Ann. Limnol. 38 (3) 2002 : 173-183

Spatial and temporal heterogeneity in succession of cyanobacterial blooms in a Spanish reservoir

D. Sanchis[1]
D. Carrasco[1]
C. Padilla[1]
F. Leganés[1]
E. Fernández-Valiente[1]
F. F. del Campo[1]
A. Quesada[1,2]

Keywords : Cyanobacteria, *Microcystis*, bloom, reservoir, Spain, phytoplankton, ecological succession.

We describe here the limnological characteristics of the Santillana Reservoir (Spain) and study the phytoplankton distribution during a typical growing season (July to November). The reservoir is a eutrophic stratified waterbody in central part of Spain, in which the average phytoplankton biomass in summer is higher than 20 µg chlorophyll a l-1. Maximum phytoplankton biomass in 1999 occurred between the end of summer and the beginning of autumn (September-October). Cyanobacteria, that were generally prevalent in phytoplankton community, clearly dominated during the peak of phytoplankton biomass. *Microcystis wesenbergii* was dominant amongst the cyanobacteria and represented almost 100 % of the biomass at the time of maximum phytoplankton value. The importance of environmental variables triggering cyanobacterial bloom events is discussed. Our results indicate that neither temperature nor N/P ratio are related to the bloom development. However, high nutrient concentration (ammonium in particular) and stability of the watercolumn seems to coincide with the maximum abundance of *Microcystis wesenbergii.*

Hétérogénéité spatiale et temporelle de la succession des blooms de cyanobactéries dans un réservoir espagnol

Mots-clés : Cyanobactéries, *Microcystis*, efflorescences, lac-réservoir, phytoplankton, succession écologique.

La succession du phytoplancton, axée sur les cyanobactéries, a été étudiée sur un réservoir proche de Madrid (Espagne). Un ensemble de variables décrivent les principales caractéristiques physico-chimiques et environnementales du réservoir. Le but principal de ce travail est d'analyser l'hétérogénéité spatiale et temporelle des facteurs environnementaux qui peuvent induire les efflorescences de cyanobactéries dans ce lac méso-eutrophe. Le réservoir peut être décrit comme un réservoir typique du centre de l'Espagne, stratifié avec un niveau trophique élevé, dans lequel la biomasse phytoplanctonique moyenne est supérieure à 20 µg.1-1 de chlorophylle *a*. Le pic de biomasse se produit entre la fin de l'été et le début de l'automne. Ce pic est essentiellement dû aux cyanobactéries; presque 100 % de la biomasse sont constitués par *Microcystis weisenbergii*, qui globalement domine la communauté phytoplanctonique. L'importance des variables environnementales est discutée en tant que facteur déclenchant des blooms de cyanobactéries.

1. Departamento de Biología, Universidad Autónoma de Madrid, 28049 Madrid, Spain.
2. Corresponding author : E-mail : antonio.quesada@uam.es

Article available at http://www.limnology-journal.org or http://dx.doi.org/10.1051/limn/2002015

1. Introduction

The presence of cyanobacterial blooms in waterbodies may produce an important detrimental economical effect, because of the consequent problems with water treatment technologies and degradation of recreational values in certain waterbodies. The potentiality of toxins production by the bloom-forming cyanobacteria (Chorus & Bartram 1999), together with the mentioned negative economical effects has made necessary understanding the dynamics of the cyanobacterial blooms, as well as the causes and consequences of these blooms.

Cyanobacterial blooms from different waterbodies at different latitudes have been described in detail (Oliver & Ganf 2000 and references therein). From those works several hypotheses have been generated to explain the causes and the consequences of cyanobacterial blooms. These hypotheses can be sorted out depending if bottom-up (environmental variables control the bloom occurrence) or top-down (biological-ecological variables control the bloom occurrence) processes are considered. In bottom-up explanations it is considered that cyanobacteria take advantage of the stability of the watercolumn, because of their buoyant capabilities some planktonic cyanobacteria can adjust their position in the watercolumn depending upon their necessities of nutrients or light (Walsby et al. 1997). This fact may be considered of adaptative value, since it would allow cyanobacteria to out-compete other planktonic organisms.

The low values of the N/P ratio are also considered important to explain the dominance of cyanobacteria (Smith 1983). Thus, when N concentration is consistently low, and P is moderately high, cyanobacteria dominance seems to be promoted.

Top-down explanations consider that the main factors responsible for bloom presence are related with predating organisms, and indirect effects derived from them (Elser 1999). However, top-down hypotheses are not explored in this paper.

Many Spanish reservoirs are in elevated trophic level (CEDEX 1995). For example in the Tajo river Basin 40 reservoirs out of 59 were eutrophic in 1995. Under these circumstances the phytoplanktonic communities are expected to be dominated by cyanobacteria, and eventually dense cyanobacterial blooms may be formed (Oliver & Ganf 2000). In fact, the published information regarding Spanish reservoirs shows an important presence of cyanobacteria (e.g. Armengol et al. 1990; Sabater & Nolla 1991).

In this work we investigated the temporal variation of the major limnological characteristics of a Spanish reservoir, that supplies water to the city of Madrid. The main objective was to describe the waterbody, paying special attention to cyanobacterial dominance. We discuss the relationship between the environmental variables considered responsible for triggering bloom episodes and the occurrence of a cyanobacterial bloom, dominated almost exclusively by *Microcystis wesenbergii*.

2. Material and methods

- Study area

The studied waterbody is Santillana Reservoir located at 40° 43' N and 3° 51' W (Fig. 1), used for human activities, mainly as drinking water supply. The reservoir is located at 900 meters above sea level on a granitic basin. As principal hydrographic features, it covers an area of 1052 ha, a maximum volume of 9.1 10^6 m^3 and a maximum depth of 40 m. It remains stratified throughout summertime. Regarding the trophic level, the reservoir has been considered as eutrophic (Avilés & González 1975).

- Sampling design

The reservoir was sampled during a typical blooming season, between late-spring and mid-autumn (from 20th May 1999 until 11th November 1999) at two time and space scales. In this way, the littoral zone of the reservoir was weekly sampled in three sites (S1, S2 and S3), and the pelagic zone was monthly monitored at three sampling stations, corresponding to the shallow basin (SC3), the deepest point (SC1) and the transition site between the former ones (SC2). The data presented in this paper correspond only to the pelagic zone and in particular to site SC1.

- Limnological characteristics

The following chemical and physical variables were determined: temperature (°C); DO (oxygen concentration and % saturation); conductivity (µS cm^{-1}) and pH. Measurements were performed using a YSI 6920 Multiparametric Probe, connected to a laptop computer for communication setting up, data acquisition and calibration, which was performed just before the sampling. High resolution watercolumn profiles of the said variables were carried out, data were collected every 20 cm. Light (PAR) extinction profiles were recorded using a 2π LI-192SA Underwater Quantum Sensor connected to a LI-COR LI-1000 data logger to establish the depth at which the irradiance was 1 % and 0.1 % of the surface irradiance ($Z_{1\,\%}$ and $Z_{0.1\,\%}$ respective-

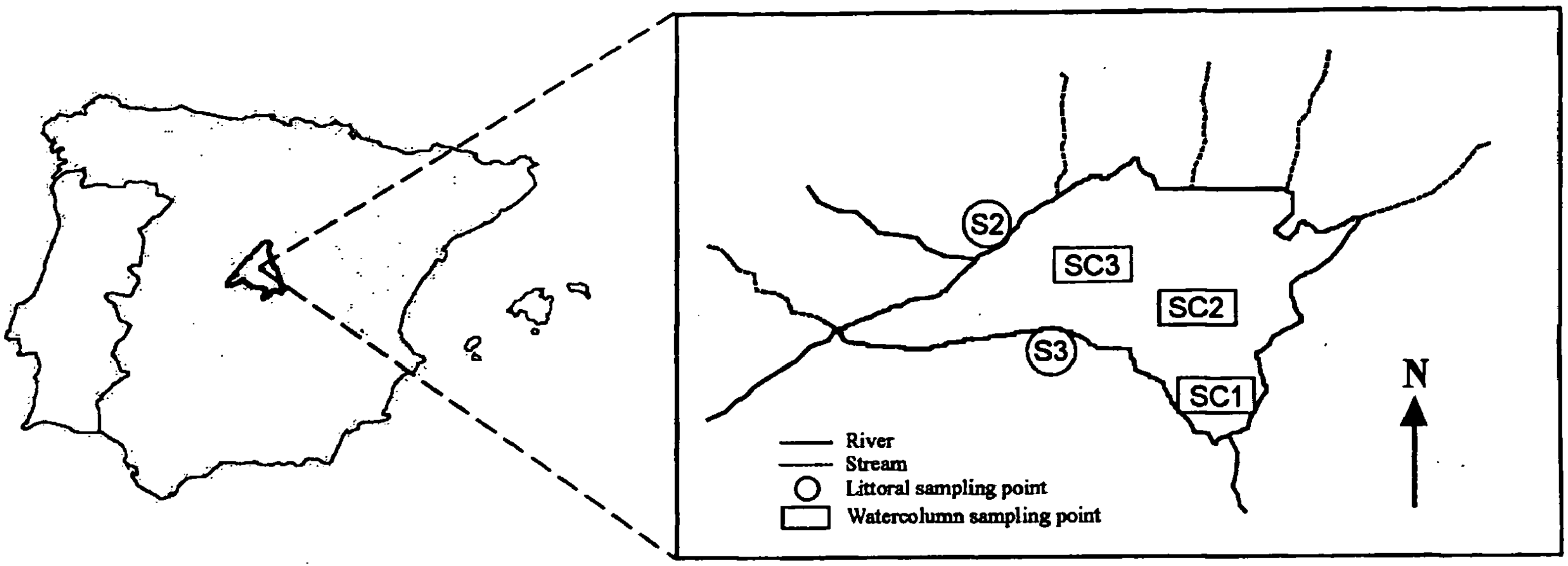

Fig. 1. Location map of the investigated reservoir, with the sampling sites. Maximum length of the reservoir is 7 Km.
Fig. 1. Localisation du réservoir étudié (Espagne), stations de prélèvement.La longueur maximale du réservoir est de 7 Km.

ly). Both light extinction profile and thermal structure of each watercolumn sampling sites were considered for water sample collection (5 different depths). Watercolumn samples were collected using a Watson-Marlow 313D/A peristaltic pump, providing flow rates up to 1100 ml min^{-1} for continuous use with an 8 mm internal diameter Tygon tubing collector attached to a 20 cm diameter stainless-steal ballasted inverted funnel. Water samples were immediately kept in darkness at 4°C until chemical and biological analyses were undertaken. Water samples were analysed in situ for ammonium-nitrogen (NH_4^+N), nitrate-nitrogen (NO_3^-N) and soluble reactive phosphorous ($SRP=PO_4^{3-}P$). Colorimetric methods, adapted from Standard Methods for the Examination of Water and Wastewater (APHA 1980), were applied to samples passed through Whatman GF/F glass microfiber filters. The equipment used was a DREL-2010 Portable Laboratory, Hach Company, USA.

NO_3^-N was measured after a modification of the cadmium reduction protocol, using gentisic acid instead of 1-naphthylamine (estimated detection limit 0.5 mg l^{-1}), and reading absorbance at 500 nm. Samples below that detection limit were measured by a low range method, which is an expanded modification of the former one, using a chromotropic acid indicator (estimated detection limit 0.01 mg l^{-1} and precision ±0.01 mg l^{-1}). NH_4^+N was measured using Nessler method (estimated detection limit 0.05 mg l^{-1} and precision ±0.015 mg l^{-1}), reading absorbance at 425 nm. $PO4^{3-}P$ was estimated with a modification of the molybdenum blue procedure (estimated detection limit 0.01 mg l^{-1} and precision ±0.01 mg l^{-1}), reading absorbance at 890 nm. Every nutrient analysis was performed three times to increase the reliability of the measurement. The standard deviation of the pseudoreplicates remained within the typical precision range of each method.

Biological analyses in water samples included phytoplankton biomass (measured as chlorophyll *a* content: Chl *a*) and algal groups distribution. Chlorophyll *a* analysis was performed spectrophotometrically following the method described by Marker et al. (1980), as well as using in situ fluorometric techniques. Algal groups distribution analyses in littoral zone and watercolumn sites were made in the field by means of fluorometric methods using a portable Fluorometer BBE-Moldaenke Algae Online Analyser, which utilises 5 LEDs for fluorescence excitation. The LEDs excitation wavelengths are 450, 525, 570, 590 and 610 nm, and fluorescence emission is measured at 680 nm. The relative fluorescence emitted upon excitation with light of the said wavelengths along with that fluorescence spectra allows to identify cyanobacteria, green algae, diatoms and cryptophytes as algal groups present in the water sample from its own typical and unique fluorescence emission spectra. Although the absolute value of chlorophyll a concentration from each group can be considered just an estimation (as every fluorometric method), the relative proportion of chlorophyll a contributed by each algal group is quite precise, because it depends basically on the unique pigment characteristics of each algal group. Laboratory calibration with cyanobacterial and green algae cultures demonstrated a high correlation between the experimental mixtures and data given by the instrument.

The identification of the dominant cyanobacterium was made following Komarek & Anagnostidis (1999).

3. Results

3.1. Physical characteristics of the reservoir

- Thermal structure

The measurements undertaken in the watercolumn indicated that the thermocline was already formed at the beginning of July (Fig. 2). Our data from previous years indicate that in this waterbody the thermocline typically forms in June (unpublished results). The depth at which the maximum temperature gradient was found, within the metalimnion, ranged between 6 and 7 meters. At mid September the water at the surface started to cool down, a fact that together with the hypolimnetic water withdrawal, pushed down the thermocline until October, when the stratification was broken and the water mass mixed, leading to a homogeneous watercolumn.

When the waterbody was stratified the hypolimnion remained at about 13°C, while the epilimnion reached 24°C in mid summer.

- Optical features

The light penetration profiles recorded in the water column indicated that until the end of September the $Z_{1\%}$ ranged between 4 and 4.5 m (vertical bars in Fig. 2). However, at the end of September $Z_{1\%}$ did not reach 2 m. This moment coincided with the most intense cyanobacterial bloom recorded during the year (see below). In November, after the mixing of the watercolumn, $Z_{1\%}$ reached 3.5 m. $Z_{0.1\%}$ reached in the two first sampling events depths between 6 and 7 m, although at the end of September was only 3 m.

Physical attributes of the reservoir corresponded to a typically stratified waterbody, with a partially aphotic

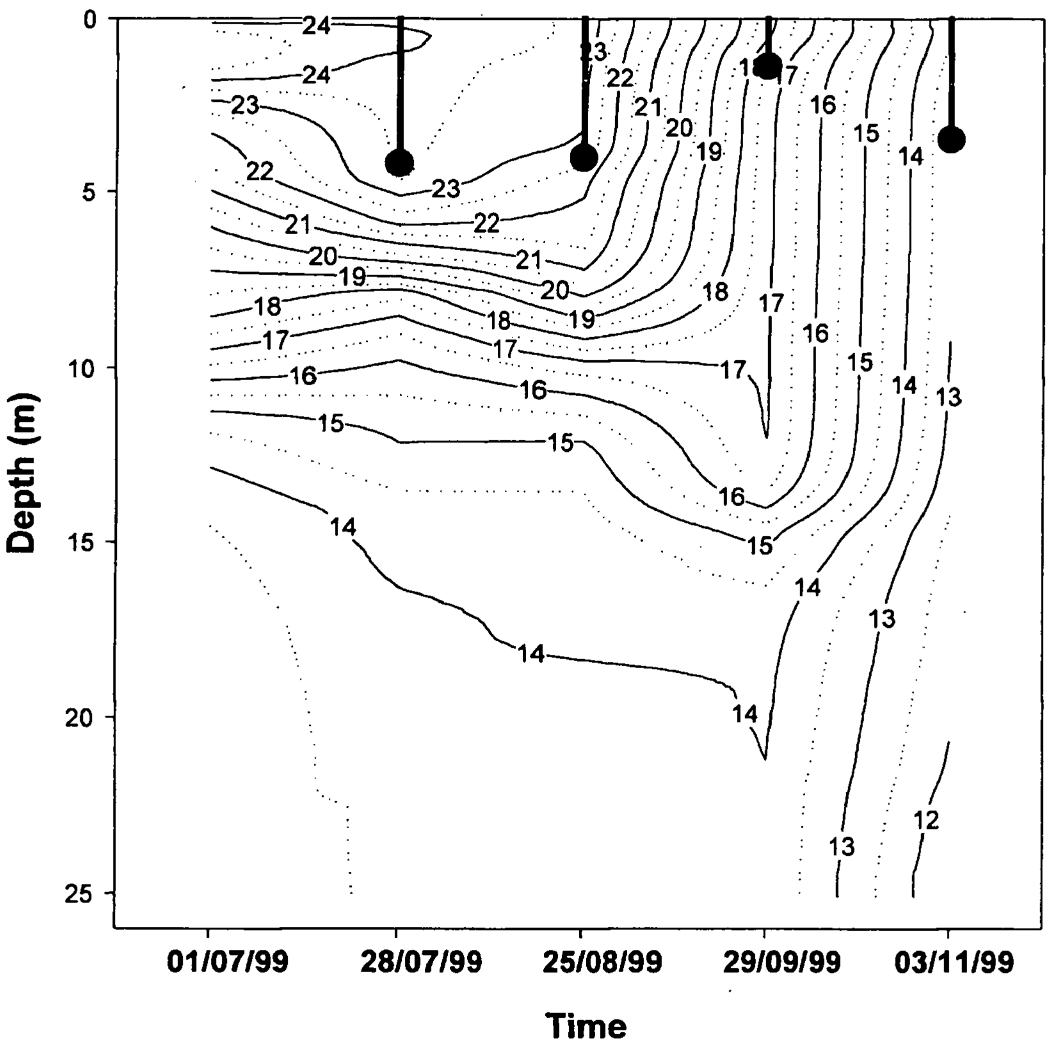

Fig. 2. Variation in temperature and light transmission characteristics in the watercolumn. The vertical straight lines represent the depth at which 1 % of the surface irradiance is reached ($Z_{1\%}$).

Fig. 2 Distribution des températures dans la colonne d'eau. Les valeurs de transmission de la lumière sont aussi représentées : la barre verticale représente la profondeur à laquelle il reste 1 % de l'intensité de surface ($Z_{1\%}$).

epilimnion (Z_{eu}<Z_{mix}), and a completely aphotic hipolimnion due to the light absorption by suspended particles, mainly the phytoplankton.

3.2. Chemical characteristics

The reservoir showed quite low concentration of dissolved salts, as evidenced by the conductivity values, always below 200 µS cm^{-1}. In the water column the values were maximum at the bottom of the hipolimnion where 194 µS cm^{-1} was reached in August. The rest of the watercolumn did not show any clear pattern of variation, and most of the year remained with similar low conductivity values (excluding the highest values; mean = 81.1 µS cm^{-1}, standard deviation = 7).

In general terms the reservoir can be considered slightly alkaline, with pH values typically between 7 and 9 (Fig. 3). The pH profile in the watercolumn, as expected, followed the phytoplankton biomass distribution, since in highly productive waters this variable is a function of the photosynthetic activity. Primary production consumes the CO2 available in the water column, shifting the carbonic-carbonate equilibrium, with the consequent increase of pH. The highest values were recorded at the surface where the photosynthetic activity is maximum, decreasing in parallel with the light extinction profile. Once the watercolumn is mixed, the pH is stable (7-7.3) through the column profile. Curiously the highest pH was not recorded when the maximum bloom development took place.

The hypolimnion was anoxic until the end of September (Fig. 4). As expected the oxycline followed the thermocline. At the end of September the concentration started to increase at the hypolimnion because of the disruption of the thermocline, reaching the water column values close to the saturation concentration in November.

Ammonium was the main source of nitrogen in the waterbody. In fact, nitrate and nitrite were lower than our detection limit (0.01 mg N-NO_3^- l^{-1}) in many occasions. However, ammonium was always well above the detection limit at every occasion (Fig. 5).

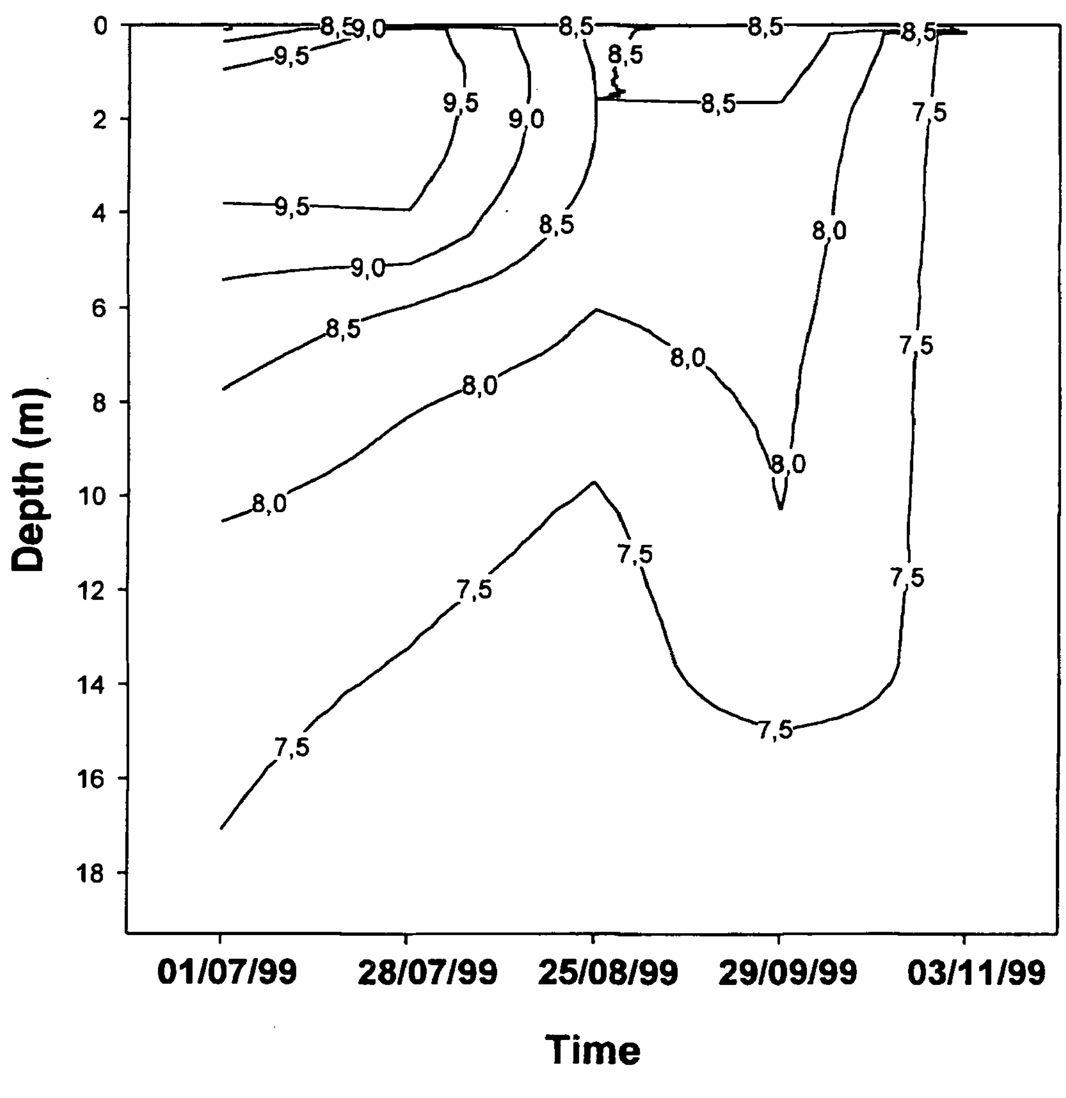

Fig. 3. pH distribution in the watercolumn.

Fig. 3. Distribution du pH dans la colonne d'eau.

Both ammonium and phosphorus concentration in the watercolumn showed a similar typical pattern, with maximum concentrations in the hypolimnion at the end of summer, and minimum concentration at the epilimnion (Figs 5 & 6). When the thermocline was disrupted, the hypolimnetic nutrient concentration decreased because of the dilution process with the poorer epilimnetic water.

The ratio DIN/SRP has been considered as a good estimate of the nutrient status of a water body, and may explain the presence of cyanobacteria versus green algae. Therefore, it is expected that values of DIN/SRP below 7.2 (in mass units) will favour cyanobacteria abundance, and higher values would favour the presence of green algae. DIN/SRP values obtained in Santillana Reservoir were low during the typical cyanobacterial bloom formation period (from July to October) (Table 1). The highest values were obtained at the end of the season after the stratification was disrupted. Thus, from the nutritional point of view we can consi-

Table 1. DIN/SRP ratios. The data represent the average for the epilimnetic and hypolimnetic results. Standard deviation is shown in brackets. Results obtained on 3/11/99 have been calculated considering all the data in the water column, since there was no stratification.

Tableau 1. Rapport DIN/SRP. Ces données représentent les valeurs moyennes dans l'Epilimnion et l'Hypolimnion - entre parenthèses : erreur standard. Les résultats obtenus le 3.11.99 ont été calculés en prenant toutes les valeurs de la colonne d'eau, non stratifiée à cette date.

Sampling period	Epilimnion	Hypolimniom
1/7/99	8.9 (1.4)	5.5 (1.1)
28/7/99	7.2 (3.9)	4.6 (0.0)
25/8/99	5.7 (0.6)	4.0 (0.7)
29/9/99	5.3 (0.5)	4.0 (0.0)
3/11/99	12.1 (1.3)	12.1 (1.3)

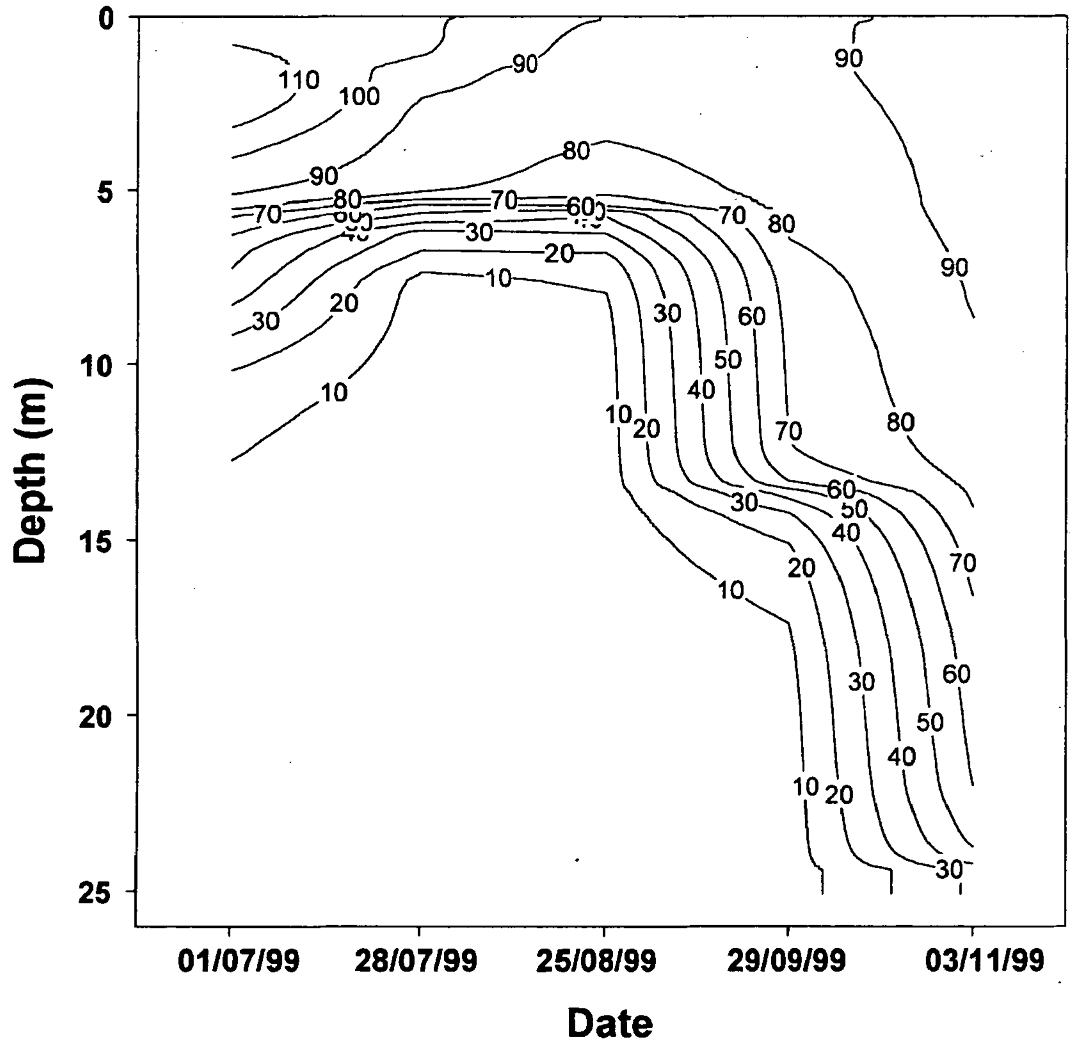

Fig. 4. Oxygen concentrations, expressed as % of saturation at the water temperature in the watercolumn.

Fig. 4. Concentrations d'oxygène (pourcentage de saturation).

der this waterbody as favourable for cyanobacterial bloom development.

3.3. Phytoplankton biomass

Regarding the phytoplankton biomass in the watercolumn we observed that the higher biomass concentration, estimated as chlorophyll a, was found in two occasions along the year, one at the end of July, with moderate values, (26.4 µg Chl *a* l^{-1}), and the other at the end of summer, in September-October, with much higher biomass (up to 90.3 µg Chl *a* l^{-1}). (Fig. 7). Most of the Chl *a* appeared, as expected, at the epilimnion. After the disruption of the thermocline the Chl *a* concentration was homogeneously low (lower than 10 µg l^{-1}) in all the water sites.

3.4. Algal groups distribution

The algal groups distribution in the watercolumn indicated that the dominant group, along the sampling period as well as along the column profile, was cyanobacteria (Fig. 8). The ecological succession of the algal groups showed a trend towards the dominance of cyanobacteria, which was maximum in October. The cyanobacterium present during the most conspicuous bloom event, was identified as *Microcystis wesenbergii*. Green algae were quite abundant in the wholewatercolumn, although usually the proportion was higher in deeper layers. Diatoms were present in several occasions, being important at the end of the sampling period, in November, after the thermocline was disrupted. It is also noticeable that when the cyanobacterial bloom took place, the epilimnetic water mass was completely dominated by cyanobacteria and not only the surface. Thus, in this case we are not finding a discrete cyanobacteria population that migrates up and down within the watercolumn, but an epilimnetic homogeneously distributed cyanobacterial population.

4. Discussion

In this paper we report the blooming process of *Microcystis wesenbergii* in a Spanish reservoir. The environmental characteristics during the typical blooming season that may be related with the bloom development are also documented.

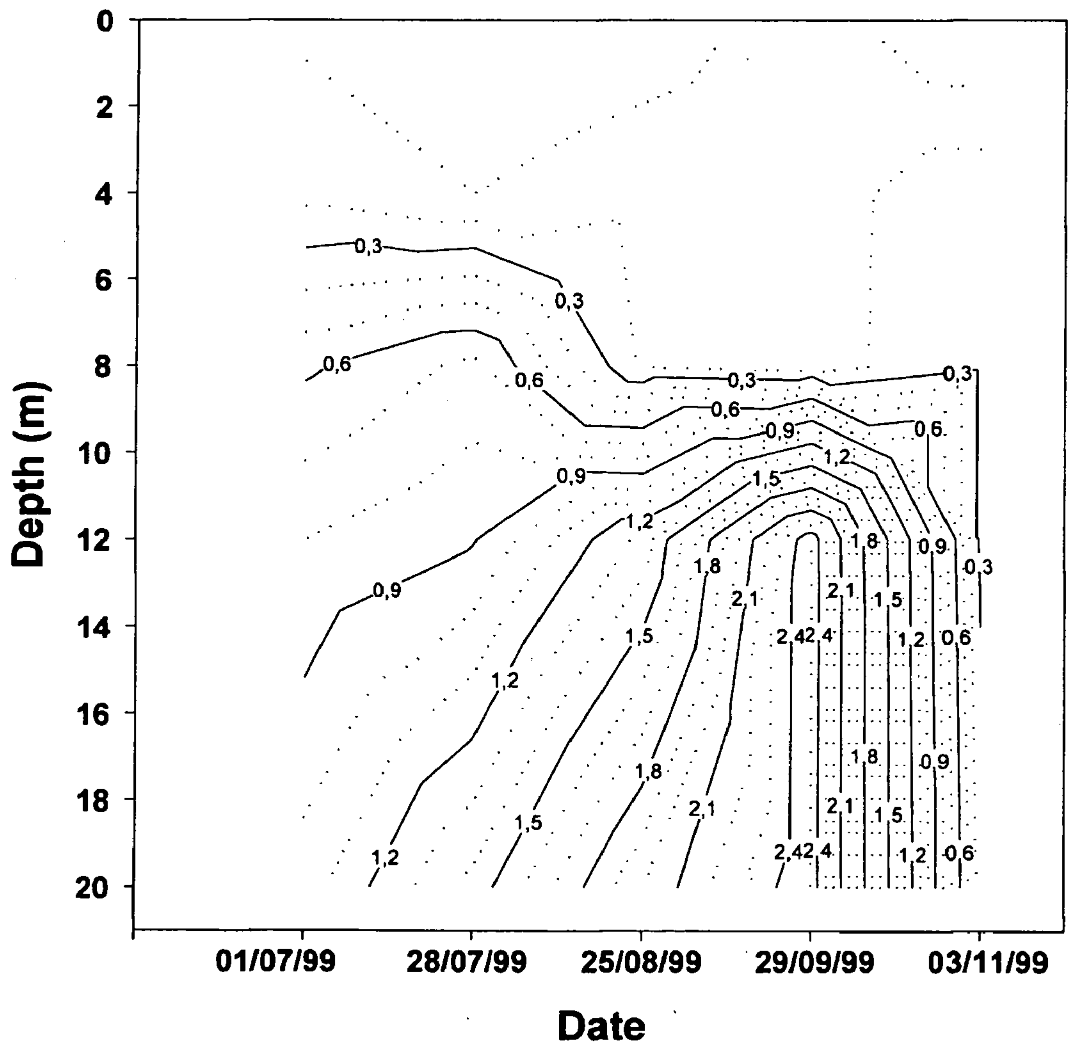

Fig. 5. Ammonium-N concentration in watercolumn. Data are expressed as mg N-NH_4^+ l^{-1}.
Fig. 5. Concentrations de N-NH_4^+ dans la colonne d'eau (mg l^{-1}).

Microcystis wesenbergii is a well known cyanobacterium that has been described worldwide. In Europe it has been found to be a bloom-forming species in all climatic conditions, from Scandinavia (Cronberg et al. 1999) to the Mediterranean Region (Tryfon & Moustaka-Gouni 1997). Nevertheless, its morphological taxonomy is not very clear, and some authors suggested a revision of its affiliation (Otsuka et al. 2000). In any case, the 'morphospecies' found in Santillana Reservoir falls precisely in the description of this species, being morphologically distinctive from other *Microcystis* species.

What environmental factors are triggering this cyanobacterium blooming?. Several authors have suggested that high temperature could be one of the reasons of cyanobacterial blooms (McQueen & Lean 1987). This idea has been discussed by Oliver & Ganf (2000) who cast doubts about this factor, as a general triggering variable, considering the data published by Robarts & Zohary (1987). Our results confirm these doubts since *Microcystis wesenbergii* bloomed in Santillana Reservoir when water temperature was 17-18°C versus the maximum temperature of over 24°C. Oliver & Ganf (2000) suggested that other variables typically associated to high temperature would be more likely related to bloom formation, since autoecological data of cyanobacteria did not show specially high temperature optimum for growth. High nutrient concentration has been considered as another triggering factor (Paerl 1988, Elser 1999). Again, no generalization can be made, because autoecological data demonstrate that cyanobacteria, as a group, are not essentially different to other algal groups regarding nutrient uptake rates or accumulation (Oliver & Ganf 2000, and references therein). However, nitrate uptake rates seem to be lower in cyanobacteria than in other algal groups when light is limiting (García-González et al. 1992). Blomqvist et al. (1994) suggested that non-nitrogen fixing cyanobacteria are favoured by high ammonium concentration while green algae are favoured by nitrate. The inorganic nitrogen, dominated by ammonium, and phosphorus concentrations found in Santillana Reservoir are quite high along the year, although in the

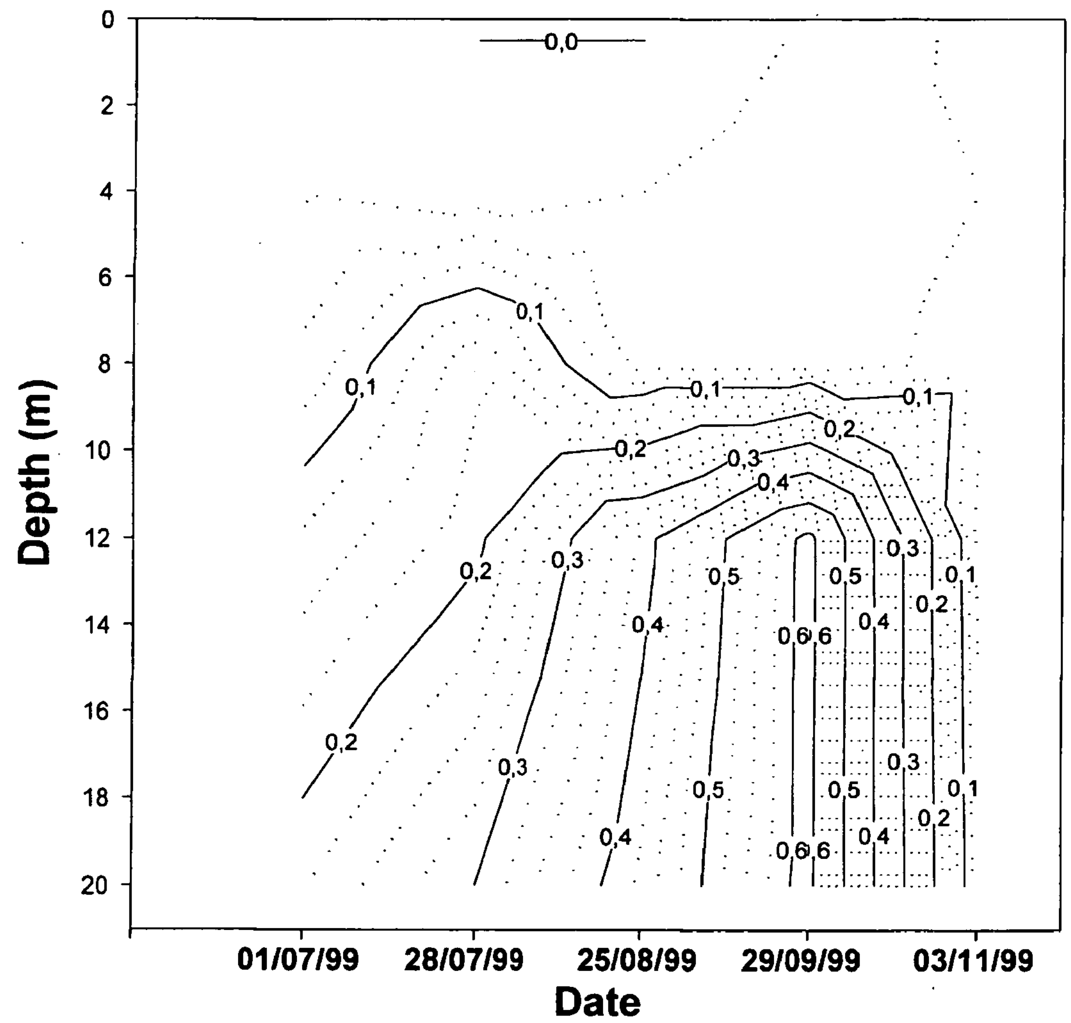

Fig. 6. $P\text{-}PO_4^{3-}$ concentrations in the watercolumn . Data are expressed as mg $P\text{-}PO_4^{3-}$ l^{-1}.
Fig. 6. Concentrations en $P\text{-}PO_4^{3-}$ dans la colonne d'eau (mg l^{-1}).

epilimnion the concentrations are low, probably due to the uptake by phytoplankton. In fact, *Microcystis* bloom coincided with an increase in the epilimnetic concentrations of ammonium and phosphorus, likely of allocthonous origin. The hypolimnetic nutrient concentration also increased notably, although it is not possible to differentiate whether this is a cause or a consequence of the bloom, because of the decaying material. Rather than nutrients, the low N/P ratio has been identified as a probable cause of cyanobacterial bloom formation (Smith 1983). Our data indicate that during the typical bloom formation period DIN/SRP ratio was below the Redfield value of 7.2 (in mass units) (Redfield 1958), indicating that this ecosystem is prone to the episodes of cyanobacterial blooms. However, many authors claim that this ratio is only adequate when the absolute concentrations of both nutrients are limiting (e.g. Reynolds 1992), which likely is not the case in Santillana Reservoir. Besides, it has been shown recently that high values of total N or total P have a bigger effect on cyanobacterial-bloom risk than total N/total P ratio (Downing et al. 2001).

In the stratification period, the watercolumn stability, together with the buoyancy regulation capabilities of cyanobacteria are considered as the most important factors explaining the cyanobacterial dominance (Oliver & Ganf 2000). As cyanobacteria can regulate their buoyancy characteristics, they can adjust their position following their nutritional/energetic requirements: they sink down when they need higher nutrient concentrations found in deeper layers, and float when they need to obtain energy through photosynthesis. In Santillana reservoir it looks like Microcystis wesenbergii takes advantage of this capability as evidenced from the maximum biomass accumulation in the surface. The optical characteristics of the studied reservoir indicate that a considerable section of the epilimnion is aphotic ($Z_{eu}<Z_{mix}$). This makes this habitat light-limited and, thus, low-light phytoplankters, might take benefit outcompeting other algal groups. Cyanobacteria are considered low light organisms, although this might not be always the case (Oliver & Ganf 2000).

Recently, several authors (e.g. Elser 1999, Oliver & Ganf 2000) have postulated that a mixture of variables

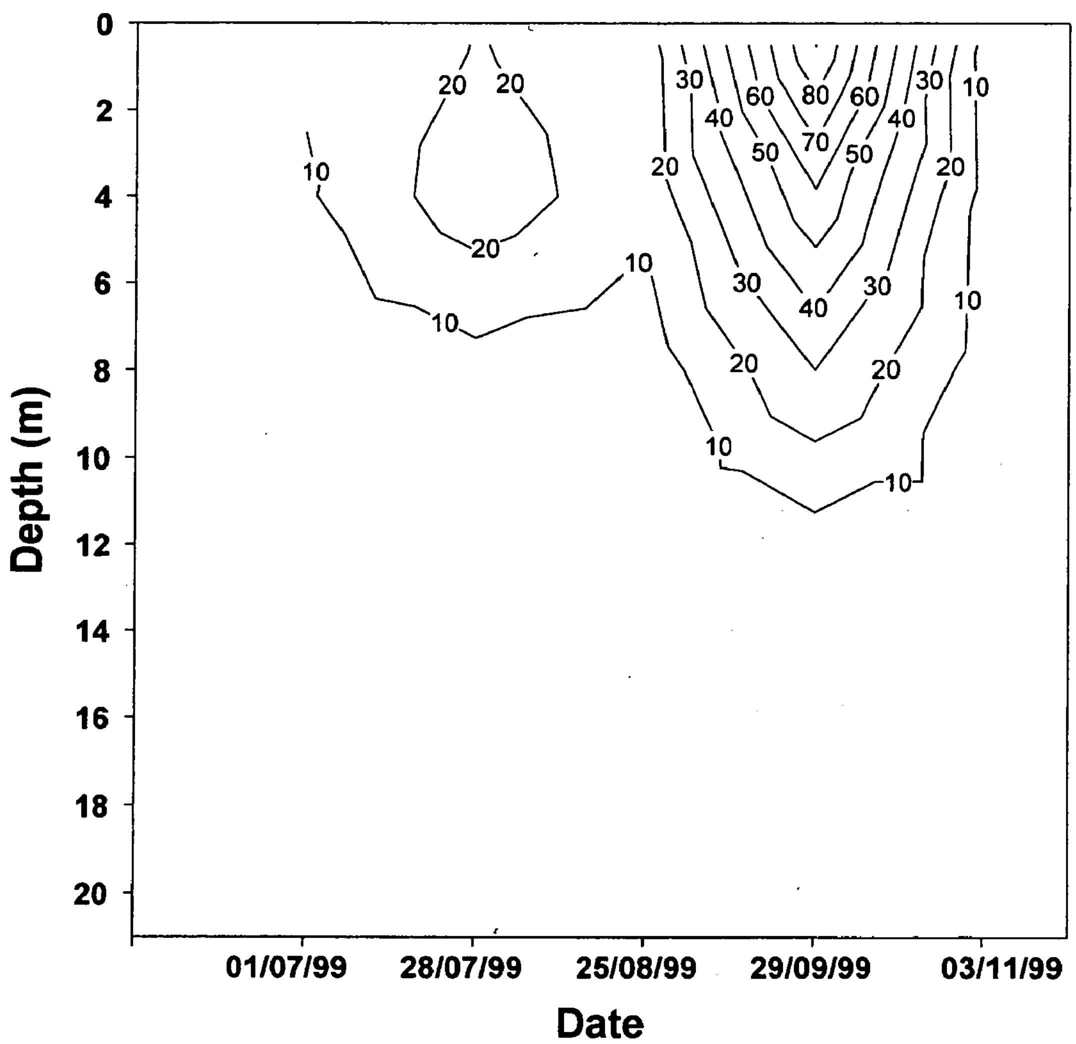

Fig. 7. Chlorophyll *a* concentrations in the watercolumn. Data are expressed as µg Chl *a* l^{-1}.
Fig. 7 Concentrations en chlorophylle *a*. (µg Chl *a*.l^{-1}).

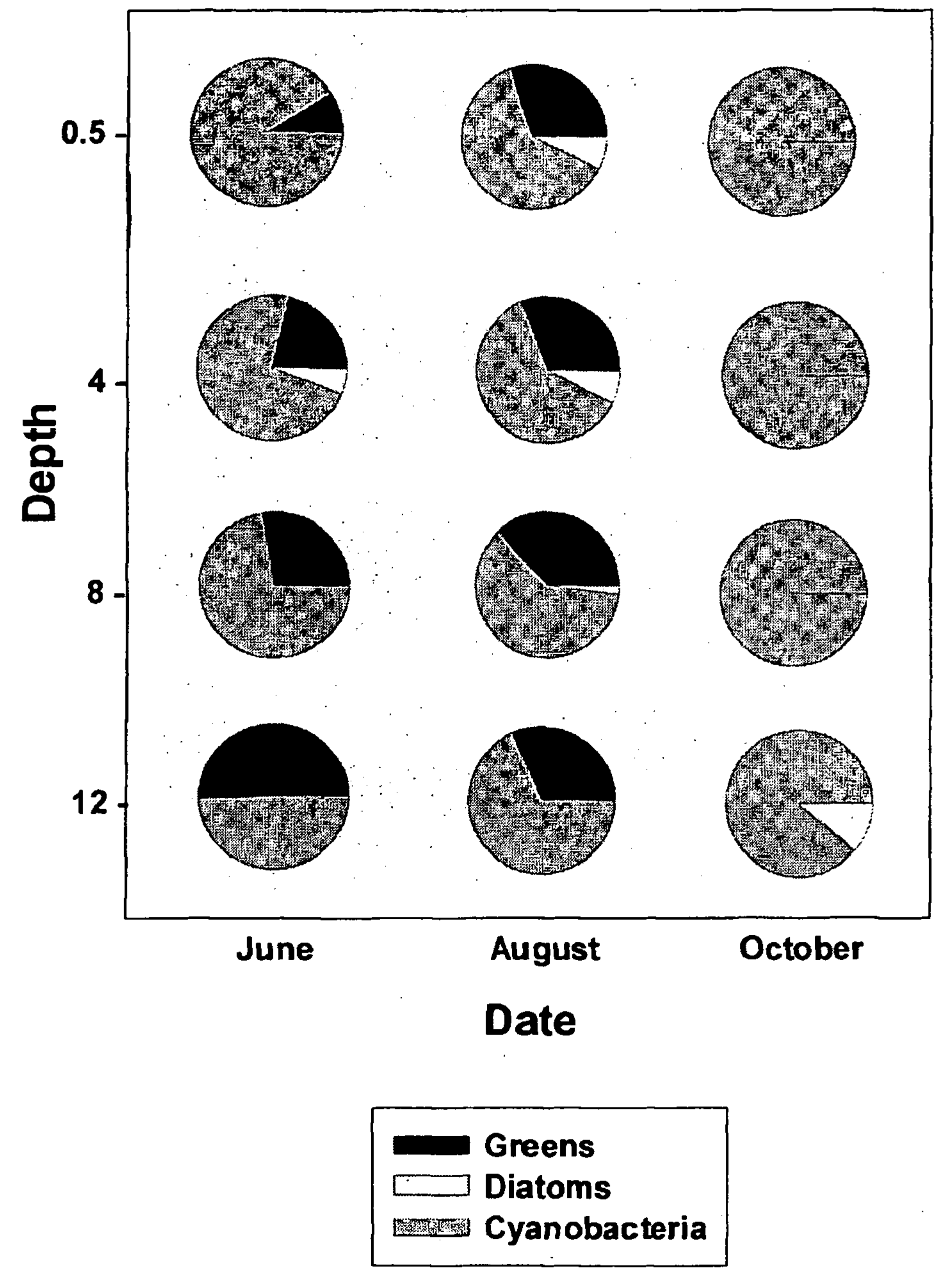

Fig. 8. Contribution of the different algal groups to the total Chlorophyll *a* concentration, determined by fluorometric methodology in the watercolumn.
Fig. 8. Contribution des différents groupes d'algues à la concentration totale en chlorophylle mesurée par méthode fluorométrique dans la colonne d'eau.

likely configure bottom-up processes responsible for the initial growth of cyanobacterial biomass, but the formation and the maintaining of the bloom may respond to a still more complex scenario in which bottom-up as well as top-down processes interact.

The main bottom-up variables that may interact in the initial growth of *Microcystis wesenbergii* in Santillana Reservoir are high nutrient concentration, in particular high ammonium concentration, and the buoyancy regulation capability of the species in this stable watercolumn. However, the top-down variables (namely grazing pressure) have not been explored in this work and might also contribute to explain the high dominance of cyanobacteria in this waterbody.

5. Conclusions

The main goal of this work was to analyse the relationships between cyanobacterial blooms and limnological parameters in a typical waterbody of central Spain. Our results show that the reservoir studied can be considered as a monomictic waterbody with anoxic hypolimnion since the formation of the thermocline. It can be considered eutrophic with high nutrient concentrations (N and P) as well as high phytoplankton biomass (estimated as Chl *a*). Cyanobacteria dominated the phytoplanktonic community during most of the sampling period, and between September and October led to a massive growth of *Microcystis wesenbergii*, which constituted more than 99 % of the phytoplanktonic organisms.

It was not possible to identify a simple variable responsible for the cyanobacterial dominance, although high nutrient concentration and stability of the water-column might be considered as variables related with the blooming process.

Acknowledgments

We thank to the Canal de Isabel II (Madrid) for allowing us to enter in the reservoir and thus, carry out this work. This work has been funded by the European Union's project CYANOTOX (IC18-CT98-0293) and the CICYT (Ministerio de EducaciÛn y Cultura, Spain; project AMB98-1787-CE. We also thank Dr. Alain Dauta for his French translation and useful comments.

References

APHA 1980. — Standard methods for the examination of water and wastewaters. 15th Ed. APHA. Washington

Armengol J., Catalán J., Gabellone N., Jaume D., de Manuel J., Martí E., Morguí J.A., Nolla J., Peñelas J., Real M., Riera J.L., Sabater S., Sabater F. & Toja J. 1990. — A comparative limnological study of the Gualdalhorce reservoirs system (Málaga, S.E. Spain). *Scientia Gerundensis,* 16 : 27-42

Avilés J. & González M.E. 1975. — Reconocimiento Limnológico de la Cuenca del Tajo. Dirección General de Obras Hidráulicas y Centro de Estudios y Experimentación de Obras Públicas. Ministerio de Obras Públicas. Madrid

Blomqvist P., Petterson A. & Hyendstrand P. 1994. — Ammonium-nitrogen : A key regulatory factor causing dominance of non-nitrogen-fixing cyanobacteria in aquatic ecosystems. *Arch. Hydrobiol.,* 132(2) : 141-164.

CEDEX 1995. — Catálogo Limnológico de embalses. Eutrofización de embalses de la cuenca del Tajo. 1974-1995. Dirección General de Obras Hidráulicas y Centro de Estudios y Experimentación de Obras Públicas. Ministerio de Obras Públicas. Madrid

Chorus I. & Bartram J. 1999. — *Toxic cyanobacteria in water.* E & F.N. Spon, London (WHO)

Cronberg G., Annadoter H. & Lawton L.A. 1999. — The occurrence of toxic blue-green algae in Lake Ringsjoen, southern Sweden, despite nutrient reduction and fish biomanipulation. *Hydrobiologia,* 404 : 123-129.

Downing J.A., Watson, S.B. & McCauley E. 2001. — Predicting cyanobacteria dominance in lakes. *Can. J. Fish. Aquat. Sci.,* 58 : 1905-1908.

Elser J. 1999. — The pathway to noxious cyanobacteria blooms in lakes: the food web as the final turn. *Freshwater Biol.,* 42 : 537-543.

García-González M., Sivak M.N., Guerrero M.G., Preiss J. & Lara C. 1992. — Depression of carbon flow to the glycogen pool induced by nitrogen assimilation in intact cells of *Anacystis nidulans. Physiol. Plant.,* 86 : 360-364

Komarek J. & Anagnostidis K. 1999. — Cyanoprokaryota 1. Teil: Chroococcales. Gustav Fisher Verlag Jena. Stuttgart,

Marker A.F., Nusch E.A., Rai, H. Riemann B. 1980. — The measurement of photosynthetic pigments in freshwaters and standardisation of methods: conclusions and recommendations. *Arch. Hydrobiol. Ergebn. Limnol.,* 14 : 91-106

McQueen D.J. & Lean D.R.S. 1987. — Influence of water temperature and nitrogen to phosphorus ratios on the dominance of blue-green algae in Lake St. George, Ontario. *Can. J. Fish. Aquat. Sci.,* 44 : 598-604

Oliver R.L. & Ganf G.G. 2000. — Freshwater blooms. In: The ecology of cyanobacteria Whitton B.A. & Potts M. (Eds.). Kluwer Academic Publishers, Dordrecht,

Otsuka S., Suda S., Li R., Matsumoto S. & Watanabe M.M. 2000. — Morphological variability of colonies of *Microcystis morphoespecies* in culture. *J. Gen. Appl. Microbiol.,* 45 : 39- 45

Paerl H.W. 1988. — Nuisance phytoplankton blooms in coastal, estuarine and inland waters. *Limnol. Oceanogr.,* 33 : 823-847

Redfield A.C. 1958. — The biological control of chemical factors in the environment. *Am. Sc.,* 46 : 205-222

Reynolds C.S. 1992.- Eutrophication and the management of planktonic algae: what Vollenweider couldn't tell us. In: *Eutrophication: Research and application to water supply Sutcliffe* D.W. & Jones J.G. (Eds.). Freshwater Biological Association, Ambleside

Robarts R.D. & Zohary T. 1987. — Temperature effects on photosynthetic capacity, respiration and growth rates of bloom-forming cyanobacteria. N.Z. J. Mar. Freshwater Res. 21: 391-399.

Sabater S. & Nolla J. 1991. — Distributional patterns of phytoplankton in Spanish reservoirs : First results and comparison after fifteen years. *Verh. Internat. Verein. Limnol.,* 24 : 1371-1375.

Smith V.H. 1983. — Low nitrogen to phosphorus ratios favour dominance by blue-green algae in lake phytoplankton. *Science,* 221 : 669-671.

Tryfon E. & Moustaka-Gouni M. 1997. — Species composition and seasonal cycles of phytoplankton with special reference to the nanoplankton of Laake Mikri Prespa. *Hydrobiologia,* 351 : 61-67.

Walsby A.E., Hayes P.K., Boje R. & Stal L.J. 1997. — The selective advantage of buoyancy provided by gas vesicles for planktonic cyanobacteria in the Baltic Sea. *New Phytol.,* 136 : 407-417.