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Temporal changes of cyanobacteria in the largest coastal Spanish Lake

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With 5 figures and 1 table in the text

Abstract: In this work, we will present long-term changes of cyanobacteria in the largest coastal, shallow, Spanish freshwater lake (the Albufera of Valencia). The lake is used as a reservoir for rice cultivation in the sorrounded lake area. The Albufera lake was in a mesotrophic state during the first half of the 20th century and at the end of 1960s, due to eutrophication, it rapidly turned into an eutrophic state with loss of submerged macrophytes and general biodiversity in the plankton, benthos and fish populations, that remains until now. Since the beginning of the century, cyanobacteria were represented in the phytoplankton of the lake, but from 1970s to 2000 became the dominant group. A total of 26 cyanobacteria species have been described between 1942 and 2000. Morphological and phenological features of the species are shortly reported in this study. Since 1991, a restoration plan of the lake started by sewage water diversion, that has reduced to half planktic chlorophyll *a* concentrations, although hypertrophic levels persist. Some alternative clear water phases appeared in which cyanobacteria contribution was reduced from 50–90% to less 5%. After nutrient diversion also a shift in cyanobacteria composition was observed. Large oligophotic filamentous species (mainly *Planktothrix agardhii*) were replaced by slender filamentous species (mainly *Pseudanabaena galeata, Planktolyngbya contorta, Pl. limnetica* and *Jaaginema* cf *metaphyticum*) and chroococcals (*Chroococcus dispersus, Ch. minutus* and *Aphanocapsa incerta*). Water stability, filament resuspension from the sediment, turbidity and benthic-planktivorous fish, were mechanisms stabilizing cyanobacteria dominance in the lake, while high flushing, nutrient depletion and increase of underwater light destabilized or prompted changes in the cyanobacteria community.

Key words: cyanobacteria, shallow lake, long-term study, Mediterranean, ricefields area, eutrophication, restoration, nutrient diversion.

Introduction

Cyanobacteria is an extensively studied group due to their success and ubiquity in aquatic systems. It has often pointed out that higher temperature is a selective factor favouring this algal group in lakes (Reynolds 1984), and there is some evidence related to their dominance in warmer lakes (Komárek 1985, Pollingher

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& BERMAN 1991), and in food webs of shallow warmer lakes (ROMO et al. 2004). In this way, studies on the ecology of cyanobacteria from shallow lakes located in warmer areas are scarce (for review see e.g. SCHEFFER 1998) and rare from the Mediterranean zone. Spain is characterized to have mainly wetlands and shallow lakes, some situated in the Mediterranean coast (CASADO & MONTES 1995). In this work, we will present long-term changes of cyanobacteria in the largest coastal, shallow, Spanish freshwater lake, the Albufera of Valencia. The Albufera has one of the longest data base on plankton from the Mediterranean countries. First records from the plankton of the lake were published at the beginning of the century (ARÉVALO 1918), which was a pioneer study on shallow lakes in Europe, since the incipient science of limnology was focussed on deep lakes. During 1960s and 1970s, eutrophication severely affected the lake, when population, industry and agriculture rapidly increased in its catchment area. The lake received huge amounts of sewage waters than turned it from a mesotrophic into a hypertrophic state that remains until nowadays (DAFAUCE 1975, ROMO & MIRACLE 1993). In 1991, a restoration plan by means of sewage water diversion started in order to desviate pollutants and nutrients from the lake. This plan has not been finishing yet, but we will report some changes accounted in the dominant cyanobacteria community. In this way, only few comprehensive investigations on phytoplankton of shallow lakes undergoing changes in nutrient load have been published and all of them located in northern temperate areas (JEPPESEN et al. 1991, DOKULIL & PADISAK 1994, MOSS et al. 1996a, PADISAK & REYNOLDS 1998, KÖHLER et al. 2000). In this work, we will analyse the main cyanobacteria species and their changes from 1942 to 2000 in the Albufera of Valencia, with special focus in the last two decades, before and after nutrient diversion, aiming to ascertain their ecology in the lake.

Site and methods

The Albufera of Valencia is a shallow, freshwater, polimictic lake located in the Natural Park of the Albufera (210 km^2) in the Mediterranean Spanish coast (39° 20' N, 0° 20' W) (Fig. 1). It is the largest Spanish lake with a surface of 23.2 km^2, a mean depth of 1 m and a high water renewal time of about 10 times per year. The lake has a belt of emergent vegetation and several small islands with reed. Since the 18^{th} century rice have been cultivated in the surrounding areas of the lake and its surface has been reduced mostly by silting in about 70 %. Originally the lake was an extensive gulf which later became separated from the Mediterranean Sea by a sand bar. Nowadays, this bar is crossed by three channels that keep the lake connected with the sea and regulates lake water level by means of sluices gates located in the outlet channels (Fig. 1). The lake is used as a reservoir for agricultural irrigation. Therefore, the Albufera has a particular hydrological cycle related to rice cultivation that markedly influences plankton dynamics (ROMO & MIRACLE 1993). The hydrological cycle of the lake is shown in Fig. 2.

Phytoplankton data were collected along eleven years during the last two decades, from 1980 to 1988 (except in 1984) and from the end of 1997 to 2000. Phytoplankton samples were taken monthly or bimonthly, except for 1980–83 that were taken seasonally.

Simultaneously, physico-chemical variables and zooplankton were recorded according to standard methods (for details see ROMO & MIRACLE 1993, OLTRA et al. 2001). In

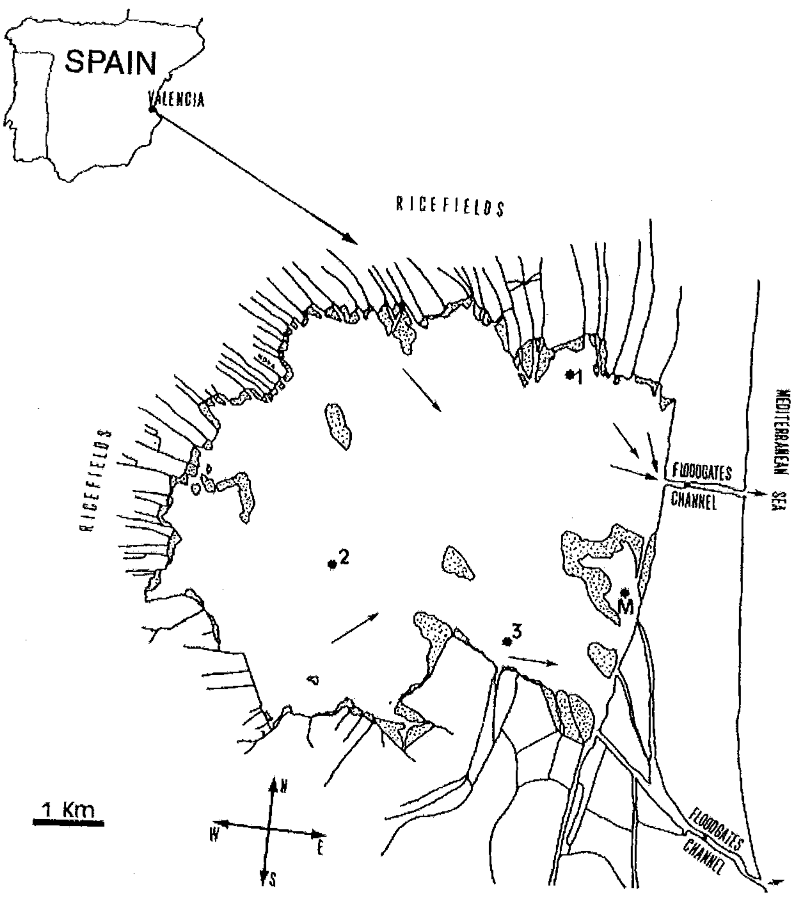

Fig. 1. Map of the lake of the Albufera of Valencia (Spain) showing location, outlet channels and sampling sites. Sampling sites nomenclature: **M** corresponds to the sampling point of 1980–81. Numbers **1, 2,** and **3** correspond to sampling sites for the remaining study periods.

the 1990s, nutrient concentrations in the lake were measured since 1994 onwards, while chlorophyll *a* was analyzed from 1995 onwards by the local Environmental Agency. Three sampling sites were selected because they represented the spatial physico and chemical zones of the lake according nutrient loading (Soria et al. 1987). Since phytoplankton temporal variations were more relevant than spatial changes between sampling points (Romo & Miracle 1993), the average of algal biomass and abundance between sampling locations will be represented. Algae were counted with an estimated error of less than 6% (Lund et al. 1958). The biovolume of phytoplankton was calculated by direct measuring and later geometrical estimation according to Rott (1981). As aforementioned, in 1991 a restoration plan started for sewage water diversion in the catchment area. Nowadays, the project is still unfinished and sewage water removal is estimated in approximately 30%.

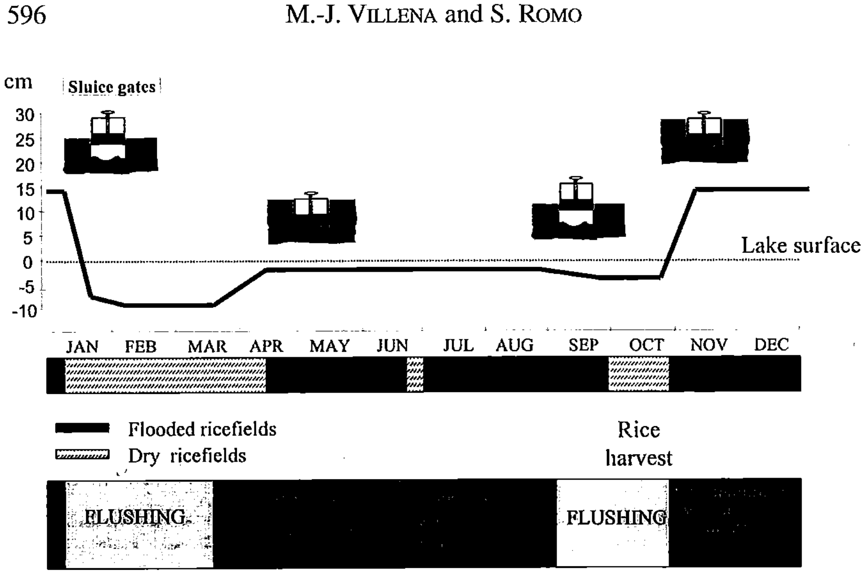

Fig. 2. General annual pattern of water-level fluctuations in the lake of the Albufera of Valencia, mainly influenced by rice cultivation in the surrounding lake area. Vertical axis values refer to water-level differences respect the lake mean depth. The lake has two annual periods of water renewal, during empting of ricefields from January–March and during rice harvest in September–October, and periods of long or intermediate water stability during the remaining months. From January to March, the sluice gates are opened and the fields are drained for tilling and sowing. This latter is completed by the end of April or early May, being preceeded by land fertilization. During summer sluices are almost closed for rice growth. From September to October, floodgates are opened to empty the fields for rice ripening and harvest. By November–December, sluices are closed again and the level of the lake is raised to flood the paddy fields for winter protection and organic matter degradation.

Results

Since the first records in 1942 until 2000, a total of 26 cyanobacteria species have been described for the lake of the Albufera of Valencia. They can be subdivided in three categories: dominant, subdominant and infrequent cyanobacteria. Some of the morphological and phenological features of the species are described (Fig 3).

Dominant cyanobacteria

The species presented in this section were dominant (more than 50% of relative abundance or biovolume) in the phytoplankton of the lake in some seasonal periods during 1942 and 2000.

• *Planktothrix agardhii* (GOM.) ANAGNOSTIDIS et KOMÁREK. It was a dominant species from January to May for 1980–88, but for 1997–2000 represent less than 1% of relative biovolume and had only small punctual increases (June 1998, 6% contribution to total phytoplankton biovolume). Mean trichome length during the study was of 180 μm with cells of 3.4 x 3.2 μm.

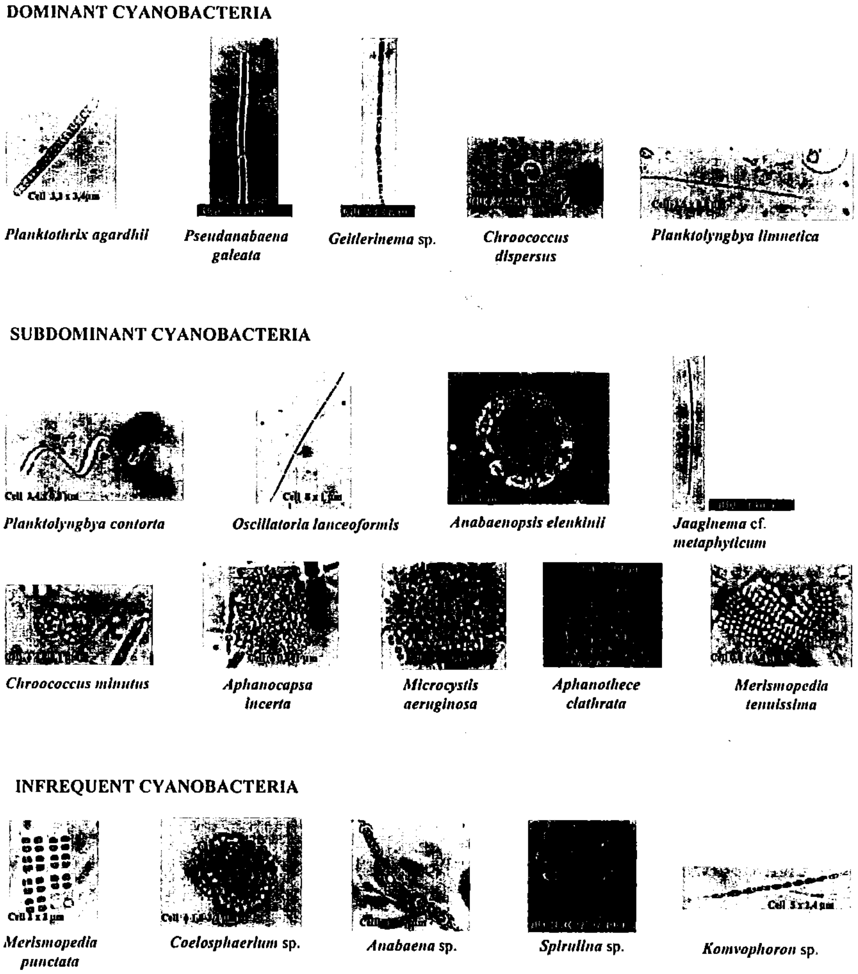

Fig. 3. Morphological characteristics of some relevant cyanobacteria from the lake Albufera of Valencia (Spain). Categories refered in the text.

• *Pseudanabaena galeata* BÖCHER 1949. BLANCO (1974) described the presence of *Oscillatoria* sp. as an important species in the lake during June to February in the 1970s. Her morphological descriptions could be refered to both *Ps. galeata* or *Geitlerinema* sp. *Ps. galeata* was a dominant species for 1980–88, specially in November–December and June, with intermediate water stagnation and nutrient levels. But it became the predominant species for 1997–2000 with the maximum peaks in May. Remarks on its taxonomy and ecology can be found in ROMO (1994 a, b) and ROMO et al. (1993 a). The mean trichome length was of 81 µm with cells of 4.2 x 2 µm.

• *Geitlerinema* sp. This species was the third dominant oscillatorial for the period 1980–88 (ROMO & MIRACLE 1993), but it was almost absent during 1997–2000. It appeared in summer under prolonged water stagnation and depletion of phosphorus. Trichomes in average of 88 µm long with cells 3.5–1.6 µm.

• *Planktolyngbya limnetica* KOMÁRKOVÁ-LEGNEROVÁ et CRONBERG 1999. This cyanobacteria has been referenced in the lake since 1942, although earlier descriptions could correspond to other slender oscillatorial cyanobacteria. This species normally co-occured in the Albufera with *Pl. contorta* since 1980. It peaked mostly during periods of prolonged water quiescence. The maximum populations were recorded in August 1987 (80 % of the total algal density, 43 % total biovolume). In the 1990s also peaked during summer-autumn, but the maximum populations recorded were ten-fold lower than in the 1980s (from 2 to 0.17×10^6 ind per ml, October 2000, 12 % of total algal abundance, 3 % of total algal biovolume). The mean trichome length was of 44 µm with cells of 2.5 x 0.8 µm.

• *Chroococcus dispersus* (KEISSLER) LEMMERMANN 1904. This species was together with *Ps. galeata* the most abundant cyanobacteria in the Albufera in the 1990s. Its maximum populations were in August 1999 (35 % and 62 % of the total algal biovolume and abundance, respectively). It forms colonies of 2–30 cells, but normally found in the lake 2 cells per colony. Cells of 3.5–4.4 µm in diameter.

Subdominant cyanobacteria

This category comprises sometimes abundant but non-dominant cyanobacteria species (less than 50 % of relative abundance or biovolume) in the lake of Albufera of Valencia, with high to moderate frequence of occurence.

• *Chroococcus minutus* (KÜTZING) NÄGELI 1849. It was first described in the lake in 1997. It occurred in late summer (August–September of 1997–2000), with maximum peak in August 1998 (10 % of the total phytoplankton biovolume). We observed solitary cells and also small colonies with 2–4 cells. Cells of 4.8–8.1 µm in diameter.

• *Anabaenopsis elenkinii* MILLER. It is a frequently occurring species in the lake since 1980. This cyanobacteria had maximum populations during July–August of the last two study decades. It contributed in July 1985 with up 27 % to total algal density and 19 % of biovolume, and in July 2000 with 4 % of the total phytoplankton abundance and 14 % of biovolume. Their populations were related to warm water temperatures, water stability and low nitrogen concentrations. Mean trichome length of 62 µm with cells of 7 x 4 µm.

• *Aphanocapsa incerta* (LEMMERMANN) CRONBERG et KOMÁREK 1994. It was recorded during July–September for 1986–88 and September–December for 1997–2000. The maximum contribution of the population to the total phytoplankton biovolume was in December 1998, which amounted 36 % of total algae biovolume (12 % of total phytoplankton abundance). Colonies of 14 µm in average and cell size of 0.8–1 µm in diameter.

• *Aphanothece clathrata* W. et G.S. WEST 1906. This species normally appeared during the summer water stability, mainly in July–August for 1980–88 and 1997–2000. Its contribution to the algal biomass and abundance was normally lower than 25 %, except in November 1980 (83 % total biovolume, 5 % in total abundance). PARDO (1942) described the presence of *Aphanothece* sp. in the Albufera mostly during winter. Colonies about 18 μm with mean cell size of 2 x 0.8 μm.

• *Merismopedia tenuissima* LEMMERMANN 1898. It was found mainly in April and September–November, during 1980–88 and 1997–2000 (maximum populations in November 1998, which amounted to 7 % of total phytoplankton biovolume). This cyanobacteria was also mentioned by PARDO (1942) during summer. Colonies of 23 μm long and cells of 0.8 x 0.8 μm.

• *Microcystis aeruginosa* (KÜTZING) KÜTZING 1846. It was described as *Anacystis cyanea* (KÜTZ.) DROUET et DAILY during summer-winter in the 1970s (BLANCO 1974). During 1980–88 appeared in July and November–December, and for 1997–2000 its greater presence was in October–November. Due to its size amounted up to 65 % of total phytoplankton biovolume in some punctual months, but their population represented less than 10 % in numbers during the 1980s. Similarly, in the 1990s contributed to 20 % of total phytoplankton biovolume but only 2 % of algal abundance. Colonies of 20 μm with cells of 4–5.4 μm in diameter.

• *Jaaginema* cf. *metaphyticum* KOMÁREK. This oscillatorial cyanobacteria had maximum presence during July–October for 1980–88 and 1997–2000. Its presence in the lake could be originated from an exogenous input from the surrounding ricefields, although developed afterwards its own populations in the lake (ROMO & MIRACLE 1994). It had an occurrence of 50 % in total samples. Its populations contributed up 40 % of the phytoplankton abundance in July 1983 and up to 32 % abundance in August 2000. Mean trichome length was of 54 μm with cells of 8 x 0.8 μm.

• *Geitlerinema amphibium* (AG. ex GOM.) ANAGNOSTIDIS 1989. It developed in the lake mainly in September, specially during 1985–1988. It is also associated to the ricefield habitats surrounding the lake. Trichomes 220–41 μm long with cells 5–2.2 x 1.6–1.2 μm. An extense study on the taxonomy and ecology of this species in the lake is reported by ROMO et al. (1993b).

• *Oscillatoria lanceaeformis* KOLBE. Since 1980, is present mainly in May and during summer, but never above 3 % of total phytoplankton biovolume. Mean trichome length of 66 μm with cells of 8 x 1 μm.

• *Planktolyngbya contorta* (LEMMERMANN) ANAGNOSTIDIS et KOMÁREK. As aforementioned, it co-occurred with *Pl. limnetica* in the Albufera. It peaked mostly in July–October for 1980–88 and 1997–2000. In August 1999 it represented up 19 % of total phytoplankton biovolume. Mean trichome length of 27 μm with cells of 2.4 x 0.8 μm.

• *Cylindrospermopsis raciborskii* (WO≥.) SEENA Raju. It was mainly found in July–October 1987 and 1988, amounting up 22 % of the algal biomass in October

1987. Thereafter, it was not recorded. Trichomes with mean length of 74 µm and cells of 7.2 x 2 µm.

• *Gomphosphaeria* sp. This cyanobacteria was only described in the lake by PARDO (1942) mainly during summer-autumn.

• *Chroococcus turgidus* (KÜTZING) NÄGELI. Similarly to the previous one, the presence of this species was only referenced by PARDO (1942) during summer-autumn.

Infrequent cyanobacteria

The frequency of occurrence of these species and their contribution to the total abundance and biomass was low in the lake.

• *Anabaena* sp. Only observed sporadically in August 1999 amounting only to 0.1 % of total phytoplankton biovolume. Trichomes with mean length of 154 µm and cells of 5 x 3.2 µm.

• *Anabaena cf. laxa* (RABENHORST) A. BRAUN. Filaments only found sporadically during 1980–88. Filaments of 198 µm long in average and cells of 4.1 x 3.2 µm.

• *Coelosphaerium kuetzingianum* NÄGELI 1849. It was observed in August 2000 when represented 5 % of total phytoplankton biovolume. Colonies with cells of 1.8–3.2 µm in diameter.

• *Gloeothece* sp. Referenced only in 1942 (PARDO 1942) appearing in the Albufera in January–February. There are no morfological data.

• *Komvophoron* sp. It was recorded during 1980–88 and in seven samples for the period 1997–2000, mainly in May 1999 (0.7 mg . l^{-1} of biovolume that represented 0.2 % of total cyanobacteria biomass). Trichomes with cell size of 5 x 2.4 µm.

• *Merismopedia punctata* MEYEN 1839. Since 1980 this cyanobacteria developed in the lake during September–November. Due to its small size, it had low contribution to the algal biovolume (less 0.3 %) and represented up 0.8 % of algal density. Colonies of 14 µm long with cell size of 2 x 2 µm.

• *Romeria* sp. It was sporadically found in 1988 (March, October and December) and 1997–2000 (May–July). The mean cell size was of 15 x 1.2 µm.

• *Spirulina* sp. It was observed in 1980–88 and in three samples for the period of 1997–2000. Mean cell size of 1.4–1.8 µm in diameter.

Ecology of cyanobacteria in the lake

The analysis from the long-term data of the Albufera reveals the presence of cyanobacteria in the lake since beginning of the 20th century (Table 1). During the first half of the century Cyanobacteria were mostly represented by chroococcals occurring mainly during summer and autumn. They coexisted seasonally with a diverse pool of other phytoplanktonic algae (Table 1), at the time when the lake

Table 1. Long-term changes in the phytoplankton of the lake Albufera of Valencia, from the first records in 1942 to 2000. Seasonal dominance of the main species and algal groups are showed.

References	**Spring** March–May	**Summer–Autumn** June–December	**Winter** January–February
PARDO (1942)	**Chlorophyta** *Coelastrum* sp. *Pediastrum* sp.	**Cyanobacteria** *Chroococcus turgidus* *Gomphosphaeria* sp. *Merismopedia* sp. *Aphanocapsa* sp. *Lyngbya* sp. *Spirulina* sp. **Dinophyta** *Ceratium hirundinella* *Peridinium* sp.	**Cyanobacteria** *Aphanotece* sp. *Gloeothece* sp. **Bacillarophyta** *Synedra ulna* *Nitzschia* spp. *Cyclotella* sp. *Navicula* sp. *Epithemia* sp. *Cymbella* sp. *Gomphonema* sp. *Pleurosigma* sp. *Amphipleura* sp. **Chrysophyta** *Dinobryon sertularia* **Chlorophyta** *Spirogyra* sp.
BLANCO (1974)	**Chlorophyta** *Chlamydomonas* sp. *Scenedesmus quadricauda* *Pediastrum boryanum* **Bacillarophyta** *Synedra ulna* *Cyclotella* sp. *Campylodiscus clypeus* *Stephanodiscus astraea* *Asterionella formosa* *Diatoma* sp.	**Cyanobacteria** *Oscillatoria* sp. *Lyngbya limnetica* *Anacystis cyanea*	
ROMO (1991)	*Planktothrix agardhii*	**Cyanobacteria** *Geitlerinema* sp. *Pseudanabaena galeata* *Planktolyngbya subtilis*	*Planktothrix agardhii*
VILLENA & ROMO (this study)	*Pseudanabaena galeata*	**Cyanobacteria** *Chroococcus dispersus* *Pseudanabaena galeata* *Planktolyngbya contorta* *Jaaginema* cf. *methaphyticum* *Planktolyngya limnetica* *Aphanocapsa incerta*	*Pseudanabaena galeata*

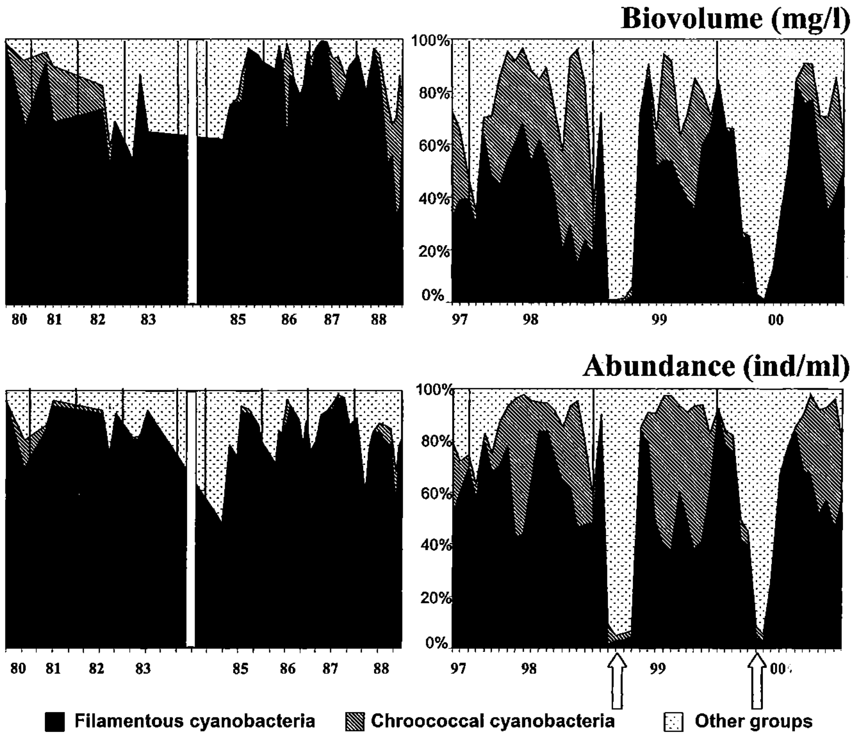

Fig. 4. Relative abundance (ind.ml^{-1}) and biovolume (mg.l^{-1} of cyanobacteria in the lake of the Albufera of Valencia, for 1980–88 and 1997–2000. Percentage of filamentous and chroococcal species are represented differently to denote the increase of this latter group in recent years.

was in a transparent state covered by submerged macrophytes. During 1960s and 1970s eutrophication turned the lake into a turbid state, which accelerated the lost of submerged vegetation and associated fauna, reduced planktonic species richness and in general the biotic biodiversity in the food web. Precise records on the phytoplankton of this period described the decrease of phytoplankton species richness and the start of dominance of filamentous cyanobacteria during most part of the year (Table 1). During 1980s and 1990s cyanobacteria overwhelmed phytoplankton during the year, and the lake became in a hypertrophic turbid state without sugmerged macrophytes. We will further describe this period of cyanobacteria dominance to study in deep their ecology in the lake.

During 1980–1988 and 1997–2000, the percentage of cyanobacteria in the Albufera represented between 50–98 % of total algal biovolume and abundance, except during punctual periods of clear water phases after sewage water diversion. In these phases of water transparence (reaching the bottom of the lake) cyanobacteria contribution in the phytoplankton declined to 5 % and were replaced by centric diatoms and chlorophytes (Fig. 4). They took place mainly

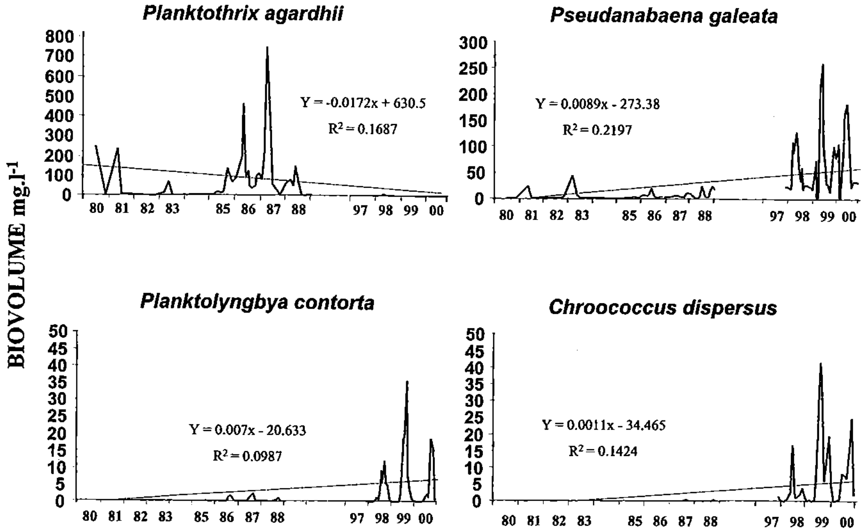

Fig. 5. Interannual changes of the dominant cyanobacteria species in the lake of the Albufera of Valencia, for 1980–88 and 1997–2000. Values for the linear regression of increase or decrease are showed.

during January–March, coincidental with higher water renewal in the lake (Fig. 2). When cyanobacteria dominated Secchi disk depth was only of 15–25 cm, specially during their maxima peaks occurring with water quiescence (May–September, Figs 2 and 4). Cyanobacteria species richness between both decades, the 1980s and 1990s, remained similar (23–21 species, respectively).

Other symptom of water quality improvement after nutrient diversion is that chlorophyll *a* declined to half, from a mean of 318 $\mu g.l^{-1}$ for 1985–88 to 163 $\mu g.l^{-1}$ for 1995–2000. After nutrient diversion cyanobacteria composition also changed. Interannual dynamics of the dominant cyanobacteria showed a trend toward smaller and less oligophotic species (Fig. 5). Large filamentous cyanobacteria, mainly *Planktothrix agardhii,* were replaced by thinner oscillatoriales, such as *Pseudanabaena galeata* and *Planktolyngbya contorta,* and by chroococcal species, the main representant being *Chroococcus dispersus* (Fig. 5). In the 1980s, *Planktothrix agardhii* represented more than 50 % of the total algal biovolume, specially during April and May (1986 and 1987 reached between 460–740 $mg.l^{-1}$ of fresh weight and 2.6–3 x 10^5 ind. per l, Fig. 5). Its population maxima were coincidental with the onset of water level stabilisation and high nutrient concentrations after ricefield fertilization. Thereafter its populations decreased ten-fold during summer and autumn, representing generally less than 25 % of the total algal abundance but up to 60 % of the total biovolume. The periodicity progressed towards *Geitlerinema* sp. in summer, with low water renewal rates and phosphate depletion, and then to *Ps. galeata* in November–December during the second period of water stability (Table 1). After the diversion of nutrients, *Ps. galeata* became the dominant cyanobacteria for the period 1997–2000 and replaced seasonally to *P. agardhii* in the lake. *Ps. galeata* amounted to 40–65% of total phytoplankton biovolume from December to June with maximum peaks in May of 1999 (260 mg. 1^{-1} of fresh weight and 1.02 x 10^6 ind. per 1, Fig. 5). Afterwards, from July to November, *Ps. galeata* decreased its populations contributing with 13–36% to the total algal biomass and 10–32% to the algal abundance. In numbers *Chroococcus dispersus* was the most abundant cyanobacteria during these months, except in September where it co-dominated with *Planktolynbya contorta.* Other relevant algae specially, between July and October, were *Jaaginema* cf. *methaphyticum* and *Pl. limnetica* (up to 14% of total algal abundance), and in September and November *Aphanocapsa incerta.* The summer-autumn period was characterized by lower levels of available nutrients, but higher light intensities and reduced pressure of zooplankton grazing.

Discussion

The Albufera of Valencia lake was in a mesotrophic state during the first half of the 20th century and due to eutrophication by the end 1960s, it rapidly turned into an eutrophic state with loss of submerged macrophytes and general biodiversity in the plankton, benthos and fish communities, that remains until nowadays. In recent years and after the diversion of sewage waters in 1991, there are some symptoms of improvement in the lake water quality. Phytoplanktic chlorophyll *a* concentrations were reduced to half, although mean values (163 μg.1^{-1}) still within a hypertrophic threshold (RYDING & RAST 1992). In addition, several intervals of clear water phases, which lasted until 5 weeks, occurred in recent years, where water transparence reached the bottom of the lake and cyanobacteria almost disappeared. This result seems to corraborate the bistability model proposed by SCHEFFER et al. (1993) in which two alternative equilibria states (turbid/clear phases) can be possible for shallow lakes. A reduction in nutrients in the Albufera lead to the system toward clear water phases and associated development of large cladocera in the lake (OLTRA et al. 2001). These clear water phases are yet short and unstable, and prevent recovering of submerged macrophytes that could stabilize the clear water equilibria (MOSS et al. 1996b, JEPPESEN et al. 1998). Although internal nutrient load by P remobilisation from the sediment have been not determined in the Albufera, this may retard and counterbalance the possitive effects of external load reduction in shallow lakes, even in flushed lakes like the Albufera (SAS 1989, JEPPESEN et al. 1991).

Restoration of the Albufera lake probably implies the idea of the restablishment and coexistence of submerged macrophytes with cyanobacteria, such as happened at the beginning of the century. The study of long-term phytoplankton data from the Albufera shows that the presence of cyanobacteria in the plankton of this Mediterranean lake was relevant since former records and with a transparent vegetated state, and experimental studies in mesocosms suggest that in warmer shallow lakes cyanobacteria can be important components of the food web and dominate phytoplankton in both clear and turbid phases (ROMO et al. 2004). Long-term data set in the Albufera support empirically these results.

Nevertheless and in accordance with other studies (JEPPESEN et al. 1991, KÖHLER et al. 2000), the high biomass and permanent dominance of cyanobacteria in the Albufera in a turbid state during the past two decades seems partly due to high nutrients concentrations and light limitation, since shade-tolerant filamentous species outcompete other algal groups (REYNOLDS 1984, SCHEFFER et al. 1997). After nutrient diversion, we observed a replacement of cyanobacteria toward thinner filamentous species that required less nutrient concentrations but higher underwater light climate, such as e.g. *Ps. galeata* or *Pl. contorta* (ROMO 1994a, ROMO & MIRACLE 1994). These species replaced the oligophotic strains of *P. agardhii* better adapted to low underwater light intensities and high P levels in shallow lakes (BERGER 1989, NICKLISCH et al. 1991). The maintenance of filamentous cyanobacteria in the Albufera could be also enhanced by its shallowness and wind exposed surface, that resuspended filaments from the sediment into the photic zone and provided inocula to the plankton, similarly to that found in other large shallow lakes (BERGER & SWEERS 1988). In fact, during the periods of clear water phases in the springs of 1999 an 2000 (Fig. 4), mats of the dominant planktic filamentous cyanobacteria were observed and recorded from the sediment.

The period of hydrological stability in the lake also favours the presence of cyanobacteria. At the start of the year when ricefields are dried before preparing them for the next crop, high water renewal prompted the increase of other algal groups (specially centric diatoms and chlorophytes), but during the remaining periods of intermediate (November–December) or long water stability cyanobacteria overwhelmed the phytoplankton in the lake. Seasonally there was a shift toward smaller species during summer after prolonged periods of water quiescence. This result can be related to lower nutrient concentrations that lead to smaller sizes (GIBSON 1975, MEFFERT 1989, ROMO 1994b) and/or a top-down effect in which summer reduction of zooplankton grazing by an increase in fish predation (unpublished data) favoured edible algae, specially in the Albufera the dominance of small chroococcal cyanobacteria, such as *Chr. dispersus* and *Chr. minutus*. Some experimental results in a Mediterranean lake seems to support this effect of planktivorous fish on cyanobacteria selectivity (ROMO et al. 2004).

Summary

Since the first limnological records of the Albufera lake in the beginning of the 20th century, cyanobacteria were well represented in the phytoplankton. Eutrophication in 1960s and 1970s increased their presence, and from 1980 to 2000 overwhelmed the phytoplankton (Table 1). After nutrient diversion in 1991, algal biovolume was reduced to half, and some clear water periods shifted cyanobacteria dominance toward other algal groups. At the same time, it was observed an interannual replacement in the predominant cyanobacteria species, in which *Planktothrix agardhii,* a large oligophotic oscillatorial with high nutrient

requirements, was replaced by smaller species, mainly *Pseudanabaena galeata* (Fig. 5). Prolonged water stability and nutrient depletion during rice growth in summer, enhanced the presence of smaller oscillatoriales, such as *Planktolyngbya contorta, Pl. limnetica* and *Jaaginema* cf. *metaphyticum,* while reduced zooplankton grazing by intense fish predation favoured small chroococcals, such as *Chroococcus dispersus* and *Chr. minutus.* Restoration of the Albufera lake probably implies the idea of reestablishment and coexistence of submerged macrophytes with cyanobacteria in a clear water state, such as occurred in the lake at the beginning of the 20th century.

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