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Hydrological cycle and interannual variability of the aquatic community in a temporary saline lake (Fuente de Piedra, Southern Spain)

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Abstract

Fuente de Piedra is a shallow, temporary saline lake whose seasonal behavior is strongly dependent on the annual hydrological budget. In this study, we outline the characteristics of Fuente de Piedra Lake for two years that had different hydrological budgets. The high precipitations in 1989–90 caused the lake not to dry as usual, and decreased both salinity and the amplitude of changes. There were also differences in nutrient dynamics, with generally lower concentrations of soluble reactive phosphorus and ammonium, whereas in the more humid year nitrate showed a distinct maximum in winter. Winter bloom chlorophyll *a* concentrations were also much higher in 1989–90 ($>600\ \mu g\ l^{-1}$) but there was also a winter productive phase that was presumably poorly coupled with consumption processes that predominate in spring. Planktonic assemblages were different between years. Highly halotolerant phytoplankton species (*Dunaliella salina* and *D. viridis*) became scarcer, and especially two previously unrecorded diatoms (*Cyclotella* sp. and *Chaetoceros* sp.) became dominant in the bloom time in the wet year. The species richness of the zooplankton increased in the wet year, with new species appearing that were not collected during 1987–88 (*Branchinectella media, Daphnia mediterranea, Macrothrix* sp., *Arctodiaptomus salinus, Cyclops* sp., *Sigara* sp...). There was also a much higher development of macrophytes (*Ruppia drepanensis, Althenia orientalis, Lamprothamnium papulosum*) and bird populations, especially flamingoes (*Phoenicopterus ruber*).

Important interannual variations in this sort of system point to the need for long term studies to observe the whole range of states that define the lake as an entity.

Introduction

Many saline lakes in endorheic basins in arid or subarid regions, are very shallow and are usually temporary since precipitation is exceeded by evaporation. These temporary waterbodies may constitute the greatest part of the natural waters in temperate latitudes. They are strongly dependent on the hydrological budget, and then limnological and ecological characteristics have a large interannual variability. As they become shallower with a surface to volume ratio (S:V) tending to be higher, they become gradually more physically controlled. These characteristics result in a higher interannual variability and lead to a quite different physical-chemical environment and behavior from one year to another mainly according to the hydrological budget and the sequence of precipitation (Comin et al., 1990; García, 1991, Comin et al., 1992; García-Ruiz et al., 1993). Although prediction of the states to be expected for each lake could *a priori* be hypothetically possible using models based on hydrological behavior, this is difficult since variability depends on many fortuitous environmental events that become more important as the S to V ratio of the lake increases. A marked effect of recent hydrological history is also important (Comín et al., 1992). On the other hand, there are not many long term limnological observations on very shallow saline lakes at present. These lakes are likely to undergo complete desiccation and they are only permanent occasionally. This makes it difficult to distinguish regularities linked to this hydrological forcing. Thus, although there are some data in the literature on the seasonality of saline lakes (see Hammer (1986) for review) there are less studies on interannual variability (Hammer, 1986; Stephens, 1990; Comín et al. 1991, 1992).

Fuente de Piedra Lake combines the morphological and limnological characteristics of these very shallow saline lakes, having some infrequent episodes of permanence but usually becoming dry in the summer. The only long term observations on Fuente de Piedra Lake are those of its hydrological budget (from 1962). Community and environmental characteristics have only been studied in 1987–88, 1988–89 and 1989–90. Unfortunately, observations for 1988–89 were few and systematically difficult to compare to those of 1987–88 and 1989–90. Seasonality characteristics of 1987–88 have been well reported (García, 1991; García & Niell, 1993; García et al., 1995). But hydrological characteristics for 1989–90 were quite different, leading to a very different behavior of the system. During 1989–90, rainfall exceeded markedly to that registered in the previous 28 years and the lake did not become dry in the summer period as usual.

In this study, we compare the physical, chemical and biological characteristics of the aquatic system of Fuente de Piedra Lake for these two hydrological cycles. The results show, as expected, drastic changes both in the water characteristics and community, with an increase in species richness for the more rainy year. The seasonal cycle follows a similar general pattern, with a productive phase in winter and a consumer phase in spring, but phytoplankton biomass values, as estimated by chlorophyll concentration, were higher in the more humid year by one order of magnitude in the winter pulse. Taxonomic differences were also very important, planktonic species not observed in 1987–88 appeared, and the macrophytes showed a much greater development. We discuss the effects of variable rainfall on the aquatic community of Fuente de Piedra, and stress the need of long term studies to understand this sort of systems, because it is necessary to register variations for several years in order to observe the whole range of states that conform the lake as an entity.

Material and methods

Fuente de Piedra saline lake is located in an endorheic basin of 152 km^2, at 400 m over sea level, in the south of the Iberian peninsula (37° 6′ N 4° 44 W) (Figure 1). The general characteristics of the aquatic community of the lake have already been described elsewhere (Niell & Lucena, 1986; García Niell, 1993, García et al., 1995).

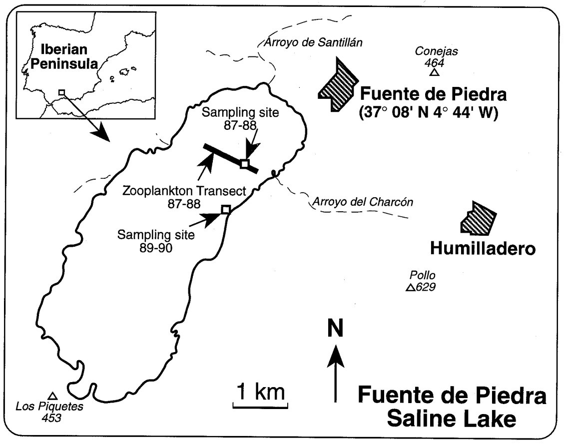

Figure 1. Location of Fuente de Piedra Lake, showing the location of sampling sites for 1987–88 and 1989–90. Zooplankton samples were taken following a transect in 1987–88.

Sampling was carried out monthly in the hydrological cycle 1987–88 (from September to July) and twice a week in 1989–90 (from December, when an unusual high rainfall was detected). Sampling stations have been represented in Figure 1.

Data of precipitation and evaporation have been taken from ‘Instituto Geológico y Minero de España’ reports (IGME, 1988, 1991).

Water samples for conductivity, salinity, nutrient and chlorophyll analyses were collected submersing a 1 l bottle in the shallow water, from the bottom to the surface, then filtered through *Whatman* GF/C ($\sim 1.2\ \mu$m) fiber filter. Water was then frozen and filters extracted in acetone to estimate pigment concentrations.

Conductivity was determined with a CRISON 525 conductivimeter with analogical temperature correction at 25 °C. Salinity was estimated as Total Dissolved Solids (TDS) that was determined by weighing 100 ml of filtered water sample (GF/C) after desiccation at 105 °C.

Nutrient analyses were carried out with a Technicon II Autoanalyzer. Nitrate and nitrite were measured using the method of Shinn (1941) and Wood et al. (1967), ammonium following Slawyk & McIsaac (1972) and soluble reactive phosphorus (SRP) following Fernandez et al. (1985).

Total particulate carbon analyses were performed on particles retained on a *Whatman* GF/F ($\sim 0.7\ \mu$m) filter. The filters were dried (80 °C, 24 h) and stored in a freezer until analysis in a *Perkin Elmer* 240-C CNH elemental analyzer at 650 °C (Culmo, 1986). These analyses were only done for 1989–90.

Chlorophyll *a* concentration was estimated from Whatman GF/C filters following Talling & Driver (1963). Filters were extracted in a refrigerator at dark for 24 h with sodium carbonate neutralized acetone.

Phytoplankton samples were preserved *in situ* with lugol-acetic acid solution (Parsons et al., 1984). Algal counts were made using an inverted microscope after sedimentation of 2.5 to 15 ml subsamples according to Utermöhl (1958) method.

Water samples for zooplankton analyses were collected monthly with a manual pump from a 30 cm diameter cylinder driven into the sediment, containing a known water volume. This water was filtered through two consecutive meshes of 500 and 100 μm grid size. Samples were concentrated *in situ* and preserved in 5% formol (final concentration). Zooplankton was counted in a Bogorov tray (Parsons et al., 1984).

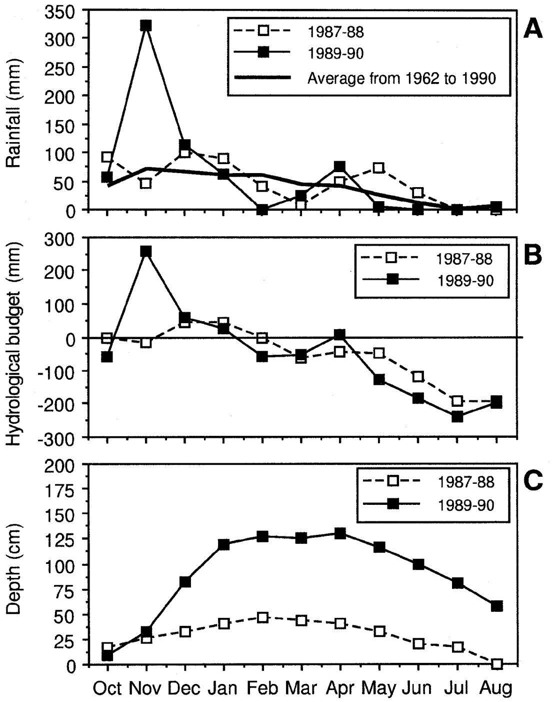

Figure 2. Precipitation (A) in the lake Fuente de Piedra in the cycles 1987–88 and 1989–90 as well as the average from 1962. (B) Hydrological budget (precipitation minus evaporation) for the hydrological cycles 1987–88 and 1989–90. (C) Water depth in the lake (cm) during 1987–88 and 1989–90.

Results

Hydrological budget, depth and salinity

The hydrological cycles that have been studied were in general more humid than the average from 1962 (I.G.M.E., 1988, 1991). Nevertheless, the hydrological cycle 1989–90 was much more rainy (713.5 mm) even more than 1987–88 (557.5 mm). Thus, precipitations in 1989–90 turned out to be the highest registered in the region from the first IGME reports (the mean precipitation for the last 28 years was 470 mm) (Figure 2A), most of the precipitation in 1989–90 occurred from late November to early December, and it can be stated that the study covers most of this anomalous cycle, with a lag of less than a month from the beginning of the highly wet conditions. Mean temperature was also higher (17.6 °C) than the 28 previous years average (15.9 °C). All hydrological cycles in the lake usually have a filling phase from the fall to the spring and a drying period that usually ends at the beginning of the summer when the lake becomes completely dry. The main preliminary difference between cycles resided in permanence, thus, during 1987–88 the lake became dry on July 18, but in 1989–90 the lake did not become dry and behaved as a permanent saline lake being quite more deeper and less saline (Figures 2C and 3).

In 1987–88 the filling phase started with the fall precipitations, and the drying phase, i.e. when evaporation exceeds precipitation, started in February, while in 1989–90 a continuous drying phase did not start until the end of April (Figure 2B). The hydrological budget is obviously related to increasing and decreasing depths of the water column in the lake, that maintained a far higher level of water in 1989–90 than in 1987–88 (Figure 2C).

Water column depths have changes correspondent to those of salinity. TDS ranged from 30 g l^{-1} in February to 220 g l^{-1} in June in the cycle 1987–88 and from 9 g l^{-1} in winter to 90 g l^{-1} at September 21 in the 1989–90 cycle (Figure 3). Therefore, difference of salinity values among years is remarkable. Whereas in 1987–88 the lake could be named as ‘hypersaline’ (>50‰) for most of the time, in 1989–90 salinity was under 20 g l^{-1} for most of the year (until summer when salinity started to rise exponentially). Thus, a

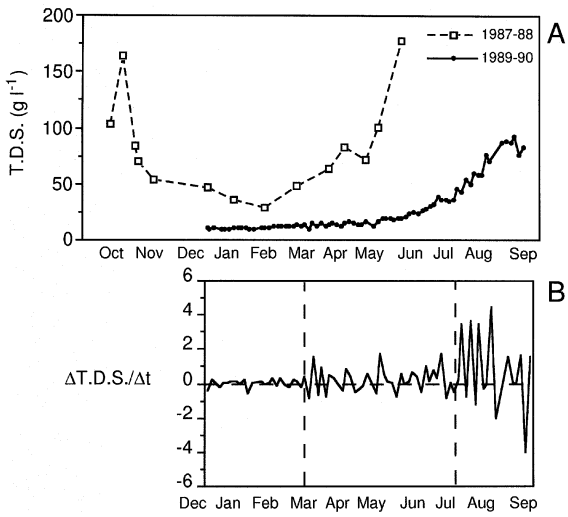

Figure 3. (A) Changes in time in Total Dissolved Solids (TDS) for the cycles 1987–88 and 1989–90. (B) Amplitude of changes per unit time in TDS values during the hydrological cycle 1989–90.

salinity value near that typical of the sea (35 g l^{-1}) is not obtained until the end of July 1990.

Changes in TDS are usually fair in the middle of the cycle, but become exponential when the drying phase advances. Figure 3B shows the result of considering increment of salinity per unit time ($\Delta S/\Delta t$) *vs* time of the year (this was done only for 1989–90 because we had salinity data twice a week). These environmental fluctuations increase gradually, specially when the drying phase is advanced. This is caused not only because salinity values are increasingly higher, but probably also by the gradual increase in the S to V ratio of the body of water.

We also present a relationship between specific conductance and TDS, built on the wide register of salinity in the lake combining data for both years. This relationship is illustrated in Figure 4 as a hyperbolic function (Eq. 1) that can be useful for future studies of this athalasohaline lake.

$$\mathrm{TDS} = 210\,C/(298.9 - C) \qquad (1)$$

C = specific conductance (mS cm^{-1});
TDS = Total dissolved solids (g l^{-1}).

Nutrient concentration

Nutrient concentration in the water also followed different patterns for each year.

Phosphate concentration in 1987–88 was in general higher (average value of 3.18 ± 6.81 μM, excluding the highest values) and with changes of higher amplitude (which is reflected also in s.d. values) than in the rainy cycle (average value of 0.54 ± 1.18 μM) (Figure 5A). For this last cycle (1989–90), peaks of exceptional concentration values as detected in 1987–88 were not observed even with a higher temporal resolution.

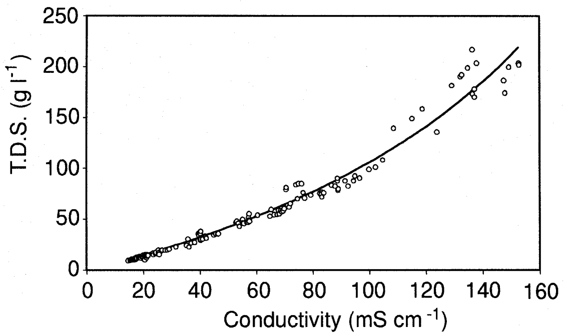

Figure 4. Hyperbolic relationship between TDS and conductivity in Fuente de Piedra Lake. Data from the hydrological cycles 1987–88 and 1989–90 have been used to obtain a wide range of possibilities.

Nitrate concentrations in the cycle 1987–88 peaked in autumn and were undetectable in winter (Figure 5B). The cycle 1989–90 presented marked differences with 1987–88 during winter. Whereas concentration values during filling phase in winter 1990 are very high, values in spring and summer remain low as in 1987–88. Nitrite concentrations have similar levels for both cycles, although slightly higher for 89–90, that has also a more marked and clear separation between winter (higher) and summer values. Values in 87–88 did not follow any clear separation in phases in spite of a peak in summer, just near complete drought (Figure 5C).

Concentration of ammonium (Figure 5D) has a clear seasonal pattern in 1987–88 parallel to both filling/drying stages and salinity. Ammonium concentration changes in 1989–90, however, appear as damped, although there is a maximum appearing just after the phytoplankton bloom ends (see also Figure 6A). Although ammonium concentration showed, in general, an opposed pattern compared to nitrate in both cycles, this fact is more evident for 1989–90.

Particulate carbon and chlorophyll concentration

Total particulate carbon in the water (1989–90) shows a slight tendency to decrease throughout the growing time in winter (Figure 6B) and then an increase from the end of spring to high summer levels. The seasonal patterns of particulate carbon in the water differ from

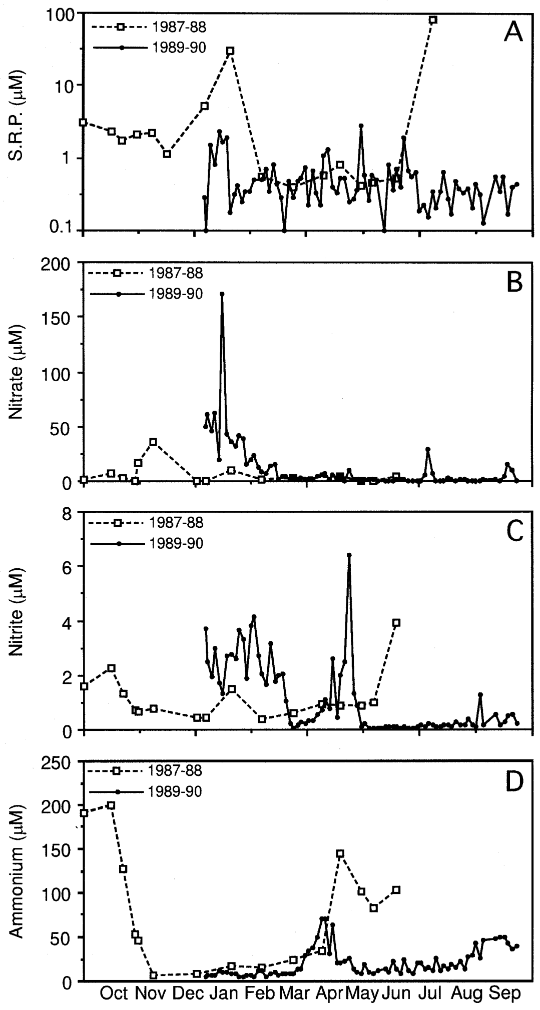

Figure 5. Seasonal variations in nutrient concentrations, soluble reactive phosphorus (A), nitrate (B), nitrite (C) and ammonium (D) during 1987–88 and 1989–90.

this of chlorophyll in 1989–90 (Figure 6A) in such a way that it suggests a gradual predominance of small heterotrophs in the water toward the summer.

Chlorophyll *a* concentration values were markedly higher in the winter bloom during the 1989–90 cycle than in 1987–88 (Figure 6A). The very high values at the end of January 1990, are followed by a phase with high levels and then fall to very low levels of chlorophyll at the beginning of the spring. Changes in 1987–88 are quite less marked compared to those of 1989–90 and the level of chlorophyll always remains moderate considering the nature of the lake.

Maximum values of chlorophyll in this saline lake usually occur during winter, linked to precipitations and filling phase. A secondary maximum is detected in both cycles; one occurring in June for the cycle 1987–88 and the other in August for 1989–90.

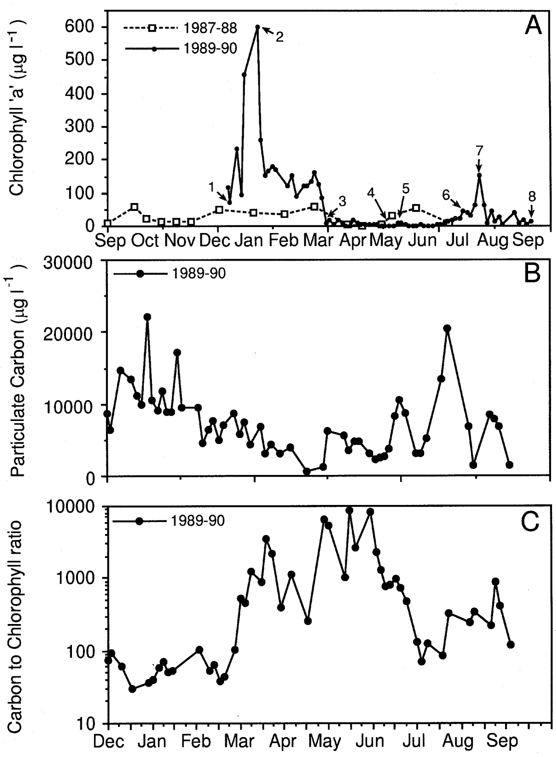

Figure 6. (A) Chlorophyll *a* concentration in the water in the cycles 198788 and 1989–90. Numbers refer to the samples taken for phytoplankton abundance analyses (B) Particulate Carbon in the water (1989–90) and (C) Carbon to Chlorophyll ratio in the water (1989–90).

Community characteristics: phytoplankton and zooplankton

Changes in the community structure in a single lake according to hydrological budget is one of the characteristics of very shallow, temporary lakes. Usual changes along a salinity gradient and that have been described by several authors for different lakes (Por, 1980; Hammer, 1986) occur in this single lake during a hydrological cycle (seasonal changes) (García & Niell, 1993) as well as in a larger, interannual time scale as is expressed in this paper and elsewhere for shallow saline lakes (Comín et al., 1991, 1992).

At the beginning of the hydrological cycle 1987–88, coinciding with a high salinity (104 g l^{-1} in October 5165 g l^{-1} in October 28), the highly halotolerant species *Dunaliella viridis* Teod. and *Dunaliel-*

Table 1. Abundance of nano and microplankton (ml^{-1}) and larger zooplankton (l^{-1}) during 1987–88.

1987–88 (ml^{-1})	October	November	December	January	February	March	April	May	June	July
Diatoms (total)	59594.6	695.8	10263.0	13480.0	17222.0	229622.0	1341.9	9534.5	12558.0	2707.5
*Nitzschia closterium**	*	*	*	*	1043.7	209400.0	*	*	*	*
Tetraselmis apiculata	–	–	–	3479.0	32877.0	10437.0	820.1	–	–	–
Oocystis sp.	*	*	–	579.8	1043.7	2609.3	670.7	8.8	–	–
Dunaliella viridis	3673.2	1913.5	2261.4	–	–	–	–	562.0	36856.0	1634.8
Dunaliella salina	17650.5	521.9	174.0	–	–	–	–	–	10600.0	1941.3
Oscillatoria sp.	*	*	–	–	1304.6	–	–	240.8	1631.0	2503.9
Other Cyanobacteria	*	*	7827.9	–	–	–	820.1	–	–	–
Gymnodinium sp.	–	7306.0	9393.5	6088.3	1826.5	652.3	1267.4	–	–	–
Other Flagellates (Total)	–	7653.9	5740.5	3903.7	18004.0	19570.0	2907.5	5459.7	9784.9	–
Fabrea salina	12.25	9.60	1.20	–	–	–	13.20	10.00	44.00	–
Strombidium sp.	*	*	159.41	234.58	–	11.2	–	–	–	–
Cyclidium sp.	*	*	50.72	69.74	–	–	–	–	–	–
Euplotes sp.	*	*	–	6.34	174.4	–	–	–	–	–
Other ciliata	1.70	174.35	14.49	–	1.6	56.8	4.10	31.60	2.80	–
Hexarthra sp.	–	1.20	2.40	0.8	2.00	–	–	–	–	–
Synchaeta sp.	–	–	–	–	7.60	–	–	–	–	–
Other (nano- microplankton)	*	*	2957	13050	26094	40444	3206	2489	27725	2452

1987–88 (l^{-1})	December	January	February	March	April	May	June	July
Cletocamptus retrogressus	40.89	99.15	73.68	538.73	684.43	101.08	51.27	–
Moina salina	0.097	0.218	0.101	0.636	254.700	203.570	0.247	–
Branchinella spinosa	0.112	0.065	0.095	0.036	0.010	–	–	–
Eucypris mareotica	0.300	0.326	0.202	0.955	0.767	2.465	0.035	–

la salina Teod., as well as several species of diatoms (mostly *Navicula* spp and *Hantzschia amphioxys* (Ehr.) Grunow) were abundant (Table 1). These are the same phytoplankters that dominated at the end of the cycle (June, July) when extreme values of salinity occurred (178 g l^{-1} June, $\sim$ 400 g l^{-1} July) and that were scarce in the samples of 1989–90, except for those of the highest salinity values (September) when *Dunaliella* spp appeared, but with a lower importance than in 1987–88. At this time the more abundant diatoms in 89–90 were represented by *Entomoneis* sp and *Nitzschia* spp. (mainly *N. closterium* (Ehr.) Smith).

Other species, common to both years, had a lower representation in 1989–90 (see Tables 1–3). This is the case for the ciliate *Fabrea salina* Henneguy, that can also be ascribed to highly saline waters (Post et al., 1983; Yufera, 1985) and that reached abundances lower by one order of magnitude, or the dinoflagellate *Gymnodinium* cf. *excavatum* Nyg. a very important winter species in 1987–88 that was very scarce in 1989–90 and developed at different salinity ranges for each year.

This is not the case for *Tetraselmis apiculata* (= *Platymonas apiculata*) Butcher that, in both cycles became the dominant phytoplankter when salinity was lower, and that constituted the dominant species in the winter bloom associated to rain events (Tables 1 and 2). This species, together with a very small centric diatom (cf. *Cyclotella* sp.) were responsible for the remarkable maximum of chlorophyll *a* concentration (600 μg l^{-1}) in January 1990.

Other phytoplankton species that were not present in the less humid cycle, were abundant in 1989–90. Thus, a solitary, very small species of *Chaetoceros* was a constituent of the initial phase of the winter bloom (Table 2). This was also the case of a species of *Chlamydomonas* and several species of flagellates that are usually assigned rather to a heterotrophic role, and that were specially abundant in the post-bloom phase.

There were also noticeable changes for small microzooplankton. Thus, besides the mentioned case of *Fabrea salina*, ciliates were quite less abundant in the wet year and this was also the case for rotifers, although a different species appears in 1989–90 (*Bra-*

Table 2. Abundance of nano and microplankton (ml^{-1}) during 1989–90. Selection of samples was made on chlorophyll results and have been marked on Figure 6.

1989–90 (ml^{-1})	29 December	23 January	27 March	22 May	29 May	27 July	10 August	27 September
Cyclotella sp.	301808.00	224399.00	4435.80	–	6958.11	260.93	–	–
Chaetoceros sp.	4348.82	–	–	–	23918.51	–	–	–
Nitzschia closterium	–	–	–	–	652.32	1043.72	9132.54	1461.21
Entomoneis sp.	–	–	–	–	–	–	–	1669.95
Other diatoms	2043.50	–	–	365.30	–	2609.30	22831.34	313.12
Tetraselmis apiculata	8697.65	266148.00	14090.20	–	–	–	–	–
Oocystis sp.	–	–	260.93	26.10	–	–	–	–
Spermatozopsis sp.	2609.30	3913.94	–	–	–	–	–	–
Chlamydomonas sp	–	–	2087.44	–	–	1956.97	5218.59	626.23
Dunaliella viridis	–	–	–	–	–	–	–	521.86
Dunaliella salina	–	–	–	–	–	–	–	104.37
Oscillatoria sp.	–	–	–	–	–	–	652.32	–
Spirulina sp.	–	–	–	–	–	–	5218.59	–
Other Cyanobacteria	–	–	–	260.93	1956.97	782.79	–	–
Gymnodinium sp.	204.35	–	–	–	–	–	–	–
Chrysophyceans	6958.12	–	–	–	–	–	–	–
Peranema sp.	–	–	–	–	–	–	–	208.74
Cryptomonas sp.	–	–	–	–	2391.85	–	–	–
Other Cryptophyceans	–	–	–	–	1304.65	–	–	–
Bodo sp.	–	–	–	78.28	–	–	–	–
Other colorless flagellates	–	–	–	1800.42	–	2087.44	–	1983.07
Amoebae	–	–	–	0.08	–	–	–	–
Fabrea salina	–	–	–	–	–	4	4.4	3.2
Other ciliata	204.35	–	1.20	0.48	–	–	–	–
Brachionus sp.	–	–	–	–	–	0.003	–	–
Turbellarians	–	–	–	–	–	–	0.002	0.017
Other (nano- microplankton)	45227.70	11741.83	2348.37	78.28	652.32	–	16308.10	–

Table 3. Abundance of larger zooplanktonic species (l^{-1}) during 1989–90.

1989–90 (l^{-1})	December	January	February	March	April	May	June	July	August	September
Cletocamptus retrogrossus	158.30	86.70	295.70	239.73	371.60	84.82	222.50	52.06	4.77	415.70
Cyclops sp.	370.10	295.00	27.23	77.80	4.30	–	–	–	–	–
Arctodiaptomus salinus	0.09	0.33	0.51	2.00	0.80	5.10	105.20	30.90	3.42	–
Copepods (larvae)	10.10	9.17	13.04	133.00	5.70	4.20	32.40	–	0.21	14.00
Moina salina	0.365	0.521	0.343	6.500	–	2.920	28.400	12.99	9.16	80.20
Daphnia mediterranea	0.155	0.034	1.566	13.520	34.5	14.1	–	–	–	–
Macrothrix sp.	–	–	–	0.010	–	–	–	–	–	–
Branchinella spinosa	0.274	0.020	0.190	0.078	–	–	–	–	–	–
Branchinectella media	0.042	–	–	–	–	–	–	–	–	–
Ostracods	2.40	3.15	2.35	43.95	5.25	5.60	34.03	4.86	12.46	2.30
Corixids (*Sigara* sp.)	0.007	–	0.009	–	0.020	0.100	0.980	2.100	0.999	0.060
Dytiscids (cf. *Hydroporus* spp.)	–	–	–	–	–	–	0.024	0.009	–	0.010
Dytiscids (larvae)	–	–	–	–	0.160	0.009	0.056	0.009	–	–
Chironomids (larvae)	0.05	1.03	–	0.01	1.47	1.60	0.99	1.43	0.56	–
Other Diptera (larvae)	–	–	–	0.04	–	–	0.09	–	–	–

chionus sp.) that did not had a maximum of abundance associated to the rain-bloom event, as was the case of *Synchaeta* sp and *Hexarthra fennica* Levander in 87–88 (Table 1). A turbellarian, not observed in 87–88, also appeared at the end of the 1989–90 cycle.

The most conspicuous changes in the aquatic community occurred for larger zooplankters. Although there were coincidences, and some species appeared during both cycles, there was a higher species richness in 1989–90.

In both cycles the copepod *Cletocamptus retrogressus* Schmankevitch was always present throughout the year and it seems to be a constant feature of this system as it was also observed in the very dry 1988–89 cycle (Sáez et al., unpublished). Nevertheless, two more species of copepods, with a more planktonic behavior, appeared in the wet year, a cyclopoid copepod and the calanoid *Arctodiaptomus salinus* Daday that has been widely registered in Spanish saline lakes (Margalef, 1947; Alonso, 1990).

The cladoceran Moina salina Daday was also present in both cycles, although in 1987–88 it had an occurrence more concentrated in time with a spectacular proliferation in April and May that coincided with a decrease in phytoplankton abundance.

Probably due to permanence and the lower levels of salinity the apparition of new cladoceran species in 89–90 is propitiated. *Daphnia mediterranea* Alonso, also registered as an usual species of the endorheic basins in the region (Alonso, 1990) was collected regularly until May, disappearing in the summer months. A species of *Macrothrix* (March) with low densities was also recorded punctually.

Among larger crustaceans, the anostracean *Branchinella spinosa* Milne-Edwards appeared during winter in both cycles, but in the more humid year, another related species, *Branchinectella media* Schmankevitsch, was also recorded just at the beginning of the rainy period (December), thus showing a rapid response to rainfall and filling of the lake. This species has also been mentioned as characteristic of Spanish saline waters and has been related to an increase in the sulphate proportion (Alonso, 1990) that is likely to occur as salinity decreases.

Another manifest change in the aquatic community was a better development of largest organisms, whereas in 1987–88 the largest aquatic organism turned out to be the anostracean *B. spinosa*, in 1989–90 several species of insects (corixids (*Sigara* sp) and dytiscids (cf. *Hydroporus* spp) as well as larvae of diptera) apart from the other anostracean *B. media* appeared. The insects moved freely in the water column and were specially abundant in summer coinciding with a phase of unusual development of benthic structure in the lake.

Observations of seasonal stages also showed a much greater importance of macrophytes in 1989–90. The most abundant species, *Ruppia drepanensis* Tin. ex Guss. that had loosely scattered small (<20 cm) plants at the bottom of the lake in 1987–88, covered extensive surfaces of the bottom in the summer of 1989–90 and reached unusual large sizes (up to 75 cm). *Althenia orientalis* subsp. *betpakdalensis* (Tzelev) García Murillo & Talavera was also more abundant and this was also the case for the charophyte *Lamprothamnium papulosum* (Wallr.) J. Gr.

Other changes in the aquatic community included the development of a neustonic fraction in some areas of the lake in the late summer (89–90), with floating aggregates of cyanobacteria (*Spirulina* sp. largely dominant).

Regarding to changes in abundance of waterbirds, the humid year 1989–90 registered a remarkable increase in the total number of flamingoes (*Phoenicopterus ruber roseus*), that reached a maximum of 50010 birds in August 1990. It was also a good reproductive year, a total of 13316 pairs attempted breeding and a record of 10417 chicks were hatched. During this year the reproduction of *Oxyura leucocephala*, *Podiceps cristatus*, *Podiceps nigricollis*, *Tachybaptus ruficollis* and *Aythia ferina*, waterbird species that did not usually reproduce in this lake (Rendón et al., 1991, Ramírez et al., 1992) was verified.

Discussion

Interannual variability and the need for long term studies

Precipitation events and general hydrological budget are undoubtedly a determinant factor explaining the behavior of temporary endorheic saline lakes. This fact is not only based on water level or salinity values that vary according to the incidence of filling and drying phases, but also on the fact that filling phases are accompanied with an input of allochtonous nutrients, whereas in drying phases these episodes have quite less importance. Not only the amount, but the sequence or extent in time of precipitation periods determines a characteristic series, typical for each year, that will determine the predominance and permanence of some organisms versus others, thus remembering the ‘yearclass' phenomena of Sanders (1968), characteristic of physically controlled systems. It is also necessary to add other tendencies in a longer term scale to this variability, that determine different states for similar salinity or environment circumstances depending on the recent history of the lake (Comín et al., 1992). These facts complicate the predictability and image of this sort of lakes very much and recommend extending research to a longer term basis (Williams et al., 1990, Comín et al., 1991).

The aquatic community and environment of Fuente de Piedra Lake has appeared as very different in each one of the three consecutive hydrological years observed (1987–88, 88–89 and 89–90) and this feature in the same way suggests understanding the entity of the lake on a long term observation basis, allowing the characterization and display of a wider range of possible states.

Salinity values and fluctuation

Regarding to salinity, an important forcing variable in these systems, the patterns are different between the two years: in 1987–88 salinity has much higher changes with a clear minimum in February, whereas in 1989–90 there is a lasting low salinity phase (remaining as 'hyposaline' *sensu* Hammer, 1986) that ends at the beginning of the summer when a period of quite more rapid changes occurs (Figure 3). The fluctuation of salinity values are much less pronounced in the winter than in the spring, when the filling phase is toward the end or in the summer, when water level decreases (Figure 3B). Presumably, an organism must cope with both, gradual increase of the absolute values of salinity, and the rate of salinity fluctuations of the environment, that become gradually more important when the drying phase is advanced (Figure 3B). The winter biota will grow in an environment with lesser values of salinity but also with a lesser degree of change. Although a physical forcing is the rule in these systems, this will favor a phase with a more important control by biological processes than usual, because environmental conditions can propitiate a certain equilibrium. This circumstance does not necessarily leads to an increase in species diversity in winter, as can be seen as a short term stability sensu Slobodkin and Sanders (1969), and reminds us that salinity has been found not to be a determinant factor interpreting the community state when considered alone (Williams et al., 1990 and references therein) and also that the influence of a recent history of permanence, and hence a more constant physical environment, in a lake can determine different final situations even for the same salinity average (Comín et al., 1992). On the other hand, there is a rapid increasing importance of physical control along the drying phase and a switch to wide euryhaline and then to highly halotolerant species. This effect is also observable in a wider time scale when comparing wet cycles, with damped salinity fluctuations throughout the year, with dryer cycles that undergo wider and more rapid changes in the physical environment. Salinity levels probably determine a general lower species richness in 1987–88 vs 1989–90 and can also be considered as determinant for changes in a seasonal scale in the dryer 1987–88, especially in the desiccation phase. Nevertheless, although salinity plays a role governing the very last seasonal changes of the more humid year 1989–90 (broad change between winter and summer), this factor is probably less important hence salinity covers a narrow range of values most of the time (Williams et al., 1990).

Nutrient dynamics and trophic aspects

In Fuente de Piedra Lake the filling phase, that turned out to end at the beginning or mid spring, has been related to a high autotrophs to heterotrophs biomass ratio for 1987–88 (García & Niell, 1993), being a time with primary production predominance and probable accumulation of organic matter. Filling and drying phases represented uncoupled phases of production (December 87 to March 88) and consumption (March to June 88) predominance respectively. Temporal patterns observed for 1989–90 for chlorophyll *a* concentration (Figure 6A) and particulate carbon to chlorophyll ratio in the water (Figure 6C) suggest the existence of similar phases also in this humid year. This fact seems to be supported by a higher abundance of heterotrophic flagellates among smaller fractions of plankton (Table 2). The end of the bloom and the beginning of the low chlorophyll phase, coincides not only with a time of lower inputs of water and hence allochtonous nutrients, but also with a switch from predominance of nitrate-nitrogen in the water to ammonium-nitrogen (Figures 5B and 5D) that can also be an expression of an autochtonous-based cycling stage that lasts until the end of the cycle. Phosphate, that seemed to be important for 1987–88 under the point of view of its proportion to nitrogen (N:P ratio) (García & Niell, 1993), reaches even lower values in 1989–90, being undetectable in some samples. Phosphate concentration fluctuates but with a lower amplitude than in 1987–88 and maintaining a low concentration. This would be an indication of a better coupling among uptake and remineralization. Nutrient dynamics turns out to be dependent on the characteristics of the year that can lead to marked differences in nutrient levels. Thus, the much dryer 1988–89 presented nutrient concentrations in the water two orders of magnitude higher than 1987–88 at least for the time of study (Sáez et al., unpublished results).

Seasonal trends

It is difficult to find constant seasonal regularities in a saline temporary lake as Fuente de Piedra but some seasonal trends can be distinguished and summarized as follow:

1. Initial stage: input of allochtonous nutrients. Predominance of allochtonous production linked to phytoplankters. When disturbance is strong (heavy rain periods) planktonic biota predominates much on other fractions and is characterized by a very low diversity. In Fuente de Piedra Lake, the alga *Tetraselmis apiculata* seems to be characteristic of these episodes.
2. When the filling period is about to end and allochtonous inputs are lower, a sedimentation and clearance phase of phytoplankton occurs. Water changes from turbid (plankton) to transparent and benthic mats increase their importance with respect to phytoplankters. Water samples have a lower autotrophs content and consumers predominate in the water. Values for reduced forms of nitrogen nutrients increase, as well as the C: Chl ratio.
3. In dryer years: Salinity and the amplitude of its change increases very much and zooplankters tend to decline and, finally, disappear. There is a further phase with an increase of producers biomass, represented by highly halotolerant species (*Dunaliella* spp).

In wetter years: Salinity and the amplitude of its change increases also but not to extreme values. There is a phase with neustonic patches (observed mainly Cyanobacteria) and a great development of macrophytes to large sizes not observable in normal years (*Ruppia drepanensis, Althenia orientalis, Lamprothamnium papulosum...*) as well as microbial mats thicker than usual in the sediment. This spring-summer phase coincides with low nitrate values and the more likely nitrogen source is ammonium, that reaches moderate concentration. There is also a new planktonic-neustonic producers predominance but not related to especially halotolerant species.

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References

Alonso, M., 1990. Anostraca, Cladocera and Copepoda of Spanish saline lakes. Hydrobiologia 197: 221–231.

Comín, F. A., R. Juliá, M. P. Comín & F. Plana, 1990. Hydrogeochemistry of Lake Gallocanta (Aragón, NE Spain). Hydrobiologia 197: 51–66.

Comín, F. A., R. Juliá & P. Comín, 1991. Fluctuations, the key aspect for ecological interpretation of saline lake ecosystems. Oecol. aquat. 10: 127–135.

Comín, F. A., X. Rodó & P. Comín, 1992. Lake Gallocanta (Aragón, NE Spain), a paradigm of fluctuations at different scales of time. Limnetica 8: 79–86.

Culmo, R. F., 1986. Low combustion temperature applications with an automated elemental (CNH) analyzer. Pittsburgh Conference Paper number 199.

Fernández, J. A., F. X. Niell & J. Lucena, 1985. A rapid and sensitive automated determination of phosphate in natural waters. Limnol. Oceanogr. 30: 227–230.

García, C. M., 1991. Estudio de un medio acuático fluctuante: la laguna atalasohalina de Fuente de piedra (Málaga). Ph.D. thesis, University of Málaga, 300 pp.

García, C. M. & F. X. Niell, 1991. Burrowing beetles of the genus *Bledius* (Staphylinidae) as agents of bioturbation in the emergent areas and shores of an athalassic inland kale (Fuente de Piedra, southern of Spain). Hydrobiologia 215: 163–173.

García, C. M. & F. X. Niell, 1993. Seasonal change in a saline temporary lake (Fuente de Piedra, southern Spain). Hydrobiologia 267: 211–223.

García, C. M., F. Echevarría & F. X. Niell, 1995. Size structure of plankton in a temporary, saline inland lake. J. Plankton Res. 17: 1803–1817.

García-Ruiz, R., C. M. García & F. X. Niell, 1993. El sistema acuático de la laguna de Fuente de Piedra después de una pluviosidad anormalmente alta (1989–90). Act VI Congr. esp. Limnol. Granada: 75–82.

I.G.M.E., 1986. Mapa geológico de España E. 1:50 000. Hoja 1023. Ministerio de Industria y Energía, Madrid.

I.G.M.E., 1988. Observaciones climatológicas e hidrogeológicas en la cuenca de Fuente de Piedra durante el año 1987–88. Nota técnica 336. Ministerio de Industria y Energía, Madrid, 39 pp.

I.G.M.E., 1991. Observaciones climatológicas e hidrogeológicas en la cuenca de Fuente de Piedra durante el año 1989–90. Nota técnica 380. Ministerio de Industria y Energía, Madrid.

Lund, J. W. G., C. Kipling & E. D. Le Cren, 1958. The inverted microscope method of estimating algal numbers and the statistical basis of estimations by counting. Hydrobiologia 11: 143–170.

Margalef, R., 1947. Estudios sobre la vida en las aguas continentales de la región endorreica manchega. P. Inst. Biol. Apl. IV: 5–51.

Margalef, R., 1983. Limnología. Omega, Barcelona, 1010 pp.

Niell, F. X. & J. Lucena, 1986. Comentarios sobre un sistema único: La Laguna de Fuente de Piedra, ideas de cómo planificar su investigación y su uso. Oxyura 3: 35–42.

Parsons, T. R., Y. Maita & C. M. Lalli, 1984. A manual of chemical and biological methods for seawater analysis. Pergamon, Oxford, 173 pp.

Post, F. J., L. J. Borowitzka, M. A. Borowitzka, B. Mackay & T. Moulton, 1983. The protozoa of a Western Australian hypersaline lagoon. Hydrobiologia 105: 95–113.

Ramírez, J. M., M. Rendón & J. M. Vargas, 1992. Reproducción e invernada de la malvasía (*Oxyura leucocephala*) en las lagunas endorreicas de la provincia de Málaga. Oxyura 6: 55–65.

Rendón, M., J. M. Vargas & J. M. Ramírez, 1991. Dinámica temporal y reproducción del flamenco común (Phoenicopterus ruber roseus) en la laguna de Fuente de Piedra (Sur de España). In 'Reunión técnica sobre la situación y problemática del flamenco rosa (*Phoenicopterus ruber roseus*) en el Mediterráneo Occidental y Africa Noroccidental.' Junta de Andalucía, Agencia de Medio Ambiente: 135–153.

Sanders, H. L., 1968. Marine benthic diversity: a comparative study. Am. Nat. 102: 243–282.

Shinn, J. A., 1941. Ind. Eng. Chem. (Annual edition), 13" 33. In Strickland, J. D. H. & T. R. Parson (eds), A Practical Handbook of Seawater Analysis. Fish. Res. Bd Can. Bull. 167.

Slawyk, G. & J. J. McIsaac, 1972. Comparison of two automated ammonium methods in a region of coastal upwelling. Deep-Sea Res. 19: 521–524.

Slobodkin, L. B. & H. L. Sanders, 1969. On the contribution of environmental predictability to species diversity. Brookhaven Symp. Biol. 22: 82–93.

Stephens, D. W., 1990. Changes in lake levels, salinity and the biological community of Great Salt Lake (Utah, USA), 1847–1987. Hydrobiologia 197: 139–146.

Talling, J. F. & D. Driver, 1963. Some problems in the estimation of chlorophyll *a* in phytoplankton. Proc. Conf. prim. Prod. Meas. Mar. Freshwat. Hawaii 1961: 142–146.

Utermöhl, H., 1958. Zur Vervollkomnung der quantitativen Phytoplankton-Methodik. Mitt. int. Ver. Limnol. 9: 1–38.

Williams, W. D., A. J. Boulton & R. G. Taaffe, 1990. Salinity as a determinant of salt lake fauna: a question of scale. Hydrobiologia 197: 257–266.

Wood, E. D., F. A. J. Armstrong & F. Richards, 1967. Determination of nitrate in seawater by cadmium-copper reduction to nitrite. J. mar. biol. Ass. UK. 47: 23–31.

Yufera, M., 1985. Las poblaciones de *Fabrea salina* (Ciliata: Heterotrichida) en las salinas de la Bahía de Cádiz. Inv. Pesq. 49: 439–500.