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Temporal variation of phytoplankton in two neighbouring Mediterranean shallow lakes in Doñana National Park (Spain)

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ABSTRACT

Temporal variation of phytoplankton in two neighbouring Mediterranean shallow lakes in Doñana National Park (Spain)

This study was aimed at describing the phytoplankton dynamics and structure of two eutrophic to hypereutrophic Mediterranean shallow lakes (Santa Olalla and Dulce). The two systems are close together and can function as one water body at times of heavy rainfall, but once separated, they evolve differently. The Shannon diversity index was low for both shallow lakes (average values of 1.11 in Santa Olalla and 1.79 in Dulce). The average phytoplankton Chl *a* concentrations and primary production rates were very high, although slightly higher in Santa Olalla (365.2 mg m^{-3} and 1.29 g C m^{-3} h^{-1}, respectively) than in Dulce (230 mg m^{-3} and 0.88 g C m^{-3} h^{-1}). Phytoplankton variation in the lakes was related to shifts in the physical and chemical features of lake water as well as hydrological conditions, a finding that is corroborated by the canonical correspondence analysis results, which showed a different pattern of evolution in each system. Eight functional groups were found in Santa Olalla (D, H_1, J, K, M, S_1, W_2 and Y), although the D, W_2 and Y groups were only predominant during the first four months of the study. For the rest of the period, the system was particularly dominated by the H_1, K and S_1 groups. Dulce exhibited a more complex distribution of phytoplankton functional groups over time. Ten functional groups were observed in this system (D, H_1, J, K, M, P, S_1, S_2, W_2 and Y). Some characteristics of these systems, such as rapid water volume fluctuations, low light penetration and low concentration of inorganic nutrients, are stressful conditions for phytoplankton, which may account for the low phytoplankton diversity and the equilibrium phases recorded for many months in both wetlands.

Key words: Phytoplankton dynamics, hypereutrophic shallow Mediterranean lakes, phytoplankton diversity, functional groups.

RESUMEN

Variación temporal del fitoplancton de dos lagunas someras mediterráneas contiguas del Parque Nacional de Doñana (España)

El presente estudio tiene como objetivo describir la dinámica y estructura del fitoplancton en dos lagunas eutróficas a hipereutróficas Mediterráneas (Santa Olalla y Dulce, España). Ambos sistemas están muy próximos y se unen superficialmente en periodos de fuertes lluvias, sin embargo, cuando el nivel desciende, evolucionan de forma separada. El índice de diversidad de Shannon fue bajo para ambos sistemas (valores promedio de 1.11 en Santa Olalla y 1.79 en Dulce). La concentración media de Chl a *y las tasas de producción primaria del fitoplancton fueron muy altas, aunque ligeramente superior en Santa Olalla (365.2 mg m^{-3} y 1.29 g C m^{-3} h^{-1}, respectivamente) con respecto a Dulce (230 mg m^{-3} y 0.88 g C m^{-3} h^{-1}). Las variaciones del fitoplancton están relacionadas con cambios en las características físicas y químicas del agua, así como con las condiciones hidrológicas, lo que es corroborado por el Análisis de Correspondencia Canónica (CCA), que muestra un patrón de evolución diferente en ambos sistemas. En Santa Olalla fueron observados ocho grupos funcionales (D, H_1, J, K, M, S_1, W_2 y Y), si bien los grupos D, W_2 y Y sólo predominaron en los primeros cuatro meses de estudio. El resto del tiempo, el sistema estuvo dominado sobre todo por los grupos H_1, K y S_1. Dulce mostró una distribución más compleja de grupos*

funcionales a lo largo del tiempo, observándose diez grupos (D, H_1, J, K, M, P, S_1, S_2, W_2 y Y). Algunas de las características de ambos sistemas, como la rápida fluctuación en el volumen de agua, la baja penetración de la luz o la escasa concentración de nutrientes inorgánicos, son condiciones de estrés para el fitoplancton, lo que puede explicar su baja diversidad y las fases de equilibrio registradas durante muchos meses en ambos humedales.

Palabras clave: *Dinámica fitoplanctónica, lagunas hipertróficas mediterráneas, diversidad del fitoplancton, grupos funcionales.*

INTRODUCTION

Very shallow lakes ($Z_{max} < 5$ m) are common wetland types in the Mediterranean region, particularly in Spain. Most of these shallow lakes are small (usually less than 10 ha) (Casado & Montes, 1995), isolated and highly interesting, both ecologically and in terms of biodiversity (Beklioglu *et al.*, 2007). During the last three decades, most of these small aquatic systems have been damaged due to human pressure. The deterioration of many northern temperate shallow lakes has been the focus of many studies, which have contributed greatly to a general understanding of the functioning of these ecosystems and the restoration of some of them (Perrow *et al*., 1997; Jeppesen *et al*., 2007; Søndergaard *et al*., 2008). Comparable information for Mediterranean shallow lakes is limited (Beklioglu *et al*., 2007), and the establishment of reference sites becomes necessary, although difficult given the intensive anthropogenic alteration of water bodies (Moss, 2007). Nevertheless, some Mediterranean shallow lakes located in protected areas appear to have remained unchanged. This is the case for Santa Olalla and Dulce, both located in Doñana National Park (Spain). Both wetlands are natural eutrophic to hypereutrophic systems, and their study could contribute to a better understanding of the behaviour of Mediterranean shallow lakes.

Phytoplankton, like other major components of aquatic systems, has been a preferred target for taxonomic study in shallow lakes, but despite the growing number of recent works on the forces that drive special and temporal phytoplankton patterns, our knowledge of phytoplankton ecology comes primarily from moderate-sized or large lakes (Padisák *et al*., 2003).

This work examines the monthly succession of phytoplankton during a two years study conducted in two mixed hypereutrophic shallow lakes in a south temperate area based on their algal functional groups (Reynolds *et al*., 2002; Padisák *et al*., 2003; Padisák *et al*., 2009), which are related to multidimensional features of the environment. A canonical correspondence analysis was used to ascertain the primary environmental variables driving phytoplankton community dynamics. This study was intended to contribute to the knowledge of phytoplankton dynamics in two unmodified shallow lakes from the Mediterranean region and evaluate the possibility of considering Santa Olalla and Dulce as reference systems in the area.

MATERIALS AND METHODS

Study Sites

The study was conducted in two shallow lakes, Santa Olalla and Dulce, over a period of 2 years, during which monthly measurements were taken from February 1998 to February 2000. Both wetlands are located on the south-western Atlantic coast of Spain (Fig. 1) in Doñana National Park. The climate of the area is predominantly Mediterranean, with dry and hot summers and little rainfall in the winters. Santa Olalla and Dulce are hypogenic shallow lakes where the main input into the systems is superficial waters from regional and local discharge flows (Manzano, 2001). Santa Olalla is larger than Dulce

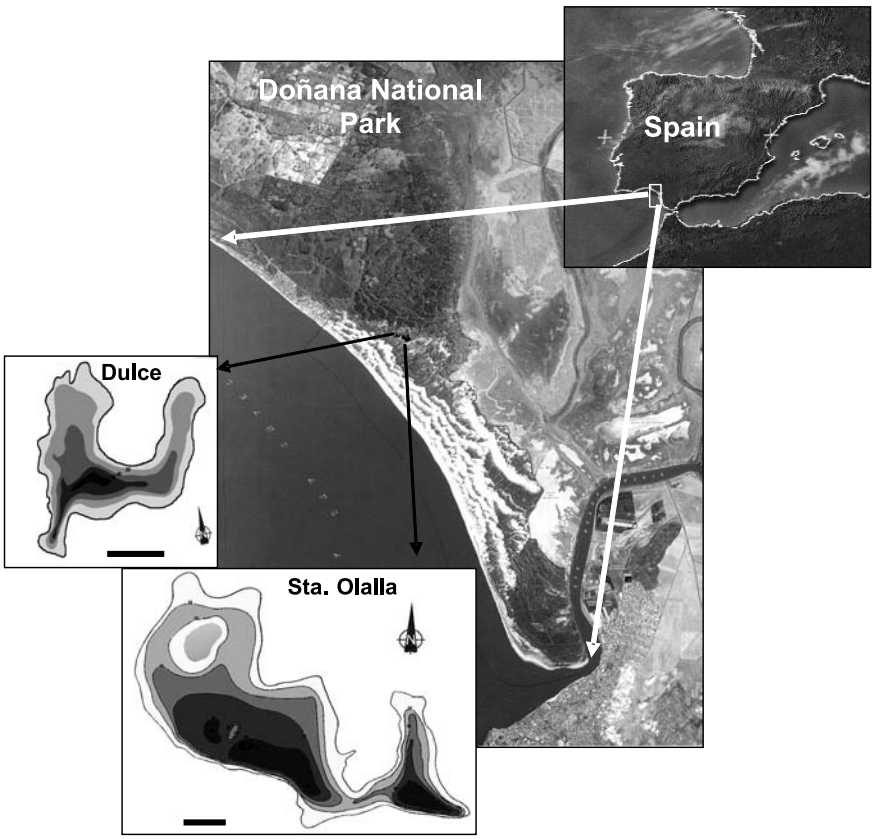

Figure 1. Location of the Santa Olalla and Dulce shallow lakes on the southwest coast of Spain. Shape and orientation of the lake basins. Bar 100 m. *Situación de las lagunas de Santa Olalla y Dulce en la costa suroeste de España. Orientación y forma de las cubetas de las lagunas. Barra 100 m.*

(Table 1), and both lakes are shallow systems with gentle slopes. The wind is strong over both shallow lakes, and vertical water mixing was observed during sampling. Santa Olalla and Dulce are only a few metres apart, and during seasons of high precipitation, they work as a single system (Toja *et al.*, 1991, Álvarez *et al.*, 2001). This behaviour was confirmed during the first months of the study, as there was very abundant precipitation early in the 1997-1998 hydrological cycle. The maximum values of water volume were registered during the initial part of the study period in both shallow lakes.

Physical and chemical parameters

Water conductivity and temperature were measured *in situ* using a WTW-LF 330/SET conductivimeter; pH and redox potential were determined using a 323 A WTW pH-meter, whereas dissolved oxygen (DO) concentrations were estimated with a WTW 340-B oxymeter. Measurements were taken 5-10 cm below the water surface at a location where the depth of the water column was approximately 0.5 m. Nutrient concentrations (NO_3, NO_2, NH_4^+, total N (TN), total P (TP) and soluble reactive phosphorus, SRP) were determined in the laboratory following standard methods (APHA 1989). Organic N was estimated by subtracting inorganic nitrogen (IN) from TN (IN = sum of NO_3, NO_2 and NH_4^+) and organic P by subtracting SRP from TP. The concentration of polyphenolic compounds was estimated according to Box's procedure (1983). The euphotic zone (Z_{eu}) was calculated as 2.7 times the Secchi depth (Cole, 1983).

Table 1. Physical and chemical variables and morphological features of the water columns of Santa Olalla (SO) and Dulce (D). (PAR) photosynthetically active radiation; (Water transp.) water transparency; (TA) total alkalinity; (PC) polyphenolic compounds; (TP) total phosphorous; (SRP) soluble reactive phosphorous; (TN) total nitrogen; (IN) inorganic nitrogen. *Características morfológicas y variables físico-químicas de la columna de agua en Santa Olalla (SO) y Dulce (D). (PAR) Radiación fotosintéticamente activa; (Water transp.) Transparencia del agua; (TA) Alcalinidad total; (PC) Compuestos polifenólicos; (TP) Fósforo total; (SRP) Fósforo reactivo soluble; (TN) Nitrógeno total; (IN) Nitrógeno inorgánico.*

	Volume (m^3)		Depth (m)		Water T (mean of 24 h) (°C)		PAR ($\mu E\ m^{-2}\ s^{-1}$)		pH		Water transp. (m)		O_2 midday (%)	
	SO	D	SO	D	SO	D	SO	D	SO	D	SO	D	SO	D
Mean	165315	34867	1.28	0.93	18.68	16.01	522.3	549.7	9.52	8.76	0.14	0.24	156.7	131.6
SD	253650	39885	0.52	0.42	4.96	5.47	142.5	287.1	0.88	0.93	0.08	0.22	65.7	47.5
Max	796776	141497	2.34	1.77	25.7	25.7	737	942.5	10.77	10.2	0.33	0.90	331	217
Min	290	3	0.44	0.0	10.8	8.39	315	65.9	7.33	6.77	0.05	0.04	28.5	45
n	23	23	23	23	15	11	15	11	24	23	24	23	24	23

	Conductivity ($\mu S\ cm^{-1}$)		TA (meq L^{-1})		PC (meq L^{-1} Tanic acid)		TP (mg L^{-1})		SRP (μg-at P L^{-1})		TN (mg L^{-1})		IN (μg-at N L^{-1})	
	SO	D	SO	D	SO	D	SO	D	SO	D	SO	D	SO	D
Mean	2692	1997	2.89	1.79	2.21	4.32	0.664	0.567	3.10	17.29	13.34	11.26	110.1	318.48
SD	2573	3373	1.28	0.79	1.93	5.56	0.367	0.521	5.00	24.54	20.72	20.67	49.1	571.01
Max	11600	16580	6.18	4.11	8.13	22.87	1.450	1.830	18.5	82.28	80.89	100.8	228.0	2445.0
Min	532	312	0.87	0.69	0.28	0.45	0.110	0.050	0.00	0.00	1.98	0.9	40.0	5.00
n	24	23	22	22	24	23	24	23	21	22	24	23	21	22

	IN/SRP		NO_2^- (μg-at N L^{-1})		NH_4 (μg-at N L^{-1})		Chl *a* (mg m^{-3})		Rate of $PP^{14}C$ (g C m^{-3} h^{-1})		Diversity Index (*H'*)		Total algae (cells ml^{-1})	
	SO	D	SO	D	SO	D	SO	D	SO	D	SO	D	SO	D
Mean	51.98	68.92	1.2	108.43	108.9	210.04	365.18	230.00	1.29	0.88	1.11	1.79	$2.29{\cdot}10^7$	$4.64{\cdot}10^6$
SD	58.52	77.43	3.6	337.77	50.2	286.02	304.86	284.38	1.11	2.92	0.91	0.79	$4.69{\cdot}10^7$	$7.61{\cdot}10^6$
Max	215.71	307.27	13.0	1318.0	228.0	1427.0	1094.40	1324.0	3.61	2.92	3.16	3.67	$2.03{\cdot}10^8$	$2.28{\cdot}10^7$
Min	71	8.7	0.0	0.00	40.0	5.00	24.40	4.01	0.098	bdl[1]	0.04	0.12	1382	171
n	21	22	21	22	21	22	24	23	24	23	24	23	24	23

[1] Bellow the detection limit.

[1] Por debajo del límite de detección.

Carlson's index (TSI) (Carlson, 1977) was used to determine the trophic status of the lakes using Secchi depth, Chl *a* and TP.

Biological parameters

Phytoplanktonic chlorophyll-*a* (Chl *a*) concentrations were estimated monthly from triplicate samples. Water samples were filtered through Whatman GF/F glass microfibre filters (0.7 μm) *in situ* and placed in 5 ml of a 90 % acetone solution for extraction over 24 h at 4º C in darkness. Chl *a* was measured using a spectrophotometer (Cary/1C/ UV-Visible spectrophotometer Varian), and its concentration was calculated using the Jeffrey & Humphrey (1975) trichromatic method. The primary productivity of phytoplankton ($PP^{14}C$) was determined using the ^{14}C method according to Goldman *et al.* (1974). Photosynthesis was measured *in situ* by suspending one dark and two light polycarbonate bottles (®Nunclon, InterMed) 15 cm below the surface

for an incubation period of 2.5 h at midday. The optimal incubation time was determined in a preliminary experiment in which 10 light bottles and 5 dark bottles were incubated simultaneously. After the first hour, 2 light bottles and a dark one were removed every 30 min. The production rate was the highest 2.5 hours from the beginning of the experiment and then declined.

Samples collected to estimate phytoplankton abundance, biovolume and diversity were fixed with formaldehyde (4 % V/V) *in situ*. Species identifications as well as phytoplankton abundance and biovolume estimations were performed with an inverted optical microscope with epifluorescence (Olympus IX50). Individual phytoplankton cells were counted after filtering 0.1 ml (or different dilutions, depending on the samples) through black Isopore membrane filters GTBP with a 0.2 μm pore size and washing the cells with citrate buffer (pH 6). Each filter was examined for the autofluorescence of cell pigments at 1000X. The measurements were made under microscope according to the method described by Fry (1990). Biomass was calculated by measuring at least 30 individuals of each species and using simple geometric approximations (Rott, 1981). Species abundance was then converted into biovolume. The dominant phytoplankton species were considered to be those representing 10 % or more of the total sample biovolume. Dominant taxa were classified into functional groups according to Reynolds *et al*. (2002), Padisák *et al*. (2003) and Padisák *et al*. (2009).

Numerical analyses

The diversity of each sample was based on the Shannon index: $H' = -\Sigma\, p_i \cdot \log_2 p_i$ where p_i is the proportion of the biovolume represented by species *i* in the sample. The Bray-Curtis dissimilarity, calculated from biovolume data between pairs of chronologically contiguous samples, was used as an estimate of the differentiation of the community along the complex environmental gradient (Bloom, 1981; Salmaso, 1996).

The relationships among the measured variables were explored using correlation coefficients (Pearson for parametric and Spearman for non-parametric variables). Normality was examined by means of the Kolmogorov-Smirnov test. Canonical correspondence analysis (CCA) was performed using XLSTAT version 3.01 (Addinsoft 1995-2008) to elucidate the relationships between the phytoplankton and the environmental variables over the study period, using all data from both shallow lakes. To satisfy the assumptions of normality and homogeneity of variance of the data, all data were logarithmically transformed before the analyses.

RESULTS

Evolution of physical and chemical parameters

The mean values of the physical, chemical and morphological variables of Santa Olalla and Dulce are summarised in Table 1. Both systems exhibited large variations in water volume. Maximum values were recorded in the beginning of the investigation period (February 1998). Santa Olalla had a maximum depth of 2.34 m and Dulce 1.77 m. In September 1999, both shallow lakes reached their lowest water volume for the study period (0.44 m for Santa Olalla, dry for Dulce), with a gradual increase in volume during the following months. Santa Olalla exhibited higher average pH, water temperature, oxygen concentration, conductivity, total alkalinity, total P and total N values, whereas Dulce exhibited higher values for water transparency, polyphenolic compounds, SRP and inorganic N. N-NO_3^- was not found in Santa Olalla during the study period and N-NO_2^- was measurable in only 4 months (March, April, October and November 1999). In Dulce Lake, the measured value for N-NO_3^- was 0 in most months except for June 1999 and February 2000, whereas N-NO_2^- was present from March–May and July–August. Inorganic nitrogen in both systems is mainly in the reduced form of ammonia. The variations in SRP and IN over the months of the study period are illustrated in Figure 2A. It should be noted that no stratification of the water column occurred in either of the two systems. The euphotic zone was

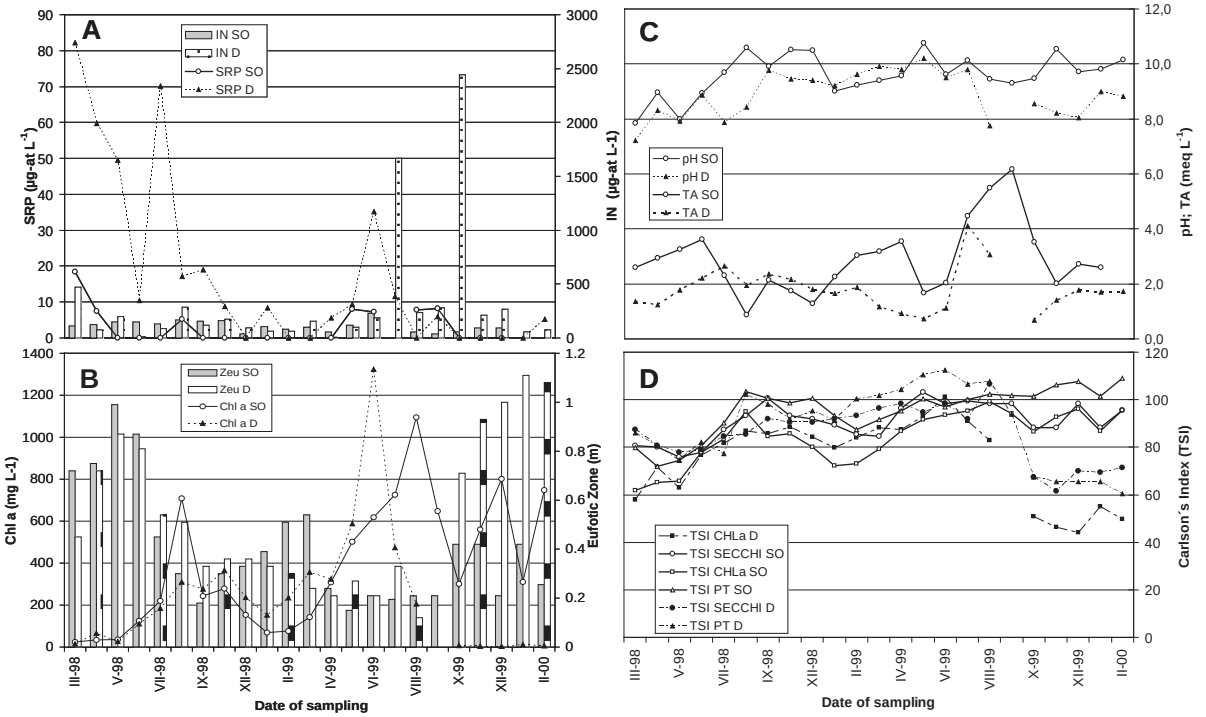

Figure 2. Changes over time in Santa Olalla and Dulce in the following variables: values of SRP and inorganic nitrogen (IN) (2A); concentration of Chl *a* and depth of the euphotic zone (2B); pH and total alkalinity (TA) (2C); Carlson's index values (calculated based on Secchi depth, TP and the concentration of Chl *a*) showing the trophic status in both systems (2D). *Cambios a lo largo del tiempo en Santa Olalla y Dulce en: los valores de SRP y nitrógeno inorgánico (IN) (2A); concentración de Chl* a *y profundidad de la zona eufótica (2B); pH y alcalinidad total (2C); valores del índice de Carlson (calculados a partir de los valores del disco de Secchi, fósforo total y concentración de Chl* a*) mostrando el estado trófico de ambos sistemas (2D).*

shallow in both wetlands (Fig. 2B), primarily due to the abundance of phytoplankton and the concentration of polyphenolic compounds.

The Carlson's index values based on Secchi depth, TP and the concentration of Chl *a* (Fig. 2D) were higher than 60 for both lakes, except for Chl *a* in September 1999 when Dulce dried up. The index tends to increase towards the hypereutrophic condition in both lakes over time. Only Dulce, after drying, showed lower index values, but in general these values remained within the range of eutrophy (Fig. 2D).

Chl *a*, primary production rates and phytoplankton abundance, biovolume and diversity

The average phytoplankton Chl *a* concentration was higher in Santa Olalla than in Dulce (Table 1). Maximum and minimum values were observed in Dulce in June 1999 (1324 mg Chl *a* m^{-3}) and in December 1999 (4 mg Chl *a* m^{-3}), respectively (Fig. 2B). In Santa Olalla, maximum phytoplankton production ($PP^{14}C$) was recorded in September 1999 (3.61 g C m^{-3} h^{-1}) and the minimum in May 1998 (0.098 g C m^{-3} h^{-1}). In Dulce, the highest primary production rate was recorded in August 1998 (2.92 g C m^{-3} h^{-1}), whereas the lowest value (below the detection limit of the scintillation counter apparatus) was recorded between October 1999 and February 2000, just after Dulce's dry period.

Eight functional groups were recorded in Santa Olalla: D, H_1, J, K, M, S_1, W_2 and Y codons (Table 2). The D (represented by *Cyclotella* spp. of small-cell size), W_2 (represented by *Trachelomonas volvocina*) and Y (*Cryptomonas phaseolus*) groups only appeared during

the first study period (February to May 1998), followed by S_1 (represented by *Planktothrix agardhii*) and H_1 (represented by nitrogen-fixing cyanobacteria species like *Anabaena spiroides* and *Anabaenopsis circularis*) groups in June and July of 1998. In July, H_1 was accompanied by the M (*Microcystis aeruginosa*) group. From August 1998 to January 1999, the system was dominated by the K group of small-celled non-vacuolate cyanobacteria types (*Aphanothece clathrata* and *Chroococcus dispersus*, which represented more than 80 % of the total phytoplankton biovolume in those months). From February to April 1999, the K group appeared together with the H_1 group (*A. circularis*) and, to a lesser extent, non-gelatinous and non-motile Chlorococcales (J group–*Tetraedron minimum*). From May 1999 until October of the same year, the S_1 group (this time with *Leptolyngbya* sp. and *Limnothrix amphigranulata*) predominated again, but the J codon (*Pediastrum boryanum* and *Tetraedron minimum*) was also present from August onwards. From November to December, the K group, accompanied by the S_1 codon, dominated once again. From January to February 2000, the K group appeared together with the H_1 group.

Dulce Lake exhibited a more complex distribution of phytoplankton functional groups over time. Ten functional groups were observed during the study period (Table 3). During the first four months (February to May 1998), the J group (*Pediastrum boryanum*, *Scenedesmus opoliensis* and *S. ovalternus*) appeared together with the W_2 (*Trachelomonas volvocina*), D (*Cyclotella*

Table 2. Dominant phytoplankton species in Santa Olalla. In parentheses: % of the biomass of species in each month. Only takes into account the % of species with a biomass equal to or greater than 10 %. The durations of the phases are taken in accordance with the results of the correspondence analysis (Fig. 4). *Especies fitoplanctónicas dominantes en Santa Olalla. En paréntesis % de biomasa de cada especie. Sólo se ha tenido en cuenta aquellas especies con un % de biomasa igual o superior al 10 %. La duración de cada fase es establecida de acuerdo con los resultados del Análisis de Correspondencia (Fig. 4).*

Santa Olalla	1st dominant specie	2nd dominant specie	3rd dominant specie	Functional groups	Phases	H'
February 98	*Trachelomonas volvocina* (35 %)	*Cryptomonas phaseolus* (28 %)	*Cyclotella* sp. (13 %)	W_2-Y-D	P1SO	2.96
March 98	*Trachelomonas volvocina* (81 %)	*Cryptomonas phaseolus* (10 %)		W_2-Y		3.16
April 98	*Cyclotella* sp. (74 %)	*Trachelomonas volvocina* (20 %)		D- W_2		1.62
May 98	*Cyclotella* sp. (52 %)	*Trachelomonas volvocina* (11 %)		D- W_2		1.12
June 98	*Anabaena spiroides* (28 %)	*Planktothrix agardhii* (28 %)	*Cryptomonas phaseolus* (28.3 %) *Trachelomonas volvocina* (13 %)	H_1-S_1-Y- W_2		0.93
July 98	*Anabaenopsis circularis* (77 %)	*Microcystis aeruginosa* (12 %)		H_1-M	P2SO	2.37
August 98	*Chroococcus dispersus* (86 %)	*Aphanothece clathrata* (10 %)		K		0.44
September 98	*Aphanothece clathrata* (84 %)	*Chroococcus dispersus* (15 %)		K		0.04
October 98	*Chroococcus dispersus* (86 %)	*Aphanothece clathrata* (12 %)		K		0.41
December 98	*Chroococcus dispersus* (60 %)	*Aphanothece clathrata* (39 %)		K		0.1
January 99	*Chroococcus dispersus* (79 %)	*Anabaenopsis circularis* (11 %)		K- H_1		0.71
February 99	*Anabaenopsis circularis* (55 %)	*Pediastrum boryanum* (25 %)	*Chroococcus dispersus* (10 %)	H_1-J-K		0.59
March 99	*Anabaenopsis circularis* (55 %)	*Chroococcus dispersus* (20 %)		H_1-K		0.51
April 99	*Chroococcus dispersus* (20 %)	*Aphanothece clathrata* (18 %) *Tetraedron minimum* (18 %)	*Chlorella* sp. (17 %) *Microcystis aeruginosa* (11 %)	K-J-M		0.91
May 99	*Leptolyngbya* sp. (44 %)	*Microcystis aeruginosa* (17 %)		S_1-M	P3SO	2.53
June 99	*Leptolyngbya* sp. (89 %)			S_1		1.53
July 99	*Limnothrix amphigranulata* (70 %)	*Microcystis aeruginosa* (10 %)		S_1-M		1.63
August 99	*Limnothrix amphigranulata* (58 %)	*Monoraphidium griffithii* (18 %)		S_1-J		2.1
September 99	*Limnothrix amphigranulata* (44 %)	*Leptolyngbya* sp. (20 %) *Pediastrum boryanum* (20 %)		S_1-J		1.8
October 99	*Leptolyngbya* sp. (34 %)	*Limnothrix amphigranulata* (27 %)	*Tetraedron minimum* (18 %)	S_1-J		2.38
November 99	*Aphanothece clathrata* (34 %)	*Limnothrix amphigranulata* (28 %)	*Scenedesmus acuminatus* (21 %)	K- S_1-J	P2SO	0.32
December 99	*Aphanothece clathrata* (39 %)	*Scenedesmus acuminatus* (22 %)	*Limnothrix amphigranulata* (18 %)	K-J- S_1		0.29
January 00	*Anabaenopsis circularis* (47 %)	*Aphanothece clathrata* (28 %)	*Scenedesmus acuminatus* (23 %)	H_1-K		0.42
February 00	*Anabaenopsis circularis* (49 %)	*Aphanothece clathrata* (32 %)	*Scenedesmus acuminatus* (13 %)	H_1-K		0.26

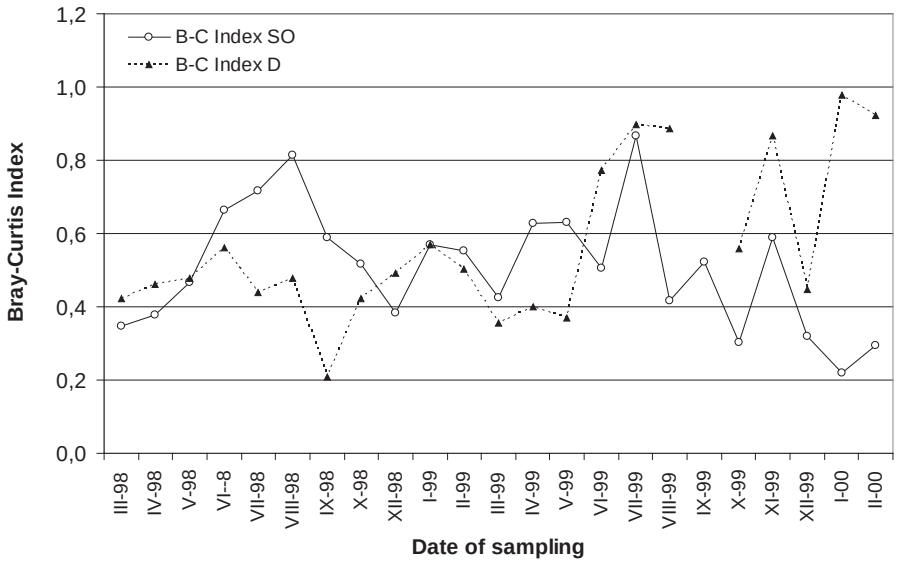

Figure 3. Rates of community change in Santa Olalla and Dulce estimated by the Bray-Curtis index, calculated from biovolume data for the chronologically contiguous phytoplankton samples. *Tasa de cambio de la comunidad fitoplanctónica en Santa Olalla y Dulce estimada mediante el cálculo del índice de Bray-Curtis a partir de los datos del biovolumen en muestras cronológicamente consecutivas.*

sp.) or P (*Aulacoseria* sp.) groups, depending on the month. From June to September 1998, the P-M groups (*Microcystis aeruginosa*) co-dominated with W_2 or several groups belonging to cyanobacteria (H_1 –*Anabaena spiroides*, S_1–*Planktothrix agardhii*, S_2–*Arthrospira platensis* or K–*Chroococcus dispersus*). In October 1998, the Y group (*Cryptomonas phaseolus*) co-dominated with the J group. From December 1998 to May 1999, the H_1 group appeared together with the J codon almost every month. In June 1999, the J and M groups predominated, whereas the Y group did so in July. In August, before its dry period, Dulce was strongly dominated by *Arthrospira platensis* (group S_2). After drying up (October 1999 to February 2000), Dulce was dominated by *Cyclotella* sp. and other small-sized diatoms (D group) except in January, where the predominant group was Y.

Figure 3 illustrates an estimate of the community change rate (Bray-Curtis Index) (Bloom, 1981). The values are normally very dependent on the time interval used. Values tend to be low for samples collected during short time intervals and show maximum values for samples collected in different seasons (Salmaso, 2003). In this study, four week intervals were used to observe the variation of the phytoplankton community. The community change rate for Santa Olalla increases gradually in the first study period (from March to August 1998), after which changes are smaller, except in July 1999, where the change rate once again had a high value. The Bray-Curtis index exhibited low values during Dulce's first hydrological cycle and increased during the second cycle, between May and June 1999, and especially just after Dulce's dry period, between November 1999 and February 2000.

Low Shannon index values (H') were obtained for both shallow lakes, with an average of 1.11 for Santa Olalla and 1.79 for Dulce (Table 1). In Santa Olalla, the highest biodiversity ($H' = 3.16$) was observed at the beginning of the study (February and March 1998). Afterwards, biodiversity decreased continuously until the winter of 1998 (though it had a peak in July 1998), when it recovered slightly only to decrease once again in the winter of 1999-2000. It is interesting to note that in September 1998 Santa Olalla was completely dominated by cyanobacteria and had a very low H' value (0.04) (Table 2). Dulce had greater biodiversity than Santa Olalla most

Table 3. Dominant phytoplankton species in Dulce. In parentheses: % of the biomass of species in each month. Only takes into account the % of species with a biomass equal to or greater than 10 %. The duration of the phases are taken in accordance with the results of the correspondence analysis (Fig. 4). *Especies fitoplanctónicas dominantes en Dulce. En paréntesis % de biomasa de cada especie. Sólo se ha tenido en cuenta aquellas especies con un % de biomasa igual o superior al 10 %. La duración de cada fase es establecida de acuerdo con los resultados del Análisis de Correspondencia (Fig. 4).*

Dulce	1st dominant specie	2nd dominant specie	3rd dominant specie	Functional groups	Phases	H'
February 98	*Scenedesmus ovalternus* (44 %)	*Scenedesmus opoliensis* (12 %)	*Cryptomonas phaseolus* (10 %) *Trachelomonas volvocina* (10 %)	J-Y- W_2	P1D	1.46
March 98	*Trachelomonas volvocina* (62 %)	*Scenedesmus opoliensis* (22 %) *Pediastrum boryanum* (22 %)		W_2-J		1.07
April 98	*Cyclotella* sp. (47 %)	*Pediastrum boryanum* (15 %)	*Trachelomonas volvocina* (13 %) *Scenedesmus opoliensis* (12 %)	D-J- W_2		2.3
May 98	*Trachelomonas volvocina* (29 %)	*Scenedesmus opoliensis* (21 %)	*Aulacoseira* sp. (13 %)	W_2-J-P		1.64
June 98	*Microcystis aeruginosa* (23 %)	*Aulacoseira* sp. (20 %)	*Anabaena spiroides* (15 %) *Trachelomonas volvocina* (11 %)	M-P-H_1-W_2		2.25
July 98	*Planktothrix agardhii* (40 %)	*Microcystis aeruginosa* (21 %)	*Aulacoseira* sp. (17 %)	S_1-M-P		1.64
August 98	*Aulacoseira* sp. (25 %)	*Arthrospira platensis* (23 %)	*Microcystis aeruginosa* (10 %)	P-S_2-M		1.61
September 98	*Arthrospira platensis* (23 %)	*Chroococcus dispersus* (19 %)	*Aulacoseira* sp. (16 %) *Anabaena spiroides* (15 %)	S_2-K-P- H_1	P2D	1.82
October 98	*Scenedesmus quadricauda* (22 %)	*Cryptomonas phaseolus* (18 %)		J-Y		3.67
December 98	*Anabaena spiroides* (47 %)	*Pediastrum boryanum* (13 %)		H_1-J		1.92
January 99	*Anabaena spiroides* (53 %)	*Monoraphidium contortum* (15 %)		H_1-J	P3D	1.195
February 99	*Anabaena spiroides* (48 %)	*Pediastrum boryanum* (42 %)		H_1-J		1.13
March 99	*Anabaenopsis circularis* (44 %)	*Pediastrum boryanum* (20 %)	*Anabaena spiroides* (17 %)	H_1-J		1.99
April 99	*Anabaena spiroides* (36 %)	*Anabaenopsis circularis* (23 %)	*Microcystis aeruginosa* (12 %)	H_1-M		2.17
May 99	*Anabaenopsis circularis* (25 %)	*Scenedesmus quadricauda* (23 %)	*Scenedesmus opoliensis* (17 %) *Anabaena spiroides* (15 %)	H_1-J		1.95
June 99	*Microcystis aeruginosa* (47 %)	*Scenedesmus quadricauda* (37 %)		M-J	P2D	0.55
July 99	*Cryptomonas phaseolus* (81 %)			Y	P4D	3.06
August 99	*Arthrospira platensis* (83 %)	*Cyclotella* sp. (13 %)		S_2-D		0.12
September 99*						
October 99	*Others small-cell diatoms* (89 %)			D		2.39
November 99	*Others small-cell diatoms* (69 %)			D	P2D	2.5
December 99	*Others small-cell diatoms* (69 %)	*Euglena gracilis* (20 %)		D- W_2		2.47
January 00	*Cryptomonas phaseolus* (81 %)	*Monoraphidium contortum* (10 %)		Y-J		1.17
February 00	*Others small-cell diatoms* (71 %)	*Monoraphidium arcuatum* (15 %)		D-J		0.85

* Dulce remained dry during September 1999.

of the time. The H' values for Dulce exhibited two peaks: October 1998 ($H' = 3.67$, maximum value) and July 1999 ($H' = 3.06$). The minimum value was observed in August 1999 ($H' = 0.12$) shortly before Dulce dried up (Table 3).

The canonical correspondence analysis (CCA) showed a significant value ($p < 0.0001$) for the permutation probe. The first two axes together explained 46.36 % of the total variability in the data. The first CCA axis separated the two shallow lakes except for the first four months of the study in Santa Olalla, which are placed next to Dulce's months (Fig. 4) since both lakes were in superficial contact over that period. Santa Olalla appears to the right, influenced by higher TN and TP concentrations, pH, conductivity and higher biovolumes of cyanobacteria (particularly *Aphanothece clathrata*, *Limnothrix amphigranulata* and *Leptolyngbya* sp.) and chlorophytes (*Scenedesmus acuminata* and *Tetraedron minimum*) (Fig. 5). Dulce is located on the left of the diagram, influenced by higher values for inorganic nitrogen (IN), phosphorous (SRP), the depth of the euphotic zone and higher total biovolumes of Bacillariophyta (*Aulacoseria* sp.), Euglenophyta (especially *Trachelomonas volvocina*) and Cryptophyta (*Cryptomonas phaseolus*). The second CCA axis indicated a grad-

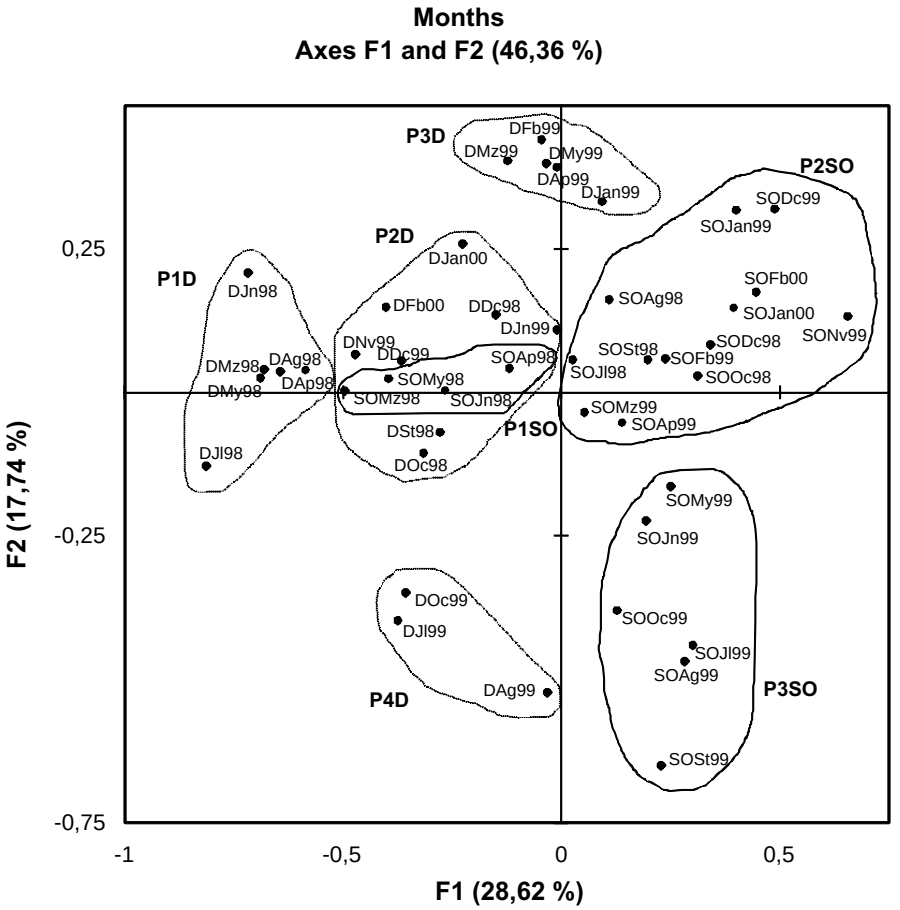

Figure 4. Score dispersion of samples along the first two CCA axes. Samples were grouped into phases over time. P1SO, P2SO and P3SO: different phases in Santa Olalla. P1D, P2D, P3D and P4D: different phases in Dulce. *Dispersión de las muestras en los dos primeros ejes del CCA. Las muestras se agrupan en fases a lo largo del tiempo. P1SO, P2SO y P3SO: Diferentes fases de Santa Olalla. P1D, P2D, P3D y P4D: Diferentes fases de Dulce.*

ual move towards hypereutrophication in both systems over the study period. There is a maximum in summer 1999 (Fig. 4), determined by high values of TN, the TN:TP ratio, conductivity, total alkalinity and temperature and low water volumes in the lakes (Fig. 5). The lakes revert to a more moderate eutrophic state in the autumn and winter of 1999-2000.

DISCUSSION

Santa Olalla and Dulce are two natural eutrophic/hypereutrophic shallow lakes with very high TN, TP and Chl *a* concentrations, phytoplanktonic biomass and, especially, primary production, along with low diversity (Table 1). Cyanobacteria dominated most of the study period in both shallow lakes , particularly in Santa Olalla, which exhibited a more eutrophic state, especially during the final months of the study (Fig. 2D).

In both Santa Olalla and Dulce, N and P are predominantly in organic form, inorganic nutrients are in very low concentrations most of the time (Fig. 2A), and the N/P ratio (Table 1) indicates a deficiency in P for most of the months in both shallow lakes (Coleto, 2003). Given the high primary production in both systems, this deficiency does not appear to be limiting phytoplankton growth. In addition, high rates of de-

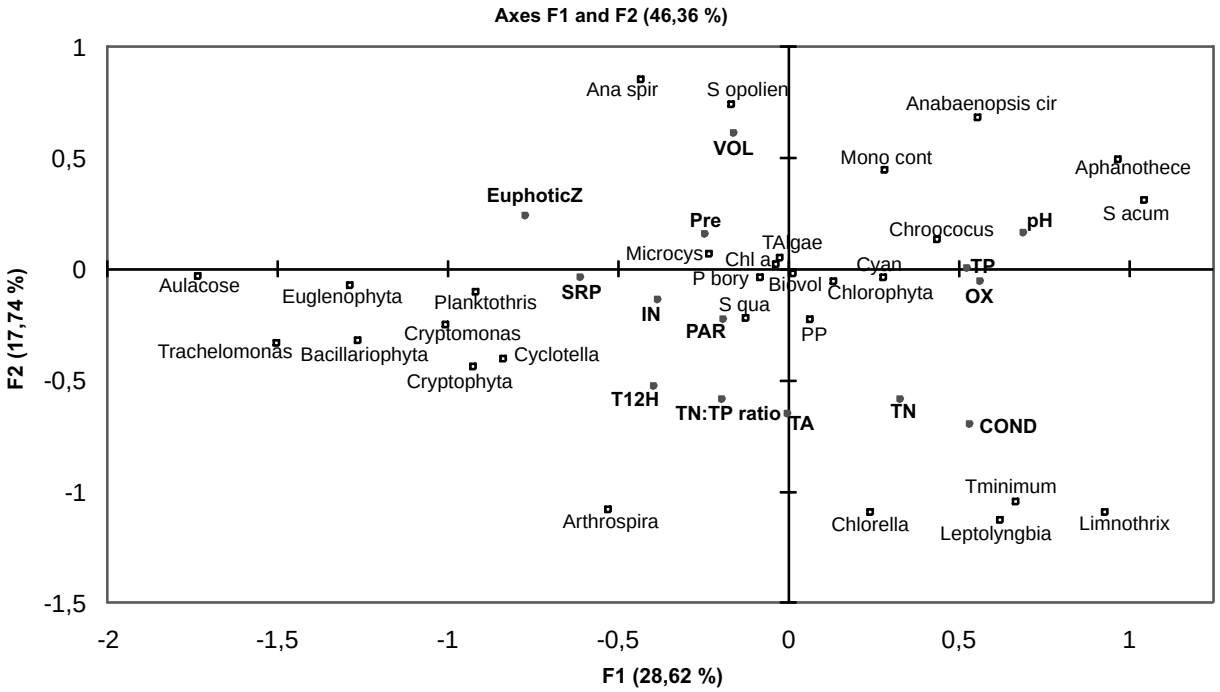

Figure 5. Scores of phytoplankton species biovolume and abiotic variables according to the correspondence analysis using all data from both shallow lakes. (Ana spir) *Anabaena spiroides*; (Anabaenopsis cir) *Anabaenopsis circularis*; (Aphanothece) *Aphanothece clathrata*; (Arthrospira); *Arthrospira platensis*; (Aulacose) *Aulacoseria* sp.; (Cyclotella) *Cyclotella* sp.; (Chlorella) *Chorella* sp.; (Chroococcus) *Chroococcus dispersus*; (Cryptomonas) *Cryptomonas phaseolus*; (Leptolyngbya) *Leptolyngbya* sp.; (Limnothrix) *Limnothrix amphigranulata*; (Microcy) *Microcystis aeruginosa*; (Mono cont) *Monoraphidium contortum*; (P bory) *Pediastrum boryanum*; (Planktothrix) *Planktothrix agardhii*; (S acum) *Scenedesmus acuminatus*; (S opolien) *Scenedesmus opoliensis*; (S qua) *Scenedesmus quadricauda*; (T minimum) *Tetraedron minimum*; (Trachelomonas) *Trachelomonas volvocina*; (Bacillariophyta) total biovolume of Bacillariophyta; (Biovol) total biovolume of phytoplankton; (Chl *a*) total Chlorophyll *a*; (Chlorophyta) total biovolume of Chlorophyta; (Cryptophyta) total biovolume of Cryptophyta; (Cyan) total biovolume of cyanobacteria; (Euglenophyta) total biovolume of Euglenophyta; (PP) primary production rate; (TAlgae) total number of phytoplankton cells; (COND) electrical conductivity; (Euphotic Z) euphotic zone depth; (OX) dissolved oxygen; (IN) inorganic nitrogen concentration; (PAR) photosyntetically active radiation; (Pre) rain precipitation; (SRP) soluble reactive phosphorus; (TA) total alkalinity; (T12H) temperature at midday; (TN) total nitrogen; (TN:TP ratio) ratio of total nitrogen: total phosphorus rate; (TP) total phosphorus; (VOL) water volume of the shallow lakes. *Situación de las variables abióticas y de las especies de fitoplancton según su biovolumen, conforme al Análisis de Correspondencia, usando los datos de ambas lagunas. (Ana spir)* Anabaena spiroides*; (Anabaenopsis cir)* Anabaenopsis circularis*; (Aphanothece)* Aphanothece clathrata*; (Arthrospira)* Arthrospira platensis*; (Aulacose)* Aulacoseria sp.*; (Cyclotella)* Cyclotella *sp.; (Chlorella)* Chorella *sp.; (Chroococcus)* Chroococcus dispersus*; (Cryptomonas)* Cryptomonas phaseolus*; (Leptolyngbya)* Leptolyngbya *sp.; (Limnothrix)* Limnothrix amphigranulata*; (Microcy)* Microcystis aeruginosa*; (Mono cont)* Monoraphidium contortum*; (P bory)* Pediastrum boryanum*; (Planktothrix)* Planktothrix agardhii*; (S acum)* Scenedesmus acuminatus*; (S opolien)* Scenedesmus opoliensis*; (S qua)* Scenedesmus quadricauda*; (T minimum)* Tetraedron minimum*; (Trachelomonas)* Trachelomonas volvocina*; (Bacillariophyta) Biovolumen total de Bacillariofitas; (Biovol) Biovolumen total del fitoplancton; (Chl* a*) Clorofila* a *total; (Chlorophyta) Biovolumen total de Clorofitas; (Cryptophyta) Biovolumen total de Cryptofitas; (Cyan)) Biovolumen total de Cianobacterias; (Euglenophyta)) Biovolumen total de Euglenofitas; (PP) Tasa de producción primaria; (TAlgae) Número total de células fitoplanctónicas; (COND) Conductividad; (Euphotic Z) Profundidad de la zona eufótica; (OX) Oxígeno disuelto; (IN) Concentración de N inorgánico; (PAR) Radiación fotosintéticamente activa; (Pre) Precipitaciones; (SRP) Fósforo reactivo soluble; (TA) Alcalinidad total; (T12H) Temperatura del agua al medio día; (TN) Nitrógeno total; (TN:TP ratio) relación Nitrógeno total: fósforo total; (TP) Fósforo total; (VOL) Volumen de agua en las lagunas.*

composition were observed in both Santa Olalla and Dulce (Álvarez *et al*., 2001), which indicates a rapid mineralisation of organic matter and suggests that primary producers assimilate dissolved nutrients almost instantaneously after mineralisation (López-Archilla *et al*., 2004). Most of the decaying organic matter is found in the sediments of the lakes. Some of the P released may be re-

tained in the sediments, to be adsorbed primarily by Fe in these systems (Coleto, 2003). However, this fraction is readily bio-available to organisms depending on the pH and redox state of the sediment-water interface (Scheffer, 1998), especially when these areas become anoxic, which occurs in several months during the study period (data not shown). The low values of oxygen in the water column in Santa Olalla and Dulce appear to be linked to a slightly higher concentration of SRP and IN (Fig. 5), favouring the presence of a higher number of species (particularly bacillariophytes, cryptophytes, euglenophytes and some species of chlorophytes). However, these species appear for short periods before being replaced by species of cyanobacteria and chlorophytes when the inorganic nutrient concentrations became even lower. These species are strongly dominant in the phytoplanktonic community, and their presence suggests that they have the ability to rapidly capture the inorganic nutrients released through decomposition and that they compete more successfully for such inorganic nutrients than cryptophytes, bacillariophytes or euglenophytes. This capacity may be related to their relatively smaller cell size (*Aphanothece clathrata, C. dispersus, T. minimum*) or their filamentous shape with small diameter (*Limnothrix amphigranulata* and *Leptolyngbya* sp.) and the consequent increase in their surface area/volume ratio.

Despite the facts that Santa Olalla and Dulce have similar physical and chemical features, are in close proximity to each other and are hydrologically connected, their phytoplankton dynamics are markedly different, which appears to be due to small environmental differences between the lakes and especially the different hydrological regimes, as shown by the CCA analysis (Figures 4 and 5). This analysis discriminates between the Santa Olalla and Dulce samples and shows a different evolution pattern in each shallow lake. Three different phases related to the increase of the trophic level could be observed in Santa Olalla (phase 1 from March 1998 to June 1998; phase 2 from July 1998 to April 1999, phase 3 from May 1999 to October 1999 and phase 2 again from November 1999 to February 2000) (Fig. 4), whereas Dulce presented a more complex pattern of four different phases: phase 1 from March 1998 to August 1998; phase 2 from September 1998 to December 1998 and phase 3 from January to May 1999; in June 1999, Dulce returned to phase 2 and entered into phase 4 from July 1999 until October 1999. From November 1999 to February 2000, the system returned to phase 2 once again (Fig. 4).

Phase 1 in Santa Olalla (Fig. 4), at the beginning of the study, is located between phases 1 and 2 of Dulce. In this period, both lakes were very similar and the phytoplankton assemblage was dominated by the D, Y and W_2 functional groups in both lakes, although the J group was also important in Dulce during this period. The D-Y-J groups are a common element in shallow enriched systems (Reynolds *et al*., 2002; Romo and Villena, 2005), whereas the W_2 group (represented by *Trachelomonas volvocina*) is found in aerated lakes (Reynolds *et al*., 2002). According to Padisák *et al*. (2003), the relationships of this functional codon with other groups and with environmental patterns that enhance its occurrence have remained rather unclear. In this study, all of those functional groups are related to low conductivity, greater depth of the euphotic zone, maximum water volume of the lakes and the presence of inorganic nutrients, especially SRP (Fig. 5). Cyanobacteria appeared in Santa Olalla for the first time during the last month of phase 1 (June 1998). *A. spiroides* (H_1 group) and *Planktothrix agardhii* (S_1 group) jointly accounted for 56 % of the total biomass, but *Cryptomonas phaseolus* (Y) and *Trachelomonas volvocina* (W_2) together represented 27 % (Table 2). June 1998, together with the first month of phase 2 (July 1998), appeared to be a period of transition to a different state, where the predominance of cyanobacteria is practically absolute.

Functional group K appeared during the first appearance of phase 2 in Santa Olalla (Fig. 4 and Table 2) and was present almost every month during this phase. Reynolds *et al*. (2002) found that this group of small-celled colonial and non-vacuolate cyanobacteria survives well at a high pH, and Padisák *et al*. (2003) observed its presence in shallow, nutrient rich, turbid lakes. In

Santa Olalla, the appearance of this group is related to high conductivity and pH, low depth of the euphotic zone, low SRP concentration and a low TN:TP ratio (Fig. 5), a feature that is shared with *Anabaenopsis circularis* (H_1), which occurs during several months in this phase.

Phase 3 (Fig. 4) corresponds to higher temperatures, conductivity and total alkalinity, low water volume in the lake and a shallow depth of the euphotic zone (all features from late spring and early summer) (Fig. 5) and the appearance of the S_1 (*Limnothrix amphigranulata* and *Leptolyngbya* sp.) functional group, which may be accompanied by the M (*Microcystis aeruginosa*) or J (*P. boryanum* or *T. minimum*) codons. Reynolds *et al*. (2002) related group S_1 to shallow enriched lakes where light is increasingly the limiting constraint, as is the case here. In contrast with *L. amphigranulata*, another species of the same genus, *L. redekei*, is a typical phytoplankton species of turbid mixed layers of the lakes and lowland rivers of Central Europe (Meffert, 1988). *Limnothrix redekei* has also been observed, but in winter/spring, in some shallow lakes such as Lake Melangee (Germany) (Mischke, 2003) or Lake Kastoria (Greece), a shallow Mediterranean lake where this species made up 99 % of the phytoplankton biomass in the winter (Moustaka-Gouni *et al*., 2007). In Santa Olalla, *L. amphigranulata* appears in months when the water reaches its most turbid and hottest state, which might suggest that this species has requirements similar to those of *L. redekei* but prefers a higher temperature. *Planktothrix agardhii*, which appeared during the last month of phase 1 (June 1998), is another member of the S_1 functional group. Wiedner (1999) investigated the influence of mixing on the proportion of *Planktothrix* vs. *Limnothrix* and showed that *Planktothrix* exhibits faster uptake kinetics that *Limnothrix* when P is provided in pulses and at low concentration. This may be the reason why *Planktothrix* only appears in June 1998, when the turbidity of the water is high but there is still some SRP in the lake, whereas inorganic P is practically non-existent during phase 3.

After phase 3, the system returned to phase 2 (Fig. 4). The depth of the euphotic zone increased slightly, as did the water volume of the lake. There was a decrease in water temperature, but the rest of the environmental conditions were similar to those found during the first occurrence of phase 2. The K and H_1 functional groups were present again in this period. Villena & Romo (2003) found that small colonies of chroococcoid cyanobacteria replaced filamentous cyanobacteria, primarily in the summer, in Lake Albufera (Spain), a shallow Mediterranean lake similar to Santa Olalla in terms of the persistent dominance of cyanobacteria and shallow water (Romo & Miracle, 1994). In Santa Olalla, there is also a co-existence or alternation between chroococcoid and filamentous cyanobacteria. Villena & Romo (2003) found experimental evidence that under conditions of TP levels lower than 0.3 mg l^{-1}, water quiescence and low rates of zooplankton grazing, filamentous cyanobacteria were replaced by chroococcoid cyanobacteria in Lake Albufera. However, in Santa Olalla, the TP level was always greater than 0.8 mg l^{-1} during this second phase 2 in which such cyanobacteria were registered. The filamentous cyanobacterium *Anabaenopsis circularis* (H_1 group) was only negatively correlated with water temperature ($P = 0.008$), whereas the chroococcoid *Aphanothece* (K group) was negatively correlated with the number of hours of light ($p = 0.001$) and light intensity ($p = 0.019$). This suggests that in Santa Olalla, the predominance of one group over another is more related to day length than it is to TP concentration.

As before, Dulce exhibited a more complex pattern than Santa Olalla, and the stages are not related as clearly to the functional groups. The J, Y, W_2, D, P, M, H_1 and S_1 functional codons alternated randomly during phase 1 (Table 3 and Fig. 4). In the last three months of this period (June to August 1998), different cyanobacteria appeared and co-dominated with *Aulacoseria* sp. (P group). Reynolds *et al*. (2002) associated the P group with lakes of lower latitudes or temperate lakes in the summer when the epilimnion is continuously mixed, although this can also happen in shallow non-stratified lakes such as Dulce, which has a water column that is completely mixed due to wind and its gentle slopes (Álvarez *et al*., 2001). The P group is characteristically associated

with desmids (Reynolds *et al*., 2002). However, these kinds of associations with cyanobacteria are not often found in the literature. Phase 1 was characterised by a high depth of the euphotic zone, high precipitation, higher SRP and inorganic N concentrations and moderate pH values (Fig. 5).

Phase 2 was characterised by lower values for the euphotic zone depth, precipitation and SRP concentration compared to those of phase 1, whereas phase 3 appeared to be marked primarily by the volume of the water body and low TA, TN:TP ratio, temperature, TN and conductivity values (Fig. 4 and 5). Both phases were defined by the dominance of filamentous cyanobacteria with heterocytes (H_1 functional group: *A. spiroides* and *Anabaenopsis circularis*) accompanied by several chlorophytes of the J functional group (*P. boryanum*, *Monoraphidium contortum* or *Scenedesmus quadricauda*) except in October, when *S. quadricauda* together with *Cryptomonas phaseolus* dominated. *Anabaenopsis circularis* also appeared in phase 2 of Santa Olalla, but *A. spiroides*, which exhibited a particular predominance in phase 3 of Dulce, was unimportant in Santa Olalla during the study period. It is possible that *A. spiroides* is not able to withstand the high pH values that *Anabaenopsis circularis* can, which would explain why *A. spiroides* is not significant in Santa Olalla where pH values are very high.

Phase 4 integrated the months before and after Dulce dried up in September (Fig. 4). In this phase, the Y, S_2 (*Arthrospira platensis*) and D functional groups alternated (Table 3). *Arthrospira platensis* was the dominant species before Dulce dried up. This is the first time that this species has been described in Dulce. Its dominance appears to be associated with a high evaporation rate (rapid loss of water), very high conductivity and a high temperature (Fig. 5). After phase 4, the system returned to phase 2 (Fig. 4). The abiotic conditions were similar to those of the previous phase 2; however, the biological variables were very different (low phytoplankton biomass, number of cells and concentration of chlorophyll *a* and a predominance of small bacillariophytes of the D group: *Nitzschia* spp. and *Synedra* sp. or *Cryptomonas phaseolus*, Y group).

Sommer *et al*. (1993) defined three criteria for the identification of equilibrium states in phytoplankton seasonal succession: (i) a maximum of three species of algae contribute more than 80 % of the total biomass, (ii) their dominance persists for more than 1-2 weeks and (iii) during that period, the total biomass does not increase significantly. Because this study is based on one sampling per month, that duration of equilibrium cannot be considered. In addition, both of the studied shallow lakes have, like many Mediterranean aquatic systems, rapid loss of water by evaporation, which increases the number of cells per volume of water and, therefore, the concentration of algal biomass. Having taken these considerations into account, we can affirm that equilibrium phases in phytoplankton assemblages are relatively frequent in Dulce and especially in Santa Olalla (Tables 2 and 3). Padisák *et al*. (2003) found that equilibrium phases are rare in 80 studied Hungarian lakes. However, lakes that experience stress conditions such as salinity or nutrient deficiencies are more likely to support phytoplankton communities in equilibrium. According to Padisák *et al*. (2003), competitive interactions are of secondary importance in stressed systems such as the above, and the primary factor of selection is the evolutionary adaptation to such stress conditions. In Santa Olalla and Dulce, high water level fluctuations, low inorganic nutrient concentrations and the low light penetration can be considered permanent stress factors for phytoplankton, and only a few species are adapted to these conditions. This could explain the low diversity and number of species found in both shallow lakes as well as the high frequency of recorded equilibrium phases.

In conclusion, Santa Olalla and Dulce are two Mediterranean shallow lakes with a natural tendency towards hypereutrophy. Cyanobacteria dominate the phytoplankton most of the time in Santa Olalla, whereas in Dulce they can co-dominate with small bacillariophytes and chlorophytes. Small differences in environmental and hydrological features between the two lakes produce differences in the characteristics and dynamics of their respective phytoplankton.

The stress that the phytoplankton in these lakes is subject to could explain the existence of a steady-state for many months. The study of these anthropologically unchanged systems can allow us a deeper understanding of the dynamics of Mediterranean shallow lakes.

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