



## Diatom and desmid relationships with the environment in mountain lakes and mires of NW Spain

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### Abstract

The mountain ranges in NW Spain have a large number of little known wetlands. We report the results of a study carried out on a group of 77 small lakes and mires in the Sierra Segundera and Cordillera Cantábrica. The main physical and chemical variables, and phytoplankton communities from littoral samples were studied. Cantabrian wetlands showed greater variability in all environmental variables measured as well as higher values in those related to mineralisation than the Segundera ones. Many of these ecosystems were oligotrophic and showed a high species richness. Desmids and diatoms were the two most abundant groups, both in the species number and in biovolume. Desmids were the most numerous group in taxa in Sierra Segundera, whereas diatoms were in Cordillera Cantábrica. Differences in species composition of algae communities between both mountain ecosystems were studied. Canonical Correspondence Analysis (CCA) was carried out on diatom and desmid flora composition. This analysis showed that alkalinity was the most important parameter in diatom distribution and pH the most important one in that of desmids.

### Introduction

Small lakes and wetlands are widespread in the mountains of the NW Iberian Peninsula. Two of the more interesting wetland complexes in this area are in Sierra Segundera and in Cordillera Cantábrica, which are the subject of this study. The biological and chemical nature of these ecosystems is still little known despite their ecological importance. Concerning microalgae, only some disperse data have been published so far (Bachmann, 1913; Margalef, 1950; Margalef, 1955; Vega et al., 1991; Velasco et al., 1999).

Mountain lakes are mainly regulated by three parameters: (1) low temperatures in winter; (2) light radiation in the lake – also low in winter due to the ice and snow cover; (3) rock composition in the catchment area – having influence on the drainage water (Bretschko, 1995). The mountain lakes in NW Spain are characterised by a heterogeneous substrate and by the Mediterranean mountain climate. Mediterranean

mountain lakes usually have low winter temperatures, allowing the formation of ice cover. However, the temperature rises considerably in summer, permitting substantial algae development.

Freshwater-phytoplankton composition depends mainly on the physical and chemical properties of the water which in its turn reflects the watershed's rock composition (Rao, 1953; Howard, 1968; Gibson et al., 1992). Water conductivity, pH, calcium concentration and carbon dioxide-bicarbonate system have great influence on algae distribution and particularly on that of diatoms and desmids (Moss, 1972, 1973; Flensburg & Sparling, 1973; Coesel, 1986; Alles et al., 1991; Dell'Uomo, 1992; Coesel & Kooijman-Van Blokland, 1994).

The aim of the present work is to study the basic chemistry and phytoplankton composition of various wetlands in the NW Spanish mountain ranges, and try to explain the relationships between them, focusing on diatom and desmid communities.

*Table 1.* Main features of the sites studied. (A) The S. Segundera sites. (B) The C. Cantábrica sites. The number code is the same as that used in Figure 1. Depth was divided into five classes: 1: <1 m, 2: 1–2 m, 3: 2–5 m; 4: 5–10 m; 5: >10 m. Total cation content was calculated by adding up  $\text{Ca}^{2+}$ ,  $\text{Mg}^{2+}$ ,  $\text{Na}^+$  and  $\text{K}^+$  concentrations

A)

Number	Name	Type	Altitude (m)	Depth (class)	Conductivity ( $\mu\text{S cm}^{-1}$ )	pH	Alkalinity ( $\text{meq l}^{-1}$ )	Silica ( $\text{mg l}^{-1}$ )	Total Cations ( $\text{mg l}^{-1}$ )
1	Aguas Cernidas	Lake	1810	4	17.8	7.1	0.12	0.04	8.14
2	Cárdena	Reservoir	1560	5	20.8	6.7	0.16	1.62	6.55
3	Carros	Lake	1340	2	12.5	7.2	0.18	1.28	2.65
4	La Clara	Lake	1600	5	8.8	6.5	0.02	0.00	1.08
5	El Cuadro	Lake	1680	4	12.4	7.1	0.06	0.01	2.71
6	Garandones	Reservoir	1620	4	17.8	6.8	0.17	0.06	6.77
7	Lacillo	Lake	1700	4	12.5	7.1	0.10	0.44	6.54
8	Mancas	Lake	1610	4	12.3	7.2	0.08	0.31	1.79
9	Patos	Lake	2000	2	25.3	4.5	0.04	0.03	3.25
10	Payón	Lake	1590	3	16.0	6.5	0.13	0.01	2.76
11	Peces	Lake	1700	3	12.9	7.5	0.12	0.04	2.13
12	Pedralba	Lake	1729	2	7.0	6.4	0.04	0.08	1.70
13	Pedrina	Lake	1730	4	9.0	6.7	0.04	0.43	2.21
14	Piatorta	Lake	1870	4	18.0	7.4	0.10	0.00	2.24
15	Playa	Reservoir	1575	3	13.5	7.0	0.12	0.00	5.07
16	Puente Porto	Reservoir	1645	5	9.0	6.5	0.04	0.4	2.09
17	La Roya	Lake	1625	4	11.5	7.3	0.08	0.37	1.71
18	Sanabresa	Lake	1745	3	8.1	6.4	0.01	0.00	1.60
19	Las Sanguijuelas	Lake	1080	2	41.3	6.1	0.07	0.56	8.48
20	Sotillo	Lake	1580	4	8.0	6.5	0.09	0.75	3.32
21	Truchas	Lake	1750	5	6.2	6.6	0.02	0.29	1.28
22	Truchillas	Lake	1870	4	4.9	6.2	0.004	0.10	1.17
23	La Yegua	Lake	1790	4	10.3	7.2	0.11	0.30	1.80
24	Vega de Conde	Reservoir	1590	5	17.4	7.2	0.08	1.01	3.90
25	Vega de Tera	Reservoir	1520	5	19.0	7.3	0.14	0.88	2.82
26	Ventosa	Lake	1825	2	10.0	8.1	0.04	0.00	2.55
27	Aguas Cernidas	Mire	1800	2	28.0	6.1	0.09	0.00	8.84
28	Camposagrado	Mire	1700	1	11.5	6.5	0.03	0.10	3.36
29	Clara	Mire	1600	3	8.0	6.8	0.06	0.00	4.15
30	Covadosos	Mire	1620	1	23.1	6.1	0.29	1.66	5.10
31	Lacillo	Mire	1920	1	12.3	5.7	0.02	1.90	6.70
32	Majadavieja	Mire	1580	2	10.9	7.0	0.09	0.01	1.78
33	Moncalvo 1	Mire	1975	1	21.5	5.4	0.06	0.71	1.38
34	Moncalvo 2	Mire	1930	1	20.2	5.5	0.06	1.37	3.07
35	Moncalvo 3	Mire	1940	1	15.7	5.2	0.02	0.49	1.85
36	Moncalvo 4	Mire	1930	1	17.3	5.8	0.11	0.05	2.95
37	Moncalvo 5	Mire	1900	1	17.3	6.1	0.06	0.18	4.73
38	Padornelo 1	Mire	1700	1	10.0	5.4	0.06	0.19	1.04
39	Padornelo 2	Mire	1680	1	6.7	6.1	0.01	0.00	1.62
40	Puente Porto	Mire	1690	1	12.0	5.6	0.04	0.00	2.12
41	La Roya	Mire	1625	2	18.5	7.2	0.13	0.36	3.75
42	Truchillas	Mire	1900	1	14.8	4.8	0.00	0.24	1.39
43	Valdecazares 1	Mire	1800	1	12.0	5.2	0.02	0.10	1.16
44	Valdecazares 2	Mire	1750	1	7.1	5.4	0.02	0.00	2.04

Continued on p. 3

Table 1. contd.

B)

Number	Name	Type	Altitude (m)	Depth (class)	Conductivity ( $\mu\text{S cm}^{-1}$ )	pH	Alkalinity ( $\text{meq l}^{-1}$ )	Silica ( $\text{mg l}^{-1}$ )	Total Cations ( $\text{mg l}^{-1}$ )
45	Ausente	Lake	1750	5	12.0	4.7	0.00	0.20	1.31
46	Bustalveinte	Lake	1000	2	97.2	7.1	0.83	0.80	19.46
47	Cerveriz	Reservoir	1660	5	246.0	8.0	1.32	0.07	19.30
48	La Cueta	Lake	1435	5	149.0	7.2	1.15	0.47	27.55
49	La Cueva	Reservoir	1600	5	214.0	8.5	1.46	0.32	18.35
50	Fuentes Carrionas	Lake	2230	4	10.5	7.1	0.08	0.91	1.97
51	Las Lomas	Lake	2060	4	44.1	6.7	0.10	0.65	3.06
52	Poza de Noja	Reservoir	740	4	24.7	6.1	0.03	0.00	9.08
53	La Serna	Lake	1000	1	1600.0	8.1	2.38	1.82	365.98
54	Tres Navas	Lake	870	2	224.0	8.2	1.14	2.31	38.62
55	Las Verdes	Lake	1720	2	77.0	7.1	0.48	0.46	13.69
56	Abiada	Mire	1100	1	2440.0	7.4	1.36	3.95	419.29
57	Ausente	Mire	1750	1	83.7	7.0	0.66	0.18	16.65
58	Cabañas de Virtus	Mire	840	2	96.5	6.8	0.58	1.14	21.17
59	Campo de la Braña	Mire	1600	1	24.4	6.1	0.07	0.25	4.79
60	Chagüño abajo	Mire	1550	2	25.1	6.2	0.09	0.14	2.03
61	Chagüño arriba	Mire	1630	2	15.3	6.5	0.02	0.00	0.96
62	Chouchinas 1	Mire	1600	2	17.4	5.2	0.02	0.07	2.96
63	Chouchinas 2	Mire	1650	1	14.4	4.9	0.00	0.04	0.61
64	Cordiñanes	Mire	900	1	231.0	6.9	1.64	1.17	27.05
65	Estacas de Trueba	Mire	1250	2	25.0	5.4	0.01	0.00	3.28
66	El Joyaco 1	Mire	1293	1	140.0	7.5	1.35	1.48	22.05
67	El Joyaco 2	Mire	1290	1	13.7	5.3	0.01	0.20	3.09
68	Llano Roñances	Mire	200	2	77.0	4.4		0.00	10.00
69	Las Lomas	Mire	2130	1	14.8	7.1	0.18	0.11	3.37
70	Peña Prieta 1	Mire	1770	2	40.0	6.4	0.14	0.52	6.20
71	Peña Prieta 2	Mire	1770	2	37.0	6.3	0.12	0.61	5.26
72	Noja	Mire	745	1	53.0	4.8	0.00	0.00	6.03
73	Reconcos	Mire	1549	2	26.8	6.4	0.13	0.32	3.77
74	Riofrío	Mire	1760	2	32.6	6.5	0.18	0.26	5.64
75	Santa Gadea	Mire	860	1	89.2	6.3	0.50	1.00	17.07
76	Los Tornos	Mire	940	2	155.7	7.2	1.37	2.40	31.50
77	Las Verdes	Mire	1720	1	130.0	7.0	0.92	0.63	20.46

### Study sites

Two mountain ranges in NW Spain were studied (Fig. 1, Table 1): Sierra Segundera and Sierra Cabrera (hereafter these two mountain ranges will be jointly called S. Segundera) and Cordillera Cantábrica (hereafter C. Cantábrica). Most of the selected wetlands were formed during the Quaternary glacial periods (Vega & Aldasoro, 1994; Pérez Alberti & Valcárcel Díaz, 1997).

The geologic substratum of S. Segundera consists of Paleozoic rocks, mainly plutonic and metamorphic ones: gneises, granodiorites, and schists (Martínez García, 1973; Vega & Aldasoro, 1994). Most of the ecosystems in this area are within the “Lago de Sanabria” Natural Park. They are in the upper part of the Tera river drainage basin, situated between 1080 and 1990 m a.s.l. Some of the lakes were converted, in 1950–1960, into reservoirs used for electricity generation and crop irrigation. Nevertheless, most of

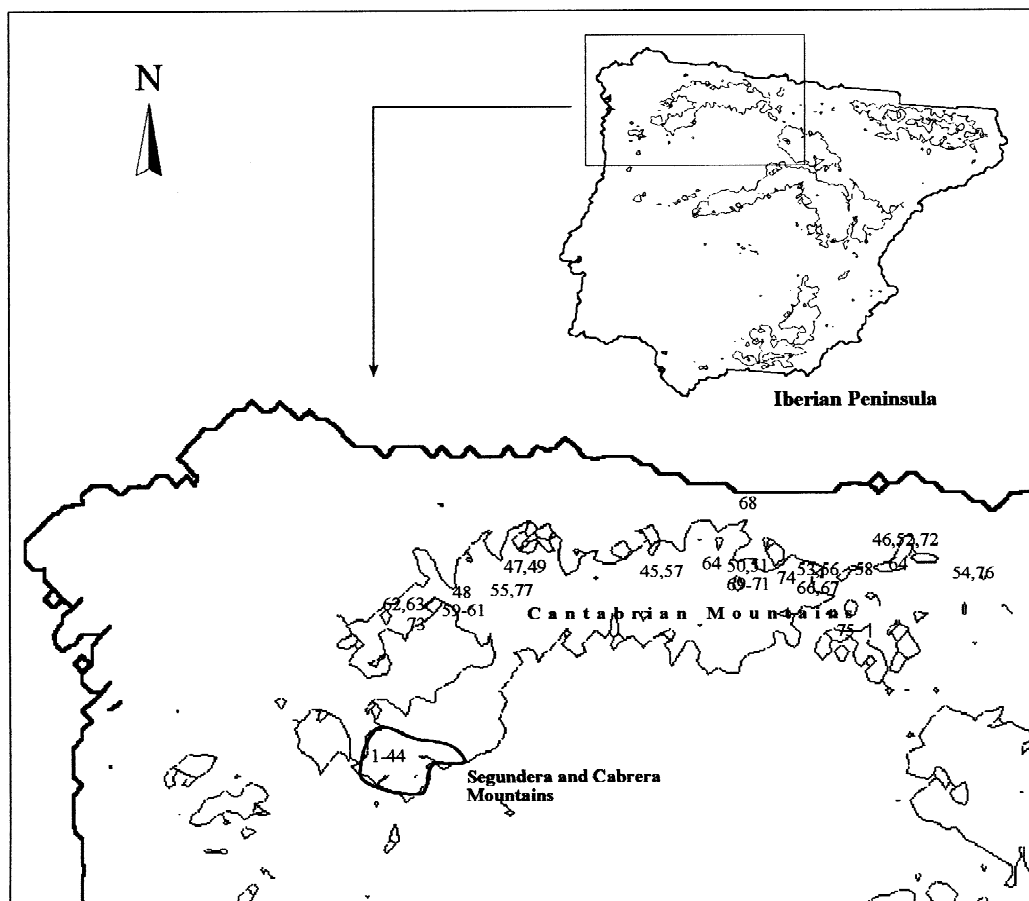


Figure 1. Geographic location of the studied lakes and mires in the Iberian Peninsula. The line corresponds to 1000 m a.s.l.

the S. Segundera wetlands maintained their original conditions and are in a good state of preservation.

The other study area (Fig. 1), C. Cantábrica, runs parallel to the northern Spanish coast. It is an extensive mountain range with both Paleozoic and Mesozoic rock materials. It is a large area of heterogeneous geology: schists, limestones, granites, conglomerates, etc. (Instituto Geológico Minero de España, 1980; Julivert et al., 1981). Here, on calcareous rocks, glacial erosion combined with karstification, resulted in a characteristic type of basin morphology (Casado & Montes, 1995). We selected a group of small lakes and mires situated in several drainage basins, between 900 and 2200 m a.s.l. Only a few of them have suffered human impact.

## Materials and methods

Surface-water samples were taken once at each site – in S. Segundera in the summer of 1993 and in C. Cantábrica in the summer of 1994 or 1995. The sampling place (for chemical variables and microalgae) was the littoral zone in lakes (at a distance of 1–1.5 m from the shore), avoiding macrophyte areas; whereas in mires it was the deepest pool.

Water conductivity, pH and alkalinity were measured in the field with portable meters. Alkalinity measurements were carried out using a potentiometric method (American Public Health Association – APHA, 1989). Nitrates, soluble reactive phosphorus (SRP), total phosphorus (TP), silica, chlorophyll *a* and chloride ( $\text{Cl}^-$ ) were determined using standard limnological methods (APHA, 1989). Water colour was measured as water absorbance at 440 nm (Cuthbert & Del Giorgio, 1992). Cations in water ( $\text{Ca}^{2+}$ ,

Mg<sup>2+</sup>, Na<sup>+</sup> and K<sup>+</sup>) were analysed using Inductively Coupled Plasma Spectroscopy (ICPS).

Water samples for microalgae observations were taken in 200 ml bottles, and preserved in Lugol's solution. Counting was carried out using the Utermöhl method (Utermöhl, 1958). A volume of 50 ml of each sample was sedimentated. Largest species were counted under 200× magnification. For the rest of the species we used 400× or 1000× magnifications, counting as many fields as necessary to obtain a significant cell number (Sournia, 1978). Algae size was determined in order to calculate biovolume (Rott, 1981).

Canonical Correspondence Analysis (CCA) was carried out using CANOCO package (Ter Braak & Smilauer, 1998). CCA ordination serves to analyse the correlation between particular environmental variables and biological assemblages species composition. It detects variation patterns within the species data that can be correlated best with the environmental variables considered (Ter Braak, 1986, 1987). Biovolume was used to quantify each species. Species data were logarithmically transformed ( $\log [x + 1]$ ).

Two preliminary desmid and diatom CCA analyses were carried out in order to select the most significant variables. From all of these variables (altitude, depth, conductivity, pH, alkalinity, nitrates, SRP, TP, silica, chlorophyll *a*, Ca<sup>2+</sup>, Mg<sup>2+</sup>, Na<sup>+</sup>, K<sup>+</sup>, total cations – Ca<sup>2+</sup>+Mg<sup>2+</sup>, Na<sup>+</sup>+K<sup>+</sup>–, Cl<sup>–</sup>, and colour, Table 2) we selected those which served to explain more than 10% of total variance. The species table shows only those present at more than 6% of the studied sites (69 diatom and 63 desmid taxa, Table 3). The final CCA analysis was carried out on the selected variables and the diatom or the desmid table.

## Results and discussion

### *Physical and chemical variables*

Water conductivity, pH and alkalinity levels were generally lower in S. Segundera than in C. Cantábrica lakes and mires (Tables 1 & 2). Also, high Ca<sup>2+</sup> levels occurred in C. Cantábrica, whereas in S. Segundera they were considerably lower (Table 2). These levels were presumably related to the higher abundance of limestone rocks in C. Cantábrica. Conversely, in the S. Segundera drainage area rocks are poorer in Ca<sup>2+</sup>, because they are mainly acid gneisses and granodiorites. Water ion content and pH tend to be low in regions

of acid igneous or metamorphic rocks (Hutchinson, 1957).

In the S. Segundera, Ca<sup>2+</sup> is mobilised faster than other cations during rock meteorisation (De Hoyos, 1996). However, in lacustrine ecosystems of the upper S. Segundera, water Na<sup>+</sup> concentration exceeded that of Ca<sup>2+</sup> (Table 2). This fact could be explained by atmospheric influence. In these water bodies, with small catchment areas, atmospheric Na<sup>+</sup> can surpass cations released from the substrate.

Due to sphagna and peat exchange activity (Kilham, 1982; Gorham et al., 1985), the lowest pH values were recorded in mires (Tables 1 & 2). Nitrate concentration was generally higher in C. Cantábrica than in S. Segundera, but that of phosphorus (both SRP and TP) was higher in S. Segundera (Table 2). However, SRP and TP mean values were low in both regions. Silica levels were generally low in S. Segundera and moderately higher in C. Cantábrica.

Water colour values were higher in S. Segundera (Table 2) due to mire influence. The colour of many S. Segundera lakes and mires was > 50 mg l<sup>–1</sup> Pt (generally considered the limit of dystrophy). Only a few C. Cantábrica sites showed a comparable water colour.

### *Phytoplankton*

#### *General description*

The analysis of phytoplankton data showed a high species number in most of the mountain water bodies included in the study (Table 4). Desmidiaceae (class Zygothryx, phylum Chlorophyta), and Diatomeae or Bacillariophyceae (phylum Chrysophyta), were the groups which contributed most to the high species number. Both groups (especially Desmidiaceae) are usually dominant in bog waters (Duthie, 1965; Flensburg & Sparling, 1973; Hosiaislouma, 1975; Fagnant, 1987). Chlorophyta, Cyanophyta and Chrysophyceae showed a higher species number in S. Segundera than in C. Cantábrica (Table 4). The highest Bacillariophyceae and Euglenophyta number was found in C. Cantábrica.

Total phytoplankton biovolume value differed in both regions (Table 5): it was higher in C. Cantábrica than in S. Segundera. The taxa which contributed most to the total biovolume were chlorophytes in mires and flagellates in lakes. Dinoflagellates and chrysophytes were the most abundant groups in lakes. A few water bodies in C. Cantábrica showed high cyanophyte and diatom biovolume.

Table 2. Variation range, means, standard deviation and medians of the physical, chemical and biological variables. SRP – soluble reactive phosphorus; TP – total phosphorus. Total cations –  $\text{Ca}^{2+} + \text{Mg}^{2+} + \text{Na}^+ + \text{K}^+$

		Segundera and Cabrera Mountains				Cantabrian Mountains			
		Range	Mean	Standard deviation	Median	Range	Mean	Standard deviation	Median
Altitude	(m)	1080–2000	1709	171.68	1700	200–2230	1392.79	466.58	1550
Conductivity	( $\mu\text{S cm}^{-1}$ )	4.9–41.3	14.3	6.8	12.5	10.5–2440.0	196.4	487.1	53.0
pH		4.5–8.1	6.4	0.8	6.5	4.4–8.5	6.6	1.0	6.7
Alkalinity	( $\text{meq l}^{-1}$ )	0.00–0.29	0.08	0.06	0.06	0.00–2.38	0.57	0.64	0.18
$\text{NO}_3^-$ -N	( $\mu\text{g l}^{-1}$ )	2–86	18.3	17.2	10.0	3–148	34.5	40.5	15.0
SRP	( $\mu\text{g l}^{-1}$ )	1–22	6.2	4.9	4.5	0.1–21	3.2	4.2	2.0
TP	( $\mu\text{g l}^{-1}$ )	1–138	20.5	23.7	12.0	2–33	10.3	6.8	9.0
Silica	( $\text{mg l}^{-1}$ )	0.00–1.90	0.37	0.51	0.14	0.00–3.95	0.68	0.87	0.32
$\text{Ca}^{2+}$	( $\text{mg l}^{-1}$ )	0.12–2.94	0.89	0.63	0.67	0.21–307.28	23.45	67.92	3.25
$\text{Mg}^{2+}$	( $\text{mg l}^{-1}$ )	0.06–0.75	0.29	0.19	0.24	0.07–147.42	8.13	26.43	0.76
$\text{Na}^+$	( $\text{mg l}^{-1}$ )	0.57–4.13	1.55	0.8	1.39	0.13–10.03	2.29	2.47	1.16
$\text{K}^+$	( $\text{mg l}^{-1}$ )	0.00–4.07	0.53	1.01	0.13	0.00–13.76	1.03	2.43	0.34
Total cations	( $\text{mg l}^{-1}$ )	1.04–8.84	3.26	2.13	2.60	0.61–419.29	34.90	93.06	9.08
$\text{Cl}^-$	( $\text{mg l}^{-1}$ )	0.00–17.99	1.94	4.19	0.50	0.00–58.98	5.23	10.94	1.50
Colour <sub>440</sub>	( $\text{mg l}^{-1}$ Pt)	0–297	47.4	54.2	28.0	0–145	39.8	39.7	26.5
Chlorophyll <i>a</i>	( $\mu\text{g l}^{-1}$ )	0.6–32.6	5.8	6.7	3.7	0.5–162.0	18.0	38.6	4.9

Chlorophyll *a* concentration was low at most sites in both mountain ranges even considering the high algae growth rate usually occurring in the summer (Table 2).

#### Desmids

Desmidiaceae were the most important group in S. Segundera with regard to species number (Table 4). Desmid abundance in the upper parts of S. Segundera could explain their high number in the largest water bodies along the river Tera course, i.e. in Sanabria lake and Valparaiso reservoir (De Hoyos, 1996; Negro et al., 2000).

Most desmids do not contribute significantly to phytoplankton biomass (Yung et al., 1986; Wojciechowska & Krupa, 1992). Many desmid and diatom species are actually part of tycho plankton, being associated with macrophytes or with the substratum. These algae are often dragged by the water flow to open water, where they can be found occasionally in the phytoplankton (Brook, 1959; Seath & Hellebust, 1978; Coesel, 1982). This was frequently observed throughout our study in mires, where we found a high number of tycho planktonic desmids, such as *Closterium acutum*, *C. depressum*, *C. humile*, *C. polygonium* var. *acutius*, *C. reniforme*, *Heimansia pusilla*, *Pleurotaenium trabecula*, *Staurastrum tetracerum*, *Staurodesmus de-*

*jectus* and *Teilingia granulata* (Brook, 1959; Coesel & Kooijman-Van Blokland, 1994). Desmid communities have been reported to be richer in bogs with open water and moss carpets than in those with moss carpets only (Yung et al., 1986). Thus, species number seems to be related to the spatial heterogeneity of mires. In our study, complex mires (with open water, hollows, hummocks, and *Sphagnum* carpets) showed a higher desmid number than simply structured ones.

Yung et al. (1986) reported a negative correlation between desmid species number and  $\text{Ca}^{2+}$  concentration in bogs, and a positive correlation to  $\text{Cl}^-$  and  $\text{H}^+$ . Thus, the higher desmid number at S. Segundera sites could be related to their lower alkalinity when compared with C. Cantábrica sites (Table 2). Also, other authors have reported a higher number of desmids than of other algae species in bogs and poor mires (Flensburg & Sparling, 1973; Hosiainluoma, 1975). Similar trends were generally found in our ecosystems studied. The S. Segundera acid ecosystems had, on average, a smaller desmid biovolume but a higher species number than the less acid C. Cantábrica ones.

Four of the 68 desmid species were not found in C. Cantábrica, but appeared at six or more sites in S. Segundera and Cabrera: *Cosmocladium constrictum*, *Heimansia pusilla*, *Staurastrum arachne* and *St. paradoxum*. *St. arachne* seems to be an uncommon species,

Table 3. Acronyms of taxa used in the CCA analysis

Bacillariophyceae		Desmidiaceae	
Label	Name	Label	Name
Amin	<i>Achnantes minutissima</i> Kütz.	Acuc	<i>Actinotaenium cucurbita</i> (Bréb. ex Ralfs) Teil. ex Ruzicka & Pouzar
Apel	<i>Amphipleura pellucida</i> (Kütz.) Kütz.	Clac	<i>Closterium acutum</i> Bréb. in Ralfs
Amp	<i>Amphora ovalis</i> (Kütz.) Kütz.	Clgr	<i>Cl. gracile</i> Bréb. ex Ralfs
Abra	<i>Anomoeoneis brachysira</i> (Bréb.) Grun.	Clin	<i>Cl. intermedium</i> Ralfs
Aser	<i>A. serians</i> (Bréb.) Cleve	Clset	<i>Cl. setaceum</i> Ehr. ex Ralfs
Ast	<i>Asterionella formosa</i> Hass.	Cab	<i>Cosmarium abbreviatum</i> Racib.
Aalp	<i>Aulacoseira alpigena</i> (Grun.) Krammer	Cam	<i>C. amoenum</i> Bréb. in Ralfs
Adis	<i>Au. distans</i> (Ehr.) Simonsen	Cbi	<i>C. bioculatum</i> (Bréb.) ex Ralfs
Agra	<i>Au. granulata</i> (Ehr.) Simonsen	Cco	<i>C. contractum</i> Kirchn. var. <i>contractum</i> + <i>C. contractum</i> Kirchn. var. <i>minutum</i> (Delp.) W. & G. S. West
Alir	<i>Au. lirata</i> (Ehr.) Ross	Cdep	<i>C. depressum</i> (Näg.) Lund. var. <i>depressum</i> + <i>C. depressum</i> (Näg.) Lund. var. <i>planctonicum</i> Reverdin
Cglo	<i>Cyclotella glomerata</i> Bach.	Cdif	<i>C. difficile</i> Lütkem.
Crad	<i>C. radiosa</i> (Grun.) Lemm.	Chum	<i>C. humile</i> (Gay) Nordst.
Cygr	<i>Cymbella gracilis</i> (Ehr.) Kütz.	Cma	<i>C. margaritifera</i> Menegh. ex Ralfs
Cymi	<i>C. microcephala</i> Grun. in Van Heurck	Cor	<i>C. ornatum</i> Ralfs ex Ralfs
Cysi	<i>C. silesiaca</i> Bleisch in Rabenh.	Cpol	<i>C. polygonum</i> (Näg.) Arch. var. <i>acutius</i> Messik
Cym	<i>Cymbella</i> spp. ( <i>C. affinis</i> Kütz. + <i>C. amphicephala</i> Näg. in Kütz. + <i>C. cesatii</i> (Rabenh.) Grun. + <i>C. cymbiformis</i> Agardh + <i>C. elginensis</i> Krammer + <i>C. helvetica</i> Kütz. + <i>C. subcuspidata</i> Krammer)	Cpun	<i>C. punctulatum</i> Bréb.
Dmes	<i>Diatoma mesodon</i> (Ehr.) Kütz.	Cpy	<i>C. pyramidatum</i> Bréb. in Ralfs
Dov	<i>Diploneis ovalis</i> (Hilse) Cleve	Creg	<i>C. regnellii</i> Wille var. <i>minimum</i> Eichl. & Gutw.
Epi	<i>Epithemia adnata</i> (Kütz.) Bréb. + <i>E. sorex</i> Kütz.	Cren	<i>C. reniforme</i> (Ralfs) Arch.
Ebid	<i>Eunotia bidentula</i> W. Smith	Csub	<i>C. subprotumidum</i> Nordst.
Ebi	<i>E. bilunaris</i> (Ehr.) Mills	Cti	<i>C. tinctum</i> Ralfs
Eex	<i>E. exigua</i> (Bréb. ex Kütz.) Rabenh.	Cos	<i>Cosmocladium constrictum</i> Arch. ex Joshua
Epe	<i>E. pectinalis</i> (Dillwyn) Rabenh.	Cyl	<i>Cylindrocystis brebissonii</i> (Menegh. ex Ralfs) De Bary
Eser	<i>E. serra</i> Ehr.	Ean	<i>Euastrum ansatum</i> Ehr. ex Ralfs
Even	<i>E. veneris</i> (Kütz.) De Toni	Ebin	<i>E. binale</i> (Turp.) Ehr. ex Ralfs var. <i>hians</i> (W. West) Krieger
Fbre	<i>Fragilaria brevistriata</i> Grun. + <i>F. pinnata</i> Ehr.	Ede	<i>E. denticulatum</i> (Kirchn.) Gay
Fcr	<i>F. crotonensis</i> Kitton	Eel	<i>E. elegans</i> (Bréb.) Kütz. ex Ralfs
Ful	<i>F. ulna</i> (Nitzsch) Lange-Bertalot	Ega	<i>E. gayanum</i> De Toni
Fvir	<i>F. virescens</i> Ralfs	Ein	<i>E. insulare</i> (Wittr.) Roy
Frus	<i>Frustulia rhomboides</i> (Ehr.) De Toni + <i>F. rhomboides</i> (Ehr.) De Toni var. <i>crassinervia</i> (Bréb.) Ross	Gac	<i>Gonatozygon aculeatum</i> Hastings
Gacu	<i>Gomphonema acuminatum</i> Ehr.	Gbe	<i>G. brebissonii</i> De Bary
Gan	<i>G. angustatum</i> (Kütz.) Rabenh.	Hpu	<i>Heimansia pusilla</i> (Hilse) Coesel
Ggr	<i>G. gracile</i> Ehr.	Hyal	<i>Hyalotheca dissiliens</i> (Sm.) Bréb. ex Ralfs
Grun	<i>G. truncatum</i> Ehr.	Net	<i>Netrium digitus</i> (Bréb.) Itzigs. & Rothe
Gyr	<i>Gyrosigma acuminatum</i> (Kütz.) Rabenh.	Oc	<i>Octacanthium octocorne</i> (Ehr.) Compère
Mcir	<i>Meridion circulare</i> (Greville) C. A. Agardh	Ptra	<i>Pleurotaenium trabecula</i> (Ehr.) ex Näg.
Ncry	<i>Navicula cryptocephala</i> Kütz.	Sppl	<i>Spondylosium planum</i> (Wolle) W. & G. S. West
Npup	<i>N. pupula</i> Kütz.	Spp	<i>Sp. pulchellum</i> Arch.
Nrad	<i>N. radiosa</i> Kütz.	Sar	<i>St. arachne</i> Ralfs
Nse	<i>N. seminulum</i> Grun.	Sbr	<i>St. brachiatum</i> Ralfs
Nsub	<i>N. subtilissima</i> Cleve	Sgr	<i>St. gracile</i> Ralfs var. <i>nanum</i> Wille
Naf	<i>Neidium affine</i> (Ehr.) Pfitzer	Sin	<i>St. inconspicuum</i> Nordst.
Nir	<i>Nei. iridis</i> (Ehr.) Cleve	Spa	<i>St. paradoxum</i> Meyen var. <i>longipes</i> Nordst.
Ngr	<i>Nitzschia gracilis</i> Hantzsch	Spse	<i>St. pseudotetracerum</i> (Nordst.) W. & G. S. West
Per	<i>Peronia fibula</i> (Bréb. ex Kütz.) Ross	Spu	<i>St. punctulatum</i> Bréb. ex Ralfs
Pgib	<i>Pinnularia gibba</i> Ehr.	Ste	<i>St. teliferum</i> Ralfs
Pint	<i>P. interrupta</i> W. Smith	Stet	<i>St. tetracerum</i> Ralfs ex Ralfs
Pmai	<i>P. maior</i> (Kütz.) Rabenh.	Stau	<i>Staurastrum</i> spp. ( <i>Staurastrum anatinum</i> Cooke & Wills in Cooke + <i>St. denticulatum</i> (Näg.) Arch. + <i>St. furcatum</i> (Ehr.) Bréb. + <i>St. polymorphum</i> Bréb. ex Ralfs)
Psub	<i>P. subcapitata</i> Gregory	Stex	<i>Stauroidesmus extensus</i> (Andersson) Teil.
Pvir	<i>P. viridis</i> (Nitzsch) Ehr.	Stgl	<i>Sta. glaber</i> (Ehr. ex Ralfs) Teil.
Rhiz	<i>Rhizosolenia longiseta</i> Zacharias	Stqui	<i>Sta. quiriferus</i> var. <i>evolutus</i> (Fritsch & Richt) Teil.
Rhop	<i>Rhopalodia gibba</i> (Ehr.) O. Müller	Staur	<i>Stauroidesmus</i> spp. ( <i>Stauroidesmus connatus</i> (Lund.) Thomasson + <i>Sta. dejectus</i> (Bréb. ex Ralfs) Teil. + <i>Sta. incus</i> (Bréb. ex Ralfs) Teil. + <i>Sta. jaculiferus</i> (West.) Teil.)
Sanc	<i>Stauroneis anceps</i> Ehr.	Tgr	<i>Teilingia granulata</i> (Roy & Biss.) Bourr.
Spho	<i>Stau. phoenicenteron</i> (Nitzsch) Ehr.	Tet	<i>Tetmemorus granulatus</i> (Bréb.) Ralfs ex Ralfs
Scu	<i>Stenopterobia curvula</i> (W. Smith) Krammer	Xant	<i>Xanthidium antilopaeum</i> (Bréb.) Kütz.
Sdel	<i>Ste. delicatissima</i> (Lewis) Bréb. ex Van Heurck		
Sbis	<i>Surirella biseriata</i> Bréb. in Bréb. & Godey		
Sli	<i>Su. linearis</i> W. Smith		
Tfe	<i>Tabellaria fenestrata</i> (Lyng.) Kütz.		
Tfl	<i>T. flocculosa</i> (Roth) Kütz.		

Table 4. Species number in each phytoplankton group in all the studied ecosystems, mean values, medians and standard deviation of species number per site. S – S. Segundera. C – C. Cantábrica

	Total species number			Mean species number per site		Median species number per site	
	S	C	S & C	S	C	S	C
<b>CHLOROPHYTA</b>							
Desmidiaceae	159	144	215	15.8 ± 15.1	11.8 ± 10.8	11.0	9.0
Rest of Chlorophyta	96	84	124	14.2 ± 8.6	8.2 ± 7.5	14.0	6.0
<b>CHRYSOPHYTA</b>							
Bacillariophyceae	80	149	161	10.8 ± 7.6	19.0 ± 10.8	9.0	18.0
Chrysophyceae	30	23	42	3.8 ± 2.2	1.4 ± 1.7	3.5	1.0
Xanthophyceae	6	9	11	0.7 ± 0.6	0.6 ± 0.7	1.0	0.0
<b>CYANOPHYTA</b>	39	34	54	5.8 ± 3.1	4.1 ± 3.4	6.0	4.0
<b>EUGLENOPHYTA</b>	24	28	42	1.8 ± 1.7	2.3 ± 2.6	2.0	1.0
<b>PYRRHOPHYTA</b>	11	13	16	2.7 ± 2.0	1.5 ± 1.7	2.5	1.0
<b>CRYPTOPHYTA</b>	8	9	10	1.7 ± 1.4	1.5 ± 1.3	1.0	1.0
<b>RAPHIDOPHYTA</b>	1	1	1	0.0 ± 0.2	0.0 ± 0.2	0.0	0.0
Total	454	494	676	57.5 ± 30.0	50.3 ± 28.2	53.5	41.0

Table 5. Variation range, means, medians and standard deviation of biovolume values per site. Data are given in mm<sup>3</sup>m<sup>-3</sup>

	Segundera and Cabrera Mountains				Cantabrian Mountains			
	Range	Mean	Standard Deviation	Median	Range	Mean	Standard Deviation	Median
<b>CHLOROPHYTA</b>								
Desmidiaceae	0–3506	519.1	995.1	37.5	0–7387	589.4	1382.0	103.7
Rest of Chlorophyta	2–1366	199.7	312.2	70.5	0–8216	843.4	2007.3	30.7
<b>CHRYSOPHYTA</b>								
Bacillariophyceae	0–1819	216.1	396.7	50.8	2–5805	580.4	1248.5	43.6
Chrysophyceae	0–391	63.6	87.4	25.6	0–874	90.4	221.1	4.8
Xanthophyceae	0–34	3.5	7.7	0.3	0–757	48.7	147.8	0
<b>CYANOPHYTA</b>	0–2733	108.2	420.5	9.9	0–69483	2332.6	12069.3	12.4
<b>EUGLENOPHYTA</b>	0–168	12.2	34.6	0.8	0–7920	276.7	1376.0	2.2
<b>PYRRHOPHYTA</b>	0–1023	209.4	260.1	90.1	0–22574	1200.3	4613.9	6.6
<b>CRYPTOPHYTA</b>	0–725	50.3	119.3	15.5	0–229	32.6	51.9	8.8
<b>RAPHIDOPHYTA</b>	0–100	2.3	15.1	0	0–1	0.03	0.2	0
Total biovolume	41–5492	1384.3	1520.0	642.0	50–84383	5994.3	15494.7	981.4

as we have not found references to it in other works. According to Cambra et al. (1998), in the Iberian Peninsula there are only two old references to *St. arachne*, both in the Galicia region, NW Spain, neighbouring with S. Segundera and Cabrera mountains.

#### Diatoms

A high diatom species number was found in C. Cantábrica ecosystems, where diatom number exceeded that of any other algae group (Table 4) and was almost

twice that of the S. Segundera ones. Diatom biovolume was very large in a few C. Cantábrica ecosystems, which increased the mean but not the median values of the group (Table 5). At most C. Cantábrica sites biovolume was small, leading to a lower median than in S. Segundera ecosystems.

C. Cantábrica, with more mineralised waters and high mean pH, had a higher number of diatom species. Many of them have not yet been reported in S. Se-



gundera region, i.e. *Amphipleura pellucida*, *Cyclotella radiosa*, *Cymbella microcephala*, *Cymbella* spp., *Diploneis ovalis*, *Epithemia adnata*, *E. sorex*, *Gyrosigma acuminatum*, *Navicula pupula* and *Rhopalodia gibba*. Total diatom number is generally related to relatively high water conductivity and pH (Rao, 1953; Eloranta, 1995). However, some species are acidophilous and prefer soft water (Round, 1957; Flensburg & Sparling, 1973; Hosiaisuoma, 1975; Kingston, 1982; Yung et al., 1986; Alles et al., 1991; Dell'Uomo, 1992). Many of these acidophilous species are common in S. Segundera lakes and mires, such as the majority of *Eunotia* species, *Frustulia rhomboides*, *Navicula subtilissima*, *Stenopterobia curvula*, and *Tabellaria flocculosa*.

#### CCA ordination

The preliminary diatom CCA analysis, covering all the variables, showed that the most significant ones were: alkalinity, pH, conductivity, cation silica content, and depth. Nutrient concentration and water colour influenced the diatom composition in some studies (Stevenson et al., 1989; Hall & Smol, 1999), but in our case, these variables explained a smaller amount of variance.

The eigenvalues of the first two axes of the CCA performed on the six variables mentioned above, were 0.36 and 0.19, respectively. The species-environment correlation was 0.89 for axis 1 and 0.81 for axis 2. The analysis showed that the main diatom variation gradient depended on alkalinity (Fig. 2) which was strongly related to axis 1 ( $r = 0.98$ ). Axis 2 was more correlated with depth ( $r = 0.75$ ) and pH ( $r = 0.73$ ). Conductivity, cation and silica content showed similar correlations to axis 1, 3 and 4 ( $r$  ca. 0.5), and a lower correlation to axis 2. The ordination plot (Fig. 2) separated the following four groups of sites:

1. Lakes, reservoirs and other deep water bodies on acid substrate, with low water alkalinity (generally  $<0.1$  meq  $l^{-1}$ ) and pH 6.5–7.5.
2. Mires and shallow water bodies on acid substrate, with low water alkalinity, and pH 4.4–6.5.
3. Mires and shallow water bodies on basic substrate, with moderate to high water alkalinity (0.5–0.9 meq  $l^{-1}$ ) and pH about 7.
4. Ecosystems on basic substrate, with high water alkalinity ( $>1$  meq  $l^{-1}$ ) and pH 7.0–8.5.

Within group 4 we could separate the deepest sites (in the upper part of the diagram) from mires and other shallow ecosystems. Geographically, most of the sites

in groups 1 and 2 are located in S. Segundera, while those in groups 3 and 4 in C. Cantábrica.

These four ecosystem groups were associated with typical diatom species. *Asterionella formosa*, *Cyclotella glomerata*, *Cymbella gracilis*, *C. silesiaca*, *Fragilaria crotonensis*, *Gomphonema acuminatum*, *G. gracile*, *Nitzschia gracilis*, *Pinnularia interrupta*, *Rhizosolenia longiseta*, *Stenopterobia curvula*, *Surirella linearis*, *Tabellaria fenestrata* and *T. flocculosa* were preferentially associated with slightly mineralised, deeper waters (group 1).

*Anomeoneis brachysira*, *Aulacoseira alpigena*, *A. distans*, *A. lirata*, *Eunotia bidentula*, *E. bilunaris*, *E. exigua*, *E. pectinalis*, *E. serra*, *E. veneris*, *Fragilaria virescens*, *Frustulia rhomboides*, *Gomphonema angustatum*, *Navicula minima*, *Peronia fibula*, *Pinnularia gibba*, *P. subcapitata* and *Stenopterobia delicatissima* were common in slightly mineralised and shallow waters (group 2).

*Achnanthes minutissima*, *Amphora ovalis*, *Anomeoneis serians*, *Aulacoseira granulata*, *Diatoma mesodon*, *Fragilaria ulna*, *F. brevistriata*, *F. pinna*, *Gomphonema truncatum*, *Navicula cryptocephala*, *Neidium affine*, *N. iridis*, *Stauroneis anceps*, and *Surirella biseriata* were distinctive of shallow, and moderate to highly mineralised waters (group 3).

*Meridion circulare*, *Navicula subtilissima*, *Pinnularia maior*, *P. viridis*, and *Stauroneis phoenicenteron* could be associated with both latter groups (group 2 and 3).

*Amphipleura pellucida*, *Cyclotella radiosa*, *Cymbella microcephala* and other *Cymbella* species (*C. affinis*, *C. amphicephala*, *C. cesatii*, *C. cymbiformis*, *C. elginensis*, *C. helvetica* and *C. subcuspidata*), *Diploneis ovalis*, *Epithemia adnata*, *E. sorex*, *Gyrosigma acuminatum*, *Navicula pupula*, *N. radiosa* and *Rhopalodia gibba* were associated with highly mineralised waters (group 4).

In the latter group *Cyclotella radiosa*, *Epithemia adnata*, *Epithemia sorex* and *Amphipleura pellucida* were found in the deepest waters. All the species in group 4 occurred only in C. Cantábrica ecosystems, except for *Navicula radiosa* and *Cymbella affinis*.

The preliminary desmid CCA analysis showed that the most significant variables were: pH, conductivity, alkalinity, depth and cation content. In the CCA performed on these five variables (Fig. 3), the eigenvalues were 0.22 for axis 1 and 0.1 for axis 2, and the species-environment correlation was 0.75 and 0.74, respectively. The first axis was related to pH ( $r = -0.71$ ) and depth ( $r = -0.47$ ), and the second one

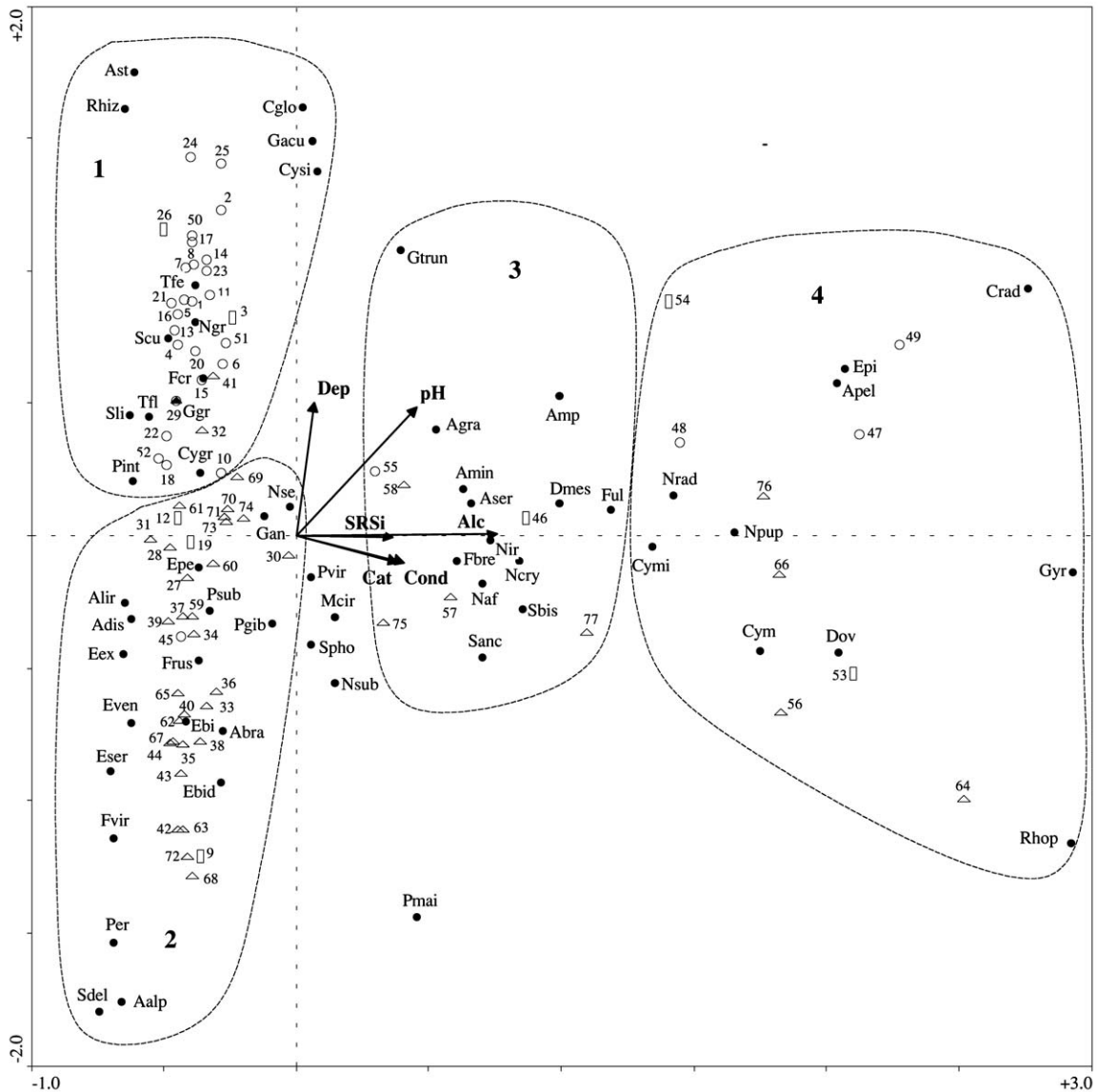


Figure 2. Triplot diagram of diatom data. Alc – alkalinity. Cat – total cation concentration. Con – conductivity. SRSi – soluble reactive silica. Dep – depth. ○ – lakes; □ – shallow lakes; △ – mires; Site numbers and taxa acronyms are listed in Table 1 and 3, respectively.

to alkalinity ( $r = 0.94$ ), conductivity ( $r = 0.89$ ) and cation content ( $r = 0.84$ ). This ordination produced the same ecosystem groups as the diatom analysis did (Figs 2 & 3). The four ecosystem groups contained typical desmid species. However, most of these species were in groups 1 and 2 which were associated with slightly mineralised waters.

The main desmid species preferring deeper, acid and weakly mineralised ecosystems (group 1) were: *Cosmarium bioculatum*, *C. contractum*, *C. margaritifera*, *C. ornatum*, *C. pyramidatum*, *C. tinctum*,

*Cosmoelidium constrictum*, *Euastrum ansatum*, *E. denticulatum*, *E. elegans*, *E. gayanum*, *Gonatozygon aculeatum*, *G. brebissonii*, *Heimansia pusilla*, *Octacanthium octocorne*, *Pleurotaenium trabecula*, *Spondylosium planum*, *Sp. pulchellum*, *Staurastrum arachne*, *St. brachiatum*, *St. gracile* var. *nanum*, *St. inconspicuum*, *St. paradoxum* var. *longipes*, *St. teliferum*, *St. tetracerum*, other *Staurastrum* species (*St. anatinum*, *St. denticulatum*, *St. furcatum*, *St. polymorphum*), *Stauroidesmus extensus*, *Std. glaber*, other *Stauroidesmus* species (*Std. connatus*, *Std. dejectus*,

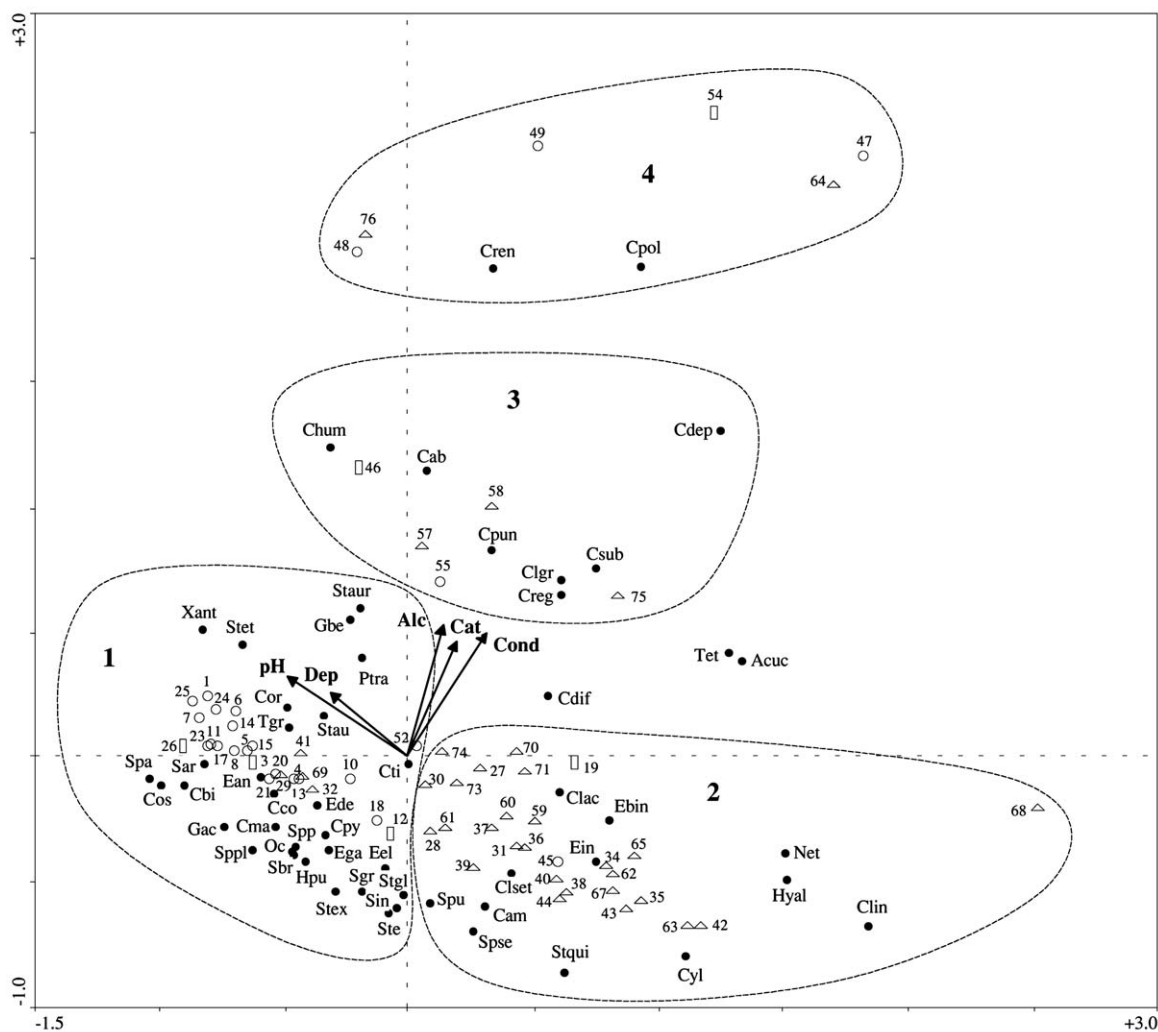


Figure 3. Triplot diagram of desmid data. Alc – alkalinity. Cat – cation concentration. Con – conductivity. Dep – depth. ○ – lakes; □ – shallow lakes; △ – mires; Site numbers and taxa acronyms are listed in Table 1 and 3, respectively.

*Std. incus*, *Std. jaculiferus*), *Teilingia granulata*, and *Xanthidium antilopaeum*. From all the above mentioned species only *Staurodesmus jaculiferus*, *Spondylosium planum*, *Xanthidium antilopaeum* and *Staurastrum anatinum* are considered strictly planktonic species (Brook, 1959).

*Closterium acutum*, *Cl. intermedium*, *Cl. setaceum*, *Cosmarium amoenum*, *Cylindrocystis brebissonii*, *Euastrum binale* var. *hians*, *E. insulare*, *Hyalotheca dissiliens*, *Netrium digitus*, *Staurastrum pseudotetracerum*, *St. punctulatum*, and *Staurodesmus quiriferus* var. *evolutus*, were present in shallow, acid and weakly mineralised waters (group 2).

The species in shallow, basic, moderately to strongly mineralised waters (group 3) were: *Closterium gracile*, *C. abbreviatum*, *C. depressum*, *C. humile*, *C. punctulatum*, *C. regnellii* and *C. suprotumidum*.

The species found as the intermediate ones between group 2 and 3 were: *Actinotaenium cucurbita*, *Cosmarium difficile* and *Tetmemorus granulatus*. They were close to group 2 regarding pH, but close to group 3 regarding mineralisation.

Finally, group 4 (ecosystems with the most strongly mineralised waters and generally deep) comprised only two species: *C. polygonium* var. *acutius* and *C. reniforme*.

Thus, *Cosmarium* species were the most successful desmids at sites with intermediate to high mineralisation and neutral to high pH (group 3 and 4).

## Conclusions

The studied water bodies in C. Cantábrica were characterized by higher mineralisation and lower colour than those in S. Segundera. Moreover, the C. Cantábrica waters were richer in nitrogen and poorer in phosphorus than those in S. Segundera. All the above mentioned factors determined the differences in phytoplankton composition and biovolume.

Regarding the species number, Bacillariophyceae were prevalent in C. Cantábrica, whereas Desmidiaceae were in S. Segundera. Diatoms and desmids were important algae groups, in both mountain ranges, regarding biovolume.

The CCA analysis of diatom communities established that diatom composition was primarily influenced by the alkalinity, conductivity and cation content variables, and secondarily by pH and depth. Conversely, the desmid CCA analysis showed that the most important variables influencing species distribution were pH and depth. The second next important ones were alkalinity, conductivity and cation content.

Those variables reveal a gradient between deep lakes and shallow, acid mires. Both CCA analyses allowed us to separate four 'ecosystem groups': (1) Lakes, reservoirs and other deep water bodies on acid substrate, with soft water and neutral pH; (2) Mires and shallow water bodies on acid substrate, with soft water and low pH; (3) Mires and shallow water bodies on basic substrate, with moderate to hard water and neutral pH; and (4) Water bodies on basic substrate with hard water and high pH.

Each of the four main groups was characterised by different algae species. Thus, different species were associated with particular environment conditions: alkalinity, pH, and spatial configuration.

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