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COLONIZATION AND DYNAMICS OF PHOTOTROPHIC BACTERIA IN A RECENTLY FORMED LAGOON IN BANYOLES KARSTIC AREA (GIRONA, SPAIN)

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RESUM

Hom ha estudiat l'evolució de la composició físico-química i microbiològica de l'aigua durant el primer cicle anual en un estanyol de recent formació al sistema càrstic de Banyoles. Després d'un mes de la seva formació, es detecten activitats microbianes anaeròbiques, principalment basades en el metabolisme de compostos de sofre, que apareixen a les capes profundes i sediments. Uns mesos després s'estableix definitivament una comunitat de bacteris fototròfics vermells del sofre (*Chromatium minus*), localitzats a la interfase oxigen-sulfhídric, que oxiden el sulfhídric que difon dels sediments i és produït d'altra banda per bacteris reductors de sulfats. El nostre treball demostra que als estanyols amb poca circulació de l'aigua, generalment s'arriba a una situació estable en què dominen dues comunitats microbianes que alteren l'estat d'òxido-reducció dels compostos de sofre (l'element més abundant a l'aigua) i constitueixen un *sulfuretum*.

RESUMEN

Se ha estudiado la evolución durante el primer ciclo anual, de la composición físico-química y microbiológica de una laguna de reciente formación en el sistema cárstico de Banyoles. Transcurrido un mes después de su formación, se detecta un progresivo aumento de las actividades microbianas anaeróbicas en las capas profundas y sedimentos (especialmente producción de sulfhídrico). Tras varios meses se desarrollan comunidades estables de bacterias fototróficas del azufre (principalmente *Chromatium minus*) situadas en la interfase oxígeno-sulfhídrico, y de bacterias reductoras de sulfatos localizadas en los sedimentos anaeróbicos.

ABSTRACT

The evolution of physico-chemical and microbiological characteristics of water in a recently formed lagoon in the Banyoles karstic area was followed during the first annual cycle. After one month from its formation, anaerobic microbial activities, mostly based on metabolizing sulfur compounds, started in bottom layers and sediments. After a few months a stable community of phototrophic sulfur bacteria (*Chromatium minus*) located at the oxygen-sulfide interphase and sulfate-reducing bacteria in the anaerobic sediments, were established.

Key words: Phototrophic bacteria, microbial ecology, sulphuretum, colonization, *Chromatium*, karstic lakes.

INTRODUCTION

Seldom, in microbial ecology of water bodies, a microbial succession could be followed in the early phases of their geological origin. The sudden formation of karstic lagoons offers a unique opportunity to study such succession in the Banyoles karstic area (Girona, Spain). Formation of waterbodies due to terrain collapse have been recorded with a certain periodicity (Sanz, 1981). They usually appears in autum (october-november) after a dry summer season when freatic water pressure is at minimum values. On november 12, 1978 a lagoon appeared near Lake Banyoles in an agriculture field located at 75 meters to the west shore of the lake. The new lagoon was named «Estanyol Nou».

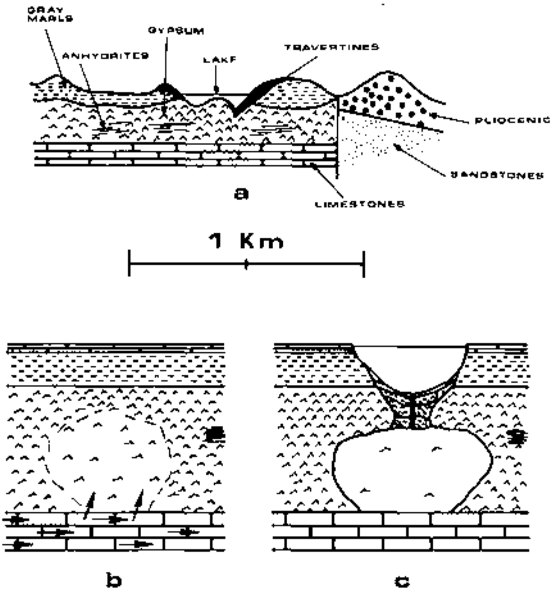


Figure 1. Schematic representation of the process of lake formation in the Banyoles karstic area. Profiles of geological strata in the nearshore of Lake Banyoles (a). Production of a gypsum solution bag in the gypsum strata (b). Sinking of the surface generating the *estanyol* (c). For explanation see the text.

Geological explanation of this event is given in figure 1. Under the surface of Banyoles karstic area, the following materials are found: travertine, gray marls, gypsum and limestone layers at the bottom part. Due to the Albanya Fault located at the East side of the lake, freatic water from limestone bottom layers is forced to flux to the surface feeding the Lake Banyoles. During this flow up water dissolves gypsum and travertinic materials, living holes filled with water. Under low water pressure conditions (a dry summer season), surface strata collapses and originates small springs or lagoons. The dissolution of the different materials of the strata results in a high contents of sulfate and bicarbonate in water.

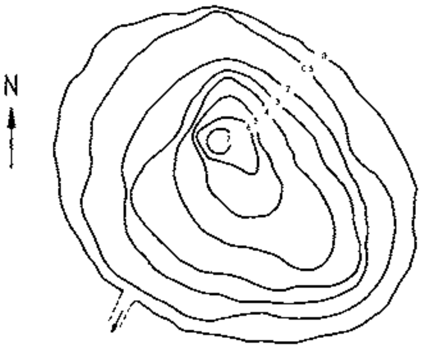
Several days after the collapse of the surface and formation of Nou lagoon, water was gray-brown colored because of abundant slime materials. The lagoon engulfed several trees which remained inside until now. Dissolved or particulate organic materials early detected in water were mainly originated from trees and other plants, before phytoplakton could start production, thus being alloctonous organic matter.

Several lagoons located in the surroundings of Lake Banyoles have been formed times ago by the above mentioned geological process. Some of them developed a community of microorganisms which actively change the redox state of sulfur compounds (the more abundant element in water) (Abellà, 1980, Montesinos, 1982). As a result of a particular microbial activity, in anaerobic sediments, sulfide is produced by sulfate-reducing bacteria (Ylla, 1981). Sulfide difusses toward upper water layers and is transformed into sulfur and sulfate by phototrophic sulfur bacteria. Planktonic phototrophic bacteria frequently forms very dense layers of deep pink, brown or green colors, at depths where light and sulfide are present in sufficient amounts (Montesinos, 1978, Guerrero & Abellà, 1978, Pfenning, 1978, Trüper & Genovese, 1968, Montesinos *et al*, 1983). This kind of anaerobic ecosystems are called *sulfureta* (Baas-Becking, 1925).

The purpose of this work was monitoring of physico-chemical and microbiological characteristics of the new formed lagoon during the first events, in order to ascertain the kind of processes leading to the situation of *sulfuretum*.

MATERIALS AND METHODS

Samples were taken beweeckly or monthly at different depths according to temperature and turbidity profiles and keeped in the cold until analysis performed not later than 48 hours. Samples at the oxygen-sulfide interphase were taken at shorter depth intervals. Physico-chemical and biological parameters were analysed as extensively described in Turet (1981), Abellà (1980) and Montesinos (1982).



z (m)	A_z (m^2)	V (m^3)
0	840	--
0.2	754	159
0.5	652	211
1	556	302
2	438	497
3	331	385
4	176	254
4.5	107	71
5	64	43
6	21	41
7	4	11
		1935

Figure 2. Bathymetric map of Nou lagoon on october 1978. For further details see Hutchinson (1957).

RESULTS

Morphometric characteristics of the Nou lagoon

In figure 2 a bathymetric map of Nou lagoon in shown. Maximum depth and the mean slope of the shore were respectively 7 meters and 25° 29′. There was no surface inlet (except during rainy days) and the outlet flux was seasonally dependent (120 $L.h^{-1}$ during the spring of 1979). The shape of the lagoon is the consequence of a single depression due to surface collapsing which is typical of karstic lakes. In the main Lake Banyoles the fusion of many dolines («holes») gived the polje basin.

Morphometric parameters according to Hutchinson (1957) are presented in table 1. Maximum lenght is 37 m and the total surface and volume were 840 m^2 and 1935 m^3 respectively. The lagoon is allmost circular with a low mean depth ($z = 2.3$ m) and surface to volume ratio ($A/V = 0.43$), indicating a relatively high influence of surface over the whole water column. The 91 % of the total volume of the lagoon was contained into the four first meters depth.

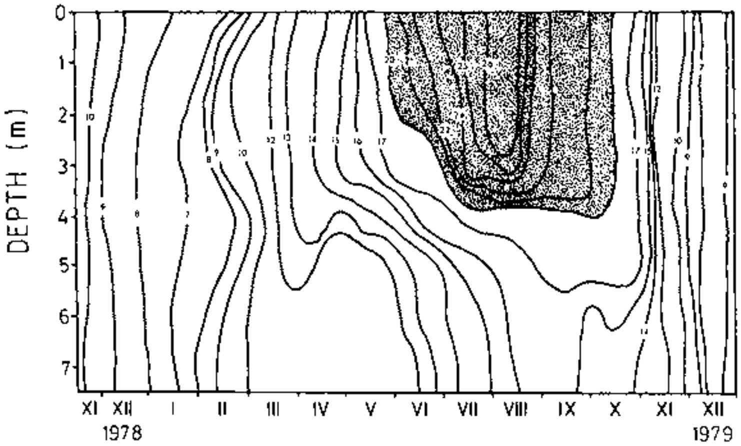


Figure 3. Depth-time distribution of temperature.

Table 1. Morphometric parameters of Nou Lagoon, following Hutchinson (1957).

A (Area)	840 m^2
V (Volume)	1935 m^3
z_m (Maximum depth)	7 m
l (Length)	37 m
b (Breadth)	33 m
$\bar{z}$ (Mean depth)	2.3 m
L (Shore line)	105 m
D_L (Development of shore line)	1.02
D_V (Development of volume)	0.99
z_r (Relative depth)	0.21
E (Mean slope)	25° 29′
A/V	0.43
$\bar{z}/z_m$	0.33

Physicochemical characteristics

Depth time profiles of temperature are shown in figure 3. The lagoon is of monomictic holomictic type, that is full overturn once a year, with a maximum temperature of 26 °C and minimum of 6 °C. Thermocline appears at the end of may and stands till october. The epilimnion reaches 3 meters depth. Apparent mixing for temperature in winter is only valid for this parameter while the other chemical and biological parameters (see figures 5, 6 and 7) demonstrates that in fact, a meromixis was present.

Vertical profiles of conductivity, pH and red-ox potential during the first annual cycle are shown in figure 4. Conductivity was high (about 1.8 mmhos. cm^{-1}) for a freshwater lake and reflected mostly the changes in the

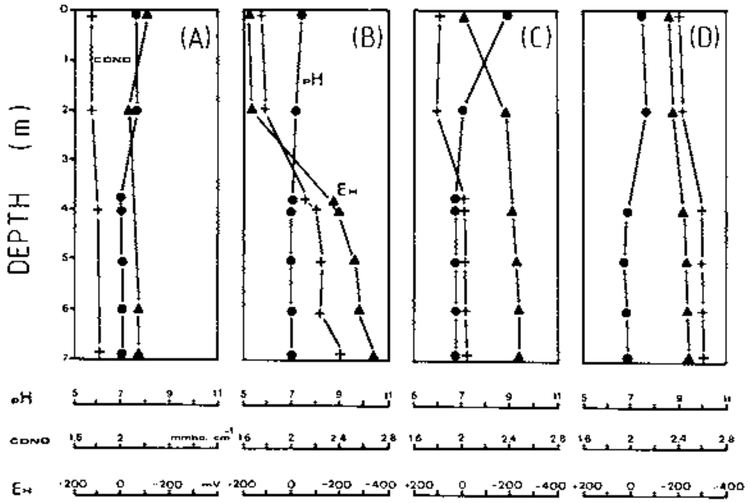


Figure 4. Vertical profiles of conductivity, pH and red-ox potential during winter (24-2-1979) (A), spring (12-5-1979) (B), summer (16-7-1979) (C) and autum (21-10-1979) (D).

main anion, the sulfate, which enters with freatic water thorought the bottom part of the lake. For that reason during the first winter after lake formation, its distribution was uniforme accross the water column (without a previous stratification period). During the spring, stratification processes caused accumulation of sulfate in the hypolimnion. Afterwords, sulfate was progressively consumed by the sulfate reduction activity which was reflected in a decrease in the conductivity of the hypolimnion. During summer, the equilibrium between accumulation and consumption of sulfate gived an intermediate conductivity profile with also lower conductivity values in the hypolimnion than during the spring. During autumn, again sulfate progressively reaches the epilimnion. The pH was always neutral or slightly acid at the bottom part. Usually the epilimnion values were slightly alkaline due to high bicarbonate concentrations.

Red-ox potential fluctuated from −400 to + 200 mV which indicated that high activity of metabolic anaerobic processes occurred. Immediately after lagoon formation, the red-ox was between 0 and −100 mV and homogeneously distributed from surface to bottom. During stratification the hypolimnion was clearly anaerobic with values below −200 mV due to the accumulation of reduced products like sulfide, amonia, etc. During fall their values again were similar accross the water column.

Depth-time distributions of oxygen and sulfide concentration are given in figure 5. Low oxygen concentrations were present at the begining in the water column (around 1-4 m) corresponding to levels usually found in freatic waters from the karstic area. Oxygen dissapears very soon (a month later) from the bottom layers because sulfide was produced due to the

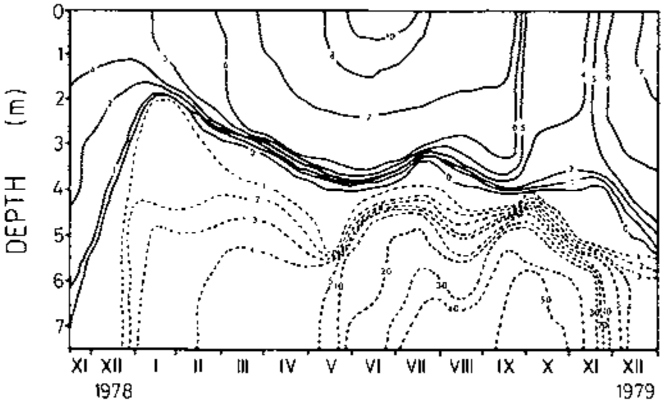


Figure 5. Depth-time distributions of sulfide (broken line) and oxygen concentrations (continuous line) in mg.L^{-1}.

activity of sulfate-reducing bacteria in sediments. The highest oxygen concentration (7-10 mg.L^{-1}) were detected during summer in the epilimnion, whereas the lowest (less than 4 mg.L^{-1}) were found between september and november, due to diffusion of sulfide from the hypolimnion favoured by an homogeneous temperature profile. As could be seen this fact indicate uncomplete mixing of the water column in spite of the temperature data. Sulfide maxima (40-50 mg.L^{-1}) were detected at the bottom part, between july and november. In the early steps of lagoon development, sulfide continuously increased, suggesting that production of sulfide by sulfate reduction was favoured by dissolved or particulate organic matter (from engulfed vegetation or from sedimented phytoplankton).

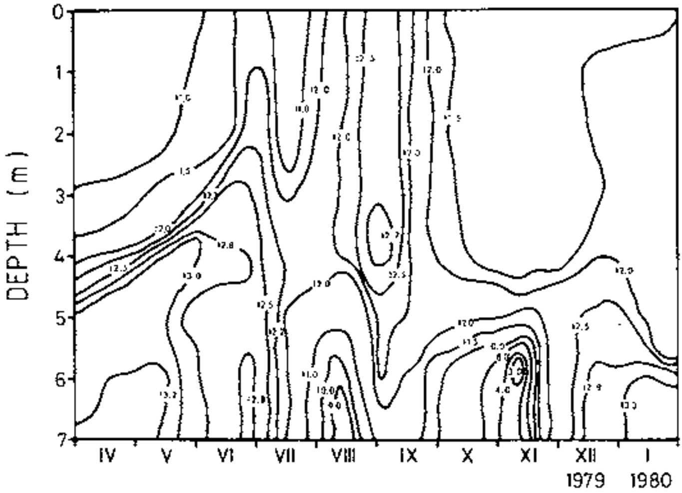


Figure 6. Depth-time distribution of sulfate concentrations in mmol.L^{-1}.

After the above-mentioned sulfide maxima, its concentration diminishes following depletion of sulfate and decrease in temperature, both being factors limiting sulfate-reduction.

Sulfate (figure 6) was found in the lagoon at very high concentrations (up to 12.7 mM) and enters the system with freatic water througouth bottom springs. Sulfate governs the chemical characteristics of the lagoon. Sulfate concentrations were the highest near the bottom, except during the summer (3-9 mmol.L^{-1}), because of the high consumption of sulfate by reduction.

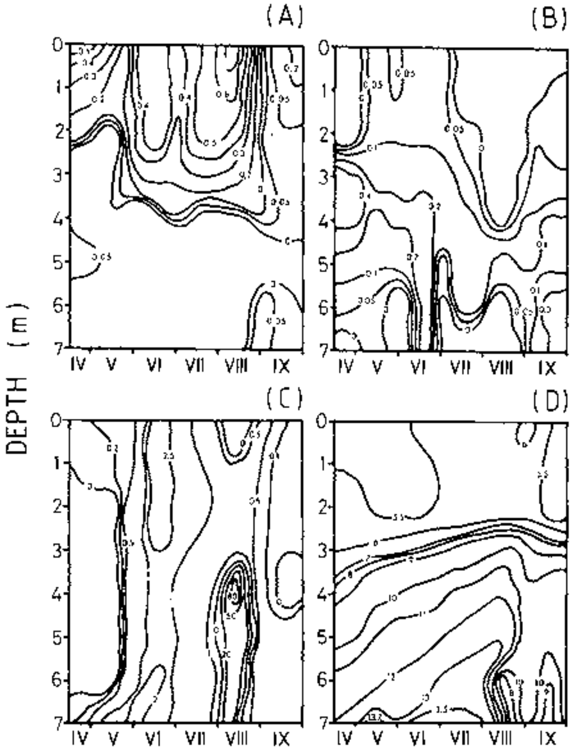


Figure 7. Depth-time distributions of nitrate (A), nitrite (B), soluble reactive phosphate (C) in μmol.L^{-1}, and total alkalinity in meq.L^{-1} (D) during 1979.

Nitrate, nitrite, soluble reactive phosphate and total alkalinity data are shown in figure 7. Analyses were only performed from april to september 1979, which coincided with the period of highest biological activity. Nitrate was very scarce in the epilimnion, with maximum values in the surface waters during august 1979, but was allmost absent in the anaerobic hypolimnion. Nitrits were also very low with relative maxima in the 3-5 m depth, at the interphase between oxygen and sulfide, where nitrate reduction was probably taking place. Depth-time profiles of soluble reactive phosphate showed an interesting pattern. The concentration was very low during early spring and autumn, but increased progressively till june-july in the whole water column. During the end of july and most of august very high values were found in the hypolimnion (up to 80 μol.L^{-1}) probably due to the release of phosphates from cells due to lysis. Total alkalinity (bicarbonate, CO_2 and carbonate) showed the same pattern accross the water column during the whole period studied: higher concentrations in the hypolimnion than in the epilimnion. This distribution reflects the two main origins of bicarbonate in water, namely the freatic and the produced by a high microbial activity in sediments.

Biological characteristics

Species composition and pigment analysis

In figure 8, the comparative absorption spectra of whole cells (*in vivo*) from cultures of *Chlorella* sp and *Chromatium minus* are presented in compari-

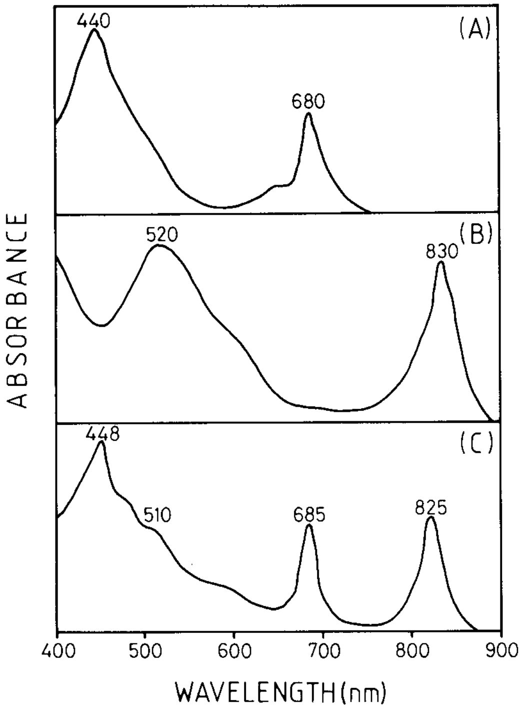


Figure 8. Absorption spectra of whole cells from cultures of *Chlorella* sp (A), *Chromatium minus* (B) and a sample taken at 4 m depth from Nou lagoon on may 26, 1979 (C).

son to a sample of 4 m depth from Nou lagoon. The wavelength maxima are sharply distinct between the algae (680 nm) and phototrophic bacteria (825-830 nm). The absorption spectrum of the sample from the bacterial layer of Nou lagoon matches both spectra and demonstrates the presence of both, algae (mainly euglenophytes and diatoms) and phototrophic bacteria (mainly *Chromatium minus*). This results were confirmed by microscopycal observation with the phase-contrast microscope.

In figure 9, the spectra of acetonic extracts from 0 and 4 m depth during the period from december 1978 to setember 1979 are presented. The oxygen-sulfide interphase containing the bacterial layer stayed at 4-5 m depth. The relative maximum at 663 nm corresponds to algal chlorophyll *a*, and the 772 nm to bacteriochlorophyll *a* from Chromatiaceae. At the surface, only chlorophyll *a* was found, with maximum amounts during february-may 1979, due to the first algal bloom of Nou lagoon, after few months of the start of colonization by phytoplanckton. At 4 m depth there was a mixture of algal chlorophyll, in higher amounts than at surface water, and bacteriochlorophyll *a*, the later starting in may.

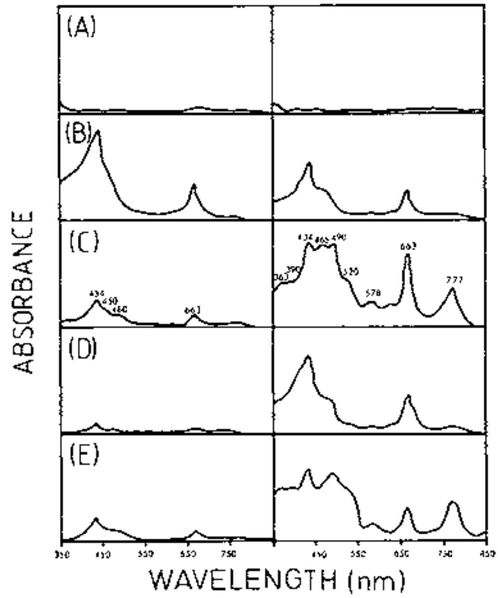


Figure 9. Absorption spectra of acetonic extracts from samples of surface (left panel) and 4 meters depth (right panel) during december 1978 (A), february (B), may (C), august (D) and september 1979 (E).

Vertical distribution of phototrophic microorganisms during stratification

Figure 10 shows the vertical distribution of pigments and cell concentration of the dominant phototrophic bacteria (*Chromatium*) and algae, in relation

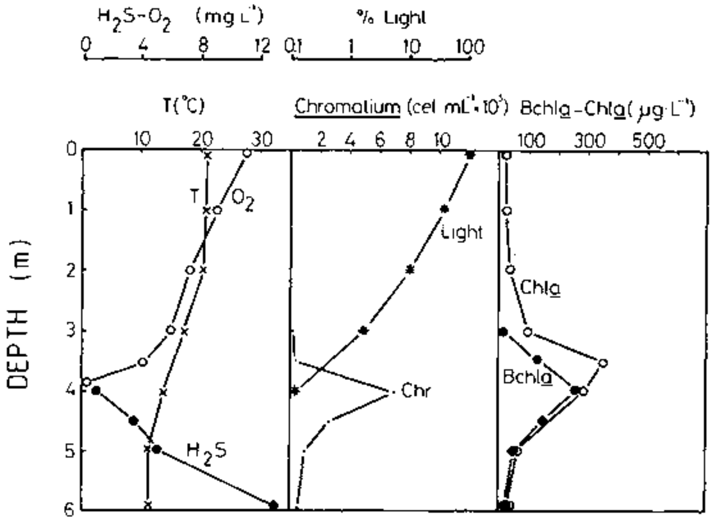


Figure 10. Vertical distribution of main physicochemical parameters, during the stratification period in Nou lagoon, in relation to cell concentration of *Chromatium* and photosynthetic pigments.

to the main physico-chemical parameters. Phototrophic bacteria formed a very dense layer (up to 7 × 10^5 cells.mL^{-1}) at about 4 m depth where oxygen and light were very low and sulfide started to increase toward the bottom part of the lagoon. The profile of chlorophyll *a* indicates that algae were growing or accumulating with maximum amounts a few centimeters up to the maximum of bacteriochlorophyll *a*, but a mixed population of algae and phototrophic bacteria is detected below 3 meters depth.

Biomass and pigment concentration of phototrophic microorganisms during the annual cycle

Once the dominant phototrophic bacterium was identified by pigment and microscopical analysis, as *Chromatium minus*, samples were taken to assess the concentration of cells in water. Results are shown in figure 11. *Chromatium minus* was first noticed at 6-7 m depth at the end of 1978, and during february 1979 it was found at low numbers in the hypolimnion (4-7 m). The highest numbers were recorded near the thermocline at 4 m depth during the rest of the year. The absolute maximum was 7.3 × 10^5 cells. mL^{-1} in may at 4 m depth.

Depth-time distribution of photosynthetic pigments in Nou lagoon (chlorophyll *a* and bacteriochlorophyll *a*) is shown in figure 12. Both pigments reflect roughly the changes in biomass of algae and phototrophic bacteria. The highest concentrations of both sets of pigments were detected during the start of stratification (april-juny) and were slightly separated in

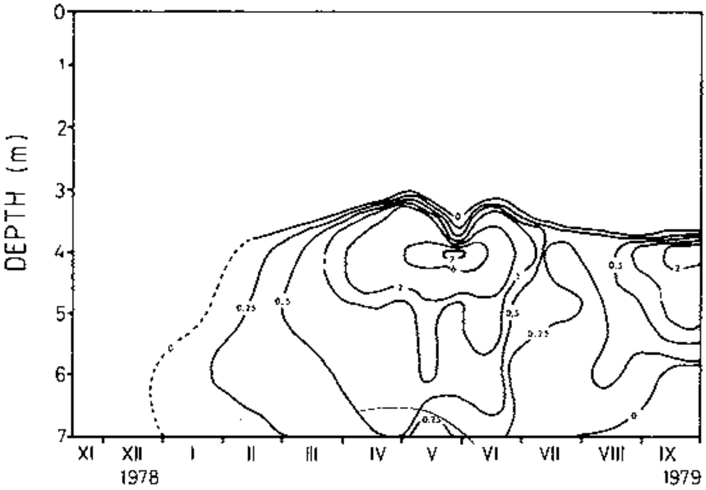


Figure 11. Depth-time distribution of the concentration of *Chromatium* in cells WmL^{-1} × 10^5.

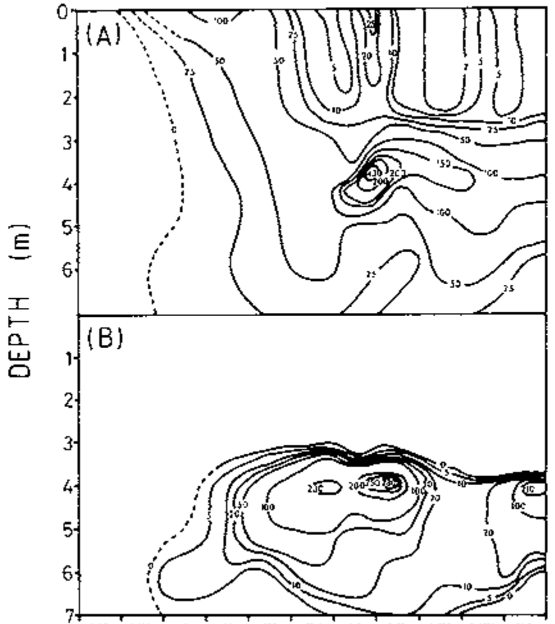


Figure 12. Depth-time distribution of the chlorophyll *a* (A) and bacteriochlorophyll *a* (B) concentrations in µg. L^{-1}.

time and space (half a meter, half a month), indicating that optimal conditions were presented for both populations (algae and phototrophic bacteria) at this time of the year. Phototrophic bacterial pigments started increasing early (december) and reached its maximum values during april-may around 4 m depth. The maximum of algal pigments was detected a few centimeters over the bacterial layer and occupied a narrower space and time (from may to june). Moreover phototrophic bacteria as a result of algal shading reached low numbers in july-august. Later on, after this period and with less algal shading effect due to chlorophyll *a*, bacteria recovered to near the optimum levels accounted during may. The shading effect of algae on phototrophic bacteria (situated below the algal layer) is clearly reflected in an increase in the amount of photosynthetic bacterial pigments per cell, which coincides with the maximum amount of algal chlorophyll detected on late may (see figure 13). During this period, *Chromatium* increased their specific okenone and Bchl *a* content to values up to 3-4 times higher than during the rest of the year. Similar results have been obtained in other lakes of the Banyoles karstic area (Abellà *et al*, 1980, Guerrero *et al*, 1980, Montesinos & Esteve, 1984).

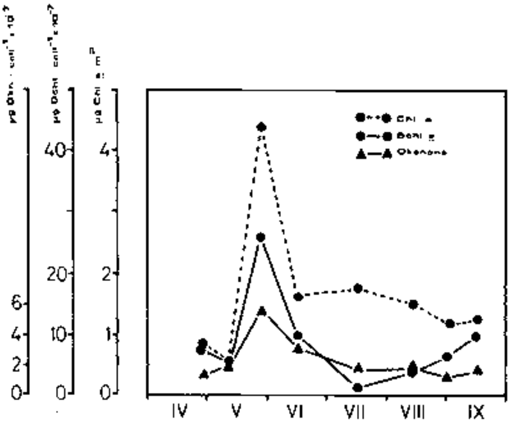


Figure 13. Effect of algal shading on the specific pigment content of *Chromatium* during the stratification period in Nou lagoon.

Production of phototrophic microorganisms

Autotrophic CO_2 fixation was measured *in situ* by means of the light-dark bottle method of Steemann-Nielsen based on the ^{14}C-CO_2 assimilation into cell components. Measurements were performed during the stratification period corresponding to august-september and at the noon time. Results are summarized in table 2. As have been shown above, algae and phototrophic bacteria coexisted in the anaerobic part of the lagoon.

Table 2. Light-dependent CO_2 uptake within the water column of Nou lagoon.

Time	Depth (m)	Production[a] (mg $C.m^{-3}.h^{-1}$)
15.8.79	0	11.2
	4	108.7
	5	53.6
	6	0.0
1.9.79	0	43.3
	4	180.8
	5	128.2
	6	0.0

[a] Light minus dark uptake.

Since 3-(3,4-Dichlorophenyl)-1,1-dimethylurea (DCMU), which inhibits photosystem II in oxygenic photosynthesis, was not used, values of CO_2 fixation were the result of activities of both, algae and *Chromatium*. Maximum light-dependent CO_2 uptake was recorded at 4-5 meters depth (180.8 mg $C.m^{-3}.h^{-1}$) being lower above and below that depths. Total daily production (resulting of integration thorought depth and light period) was 1535 mg $C.m^{-2}.day^{-1}$ (15-8-1979) and 3918 mg $C.m^{-2}.day^{-1}$ (1-9-1979).

On assuming that algae (mostly euglenophyts and diatoms) were photosynthetically inactive at depths where sulfide is high (below 4-5 m), all CO_2 uptake below that depth should be due to phototrophic bacteria. Therefore production by *Chromatium* may account for a 56 to 70 % of the total production in the lagoon.

DISCUSSION

Nou lagoon is a holomictic monomictic waterbody originated near Lake Sisó on november 1978. Thermal stratification occurs from spring to early autumn, dividing the water profile into an aerobic epilimnion (3 to 4 meters depth) and an anaerobic hypolimnion of approximately equal extension. Evolution toward anaerobic conditions, mainly in the hypolimnion, happens very rapidly. After one to two months of its formation, sulfide have been detected into the bottom layers and a stale «sulfuretum» was developped. This was mainly due to the fact that sulfate and bicarbonate are the main anions in the water.

At the start of its evolution, very low oxygen concentrations were detected in the whole water column of the lagoon and water was turbid due to suspended clay and marl particles which considerably attenuates light penetration. This causes phytoplankton to develop only at the very surface level. In the rest of the lagoon, quimioorganotrophic processes, first aerobic respiration, consumed oxygen simultaneously to the degradation and mineralization of organic matter engulfed during its formation. When oxygen was exhausted, mainly in the bottom part and sediments, organic matter was oxidized by anaerobic respiration or fermentation processes. During this time most of organic matter available was alloctonous coming from particulate organic matter (trees, leaves or small plants) which sedimented progressively.

Evidence of the profound effect of this anaerobic mineralization processes is gived by the fact that redox potential was progressively more negative and reduced substances appeared into the bottom layers. In the hypolimnion, nitrate was allmost absent, nitrite accumulates in the thermocline and sulfide and bicarbonate increased toward the bottom part, thus reflecting the impact of the above mentioned microbial activities such as fermentation and anaerobic respiration of nitrates, nitrites or sulfates.

During the stratification period, the stability of layers below the epilimnion permits significant sedimentation of particulate materials and water becames more transparent, thus permitting light to penetrate in deeper layers favouring the development of phototrophic organisms.

The formation of interphases during this time, namely the oxygen-sulfide and the water-sediment interphases, had a pronounced effect on the consolation of very especialized microbial communities: the autotrofs and the sulfate respiring quimioorganotrofs. Among the autotrofs, phytoplankton and purple sulfur bacteria were the most important. Phytoplankton initially developed in the aerobic epilimnion but later soon, they established a few centimeters over the anaerobic sulfide-containing hypolimnion. This fact is apparently difficult to understand since at this depth light limitation for algae was very strong (less than 1 % of incident light in the surface) and microaerophyllic conditions occurred. One possibility to explain this fact is that at the oxygen-sulfide interphase, high concentrations of nutrients are diffusing toward the epilimnion sink hypolimnetic waters were very rich in phosphates, bicarbonate and ammonia. Phototrophic sulfur bacteria, mainly represented by purple sulfur bacteria of the genera *Chromatium*, use sulfide as electron-donor for the photosynthesis, do not produce oxygen, accumulate elemental sulfur inside the cells and gived sulfate as final product of this oxidation. They situate a few centimeters below depths where sulfide start increasing and enough light exist.

Once the above mentioned populations of autotrofs were developped, they accounted for most of the autoctonous organic matter input into the lagoon. Their activity was very high, especially during thermal stratification. Values of 3.9 g $C.m^{-2}.day^{-1}$ were recorded during this time, being the highest observed in the Banyoles karstic area (Turet, 1981). Their biomass at this time of the year was also very high as can be judged by the high total pigment content of the Nou lagoon (up to 1300 $mg.m^{-2}$).

The other community, the sulfate-reducing bacteria, developped mainly in the anaerobic sediments. Their metabolism is based in the utilization of low molecular weight reduced organic substances produced by hidrolysis and fermentation of organic matter entering the sediments (mainly phytoplankton, zooplankton and phtototrophic bacteria). Oxidation of this organic compounds by sulfate-reducing bacteria is coupled to sulfate respiration resulting into production of sulfide and CO_2. Rates of sulfide production of 19 $mmol.m^{-2}.day^{-1}$ have been observed in the anaerobic sediments of Nou lagoon during the stratification period (Ylla, 1981). Sulfide production by simple decomposition of organic matter is very low (macromolecules containing sulfur) in comparison to sulfate respiration, specially if it is taken into account that sulfate is extremely abundant in waters from Nou lagoon (from 3 to 12.7 mM). The magnitud of such processes of sulfate respiration was reflected in the strong decrease in sulfate concentration in the hypolimnion during october-november 1979, after the decline of the bloom of photosynthetic organisms. This sulfate minimum coincided with the sulfide maximum. Therefore one may assume that limitation of sulfide production by organic matter was released after dying cells of phytoplankton and phototrophic bacteria reached the sediments.

Except for the initial steps, Nou lagoon does not received alloctonous organic matter. In spite of this, once autotrophic processes started, autoctonous organic matter was generated and this was enough to permit the development of a stable sulfuretum. This was confirmed by the presence of phototrophic bacteria and anaerobic hypolimnion during the following annual cycles of the lagoon. Fortunatelly anaerobic conditions remained restricted to the bottom layers and an aerobic epilimnion permanently exist during the stratification period. Therefore one should think in the implications of the results presented in this study, because naturally occuring inputs of organic matter are intrinsically enough to develop a stable sulfuretum in karstic lakes. Addition of organic matter estimulates greatly sulfide production because sulfate is very abundant and is allmost continuously supplied by underground water.

Our general conclusion is that the climax of many *estanyols* is the development of a stable sulfuretum of different importance depending on the particular degree of stratification of each waterbody. Physicochemical stratification is mainly governed by factors affecting water mixing such as the presence of vegetation protecting the water surface from wind, the surface to volume ratio, and the activity of microbial processes into the sediments (mainly organic matter degradation and sulfide production). Examples of the above mentioned situations exist among the *estanyols* of the sorroundings of Lake Banyoles.

Finally care should be taken since aquatic ecosystems of karstic origin are extremely sensible to eutrophication, which especially during summer may result in a complete anaerobization of the lake with fatal consequences for the life of animals and plants.

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Bibliography

ABELLÀ, C.A. (1980). *Dinàmica poblacional comparada de bacteris fotosintètics planctònics*. Tesi doctoral. Universitat Autònoma de Barcelona.

ABELLÀ, C.A., MONTESINOS, E. and GUERRERO, R. (1980). Field studies on the competition between purple and green sulfur bacteria for available light (Lake Sisó, Spain). *Developments in Hidrobiology* 3: 173-181.

BAAS-BECKING, L.M. (1925). Studies on the sulphur bacteria. *Am. Bot. Soc. Lond.* 39: 613-650.

GUERRERO, R. & ABELLÀ, C.A. (1978). Dinámica espaciotemporal de las poblaciones bacterianas fotosintéticas en una laguna anaerobia de aguas sulfurosas. *Oecol. Aquat.* 3: 193-205.

GUERRERO, R., MONTESINOS, E., ESTEVE, I. and ABELLA, C.A. (1980). Physiological adaptation and growth of purple and green sulfur bacteria in a meromictic lake (Vilar) as compared to a holomictic lake (Sisó). *Developments in Hidrobiology* 3: 161-171.

HUTCHINSON, G.E. (1957). *A treatise on Limnology, I. Geography, physics and chemistry of lakes*. J. Wiley & Sons, New York.

MONTESINOS, E. (1978). *Biomasa i activitat dels bacteris fototròfics en dos medis aquàtics de diferent nivell tròfic (Banyoles i Sisó)*. Tesina de llicenciatura. Universitat Autònoma de Barcelona.

— (1982). *Ecofisiologia de la fotosíntesi bacteriana*. Tesi doctoral. Universitat Autònoma de Barcelona.

MONTESINOS, E., GUERRERO, R., ABELLÀ, C. and ESTEVE, I. (1983). Ecology and physiology of competition for light between *Chlorobium limicola* and *Chlorobium phaeobacteroides* in natural habitats. *Applied and Environmental Microbiology* 46: 1007-1016.

MONTESINOS, E. and ESTEVE, I. (1984). Effect of algal shading on net growth and production of phototrophic sulfur bacteria in lakes of the Banyoles karstic area. *Verh. Internat. Verein. Limnol.* 22: 1102-1105.

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

SANZ, M. (1981). *El sistema hidrogeológico de Banyoles-La Garrotxa*. Tesis doctoral. Universitat Autònoma de Barcelona.

TRÜPER, H.G. & GENOVESE, S. (1968). Characterization of photosynthetic sulfur bacteria causing red water in Lake Faro (Messina, Sicily). *Limnol. Oceanogr.* 12: 225-232.

TURET, J. (1981). *Colonització i dinàmica poblacional dels bacteris fotosintètics en un estanyol de nova formació a la zona càrstica de Banyoles*. Tesina de llicenciatura. Universitat Autònoma de Barcelona.

YLLA, J. (1981). *Activitat reductora de sulfat en els sediments anaeròbics de la zona càrstica de Banyoles*. Tesina de llicenciatura. Universitat Autònoma de Barcelona.