESULTS AND DISCUSSION

Data have been collected from two different sources. The first source was our own data, obtained from different campaigns donde during the last five years. The second one comes from the bibliography for discussion purposes.

Lake Vechten

This is a gravel man-made lake, located centrally in The Netherlands (near Utrech), and having its origin in excavation (sand digging) in 1941. It has two similar basins, each with a maximum depth of 11 meters. Some aspects of its limnology and physiography are yet described in Gulati & Parma (1982) and Steenbergen & Verdow (1982) among others. The samples were taken in the eastern basin of the lake on August 13th 1988.

Steenbergen et al. (1987) describe it as a warm-monomictic lake, which agrees with our data. As shown by the vertical profile of temperature (Fig. 1a), a pronounced thermocline (12 °C between 3 and 6 meters depth) divides a cold hypolimnion (4-5 °C) from a warm epilimnion (17-18 °C). The chemocline starts below the thermocline (Fig. 1a). The physico-chemical properties of the metalimnion will be determinant for the biology of the microaerophilic-anaerobic part of the lake.

The pH values range down between 6.8-7.2 in the epilimnion to 6.3-6.8 in the metalimnion and 6.1-6.3 in the anaerobic hypolimnion. This distribution agrees with a typical summer stratification, where the acidic behaviour of

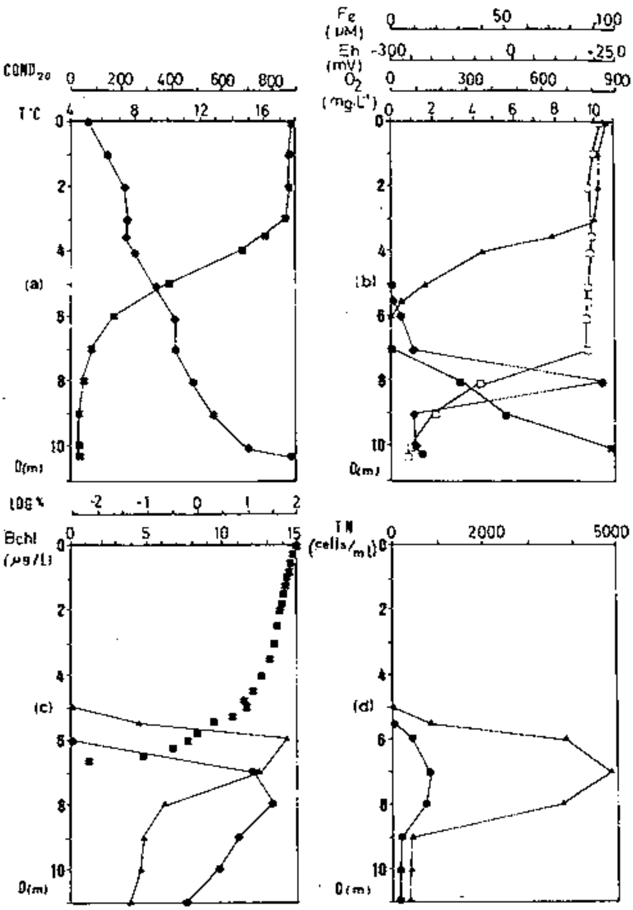

Figure 1. Physico-chemical and biological conditions of lake Vechten on August 1988. (a) vertical profiles of temperature (■) and conductivity at 20°C (●). (b) vertical profiles of oxygen (▲), sulfide (●), redox potential (□) and total iron (Fe) ■). (c) vertical profiles of bacteriochlorophylls *d* (▲) and *e* (●) and the extinction of incident light (■). (d) vertical profiles of total number (TN) of *Chloronema spiroideum* (▲) and *Chloronema giganteum* (●).

some reduced compounds from the hypolimnion (mainly sulfide and ammonium) decreases the pH values.

The combined vertical distribution of oxygen (mg.L^{-1}), sulphide (µM) and redox potential (mV) follows both thermal and saline stratification pattern (Fig. 1b): the well stratified water column becomes divided into three major zones, epilimnion (0 to 5 meters depth), metalimnion (5 to 7 meters depth) and hypolimnion (7 to 11 meters depth).

The epilimnion is homogeniously aerobic until 4 meters, decreasing progressively the oxygen concentration under this depth. The metalimnion shows a coexistence of oxygen and sulphide, both at low levels. The redoxcline, as well as the oxycline, is located also in the metalimnion, where a sharp gradient of more than 400 mV appears. Although metalimnetic sulphide concentrations range in the micromolar level, hypolimnetic sulphide concentrations range nearly in the milimolar level (at 8 meters). Under this maximum, free sulphide decreases largely mainly due to the increase in the ferrous iron concentration (Fig. 1b). Iron availability seems to control the concentration of free sulphide in the hypolimnion (Verdouw & Dekkers, 1980; Brugada, 1986).

In the metalimnetic layer (between 5 and 7 meters), where the thermocline ends and the chemocline starts, dense populations of phototrophic bacteria develop. Two peaks appeared in the vertical distribution of bacteriochlorophylls (Bchl) in the water column (Fig. 1c). The first one, at 6 meters depth, concerns a Bchl *d* peak and, the second one, at 8 meters depth, concerns a Bchl *e* peak. No members of Chromatiaceae were found, maybe due to the shading carried out by a cyanobacteria population in the upper metalimnion. Brown Chlorobiaceae populations were also found, mainly *Chlorobium phaeobacteroides*. Finally, two different species of filamentous gas vacuolated *Chloronema* (green Chlorobiaceae) were found. Vertical distribution of their total numbers (Fig. 1d) shows that *C. spiroideum* (5×10^3 filaments $\cdot$ mL^{-1}) was predominant over *C. giganteum* (5×10^2 filaments $\cdot$ mL^{-1}).

Brown Chlorobiaceae underlies the green Chlorobiaceae layer due to their better adaptation to lower light intensities and higher sulphide concentrations. Green Chlorobiaceae developed a plate at a sulphide concentration of 50 µM. However, brown Chlorobiaceae developed it at a sulphide concentration of 870 µM. Vertical extinction of light (Fig. 1c) shows two main depths where light extinction increases; at 5 meters depth, mainly due to a dense population of the cyanobacteria *Synechococcus*-type cells (Steenbergen et al., 1987), and at 6.25 meters depth, mainly due to the green Chlorobiaceae populations. That means, that brown Chlorobiaceae grew under very low light intensities (about 0.001 % of incident surface light). On the other hand, an increase in the sulphide and total iron concentration associated to the brown Chlorobiaceae peak was found. Thus, the presence of ferrous sulphide (FeS) at this layer might be in part responsible for the total extinction of light at this depth.

Schleinsee

The Schleinsee is located at northeast of Langenargen, near the Bodensee. It has a singular bathymetry, without high slopes and with a very flat bottom. The samples were taken on September 25th, 1985 and on August 15th, 1988, in the maximal depth point (11 meters). The inital studies on this lake comes from Vetter (1937), who started to study the phytoplankton of this lake in 1934.

The vertical profiles of temperature (Fig. 2a) shows the typical summer stratification, being the thermocline deeper and weaker in September than in August. A relatively wide metalimnion (about 3 meters) divides a cold hypolimnion (4 to 6 °C) from a warm epilimnion (20 to 24 °C). Conductivity (Fig. 2a) follows the thermal distribution on September 1985 and on August 1988. However, both gradients, thermal and saline, are smooth.

The vertical combined distribution of oxygen ($mg \cdot L^{-1}$) and sulphide (μM) follows the thermal stratification (Fig. 2b). The oxycline on September 1985 was smooth, with values of 15-16 $mg \cdot L^{-1}$ of dissolved oxygen in the upper part of the epilimnion (between 0 and 2 meters). The metalimnetic layer shows both oxygen and sulphide concentrations under 2 $mg \cdot L^{-1}$ and 15 μM respectively. In the hypolimnion, sulphide concentration increases up to 70 μM. Ferrous sulphide (FeS) does not seem to control the free-sulphide concentration because of its low level of about 2 μM (Eichler, 1988). On August 1988, similar profiles of both oxygen and sulphide were obtained.

The distribution of pH follows the stratification of the water column. The aerobic epilimnion had, on September 1985, pH values greater than 8, mainly due to the high photosynthetic activity of phytoplankton. In the metalimnion, the pH started to decrease just nearly 7. Finally, in the anaerobic reduced hypolimnion the pH values decreased until 6.8.

Hence, this low concentration of hypolimnetic sulphide determines the biology of purple and green sulphur bacteria present in the meta and hypolimnion of Schleinsee.

On August 1988, two kinds of bacteriochlorophylls appeared, Bchl *a* and *d*, showing both a peak at 6 meters depth in the upper part of the metalimnion (Fig. 2c). This dynamics shows the coexistence of both green and purple sulphur bacteria at this depth. Bchl *d* concentration was 3.5 times higher than Bchl *a* concentration. Nevertheless, total number of Chromatiaceae was 2.5 higher than total number of Chlorobiaceae (Fig. 2d). This topic can be explained by their own morphology. The main green Chlorobiaceae found was a filamentous gas vacuolated *Chloronema giganteum*, being a small motile *Chromatium* sp the main member of Chromatiaceae. Therefore, no individual cells but filaments were counted as *C. giganteum;* so, the number of individual cells is rather higher than the number of filaments in this case.

Vertical extinction of light (Fig. 2c) shows a three steps distribution pattern. The strongest quenching of light takes place between 4 and 6 meters depth, just over the metalimnion; it might be due to cyanobacterial populations developing at this depth. Below the phototrophic bacterial plate, light intensity decreases until undetectable levels.

Buchensee

Buchenseen are three small lakes in Gütthingen, northwest from Bodensee (Federal Republic of Germany). The central Buchensee has been the object

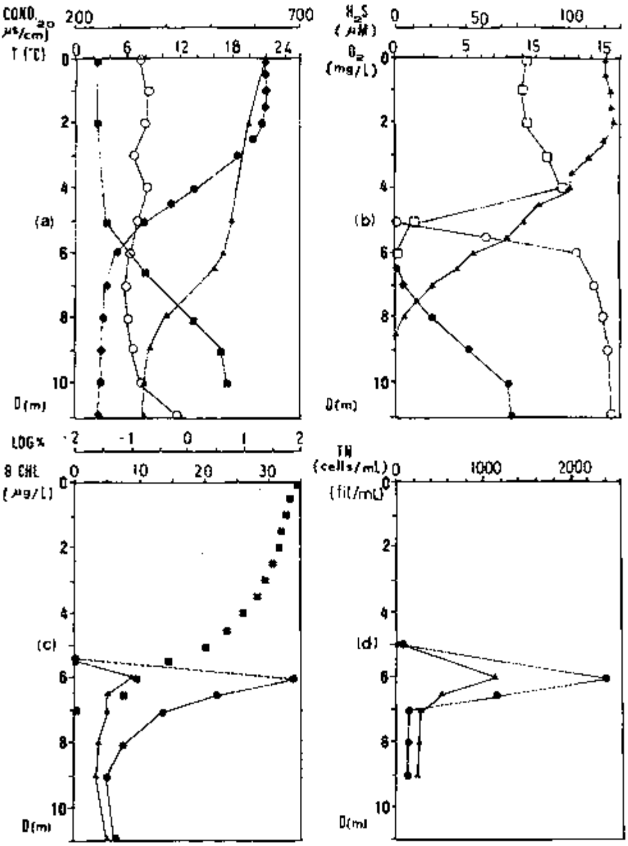

Figure 2. Physico-chemical and biological condittions of Schleinsee on September 1985 and August 1988. (a) vertical profiles of temperature (▲ & ●) and conductivity at 20 °C (■ & ○) on both dates respectively. (b) vertical profiles of oxygen (▲ & □) and sulphide (● & ○) in both dates respectively. (c) vertical profiles of bacteriochlorophylls *a* (▲) and *d* (●) and the extinction of incident light (■) on August 1988. (d) vertical profiles of total number (TN) of *Chromatium* sp (●) and *Chloronema giganteum* (▲) on August 1988.

of the study. It is a circular basin with a maximum depth of 12 meters. The samples were taken on September 1985 and August 1988 in the maximal depth point.

As in the other lakes, the vertical profiles of temperature (Fig. 3a) show a thermal stratification, deeper on September 1985 than on August 1988, as well as a higher pH (8-8.2) in the epilimnion than in the hypolimnion (6.5-7). Conductivity follows the thermal distribution in both cases. However, the biology of both anaerobic hypolimnion is quite different, mainly due to the distribution of oxygen and sulphide.

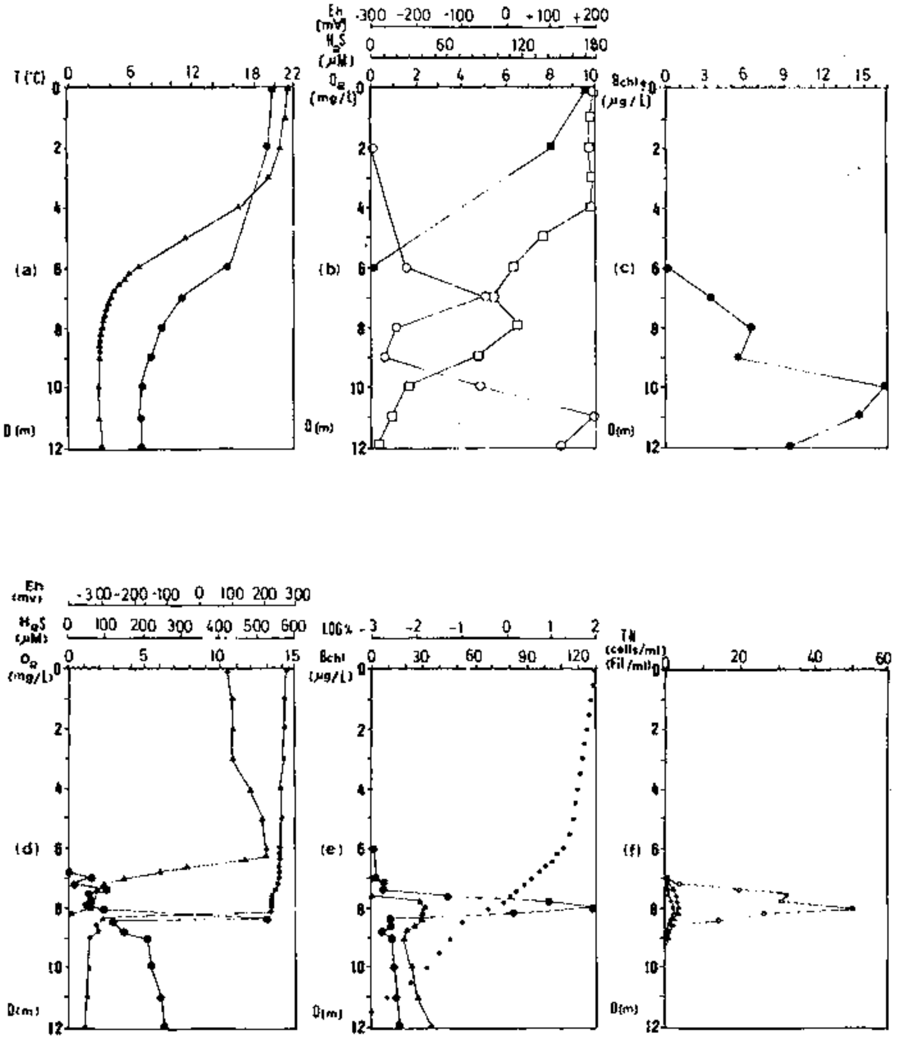

Figure 3. Physico-chemical and biological conditions of Buchensee on September 1985 and August 1988. (a) vertical profiles of temperature (● & ▲) on both dates respectively. (b) Vertical profiles of oxygen (■), sulphide (○) and redox potential (□) on September 1985. (c) vertical profile of bacteriochlorophyll *e* on September 1985. (d) vertical profiles of oxygen (▲), sulphide (●) and redox potential (·) on August 1988. (e) vertical profiles of bacteriochlorophylls *a* (●) and *d* (▲) and vertical extinction of incident light (·) on August 1988. (f) vertical profiles of total number (TN) of *Chromatium okenii* (□), *Chloronema spiroideum* (○) and *Chloronema giganteum* (▲) on August 1988.

On September 1985, there was a clear division between both aerobic epilimnion and anaerobic hypolimnion (Fig. 3b), because no metalimnetic coexistence was found. Sulphide shows two peaks, one below the oxygen/sulphide interphase (at 7 meters depth) with a value of 100 μM and other over the bottom with a value of 200 μM. This irregular distribution might be the origin of the smooth redoxcline found.

There was also a dense population of phytoplankton, which is responsible for the strong extinction of light quality in the epilimnion. Under such conditions, brown phototrophic bacteria populations develop in the anaerobic hypolimnion. As shows the vertical profile of bacteriochlorophyll *e* (Bchl *e*), there were two peaks (Fig. 3c), one at 8 meters and another one at 10 meters. There are two topics to be discussed in order to ascertain the biology of phototrophic bacteria in the anaerobic hypolimnion of Buchensee on September 1985: why brown Chlorobiaceae and no other phototrophic bacteria? and why was not there a plate just at the oxygen/sulphide interphase but 4 meters below it? The development of phototrophic bacteria is directly controlled by sulphide levels and both light intensity and quality (Pfenning, 1967). In this case, light seems to be the major physical factor controlling their development, mainly due to the algal shading and the depth at which phototrophic bacteria develop. Light intensity seems to be less important than light quality for phototrophic bacteria growing because of the depth of the plate. Thus, selective spectral shading by phytoplankton (Parkin & Brock, 1980; Montesinos et al., 1983) is the responsible of the occurrence of brown phototrophic bacteria and no others in this lake.

The main phototrophic bacteria present in the lake was *Pelodictyon phaeoglomerans* strain 7502 (Abella & Montesinos, 1986; Abella et al., 1986), a branched vacuolated bacteria which forms microcolonies growing under both field and laboratory conditions.

However, on August 1988 the behaviour of phototrophic bacteria populations was rather different than on September 1985 because of its different physico-chemical conditions.

There was a sharp thermal gradient; therefore, a well structured metalimnetic layer appeared. The combined distribution of oxigen (mg $\cdot$ L^{-1}), sulphide (μM) and redox potential (mV) follows this distribution pattern (Fig. 3d). The aerobic epilimnion shows both an homogeneous concentration of oxygen (between 10 and 12 mg $\cdot$ L^{-1}) and an oxidant redox potential (between +200 and +300 mv). The anaerobic hypolimnion had sulphide concentrations ranging between 200 and 550 μM, depending on the depth; there was a peak just below the redoxcline (at 8.4 meters depth). The pH values ranged between 7 to 8 in the epilimnion and between 6.5 to 7 in the hypolimnion.

The metalimnion is clearly the most physicochemically interesting layer, mainly due to the distribution of both oxygen and sulphide. Between 6 and 8 meters, a weak coexistence was found, both at low concentration levels. Metalimnetic sulphide concentrations ranged between 10 and 80 μM, with a maximum of about 100 μM at 7.4 meters depth. However, the oxygen concentration decreased progressively with depth, from 12 mg · L^{-1} (at 6 meters depth) until it dissapears (at 8.2 meters depth). The redoxcline (between 8.2 and 8.4 meters depth) mainly follows sulphide distribution, because the decreasing of redox potential (from +200 mV to −300 mV in 20 centimeters) occurs simultaneously with the increasing in sulphide concentration (from 80 to 550 μM at the same depth). So, this sharp redoxcline is the border between metalimnion and hypolimnion.

Purple and green sulphur bacteria were found in the metalimnion and upper epilimnion, as show the vertical profiles of their bacteriochlorophylls, Bchl *a* and *d* (Fig. 3e). Purple sulphur bacteria were predominant over the green ones. As happened in lake Vechten, total number of Chromatiaceae (5×10^4 cells · mL^{-1}) was 10 times higher than total number of green Chlorobiaceae (5×10^3 filaments · mL^{-1}); but Bchl *a* concentration was only 5 times higher than Bchl *d* because of their different morfology (Fig. 3f). The main member found of Chromatiaceae was *Chromatium okenii.* Two species of green filamentous gas vacuolated Chlorobiaceae were found, *Chloronema giganteum* and *Chloronema spiroideum.* The distribution of total number of phototrophic sulfur bacteria follows the dynamics of their own pigments; however, there was an spatial seggregation between both *Chloronema. C. giganteum* populations were found slightly overliying *C. spiroideum* populations; no clear reasons could be found in order to explain this fact or define its ecological niche.

The vertical extiction of light (Fig. 3e) shows that the higher extinction of light took place between 7.8 and 8.5 meters depth, concerning to purple and green sulphur bacteria plates.

On September 1985, brown Chlorobiaceae were found instead of Chromatiaceae and green Chlorobiaceae (found on August 1988). This fact can be explained by the higher shadowing effect due to the phytoplankton that took place on September 1985; however, on August 1988 there was not a dense phytoplankton population as shows the low extinction of light in the epilimnion. The increase in light intensity and the decrease in partial spectral shadowing could be the main selective factor controlling the presence of purple and green instead of brown sulfur bacteria on August 1988.

Global discussion and modeling of these lakes

The ecology and physiology of phototrophic bacteria have been yet modeled by several authors (Montesinos 1982; Riera, 1987; Abella & Garcia-Gil, 1988). However, the ecology models become more qualitative than quantitative.

One of the first attempst to quantify the relationship between phototrophic bacteria and their environmental conditions was carried out by Abella & Montesinos (1986). Their preliminary model mixes qualitative and quantitative features (Fig. 4), and tries to explain the selective growth of phototrophic

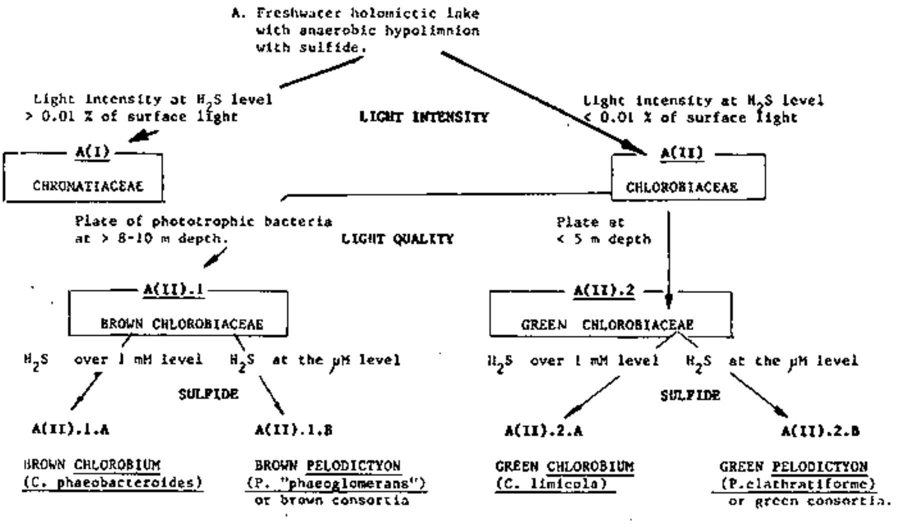

Figure 4. A model explaining the selective growth of phototrophic bacteria in freshwater holomictic lakes.

bacteria in freshwater holomictic lakes. The main selective environmental factors used to build up the model were light, both quality and intensity, sulphide concentration, type of pigments and presence of gas-vacuolate bacteria.

The results of lake Vechten in 1988 agrees well with those predicted by the model. There was a green phototrophic bacteria plate over a brown one. The environmental conditions concerning the green sulphur bacteria were very similar to those described in the model, as occurs with the brown sulphur bacteria. Thus, the model predicts the development of individual populations, but not both at the same time. However, this plate coexistence, not predicted by the model, was present.

This model has been built up from the ecology of phototrophic bacterial populations assuming a steady state dynamics, defined as no apparent net growth of the populations (growth minus loss); hence, the selective factors have yet performed and the competition processes have finished. On August 1988, in lake Vechten, selective factors were still performing and therefore, the results does not adjust to the model because it only predicts the steady state.

The results of Schleinsee from 1985 agree with the model because a plate of brown phototrophic bacteria was found at 8 meters depth. However, as comented above for lake Vechten, a coexistence of purple and green sulphur bacteria was found in 1988 for similar reasons.

The results of Buchensee during August 1988 agree with the model, as well as the results from 1985. In 1988, there was a dense population of purple suphur bacteria at 8 meters depth, more than 0.01% of surface incident light and µM level of sulphide. Under them, no brown but green sulphur bacteria developed. Thus, there were two plates of phototrophic bacteria below 8 meters depth and none of them were brown. On the other hand, this model has not been yet well developed for purple sulphur bacteria; hence, more data should be necessary in order to adjust this model to their behaviour. Obviously, these populations were not at the stationary state.

This model seems to explain better the main group of phototrophic bacteria that would develop under any environmental conditions in stationary state than the concret species. Surely, more parameters as spectral characteristics, buoyancy, motility, surface versus volume ratio, Ks and Ki for sulphide, size, nutrient uptake (phosphate, ammonium), vitamins, form,... must be considered in order to adjust better the predictibility of this model to the field data.

Aknowledgements

We wish to thank L. Sala-Genoher for his help and friendship. We are also grateful to the Laboratori de Microbiologia, Estudi General de Girona, for its economical support.

References

ABELLA, C.A. & MONTESINOS, E. (1986). *Pelodictyon* sp strain 7502. The brown counterpart of *Pelodictyon clathratiforme*. Preliminary Characterization. Abstracts of the 4th International Symposium on Microbial Ecology.

ABELLA, C.A., GARCIA-GIL, J. & BRUNET, R. (1986). Ecological comparison between *Pelodictyon phaeglomerans* strain 7502 and *Pelodictyon clathratiforme* in their natural habitats. Abstracts of the 4th International Symposium on Microbial Ecology.

ABELLA, C.A. & GARCIA-GIL, L.J. (1988). Diel migration as a mechanism for enrichment of natural populations of branching species of *Pelodictyon*, In: Green Photosynthectic Bacteria. J.M. Olson, J.G. Ormerod, J. Amesz, E. Stackebrandt & H.G. Trüper (eds.). Plenum. New York.

BAVENDAMM, W. (1924). Die Farblosen und roten Schwefelbakterien des Süss und Salzwassers. Gustav Fisher. Jena.

BRUGADA, D. (1986). Metabolisme del sofre i funció detoxificadora dels bacteris fototròfics de l'estanyol del Vilär (Banyoles). Tesi de Llicenciatura. Universitat Autonòma de Barcelona.

EICHLER, B. (1988). Untersuchungen zur Ókophysiologie und systematik gasvacuolenhaltiger Chromatiaceen. Dissertation zur Erlangung des akademischen Grades des Doktors der Naturwissenschaften. Universität Konstanz.

FITZ, R. (1986). Die Sukzession des Phytoplanktons im mittleren Buchensee und ihre Beziehung zu relevanten Umweltfaktoren. Diplomarbeit. Univerität Konstanz.

GLOE, A., PFENNING, N., BROCKMANN, H. & TROWITZSCH, W. (1975). A new bacteriochlorophyll from brown coloured Chlorobiaceae. *Arch. Microbiol.*, 102:103-109.

GULATI, R.D. & PARMA, S. (1982). Studies on Lake Vechten and Tjeukaemeer, The Netherlands. *Hydrobiol.*, 95:1-383.

MONTESINOS, E. (1982). Ecofisiología de la fotosíntesis bacteriana. Tesis Doctoral. Universitat Autònoma de Barcelona.

MONTESINOS, E., GUERRERO, R., ABELLA, C. & ESTEVE, I. (1983). Ecology and physiology of the competition for light between *Chlorobium limicola* and *Chlorobium phaeobacteroides* in natural habitats. *Appl. Environm. Microbiol.*, 46:1007-1016.

PARKIN, T.B. & BROCK, T.D. (1980). Photosynthetic bacterial production in lakes: The effects of light intensity. *Limnol. Oceanogr.*, 25:711-718.

PFENNING, N. (1967). Photosynthetic bacteria. *Annu. Rev. Microbiol.*, 21:285-324.

PFENNING, N. (1978). General physiology and ecology of photosynthetic bacteria. In: R.K. Clayton Sistrom, W.R. (eds.). *The photosynthetic bacteria*. Plenum Press. New Yorl.

RIERA, X.G. (1987). Cicle limnològic i ecologia de les poblacions de bacteris fototròfics en la llacuna costanera de «La Massona» (Alt Empordà, Girona). Tesina de Llicenciatura. Universitat Autònoma de Barcelona.

SMITH, J.H. & BENÍTEZ, A. (1955). Chlorophylls. Analysis in plant materials. In: Modern methods of plant analysis. V.H. Springer Verlag. Heidelberg.

STEENBERGEN, C.L.M. & H. VERDOUW. (1982). Lake Vechten: aspects of its morphometry, climate, hydrology and physico-chemical characteristics. *Hydrobiol.*, 95:11-23.

STEENBERGEN, C.L.M., KORTHALS, H.J. & van Nes, M. (1987). Ecological observations on phototrophic sulfur bacteria and the role of these bacteria in the sulfur cycle of monomictic lake Vechten (The Netherlands). *Acta Acadamieae Aboensis.*, 47 (2):97-115.

TAKAHASHI, M. & ICHIMURA, S. (1970). Photosynthetic properties and growth of phototrophic bacteria in lakes. *Limnol. Oceanogr.*, 15:924-944.

VERDOUW, H. & E. M. DEKKERS. (1980). Iron and manganese in lake Vechten (The Netherlands); dynamics and role in the cycle of reducing power. *Arch. Hydrobiol.*, 89:509-532.

VETTER, H. (1937). Limnologische Untersuchungen über das Phytoplankton und seine Beziehungen zur Ernährung des Zooplanktons im Schleinsee bei Langenargen am Bodensee. *Int. Rev. ges. Hydrobiol. Hydrogr.*, 34:499-561.

VOGEL, A.I. (1978). Text-book of quantitative inorganic analysis (4 th edition). Longman.