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Relationships between diatoms and the environment in Spanish reservoirs

A. I. Negro & C. De Hoyos

Área de Ecología, Facultad de Biología. Universidad de Salamanca. Campus Miguel de Unamuno. 37071 Salamanca. España. E-mail: negro@usal.es

ABSTRACT

Diatoms are very useful environmental indicators in limnological and paleolimnological studies. Spanish reservoirs offer a valuable opportunity for the study of relationships between diatoms and environmental conditions, since these ecosystems are abundant in this country and the patterns of their regional limnology are well established.

We report the results from a study carried out on diatom communities in 40 reservoirs from several Spanish water basins. More than 200 diatom taxa were found. A canonical correspondence analysis was applied to the abundance data of the most common taxa and the main physical and chemical variables. This analysis showed that mineralisation (conductivity and alkalinity) was the most important environmental factor explaining diatom distribution, while trophic state was the second most important. These results are similar to those in previous studies on phytoplankton in Spanish reservoirs. Conductivity and alkalinity optima of the selected taxa allow us to consider these taxa as good indicators of water mineral content in similar ecosystems.

Keywords: diatoms, reservoirs, water mineralisation, trophic state, canonical correspondence analysis

RESUMEN

Las diatomeas son indicadores ambientales muy útiles en estudios limnológicos y paleolimnológicos. En España los embalses ofrecen una gran oportunidad para el estudio de las relaciones entre las diatomeas y las condiciones ambientales, ya que son ecosistemas muy abundantes y las principales características de su limnología regional están bien estudiadas.

Se presentan aquí los resultados de un estudio sobre las comunidades de diatomeas efectuado en 40 embalses de diversas cuencas hidrográficas españolas. En ellos se encontraron más de 200 taxones de diatomeas. Se efectuó un análisis de correspondencias canónicas con los datos de abundancia de los taxones más frecuentes y las principales variables físico-químicas. Este análisis muestra que el factor con mayor influencia sobre las comunidades de diatomeas es la mineralización (conductividad y alcalinidad), y en segundo lugar el grado trófico. Estos resultados son similares a estudios previos sobre el fitoplancton de embalses españoles. Los valores de los óptimos respecto a la conductividad y alcalinidad de los principales taxones, permiten considerar dichos taxones como buenos indicadores del contenido mineral del agua en ecosistemas similares.

Palabras clave: *diatomeas, embalses, mineralización del agua, estado trófico, análisis de correspondencias canónicas*

INTRODUCTION

Diatoms are currently among the most studied organisms in freshwater ecosystems, due to their role as environmental indicators (Stoermer & Smol, 1999). The response of individual species to some environmental factors allow us to infer the magnitude of those factors considering only the community composition, which is especially useful in paleolimnology. With data from modern diatom communities we can calculate species' optima and tolerances (Charles, 1985; Cumming *et al*., 1995; Joynt & Wolfe, 2001). These optima and tolerances serve to design transfer functions which, when applied to fossil diatom assemblages, allow us to estimate the magnitude of environmental factors over time (Stevenson *et al*., 1989; Battarbee *et al*., 1999; Enache & Prairie, 2002). Sediment-diatom records have revealed eutrophication processes (Lotter, 1998; Reavie *et al*., 2000), acidification (Tolonen & Jaakkola, 1983; Jones *et al.*, 1993; Dixit *et al.*, 2002), land-use changes (Siver *et al.*, 1999), and climate changes (Verschuren *et al.*, 2000; Joynt & Wolfe, 2001).

Generally, species optima and tolerances are calculated with data from a large number of lakes (as many as possible), covering a broad gradient range of environmental factors in the area. In Spain, where deep lakes are scarce, reservoirs offer a better opportunity for this type of studies.

The most extensive and detailed work performed in Spain on reservoir limnology is that of Margalef *et al.* (1976), who studied the physical and chemical variables, zooplankton, phytoplankton, and benthos in about one hundred reservoirs all over the country. A part of the phytoplankton data had been previously treated by Planas (1975). About fifteen years later, a second sampling was carried out in the same reservoirs, and their regional limnology was discussed by Armengol *et al.* (1991) and Riera *et al.* (1992). On the second occasion Sabater & Nolla (1991) studied the phytoplankton community as a whole, and Sabater (1991) focussed on Centrales (Bacillariophyceae).

The present work deals with diatom communities in forty Spanish reservoirs from the main administrative water basins. The foremost objectives were: 1. to study the most important factors affecting the distribution of the main diatom taxa; 2. to calculate the ecological optima and tolerances for these factors in some selected taxa so as to analyse their utility as local environmental indicators.

STUDY SITES AND METHODS

We studied 40 reservoirs located in the main administrative water basins of Spain: Duero, Ebro, Guadalquivir, Guadiana, Júcar, Miño, Segura, Tajo, Norte I, and Norte II (Table 1, Fig. 1).

Figure 1. Distribution of the studied water reservoirs in the administrative Spanish water basins. *Distribución de los embalses estudiados en las cuencas hidrográficas en las que se divide administrativamente el territorio español.*

Table 1. Names of the studied reservoirs, administrative water basins they belong to, number of phytoplankton samples taken for quantitative estimates (N), and year of sampling in each reservoir. *Nombre de los embalses estudiados, cuenca hidrográfica administrativa a la que pertenecen, número de muestras de fitoplancton utilizadas para estimaciones cuantitativas (N) y año de muestreo en cada embalse.*

Water basin	Reservoir name	N	Year
Duero	Agavanzal	6	2000
	Campillo Buitrago	8	2001
	Cuerda del Pozo	8	2001
Ebro	Cereceda	6	1999
	Flix	6	1999
	Gonzalez La-Casa	6	1999
	Mansilla	6	1999
	Sobrón	6	1999
	Talarn	6	1999
	Ullivarri	4	2000
	Urrunaga	5	2000
Guadalquivir	Guadalmellato	13	2001
	Huesna	6	2000
	Sierra Boyera	12	2001
Guadiana	Brovales	6	1999
	Gasset	9	2001
	La Cabezuela	9	2001
	Peñarroya	9	2001
	Piedra Aguda	9	2001
	Ruecas	5	2000
	Valuengo	6	1999
	Vega de Jabalón	9	2001
	Villar del Rey	9	2001
	Zafra	6	1999
Júcar	Alarcón	6	1999
	Mª Cristina	5	1999
	Tous	6	1999
Norte I	Belesar	3	2001
	Bárcena	6	2001
	Castrelo	1	2001
	San Cosmade	4	2000
	Villagudín	3	2000
Norte II	La Granda	6	2000
	Trasona	6	2000
Segura	Cenajo	6	1999
	Crevillente	6	1999
Tajo	La Jarosa	6	2000
	La Tajera	4	2000
	Navacerrada	5	2000
	Santillana	4	2000

Sample collection and analyses of physical and chemical variables were performed by CEDEX (Centro de Estudios y Experimentación de Obras Públicas) staff. Temperature, pH, conductivity, and oxygen were measured with portable meters. Alkalinity was measured by colorimetric titration (APHA–AWWA–WPCF, 1985). Ammonia was analysed using the Spectroquant 14752 method (detection limit of the method: 20 µgN/l) and nitrates were determined using the Spectroquant 14773 method (detection limit: 230 µgN/l), while for nitrites the Spectroquant 14776 was used (detection limit: 15 µgN/l). Orthophosphates and total phosphorus (TP) were analysed using the ascorbic acid method (detection limit: 10 µgP/l). Water for orthophosphate determination was filtered immediately (GF/C filters) and stored in a freezer until analysed in the laboratory. Water for TP analysis was fixed with acid after sampling and was digested in the laboratory prior to analysis using a DR LANGE HT200S digestor in acidic conditions (APHA–AWWA–WPCF, 1985). Chlorophyll *a* was determined using the formulae of Parsons & Strickland (1963).

Table 2 shows the variation range and median value of the environmental variables analyzed, at the dates and depths included in the study. Some environmental data could not be measured as they were under the detection limit of the analytical method. For their inclusion in the analysis we considered a magnitude equal to one unit smaller than the detection limit in the case of orthophosphates, TP, ammonia, and nitrites, and ten units smaller in the case of nitrates.

Table 2. Minimum, maximum**,** and median values of the physical and chemical variables in the data set for the forty reservoirs. Ab: abbreviation used in figure 2; N: number of samples. *Valor mínimo, máximo y mediana de las variables físico-químicas para el conjunto de los 40 embalses. Ab: abreviatura utilizada en la figura 2; N: número de muestras.*

	Ab	Min	Max	Median	N
Secchi depth (m)	Sec	0.1	9	1.8	250
Alkalinity (mg $CaCO_3$/l)	Alk	12	296	108.5	240
Temperature (ºC)	Tem	3.9	29.3	17.4	252
Dissolved oxygen (mg/l)	Ox	0.2	31.68	8.6	252
pH	pH	5.7	9.6	8.1	252
Conductivity (µS/cm)	Cond	24	1677	290	252
Ammonia (µg N/l)	NH4	<10	510	40-50	243
Nitrite (µg N/l)	NO2	<10	150	20-30	244
Nitrate (µg N/l)	NO3	<200	3730	400-600	250
Soluble reactive phosphorus (µg P/l)	SRP	<10	250	<10	196
Total phosphorus (µg P/l)	TP	<10	1668	40-50	226
Chlorophyll *a* (mg/m^3)	Chl	0.06	75.24	3.61	171

We examined phytoplankton samples taken on three or four occasions (winter, spring, summer, and autumn) from each reservoir in 1999, 2000, or 2001 (Table 1). Samples were taken at two sampling points: near the dam (P1), and near the river inflow (P2). In some Guadiana reservoirs and those of the Ebro, Júcar, Tajo, Segura, and Norte II water basins, epilimnion samples were combined. The rest of the reservoir samples were collected generally at 2 and 5m depth at P1, and at 2m depth at P2. Net samples were also taken from most of the reservoirs so as to help in taxa identification. Phytoplankton counts were performed using an inverted microscope according to the Utermöhl method (Utermöhl, 1958). As many fields as necessary were counted to obtain a significant cell number (Sournia, 1978). The magnification was from 100x to 1000x, depending on the size and density of each taxon. The results were expressed as cells per ml.

Diatom taxonomy follows Krammer & Lange-Bertalot (1991a, b; 1997a, b). Taxa were generally identified to species or variety level.

A Canonical Correspondence Analysis (CCA) was carried out using the CANOCO package (Ter Braak & Smilauer, 1998) with the environmental variables shown in Table 2 and the diatom taxa listed in Table 3. The CCA detects variation patterns within the species data that can be explained best by the environmental variables considered (Ter Braak, 1986). In this analysis it is assumed that the species have a unimodal response to environmental variables, which can be previously checked by the Detrended Correspondence Analysis (Ter Braak & Smilauer, 1998). A strong unimodal response can be deduced if the maximum gradient length of the Detrended Correspondence Analysis exceeds 4 SD, as it occurred in our study.

Only taxa present in 10% or more of the reservoirs were included in the CCA, except for those with maximum population density lower than 1 cell/ml. The selected taxa are shown in Table 3. The number of samples considered in the analysis was 252. The data for some environmental variables were not available in all samples (Table 2). Physical and chemical data (except for pH), and diatom data were logarithmically transformed (log [x+1]). The statistical significance of the ordination axes was assessed by the Monte Carlo permutation tests (999 permutations).

In the CCA ordination diagrams, the species' position approximately indicates the environmental optima for each species relative to the other taxa (Ter Braak, 1986). The CCA is a

Table 3. Names of the main taxa in this study. Ab: abbreviations used in figures 2 and 3. N: number of quantitative samples where each taxon occurred. Max: maximum number of individuals counted (cells/ml). The most abundant and/or commonest taxa are marked with an asterisk. *Nombre de los principales taxones del estudio. Ab: abreviatura utilizada en las figuras 2 y 3. N: número de muestras cuantitativas donde apareció cada taxón. Máx: número de individuos máximo encontrado (células/ml). Se señalan con un asterisco los taxones más abundantes y/o frecuentes.*

Name	Ab	N	Max
Achnantes lanceolata (Bréb.) Grun. in Cl. & Grun. 1880	Acl	5	21.9
*_A. minutissima_ Kütz. 1833	Acm	72	552.7
Amphora ovalis parvulum (Kütz.) Kütz. 1844	Amo	10	11.7
Anomoeoneis vitrea (Grun.) Ross 1966	Anvi	8	7.5
*_Asterionella formosa_ Hassall 850	Asfo	80	5615.6
*_Aulacoseira distans_ (Ehr.) Simonsen 1979	Audi	37	5077.3
*_A. granulata_ (Ehr.) Simonsen 1979	Augr	143	5136.2
Caloneis amphisbaena (Bory) Cl. 1894	Caam	6	7.8
C. silicula (Ehr.) Cl. 1894	Casi	4	1.4
Cocconeis pediculus Ehr. 1838	Cpe	11	13.2
C. placentula Ehr. 1838	Cpl	20	47.3
*_Cyclotella comensis_ Grun. in Van Heurck 1882	Cco	28	12 655.5
*_C. meneghiniana_ Kütz. 1844	Cme	21	1045.0
*_C. ocellata_ Pantocsek 1901	Coc	75	41 364.1
*_C. stelligera_ Cl. & Grun. (in Van Heurck) 1882	Cst	18	535.8
Cymatopleura elliptica (Bréb.) W. Sm. 1851	Cye	13	3.4
*_C. solea_ (Bréb.) W. Sm. 1851	Cys	27	3.3
Cymbella affinis Kütz. 1844	Caf	8	11.7
C. aspera (Ehr.) Peragallo 1849	Cas	6	1.5
C. helvetica Kütz. 1844	Che	7	11.3
C. microcephala Grun. in Van Heurck 1880	Cmic	18	25.5
C. minuta Hilse ex Rabh. 1862	Cmi	18	85.2
*_C. silesiaca_ Bleisch in Rabh. 1864	Csi	23	24.1
C. sinuata Gregory 1858	Csin	4	14.4
Diatoma moniliformis Kütz.1833	Dmo	18	14.8
*_D. tenuis_ Agardh 1812	Dte	7	102.8
*_D. vulgaris_ Bory 1824	Dvu	26	16.1
Fragilaria arcus (Ehr.) Cl. 1898	Far	9	8.0
*_F. capucina_ Desmazières 1925	Fca	43	596.7
*_F. crotonensis_ Kitton 1869	Fcro	49	24 156.1
F. tenera (W. Sm.) Lange-Bertalot 1980	Fte	13	581.3
*_F. ulna_ (Nitzsch) Lange-Bertalot 1980	Ful	62	46.3
*_F. ulna_ var. _acus_ Kütz. Lange-Bertalot 1980	Fac	54	4327.3
Gomphonema acuminatum Ehr. 1832	Gac	6	29.1
G. clevei Fricke 1902	Gcl	8	32.7
G. olivaceum (Hornemann) Bréb. 1838	Gol	10	17.4
G. parvulum (Kütz.) Kütz. 1849	Gpa	4	21.4
*_Gyrosigma acuminatum_ (Kütz.) Rabh 1853	Gya	30	1.4
Hantzschia amphioxys (Ehr.) Grun. in Cl. & Grun. 1880	Ham	10	1.1
Meridion circulare (Grev.) Agardh 1831	Mcir	8	5.2
Navicula capitata Ehr. 1838	Nc	7	8.8
*_N. capitatoradiata_ Germain 1981	Nca	30	14.7
N. cryptocephala Kütz. 1844	Ncry	9	5.7
N. cuspidata (Kütz.) Kütz. 1844	Ncus	10	6.6
N. lanceolata (Agardh) Ehr. 1838	Nla	6	21.5
*_N. margalithii_ Lange-Bertalot 1985	Nma	29	12.5
*_N. phyllepta_ Kütz. 1844	Nph	41	37.9
N. pupula Kütz. 1844	Npup	12	32.4
N. radiosa Kütz.1844	Nrad	16	16.1
N. trivialis Lange-Bertalot 1980	Ntri	12	67.1
*_Nitzschia acicularis_ (Kütz.) W. Sm. 1853	Nac	89	365.3
N. angustata (W. Sm.) Grun. in Cl. & Grun. 1880	Nan	11	7.2
N. dissipata (Kütz.) Grun. 1862	Ndi	20	9.7
N. flexa Schumann 1862	Nfl	12	3.0
N. linearis (Agardh) W. Sm. 1853	Nli	13	32.2
*_N. palea_ (Kütz.) W. Sm. 1856	Npa	11	3519.1
N. recta Hantz. in Rabh 1861-1879	Nre	7	2.94
N. vermicularis (Kützh) Hantz. in Rabh 1860	Nve	16	7.2
*_Stephanodiscus hantzschii_ Grun. in Cl. & Grun. 1880	Shan	52	103 509.8
Surirella angusta Kütz. 1844	Suan	9	14.3
*_Tabellaria fenestrata_ (Lyngb.) Kütz. 1844	Tfen	17	457.3
T. flocculosa (Roth) Kütz. 1844	Tflo	7	27.8

method based on weighted averaging (WA). In WA, the optimum for an environmental factor of a species is estimated as the average of the values of this factor, at the sites where the species occurred, weighted by its abundance (Ter Braak, 1986, 1987):

$$u_k = \Sigma y_{ik}\, x_i / \Sigma y_{ik}$$

u_k: optimum of species k.
y_{ki}: abundance of species k at site i.
x_i: value of the environmental factor at site i.

The tolerance of a species can be estimated as the weighted-average standard deviation:

$$t_k = (\Sigma y_{ik}(x_i - u_k)^2 / \Sigma y_{ik})^{1/2}$$

RESULTS

Relevant taxa

We found 40 diatom genera, both in quantitative and net samples, 215 species and varieties (32 Centrales and 183 Pennales). The major part of the taxa belonged to *Navicula* (27 taxa), *Cymbella* (25 taxa), *Nitzschia* (22 taxa), *Fragilaria* (19 taxa), and *Cyclotella* (13 taxa).

Some species of the remaining genera, such as *Acanthoceras zachariasii*, *Actinocyclus normanii*, *Ellerbeckia arenaria*, *Pleurosira laevis,* and *Campilodiscus hibernicus*, only appeared in reservoirs of the Ebro basin and in the SE part of Spain. *Pinnularia* and *Eunotia* taxa, i.e. *Pinnularia viridis*, *P. subcapitata,* and *Eunotia bilunaris,* were very scarce and occurred mainly in reservoirs in the west. Also *Frustulia rhomboides* and *Neidium affine* were found in the west.

The most common taxa and those with important population densities are shown in Table 3. We find among them *Achnantes minutissima*, *Asterionella formosa*, *Aulacoseira granulata*, most of *Cyclotella* species, *Fragilaria capucina*, *F. crotonensis*, *F. ulna*, *F. ulna* var. *acus, Nitzschia acicularis, Stephanodiscus hantzschii,* and *Tabellaria fenestrata*.

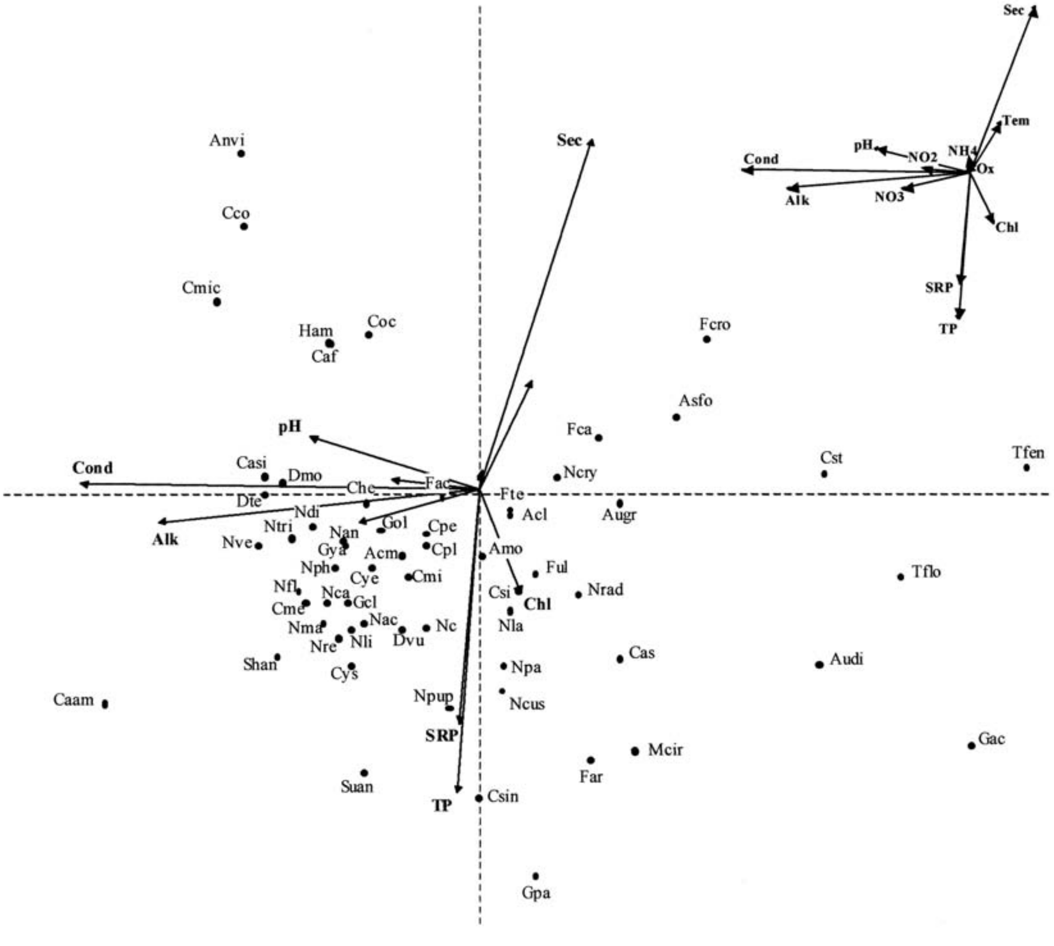

Figure 2. CCA biplot of the environmental variables (arrows) and species (points). Only the most important variables are labelled. The complete plot of the environmental variables is shown in the upper-right-hand corner of the figure. See tables 2 and 3 for abbreviations. *Representación gráfica de los resultados del ACC, variables ambientales (flechas) y las especies (puntos). Solamente se señala el nombre de las variables más importantes. En el ángulo superior derecho se muestra el diagrama completo de las variables ambientales. Abreviaturas como en las tablas 2 y 3.*

Diatoma, *Gyrosigma* and *Cymatopleura* species were also common, mainly in reservoirs of Ebro, Júcar, Segura, and in some of the Guadiana reservoirs, but their population densities were generally low.

Canonical Correspondence Analysis

The eigenvalues of the first two CCA axes were 0.34 and 0.22 respectively. These two axes collectively explain 10.3% of the variance in the diatom species data (axis 1: 6.3%; axis 2: 4%). The species-environment correlation was 0.82 for axis 1 and 0.64 for axis 2, and the amount of species-environment variance explained was 36.4% and 23.2% respectively. The first canonical axis and the sum of all canonical axes were statistically significant (p=0.001).

The first axis represents the mineral-content gradient, as it is strongly correlated to conductivity (r=-0.942) and alkalinity (r=-0.757). Also pH is associated with the first axis (r=-0.398). The second axis is related to the trophic gradient: Secchi depth and total phosphorus show the highest correlation to this axis (r=0.769 and r=-0.667 respectively). Chlorophyll *a* and SRP are also related to the second axis, but correlation coefficients are lower (r=-0.231 for chlorophyll *a* and r=-0.517 for SRP).

Figure 2 shows the CCA biplot of environmental variables and diatom scores for the first two axes. Most of the taxa appear in the lower-left quadrant of the CCA, i.e. they are related to intermediate to high levels of mineral content and trophic state.

The species associated with higher values of the mineral-content gradient (i.e. with a more extreme position in the left part of the first CCA axis) were *Caloneis amphisbaena*, *Cymbella microcephala*, *Cyclotella comensis*, *Anomoeoneis vitrea*, *Nitzschia vermicularis*, *Diatoma tenuis*, *Caloneis silicula*, *D. moniliformis*, *Stephanodiscus hantzschii*, *Navicula trivialis*, *Nitzschia flexa*, and *Cyclotella meneghiniana*. Whereas those associated with the lower gradient values were *Tabellaria fenestrata*, *Gomphonema acuminatum*, *Tabellaria flocculosa*, *Aulacoseira distans*, *Cyclotella stelligera*, *Fragilaria crotonensis,* and *Asterionella formosa*.

With regard to the second axis (trophic gradient), *Gomphonema parvulum*, *Cymbella sinuata*, *Surirella angustata*, *Fragilaria arcus*, *Meridion circulare*, *Gomphonema acuminatum*, *Navicula pupula*, *Caloneis amphisbaena*, and *Navicula cuspidata*, seemed to be related to the highest trophic level. In contrast, *Anomoeoneis vitrea*, *Cyclotella comensis*, *Cymbella microcephala*, *Cyclotella ocellata*, *Fragilaria crotonensis*, *Cymbella affinis*, and *Hantzschia amphyoxis* were in the lower extreme of the trophic gradient in the CCA biplot.

Optima and tolerances

Optima and tolerances for conductivity and alkalinity were calculated, since they were the variables revealed in the CCA as the most important ones explaining diatom distribution. We only considered the 24 taxa that developed dense populations and/or were very common (w/asterisk in Table 3). The optima and tolerances of these taxa are represented graphically in figure 3 in order of decreasing optima.

Both conductivity and alkalinity optima are quite different for the 24 selected taxa. As was to be expected, the arrangement of the taxa in figure 3 resembles the one of the CCA biplot. Thus, the taxa with the lowest alkalinity and conductivity optima are *Tabellaria fenestrata*, *Aulacoseira distans*, *Cyclotella stelligera*, *Fragilaria crotonensis,* and *Asterionella formosa*; whereas the highest optima are for *Cyclotella comensis*, *C. meneghiniana*, *Diatoma tenuis*, *Stephanodiscus hantzschii,* and *Navicula margalithii*.

The range of the alkalinity tolerance intervals was very similar for the 24 selected taxa. There were greater differences in conductivity. We could mention *Cyclotella stelligera*, *Aulacoseira distans,* and *Tabellaria fenestrata*, as those having the narrowest conductivity tolerance. *Diatoma tenuis* showed narrow tolerance for both variables.

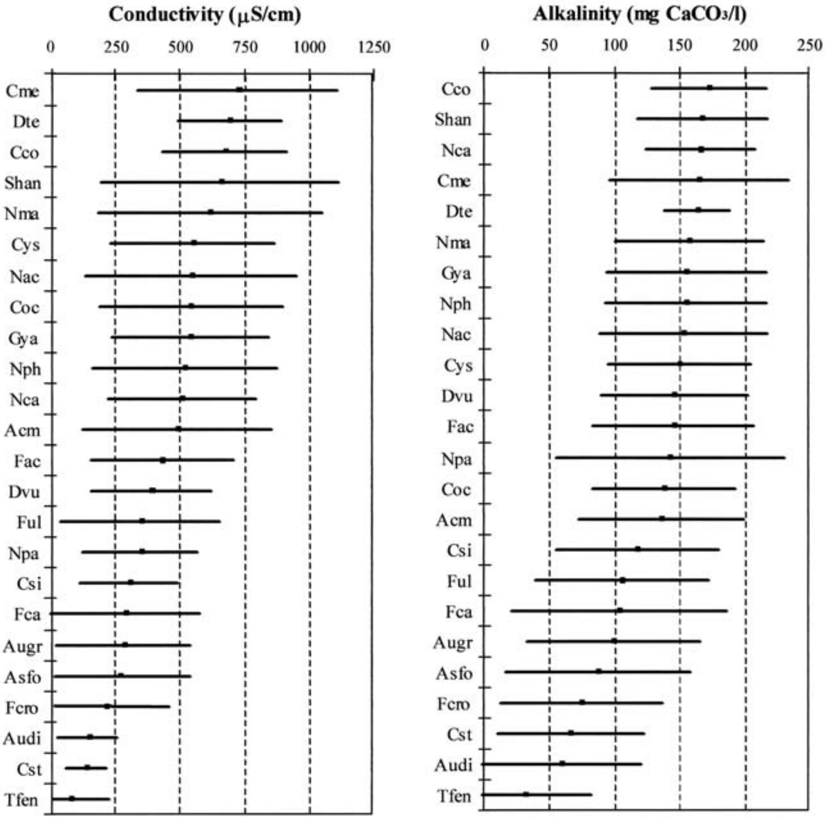

Figure 3. Alkalinity and conductivity optima (points) and tolerances (bars) of the 24 most relevant taxa, arranged in order of decreasing optima for conductivity and alkalinity. See Table 3 for abbreviations. *Óptimos (puntos) y tolerancias (barras) respecto a la conductividad y alcalinidad, de los 24 taxones más importantes del estudio. Se representan en orden decreciente de los óptimos. Abreviaturas como en la Tabla 3.*

DISCUSSION

It has been demonstrated, on a broad geographic scale, that phytoplankton in Spanish reservoirs is mainly influenced by the water mineral content and trophic state (Margalef *et al*., 1976; Sabater & Nolla, 1991; Riera *et al*., 1992; De Hoyos *et al*., in press), and this again becomes apparent in our study. The ionic composition will probably always be the most important of the two factors because it depends on bedrock geology and climate (Margalef *et al*., 1976; Riera *et al*., 1992).

Margalef *et al*. (1976) divided Spanish reservoirs, according to the water mineral content, into two basic groups: 1) soft-water reservoirs, on siliceous bedrock (West part of the Iberian Peninsula), and 2) hard-water reservoirs, on calcareous bedrock (Central and Eastern part of the Iberian Peninsula). Only the taxa-presence/absence data in our study, without considering any other ones, had already revealed a difference between the two groups of reservoirs. Genera, such as *Acanthoceras*, *Actinocyclus*, *Ellerbeckia*, *Campilodiscus*, *Cymatopleura*, *Gyrosigma,* and *Pleurosira*, were much more common (and some of them exclusive) in the eastern reservoirs. *Eunotia*, *Pinnularia*, *Frustulia, and Neidium*, appeared mainly in the west area. The latter genera are very common in soft-water mountain lakes (De Hoyos & Negro, 2001; Negro *et al*., 2003).

Regarding the influence of the water mineral content on the most relevant taxa (first CCA axis), our results are consistent with those of other authors. That is to say, *Asterionella formosa*, *Aulacoseira distans*, *Fragilaria crotonensis*, *Tabellaria fenestrata,* and *T. flocculosa*, can be considered to be related to soft waters, which was also shown by Margalef *et al*. (1976) and Sabater & Nolla (1991). Negro *et al*. (2000) reported that *T. fenestrata* and *A. formosa* contributed to the major part of the phytoplankton biomass during the circulation period in the Valparaíso Reservoir (Duero basin), where mean conductivity was only 24 µS/cm. In the CCA biplot, *Aulacoseira granulata* is in an intermediate position, which reflects its wide distribution in the Spanish reservoirs (Sabater, 1991). *Cyclotella stelligera* prefers waters with a lower pH level and a lower calcium concentration than other *Cyclotella* species, such as *Cyclotella meneghiniana and C. ocellata* (Dixit *et al*., 2002; Enache & Prairie, 2002). This can be seen in the CCA biplot (Fig. 1). In the Spanish reservoirs with the hardest water, *C. meneghiniana*, *C. radiosa*, and *C. comensis* are abundant, and *Stephanodiscus hantzschii* and *Cyclostephanos dubius* also occur but are more sporadic (Margalef *et al*., 1976; Sabater, 1991; Sabater & Nolla, 1991). In our study *C. radiosa* (not included in the CCA analysis) was less common than *C. comensis* or *C. meneghiniana*, whereas *C. ocellata* was more common. On the other hand, *Stephanodiscus hantzschii* as well as other *Stephanodiscus* species and *C. dubius* also occurred in the hard-water reservoirs. But, because of their low occurrence and identification problems, we did not include *Stephanodiscus* spp. and *C. dubius* in the CCA.

Conductivity and alkalinity optima differed between the selected taxa, indicating that they could be considered as good mineral-content indicators. This is of great interest in paleolimnological studies, because water conductivity variation can be related to changes in patterns of precipitation and evaporation and thus to climate changes (Anderson *et al*., 1999; Verschuren *et al*., 2000). Besides a well-defined optimum, a good environmental indicator must have a narrow tolerance, because taxa with broad tolerance will not be affected by changes in the environment (Racca *et al*., 2001; Enache & Prairie, 2002). The tolerances we have obtained do not differ very much, especially for alkalinity. Nevertheless, it must be emphasized that the tolerances of taxa showing the highest optima hardly overlapped those of the taxa with the lowest optima (Fig. 3).

Regarding the relationship between diatoms and trophic state (second CCA axis), our results on soft-water reservoirs differ slightly from other studies. Namely, *A. granulata, A. formosa,* and *F. crotonensis* are generally considered to be eutrophic species (Margalef *et al*., 1976; Carney, 1982; Lepistö & Roseström, 1998; Reavie *et al*., 2000). In our study, *F. crotonensis* is in the lowest extreme of the trophic gradient (Fig. 2), and *A. granulata* and *A. formosa* (particularly the former) are near the center of the gradient. Conversely, *Aulacoseira distans*, a species abundant in oligotrophic lakes (De Hoyos, 1996), seems to prefer waters with a higher trophic state than the three species mentioned, as seen from their position in the CCA biplot. Some studies have pointed out that Spanish reservoirs are becoming increasingly eutrophic, especially the soft-water ones (Sabater & Nolla, 1991; De Hoyos *et al*., 2004). Eutrophication-indicator diatoms could be useful tools for future management of these reservoirs, so our results need to be confirmed in further studies. In hard-water reservoirs, the main taxa did show the expected relation with trophic state. *Stephanodiscus hantzschii* is in the upper extreme of the trophic gradient (Fig. 2). Other *Stephanodiscus* species and *Cyclostephanos dubius* sometimes occur together with *S. hantzschii*. In lakes of eutrophic conditions *Stephanodiscus* spp. and *C. dubius* are common (Carney, 1982; Lotter, 1998; Temponeras *et al*., 2000; Reavie *et al*., 2000). *Cyclotella* species in hard-water reservoirs mainly inhabit the oligo-mesotrophic ones (Dasí *et al*., 1998), as it occurred in our study.

CONCLUSIONS

Water mineral content appears, once again, as the most important factor explaining phytoplankton distribution in Spanish reservoirs.

Some of the most common and abundant diatoms in the reservoirs can be considered as good mineral-content indicators, which is very useful, especially in paleolimnological studies. The alkalinity and conductivity optima of these taxa are well defined, but the extreme values of tolerances require a more precise determination.

Variables related to trophic state also influence diatom communities, but in soft-water reservoirs it is difficult to determine the indicator taxa. A more detailed study on these reservoirs is of great interest, in order to find the best trophic-state indicators for their management.

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