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Phytoplankton diversity and cyanobacterial dominance in a hypereutrophic shallow lake with biologically produced alkaline pH

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Abstract In this work, we have characterized the diversity of phytoplanktonic species in a highly alkaline and hypereutrophic shallow lake, Santa Olalla (southwestern Spain), the evolution of their relative abundances, and that of several physicochemical parameters over 2 years. In the absence of an external input of alkaline water, Santa Olalla's stable high pH (average pH 9.52, with several maxima >10.5) is explained by an extremely high photosynthetic primary productivity. A variety of phytoplankton species was observed even during pH maxima. These included several species of green algae, diatoms, and euglenoids and several cyanobacteria from the orders Nostocales and Chroococcales. Quantitatively, cyanobacteria dominated. A blooming event due to *Aphanothece clathrata* was observed at one pH maximum, during which the diversity as measured by the Shannon-Weaver index was extremely low. Santa Olalla's cyanobacteria are alkaliphilic and/or extremely alkalitolerant and appear to be responsible for the generation and maintenance of stable high-pH conditions in their environment.

Keywords Alkaliphiles · Cyanobacteria · Freshwater shallow lake · Hypereutrophic · Microbial diversity Phytoplankton · Primary production

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Introduction

Alkaliphiles have attracted much scientific attention because of their adaptations to life under high pH (optimal growth at or above pH 9) and also because of the biotechnological applications derived from many of their enzymatic activities (Grant 1992; Horikoshi 1999). Most alkaliphiles have been isolated from a variety of environments ranging from soda lakes, soils, and industrial settings to some marine fjords and the deep sea (Takami et al. 1997; Jones et al. 1998; Horikoshi 1999; Stougaard et al. 2002). Among these, soda lakes have been widely studied, as they are the most extensive and stable alkaline environments, where pH values greater than 11.5 can be maintained by the presence of large amounts of mineral carbonates (Grant 1992; Jones et al. 1998). Since they exhibit salt concentrations varying from 5% to saturation levels (~30%), microorganisms isolated from soda lakes are usually halophilic or halotolerant at the same time (Jones et al. 1998). However, this is not a general rule for alkaline inland water bodies, since high pH can be produced in the absence of elevated salt concentrations, as occurs in the largest alkaline lake, Lake Van in Turkey (pH ~9.7) (Kempe et al. 1991).

Alkaline environments can be generated not only by particular geochemical conditions but also by natural biological activity. Thus, microbial ammonification and sulfate reduction in soils can locally increase the pH even to values above 10, but these are rarely stable (Jones et al. 1998). Carbon fixation as a consequence of photosynthetic activity can displace the carbon dioxide/bicarbonate/carbonate equilibrium that is the most common pH-buffering mechanism in freshwater systems. Photosynthesis thus tends to increase the environmental pH, counterbalancing the buffering effect of carbon dioxide, which globally leads to neutral or acid pH. This pH increase is particularly remarkable in hypereutrophic systems, as a consequence of a very high primary production. In turn, photosynthesis is favored

under more alkaline conditions, since alkaline systems act as a trap for atmospheric carbon dioxide (Imhoff et al. 1979). Thus, the highest primary production levels are encountered in alkaline lakes (Melack 1981; Talling et al. 1973). Nevertheless, although the diversity of alkaliphilic or extremely alkalitolerant microbes thriving in soda lakes has been extensively studied, that of microorganisms living in high-pH freshwater lakes remains largely unexplored.

In this work, we present a study of a shallow lake, Santa Olalla (southwestern Spain), with a microbiologically produced highly alkaline pH. During the 2-year period of study (1998–1999), Santa Olalla had an average pH of 9.52, reaching several maxima of pH >10.5. These values are similar to those recorded during the last 30 years (Margalef 1976), suggesting that Santa Olalla is a stable alkaline system. We have analyzed the diversity of the phytoplankton community, which is overwhelmingly dominated by cyanobacteria, in parallel with the evolution of pH and primary productivity.

Materials and methods

Study site and sampling

Santa Olalla is located at the Doñana National Park, southwestern Spain, and belongs to a system of peridune wetlands in an area dominated by a Mediterranean-type climate with dry, hot summers and low-rainfall winters. Samples and measurements were taken monthly from February 1998 to February 2000. However, phytoplankton cell counts were not done from July 1999, and therefore parameter values from only February 1998 to June 1999 are shown in Fig. 1. Samples to study phytoplankton abundance and diversity were fixed in situ with 4% formaldehyde.

Physicochemical parameters

Conductivity, temperature, pH, and redox potential were measured in situ in the water column by means of field probes. Dissolved oxygen concentration was measured both at 5 cm beneath water surface and close to the bottom sediment. Nutrient concentrations (NO_3^-, NO_2^-, NH_4^+, organic nitrogen, organic phosphorous, and soluble reactive phosphorus) were determined in the laboratory following normalized methods (APHA-AWWA-WPCF 1989).

Biological parameters

Triplicate water samples were filtered in situ through Whatman GF/F glass microfiber filters (0.7 μm pore size). Chlorophylls *a* and *b* were extracted with 5 ml of 90% v/v acetone for 24 h at 4°C in the dark. Chlorophyll concentrations were measured using a spectrophotometer applying the Jeffrey and Humphrey trichromatic method (Jeffrey and Humphrey 1975).

Primary phytoplanktonic productivity was determined using the ^{14}C method (Goldman et al. 1974). Briefly, photosynthesis was measured in situ by suspending sets of two light and one dark of polyethylene bottle at 15 cm from the surface and allowing an incubation time of 2.5 h at midday (the optimal incubation time was determined in a preliminary experiment). In total, 10 light bottles and 5 dark bottles were incubated simultaneously. After the first incubation hour, two light and one dark bottle were removed every 30 min. The highest production was estimated at 2.5 h from the beginning of the experiment.

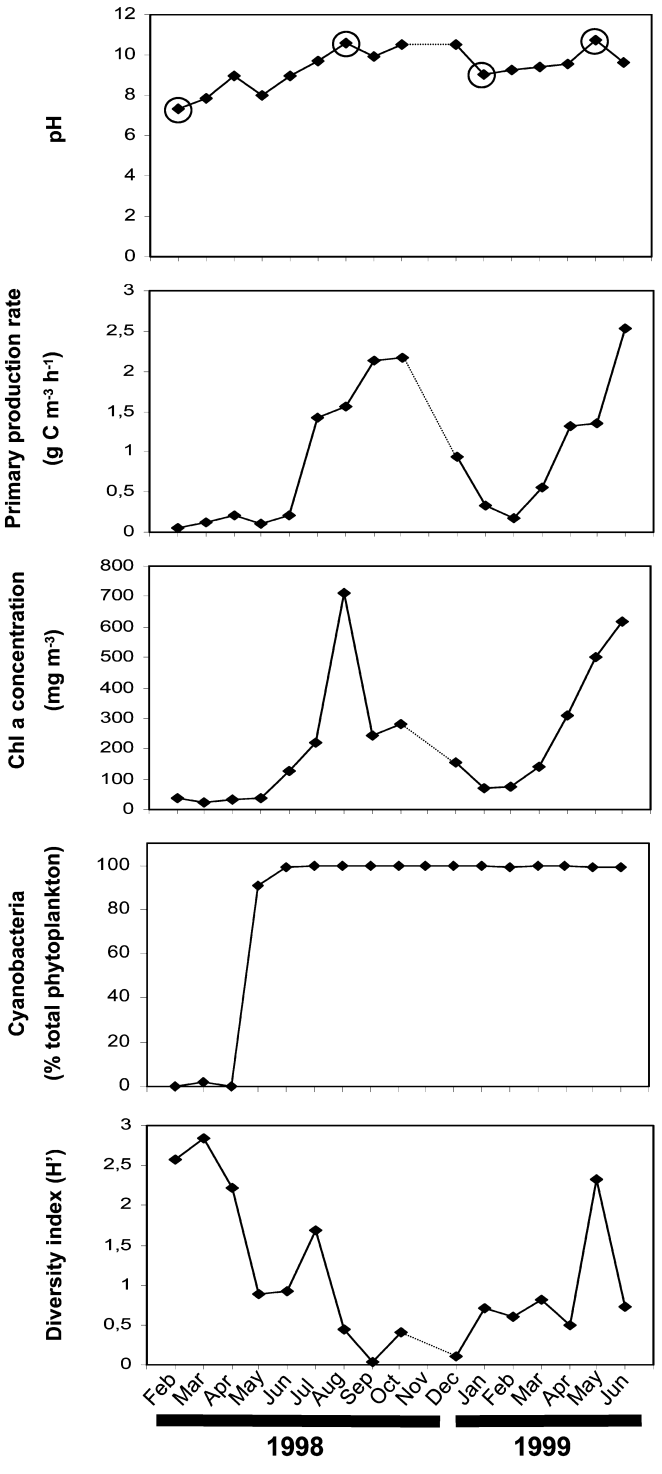

Fig. 1 Evolution of pH, primary production rate, chlorophyll *a* (Chl *a*) concentration, proportion of cyanobacteria in the phytoplankton and Shannon-Weaver indices (H′) for phytoplankton diversity in the shallow lake Santa Olalla during the period February 1998–June 1999. *Dotted lines* correspond to one missing point in the dataset. The pH values enclosed by a *circle* indicate the points at which the physicochemical and biological parameters shown in Table 1 were taken

Microscopy observation and taxonomic identification

Species identification was carried out using an inverted optic microscope (Olympus IX50). Enumeration of phytoplankton cells was always done in duplicate after filtering 0.1 ml (or different dilutions depending on the samples) of the fixed samples through black Isopore GTBP membrane filters (0.2 μm pore size) and then washing with citrate buffer pH 6. Each filter was examined for the autofluorescence of cell pigments at 1,000× with a UV fluorescence filter. Quantitative microscope observations were done according to Fry (1990).

Biodiversity and statistical analyses

Phytoplankton biodiversity estimates were calculated using the Shannon-Weaver equation in base 2 in order to take into account both species diversity and relative abundance (Shannon and Weaver 1963). Relationships among variables were explored using correlation coefficients (Pearson for parametric variables and Spearman for non-parametric). Statistical correlations were done using the program SPSSwin 10.0 (SPSS) and included all monthly data from February 1998 to February 2000 (data not shown).

Results and discussion

High primary production rates and alkalinity in Santa Olalla

Santa Olalla is a hypogenic (groundwater-fed) shallow lake where the main water input is subsurface, coming from regional and local discharge flows (Sacks et al. 1992). In contrast to neighboring shallow lakes also in the Doñana National Park, this is a permanent system. It has an average water volume of 165,315 m^3, although due to its smooth slopes and to the climate conditions, it can fluctuate considerably, with water levels varying from 250 to 70 cm depth (see also Table 1). During particularly rainy winters, Santa Olalla overflows and can fuse with the neighboring non-permanent and non-alkaline, shallow Lake Dulce. This circumstance occurred at the beginning of our study in February 1998 and is the reason that the pH (7.33) was the lowest recorded during the 2 years of study (Table 1, Fig. 1). Historical pH records in Santa Olalla correspond to alkaline values; the pH was 9 on average in January 1973 (Margalef 1976) and fluctuated between 8 and 11 in the year 1986–1987 (López et al. 1991). The evolution of pH during 1998–1999 is shown in Fig. 1. From the minimum observed in February 1998, pH values increased rapidly, reaching stable pH values ≥9 in 2 months and exhibiting various maxima of more than 10.5. Table 1 shows different physicochemical and biological parameters measured at two of these pH maxima (August 1998, pH 10.58 and May 1999, pH 10.77) compared with data from the minimum observed in February 1998 and a minimum intermediate point between the two maxima (January 1999, pH 9.02). Taken together, these data suggest that Santa Olalla, despite fluctuations mostly due to increased rainfall, is a stable high-pH system and that high pH levels can recover rapidly.

Santa Olalla's alkaline pH is not due to groundwater input. Underground water flowing into the lake has neutral pH values of 6.7–6.8 on average (M.C. Coleto, personal communication). This is accompanied by the absence of measurable levels of carbonate in the input water, carbonates being detectable only above pH 8.3. Input groundwater bicarbonate content corresponds to 0.4–0.6 mEq l^{-1}. Both groundwater pH and alkalinity (capacity of solutes in an aqueous system to neutralize acid) are far from those found in the Santa Olalla water column (Table 1). Nevertheless, although pH can reach elevated values close to 11, alkalinity remains quite moderate (1.66–2.26 mEq l^{-1}) when compared to some soda lakes, such as the Mono Lake (618 mEq l^{-1}) (Council and Bennett 1993) or Lake Nakuru (122.5 mEq l^{-1}) (Millbrink 1977), and other alkaline systems such as Lake Van (152.7 mEq l^{-1}) (Kempe et al. 1991). Its alkalinity is, however, comparable to that of alkaline lakes such as Tanganika (6.6 mEq l^{-1}) (Cohen and Thouin 1987). According to Talling and Talling (1965), Santa Olalla would belong by its alkalinity to Class I lakes, including lakes such as Malawi or Victoria, which are characterized by total alkalinity of less than 6 mEq l^{-1}, although Santa Olalla's conductivity is much higher (Table 1) than that of typical Class I lakes (< 600 μS).

Therefore, the high pH in Santa Olalla is rather the consequence of high primary production. This shallow lake is a eutrophic to hypereutrophic system. As can be seen in Table 1 and Fig. 1, the primary production rate is extremely high, reaching values above 1.5 g C m^{-3} h^{-1}. These values greatly exceed those recently reported from two shallow saline and alkaline pools as the highest records of productivity in natural aquatic ecosystems (0.925 gC m^{-3} h^{-1}) (Kirschner et al. 2002). This high productivity is accompanied by the presence of large amounts of chlorophyll, particularly chlorophyll *a* (Chl *a*, 365.2 mg m^{-3} on average). In fact, the curves for productivity and Chl *a* concentration show similar shapes during the time period studied (Fig. 1). Chl *a* values higher than 100 mg m^{-3} are characteristic of hypereutrophic systems (OECD 1982). Furthermore, the turbidity of the water column was sometimes so high that Secchi disks were no longer visible below 5 cm from the surface (Table 1). Hypereutrophic systems are characterized by very low water transparency (Secchi disks no longer seen below 40–50 cm depth). These parameter values confirm the hypereutrophic nature of Santa Olalla. In addition to the detection of a variety of cyanobacterial species, cyanobacteria were found to be the most abundant members of the phytoplanktonic community (Table 1). This is reflected not only in direct cell counts but also by the total amount of Chl *a* together with the Chl *a*/Chl *b* ratio. The Chl *a* (found in cyanobacteria and algae) concentration was especially elevated during the pH maxima, overwhelming the corresponding values for Chl *b* (characteristic of green algae, plants, and euglenoids). In fact, a variety of green algae were detected also during pH maxima, but their numbers were much lower (Table 1).

Table 1 Physicochemical and biological parameters in Santa Olalla. *n.d.* Not determined, *b.d.l.* below detection limits

	February 1998	August 1998	January 1999	May 1999
pH	7.33	10.58	9.02	10.77
CO_3^{2-} (mEq l^{-1})	0	0.26	0.05	0.41
HCO_3^- (mEq l^{-1})	2.18	1.8	2.22	1.26
Total alkalinity (mEq l^{-1})	2.18	2.06	2.26	1.66
Volume (m^3)	>1,896,326[a]	139,303	67,644	28,982
Maximal depth (m)	2.38	1.49	1.29	1.04
Average depth (m)	1.04	0.19	0.34	0.25
Precipitation (mm m^{-2})	90.4	0	80.7	8.3
Daily light time (h)	11.33	14	10.83	15
Midday water temperature (°C)	15.2	30	11	26.7
Maximal water temperature (°C)	n.d.	34	n.d.	33
Minimal water temperature (°C)	n.d.	20	n.d.	15
Conductivity (μS cm^{-1})	532	1,163	1,478	2,480
Redox potential (mV)	86	n.d.	34	13
Transparency (Secchi depth, cm)	22	10	13	5
Dissolved O_2 close to bottom (%)	28.5	235	120	27
Dissolved O_2 near surface (%)	28.5	217	126	200
NO_3^{2-} (g m^{-3})	0.025	0	0	0
NO_2^{2-} (g m^{-3})	0.005	0	0	0
NH_4^+ (g m^{-3})	0.12	0.09	0	0
Organic nitrogen (g m^{-3})	3.1	5.88	7	8.4
Organic phosphorous (g m^{-3})	0.23	0.97	0.48	0.79
Soluble reactive phosphorous (g m^{-3})	0.04	0	0	0
Total phytoplankton (cells ml^{-1})	1,382	40,156,013	14,144,513	30,206,756
Cyanobacteria (cells ml^{-1})	1	40,149,803	14,137,000	29,960,000
Heterocytes (cells ml^{-1})	0	12,400	150,000	9,210
Green algae (cells ml^{-1})	821	6,210	7,513	237,546
Euglenoids (cells ml^{-1})	83	0	0	0
Diatoms (cells ml^{-1})	79	0	0	0
Cryptophytes (cells ml^{-1})	398	0	0	0
Shannon–Weaver index (H′)	2.58	0.44	0.71	2.32
Primary production rate ($g^{14}C$ $m^{-3}h^{-1}$)	0.06	1.56	0.33	1.36
Chlorophyll *a* (mg m^{-3})	35.4	708.8	68.9	502.1
Chlorophyll *b* (mg m^{-3})	3.82	b.d.l.	b.d.l.	23.8

[a]Precise volume measurement was impossible because the shallow lake was overflowed during February 1998

Diversity of dominant cyanobacterial species

As mentioned above, cyanobacteria dominated Santa Olalla's phytoplankton. After a massive rainfall when Santa Olalla overflowed (winter 1998) and the pH began to be stabilized at values ≥9, cyanobacteria increased from very low counts (near 0%) up to 99–100% of the total phytoplankton (Fig. 1). Although the dominant cyanobacterial community was relatively varied, species composition was not always the same, as significant changes in cyanobacterial diversity were observed during the time period studied.

A list of cyanobacterial and other phytoplanktonic species identified during the two pH maxima (August 1998, pH 10.58; May 1999, pH 10.77) is given in Table 2. Their taxonomic identification was done by classical morphological criteria (Anagnostidis and Komárek 1985; Waterbury 1991). We identified members of two cyanobacterial orders, Chroococcales and Nostocales. Within the Chroococcales, we detected representatives of four families: Gloeobacteriaceae (genus *Aphanothece*), Merismopediaceae (genera *Aphanocapsa* and *Merismopedia*), Microcystaceae (genus *Microcystis*), and Chroococcaceae (genus *Chroococcus*). Within the Nostocales, we observed representatives of two families: Nostocaceae (genera *Anabaena* and *Anabaenopsis*) and Oscillatoriaceae (genera *Limnothrix*, *Leptolyngbya*, *Oscillatoria*, *Pseudanabaena*, and *Raphidiopsis*). Micrographs of some of the species most frequently encountered during the two Santa Olalla pH maxima are shown in Fig. 2.

During the two high-pH peaks (pH >10.5) in August 1998 and May 1999, cyanobacteria accounted for more than 99% of phytoplankton cells (Fig. 1). However, the percentage of cells from the different species with respect to the total cyanobacteria varied considerably (Table 2). Thus, *Aphanothece clathrata* clearly dominated phytoplankton in August 1998 (92.5%), whereas dominant species were more diversified in May 1999, with *Leptolyngbya* sp., *Anabaena aphanizomenoides*, and *Merismopedia tenuissima* being 50%, 23.6%, and 9.3% of the total cyanobacterial population, respectively. These results reflect blooming events of different cyanobacterial species at given moments. In fact, several of these species are known to bloom in eutrophic systems, such as *Microcystis aeruginosa* and *Anabaena* spp. (Cohen and Gurevitz 1991; Haider et al. 2003; Paerl et al. 2001). Although the factors that trigger these specific blooms in Santa Olalla have not been identified with certainty, it is clear that the species that bloomed during the pH maxima must be at least highly alkalitolerant, being able to grow at pH close to 11. Interestingly, and for comparison, a very large number of isolated alkaliphilic prokaryotic species have maximal growth pH values not higher than 10–10.5. Many of these cyanobacteria living

Table 2 Phytoplankton species observed during the two highest pH maxima that occurred in Santa Olalla during 1998–1999. The percentage of cyanobacterial species with respect to the total cyanobacteria is given in brackets

Cyanobacteria	August 1998 (pH 10.58)	May 1999 (pH 10.77)
Anabaena aphanizomenoides	+ (< 0.1)	+ (11.9)
Anabaena sp.	–	+ (< 0.1)
Anabaena spiroides	+ (< 0.1)	–
Anabaenopsis circularis	+ (< 0.1)	+ (0.6)
Anabaenopsis tanganikae	+ (< 0.1)	+ < 0.1)
Aphanocapsa delicatissima	+ (< 0.1)	–
Aphanothece clathrata	+ (92.5)	+ (< 0.1)
Chroococcus dispersus	+ (7.2)	+ (< 0.1)
Leptolyngbya sp.	–	+ (50.1)
Limnothrix amphigranulata	–	+ (< 0.1)
Merismopedia tenuissima	–	+ (23.6)
Microcystis aeruginosa	+ (< 0.1)	+ (9.3)
Oscillatoria sp.	+ (< 0.1)	+ (< 0.1)
Pseudanabaena limnetica	–	+ (< 0.1)
Raphidiopsis mediterranea	+ (0.3)	+ (4.4)
Chlorophyta		
Coelastrum sp.	–	+
Golenkinia sp.	–	+
Monorraphidium contortum	–	+
Lagerheimia ciliata	+	+
Oocystis parva	–	+
Pediastrum boryanum	+	+
Pediastrum tetras	–	+
Scenedesmus acuminatus	–	+
Scenedesmus acutus	–	+
Scenedesmus opoliensis	+	+
Scenedesmus quadricauda	+	+
Scenedesmus sp.	–	+
Tetraedron minimum	+	+
Tetraedron triangulare	–	+
Tetrastum staurogenieformis	+	–
Euglenophyta		
Trachelomonas sp.	–	+
Diatoms (Bacillariophyta)		
Cyclotella meneghiniana	–	+
Stauroneis sp.	–	+

in Santa Olalla are also frequent at near-neutral pH, such as several species of the genera *Microcystis*, *Aphanothece*, and *Anabaena*. This indicates that these cyanobacteria have very wide ranges of optimal pH conditions from neutral to very alkaline levels, as they reach very high numbers under alkaline conditions. Cyanobacteria are indeed among the best-adapted bacterial groups to very diverse extreme conditions since, with the exception of very low pH, they can also tolerate high salt concentrations, below-zero temperatures to very high temperatures (up to ~70°C), and strong irradiation and xerophilic conditions (Cohen and Gurevitz 1991; Gordon et al. 2000; Paerl et al. 2000).

Other phytoplankton components

Despite the overwhelming cyanobacterial dominance in Santa Olalla under alkaline conditions, various species of phytoplanktonic eukaryotes were identified in the lake water (Table 2, Fig. 2). Interestingly, the diversity observed was broader during the highest pH maxima (pH 10.77), although most likely other environmental circumstances concurred that allowed their development (temperature, nutrient availability). Most eukaryotic photosynthesizers identified were chlorophytes, although some euglenoids and diatoms were also detected (Table 2). In contrast to the situation observed at pH > 9, phytoplanktonic eukaryotes were very abundant and diverse at the starting point of our study at near-neutral pH. This suggests that those eukaryotes were more sensitive to alkaline conditions, since they appeared to be largely outcompeted by cyanobacteria.

In addition to phytoplankton, we observed other planktonic components, primarily bacteria, which were particularly abundant, but also protozoa, although their study was outside the scope of this work. The presence of very abundant communities of heterotrophic bacteria associated with phytoplankton blooms in shallow lakes is well documented (Kirschner et al. 2002), including Santa Olalla itself, as can be deduced from the nature and abundance of the lipids accumulated in sediments (Grimalt et al. 1991).

Overall, Santa Olalla's phytoplankton diversity was low as confirmed by the Shannon-Weaver index (Table 1, Fig. 1). Low-diversity environments give Shannon-Weaver indices (H′) ≤ 2.5 (Margalef 1972; May 1975). In our case, values slightly above 2.5 were seen only in February–March 1998, after intense rainfall, before cyanobacteria became dominant. In general, the values calculated monthly during the 2 years were lower than 1, which implies very low diversity levels (Fig. 1). The lowest H′ values were calculated from August to December 1998 (Fig. 1), coincident with the *A. clathrata* bloom (which accounted for 92.15–99.60% of the total cyanobacteria during this period). Only two Shannon-Weaver index values were higher than 1 after the pH stabilized at > 9, those corresponding to July 1998 (1.69) and May 1999 (2.32). The latter value is surprising, since it corresponds to the highest pH value measured (10.77). Although there is not a clear explanation for this observation, a possible cause for the diversity increase would be a higher nutrient input provided by spring rainfalls. Nevertheless, statistical tests show a slight but significant negative correlation between pH and diversity ($r = -0.568$, $P = 0.022$). At any rate, shallow lakes of these characteristics are very fluctuating systems, and it is very difficult to identify the impact of each of the different environmental parameters upon the diversity and temporal evolution of the microbial community.

Conclusions

We have studied the phytoplankton diversity and abundance in the permanent shallow lake Santa Ollala, which showed stable alkaline pH values (average 9.52) during 1998 and 1999. Historical records of alkaline pH

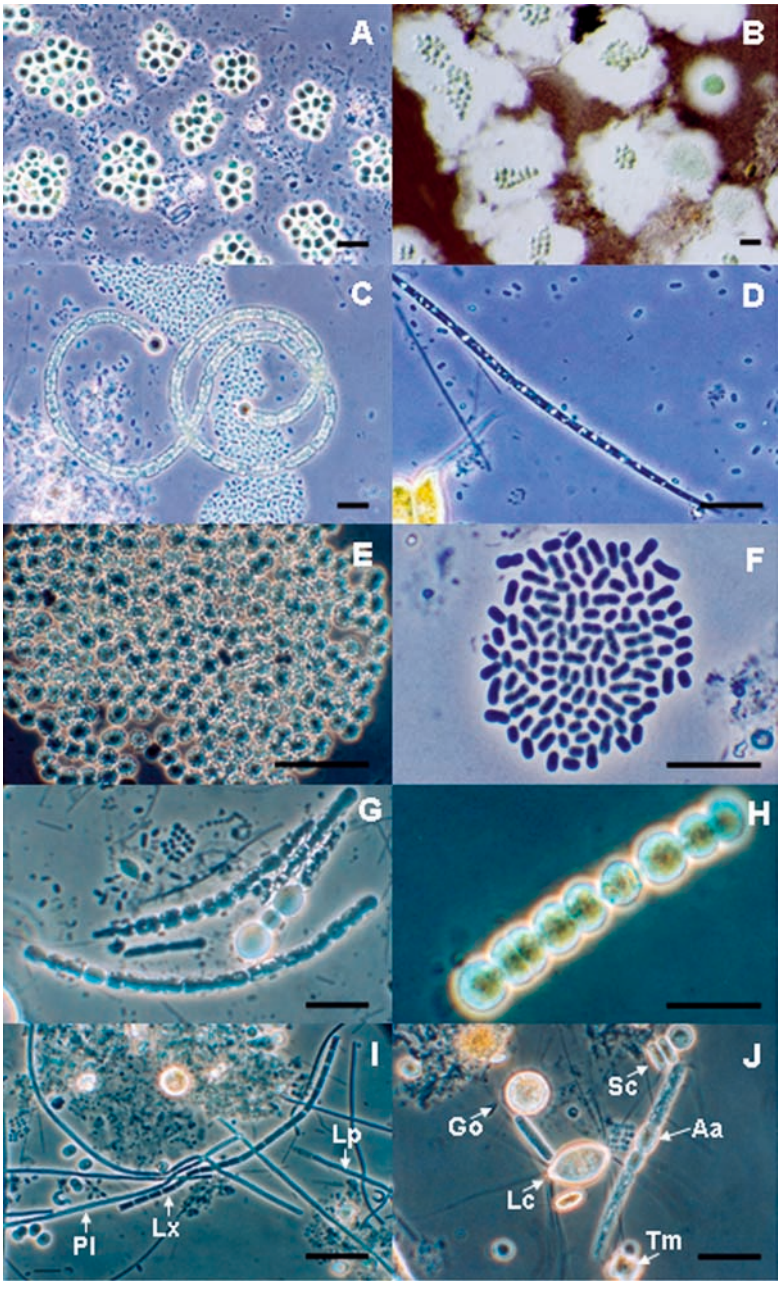

Fig. 2 Micrographs of different phytoplanktonic species observed by optical microscopy in Santa Olalla during two pH maxima (August 1998, pH 10.58 and May 1999, pH 10.77). Panels correspond to **A** *Chroococcus dispersus* colonies; **B** *C. dispersus* colonies stained with Indian ink and seen using bright field to show the extent of surrounding mucilage; **C** *Anabaenopsis tanganikae*; **D** *Raphidiopsis mediterranea*; **E** *Microcystis aeruginosa*; **F** *Aphanothece clathrata*; **G** *Anabaena aphanizomenoides*; **H** *Anabaena spiroides*; **I** cells of the cyanobacteria *Leptolyngbya* sp. (*Lp*), *Limnothrix amphigranulata* (*Lx*), and *Pseudanabaena limnetica* (*Pl*); and **J** filament of the cyanobacterium *A. aphanizomenoides* (*Aa*) and cells of the green algae *Golenkinia* sp. (*Go*), *Lagerheimia ciliata* (*Lc*), *Scenedesmus* sp. (*Sc*), and *Tetraedron minimum* (*Tm*). Pictures **A–F** and **H** correspond to August 1998; panels **G**, **I**, and **J** correspond to May 1999. All micrographs were taken under phase contrast unless otherwise specified. *Scale bars* correspond to 10 μm

during the last 30 years indicate that it is a stable, highly alkaline system. This stability may be disrupted by episodic massive rainfall periods, but it is very rapidly recovered. Santa Olalla's microbial populations must therefore be alkaliphilic and/or highly alkalitolerant, since pH can frequently exceed 10.5. Furthermore, since underground input water is neutral, the high-alkaline conditions of the system appear to be a consequence of cyanobacterial activity. Not only is primary production extremely high in this hypereutrophic lake, but also cyanobacteria dominate phytoplankton to reach levels of up to 98–100%, sometimes due to blooms of single species (*A. clathrata*). The high pH generated establishes a positive feedback in the system since, in turn, more carbon is available for primary production and nutrients such as phosphorous become more soluble (Talling and Talling 1965). Santa Olalla is therefore a system where the extreme conditions, high pH in this case, are produced and sustained by the biological components of the ecosystem. The situation is equivalent to that observed in some acidic settings where extremely low pH values are generated by the activity of chemolithoautotrophic bacteria, mostly *Acidithiobacillus* and *Leptospirillum*, which release sulfuric acid to the environment and are strict acidophiles (Harrison 1984). In this context, the systematic exploration of non-hypersaline, high-pH environments, such as Santa Olalla and other hypereutrophic lakes, will allow the identification of new alkaliphilic and alkalitolerant microorganisms. It will also increase our understanding on how microbial

communities generate and maintain the homeostasis of biologically generated extreme environments.

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