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Macrophytes from lakes in the eastern Pyrenees: community composition and ordination in relation to environmental factors

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SUMMARY

1. Thirty-six species of macrophytes (fourteen flowering plants, two quillworts, sixteen mosses and liverworts, and two algae) were collected in an extensive survey of 116 high mountain lakes in the eastern Pyrenees. Seventy per cent of the lakes showed macrophyte development.
2. The isoetids (*Isoetes lacustris, Isoetes setacea* and *Subularia aquatica*) were the dominant growth form, although the natopotamid *Sparganium angusifolium* was the most widespread species. Potamids (*Potamogeton* spp., *Ranunculus* spp.), the alga *Nitella* gr. *opaca* and some mosses (*Warnstorfia exannulata, Sphagnum denticulatum*) were often present.
3. A multivariate ordination analysis (RDA-redundancy analysis) revealed that water chemistry, altitude and vegetation cover of the catchment, and nutrient availability are major environmental factors associated with macrophyte distribution along the eastern Pyrenean lakes. Isoetids prevailed in softwater oligotrophic lakes, potamids in relatively hardwater oligotrophic lakes, and *Potamogeton natans* and *Callitriche palustris* in small and eutrophic water bodies affected by the presence of cattle.

Introduction

The structure and composition of aquatic vegetation is related to the chemical composition of water (Moyle, 1945; Hutchinson, 1975; Pip, 1979; Raven, 1988) and this relationship can be used to classify the water bodies as well as to survey possible changes occurring due to acidification or eutrophication (Grahn, 1977; Roelofs, 1983). Comparative studies of macrophyte communities related to water chemistry include measurements of a wide range of the chemicals dissolved in water of the systems studied. According to Peet (1980) vegetational changes taking place on an extensive environmental gradient can hide significant relationships occurring over narrower ranges of environmental variables. Peet (1980) advocates, therefore, the study of more homogeneous systems. The Pyrenean lacustrine district allows work to focus on one extreme of the gradient, since it includes only softwater oligotrophic lakes mainly located in granodioritic basins.

Submerged vegetation from the eastern Pyrenean lakes has been studied only within the context of the local flora (e.g. Llenas, 1912; Coste & Soulié, 1913; Font i Quer, 1948; Losa & Montserrat, 1950; Montserrat Martí, 1981; Canalis *et al.*, 1984; Ballesteros, 1989; Carrillo & Ninot, 1992) or for the purposes of describing and classifying plant communities (Braun Blanquet, 1948; Campàs, 1979; Carrillo, 1984; Ballesteros, Gacia & Camarero, 1989; Ballesteros &

Gacia, 1990, 1991). The only studies providing data on the chemical composition of the water in relation to submerged macrophytes inhabiting Pyrenean lakes are those of Margalef-Mir (1981) and Ballesteros & Gacia (1990, 1991), but no extensive study has been published.

The aim of this study is to provide more complete documentation and analysis of the aquatic flora of the Pyrenean lakes and to determine whether there is any relationship between aquatic vegetation and water chemistry, which will be useful for both lake classification and monitoring future long-term changes.

Material and Methods

A total of 116 lakes and small water bodies were sampled in July–August 1987 in the eastern Pyrenees (Fig. 1). Sampling was performed in order to include all kinds of lakes: cirque and valley lakes, natural and dam lakes, different altitudes and different productivities. All the lakes have glacial origin, and most of them were situated between 2000 and 2600 m above sea level and have small catchments (<200 ha). The lakes themselves are small (<60 ha) with shallow (<50 m) basins and 80% of them lie on granodioritic batholites, while the others are located on Cambro-Ordovician schists or Devonian limestones. The lakes are situated in the alpine or subalpine zone; vegetation in catchments consists of meadows dominated by different species of *Festuca*, *Carex*, scrub, and small woodlands of *Rhododendron ferrugineum* L. and *Pinus uncinata* Miller ex Mirbel. Small wet meadows of *Nardus stricta* L., boreo-alpine peat fens and peat-moss bogs were common near the lakes, replacing the dominant alpine and subalpine communities. A helophytic belt of *Carex rostrata* Stokes and *Eriophorum angustifolium* Honckeny was sometimes present in shallow waters.

Macrophytes were sampled by diving, and taxonomic identifications were made following Tutin *et al.* (1964). Vouchers of most of the specimens collected were deposited in the herbariums of the Institut Botànic de Barcelona (BC) and the Centre d'Estudis Avançats de Blanes (CEAB). Only presence–absence data of the macrophytes were recorded, since patchiness in the distribution of the species in the lakes prevented us from obtaining abundance estimates.

Water sampling was performed at half the Secchi depth or at half the maximum depth of the lake (if the Secchi disc depth was greater than the maximum depth). Conductivity, pH and alkalinity were measured within 12 h of collection of water samples. Samples for nutrient and elemental analysis were frozen and stored. Nutrients [total phosphorus (TP), ammonium (NH_4^+) nitrites (NO_2^-) and nitrates (NO_3^-)], anions (Cl^-, SO_4^{2-}) and cations (Ca^{2+}, Mg^{2+}, Na^+, K^+) were analysed as described in Catalan *et al.* (1993). Lake altitude, area and basin were estimated from the 1:25 000 maps of the Instituto Cartográfico Español. Total vegetation coverage of the catchment and the coverage of fens bordering the lake were estimated from previous cartography, aerial photographs and field observations.

A multivariate, direct gradient analysis was performed to relate species presence–absence data to environmental factors using the program CANOCO

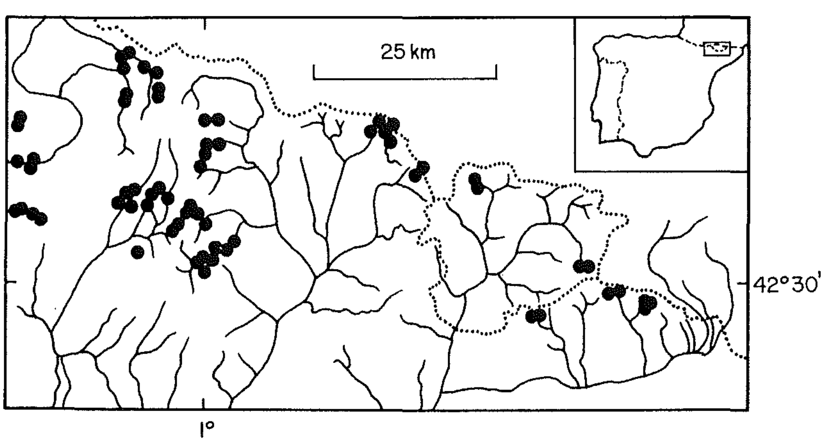

Fig. 1 Location of the lakes sampled in the eastern Pyrenees. The circles represent lakes or groups of lakes.

(Ter Braak, 1988). Redundancy analysis (RDA) was chosen over canonical correspondence analysis (CCA) since the range of variation of the environmental variables was narrow, and an underlying linear response model could be assumed (Ter Braak, 1987). To perform the analysis, lakes without macrophytes or lakes lacking some environmental data were rejected. Only flowering plants which appeared in more than 2% of the remaining lakes were taken into account. Mosses and liverworts usually had a scattered distribution in the lakes and their coverage was usually negligible; thus, only two species which were relatively abundant and occurred in more than 6% of the lakes were considered. Alkalinity and calcium concentrations were not considered in the analysis because they were strongly correlated with conductivity ($P < 0.0001$). A total of seventeen macrophytes, eighteen environmental factors and fifty-two lakes were used in the analysis.

Results

Nearly 70% of the lakes sampled had submerged aquatic macrophytes. These were mainly distributed around 2200 m above sea level (Fig. 2). Thirty-six species of submerged macrophytes were collected (Fig. 3). *Sparganium angustifolium* was the most frequent (66% of lakes). The isoetid species *Isoetes lacustris, Subularia aquatica* and *Isoetes setacea* were present in 38, 36 and 35% of the lakes, respectively. A widespread species of *Nitella* of the *N. opaca* group was present in 35% of lakes. Different species of *Potamogeton* (*P. berchtoldii, P. alpinus*), *Ranunculus* [*R. aquatilis, R. trichophyllus* ssp. *eradicatus* (Laest) C.D.K. Cook], *Myriophyllum alterniflorum* and *Callitriche palustris* were rather abundant (>10% of the lakes). Finally, several species of mosses, liverworts and other vascular plants were only found occasionally (<10% of the lakes; Fig. 3).

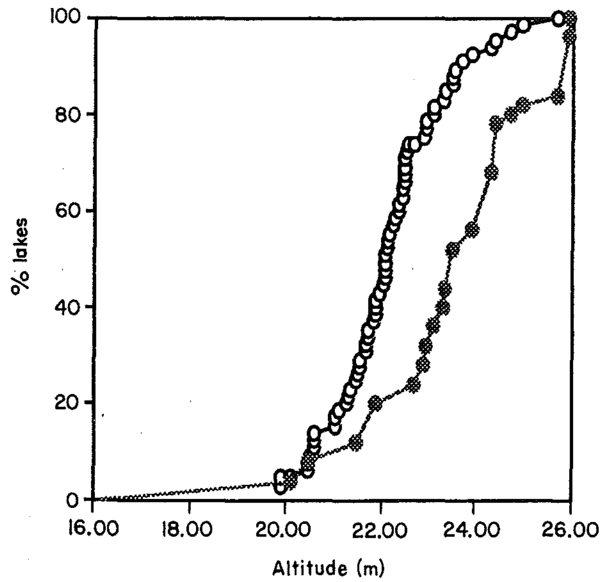

Fig. 2 Cumulative percentage of lakes with and without macrophytes in relation to lake altitude. •, Without macrophytes; ○, with macrophytes.

Data on selected environmental factors and species composition of the lakes chosen for the analysis are summarized in Tables 1 and 2.

The ordination of the species and lakes in the RDA shows that pH and conductivity are the selected environmental factors most strongly positively related with the first axis (Fig. 4a), which can be described as a 'dissolved ions axis'. The macrophytes associated with relatively high values of pH and conductivity are different species of the genus *Potamogeton, Myriophyllum alterniflorum, Nitella* gr. *opaca* and *Ranunculus trichophyllus* ssp. *eradicatus. Ranunculus aquatilis, Isoetes setacea* and *Sparganium angustifolium* are associated with intermediate values of ions, while *Isoetes lacustris* and *Sphagnum denticulatum* appear in water bodies with low pH and conductivity. The distribution of the lakes along the gradient (Fig. 4b) shows that lakes with low to very low pH and conductivity values are the most abundant.

The second axis of the RDA is positively related to variables such as nitrites, altitude and lake area, and negatively related to the percentage of vegetation coverage of the basin and the fen coverage around the lake. The inverse relationship between altitude and vegetation coverage of the basin was expected, since altitudes around 2300–2500 m above sea level are the limit for the development of pines and scrubs in the Pyrenees (Bolòs, 1957). Furthermore, small lakes are usually surrounded by fens and bogs. The relationship between the second axis and the nitrite concentration is explained by the chemistry of some lakes, which are frequently visited by cattle. The species *Subularia aquatica, Isoetes setacea* and *Sparganium angustifolium* appear at low values of the second axis, while *Sphagnum denticulatum* and *Ranunculus trichophyllus* ssp. *eradicatus* appear at high values.

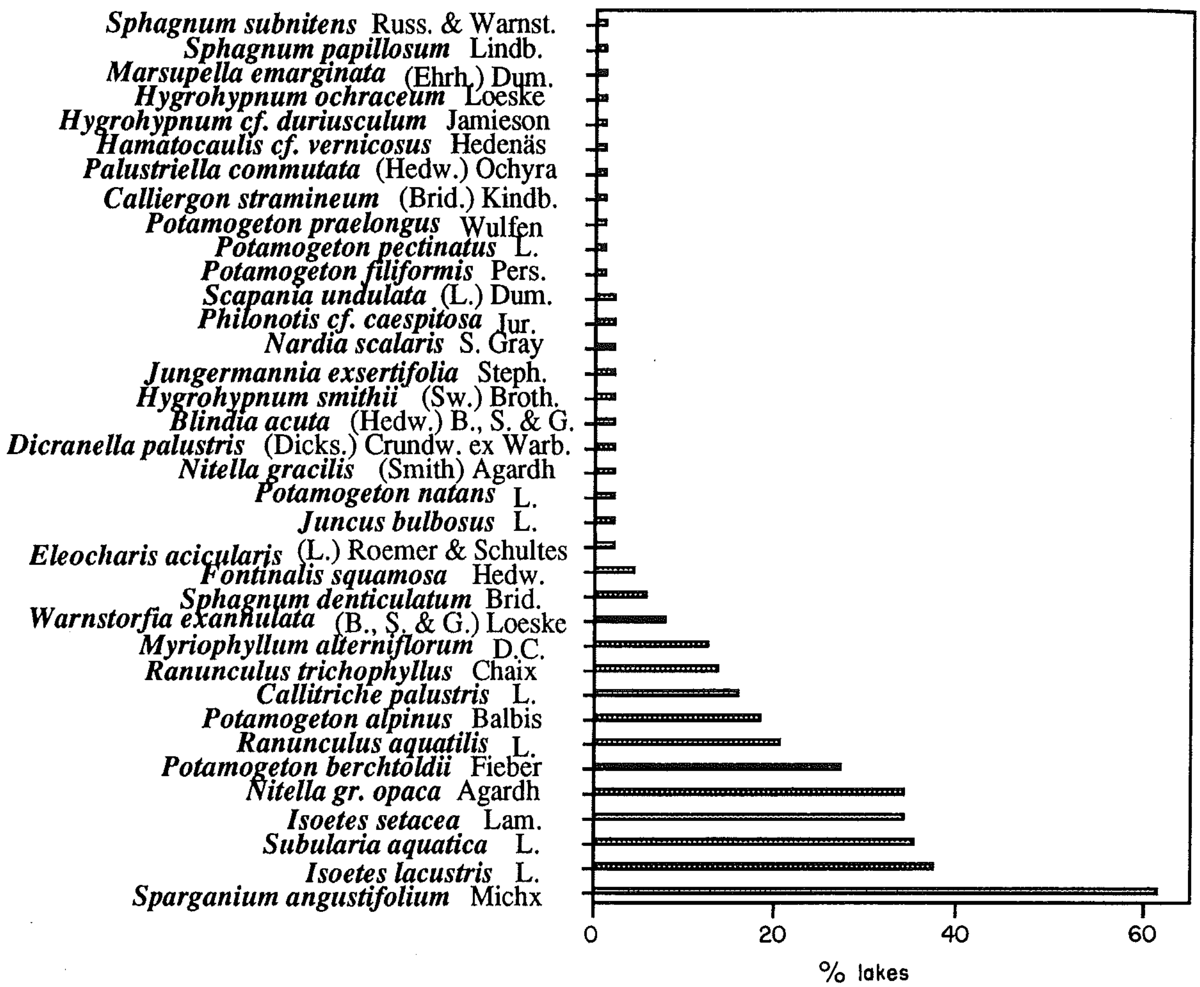

Fig. 3 Percentage of presence of the main submerged macrophytes in Pyrenean lakes with macrophytes development.

The third axis of the RDA (Fig. 5) is related to the factors K^+, Na^+, fen coverage, TP and NO_3^-, which indicate rather eutrophic conditions. Lakes appearing on high values of this axis are either small, very shallow and strongly influenced by cattle, or have an extensive coverage of surrounding fens, or are small reservoirs with macrophytes development. *Potamogeton natans* and *Callitriche palustris* are species positively associated with this axis, while *Isoetes lacustris* is negatively associated with it (Fig. 5).

The values of the three first eigenvalues are 0.14, 0.11 and 0.07, respectively. They indicate that, even though the first axis is the most important in the ordination, the other two are also significant. In total, the three first axes of the ordination explain 32% of the variation in species distribution.

Discussion

Pyrenean lakes show a higher diversity of macrophytes than lakes from other mountain ranges in Europe (e.g. Braun Blanquet, 1948). The fraction of lakes with macrophytes is higher at low altitudes (around 2200 m a.s.l.). The reason is that above 2400 m a.s.l. ice covers the lakes for more than 7 months of the year and water temperature remains very low in summer, strongly affecting the whole vegetative development cycle in vascular plants (Braun Blanquet, 1964).

In addition to altitude, water level fluctuations also affect macrophyte development in lakes, through desiccation, sediment resuspension or light limitation in periods of high water level. These fluctuations can be found in natural lakes due to seasonality

Table 1 Selected environmental factors at the lakes analysed. The following data are indicated: identification number (ID), name of the lake, altitude (Alt.), lake area (A_{lake}), dominant vegetation of the basin (DV), pH, conductivity (Cond.), total phosphorus (TP), nitrates (NO_3) and potassium (K). Abbreviations for dominant vegetation are as follows: 1, bare rock; 2, *Festuca eskia* Ramond ex DC meadows; 3, *Carex curvula* All. meadows; 4, *Rhododendron ferrugineum* shrubs; 5, *Pinus uncinata* forests; 6, *Festuca gautieri* (Hackel) K. Richter meadows; 7, other

ID	Lake	Alt. (m)	A_{lake} (ha)	DV	pH	Cond. ($\mu S\ cm^{-1}$)	TP (μM)	NO_3 (μM)	K (μM)
3	Redó Lake	2568	1.6	2	6.90	38.5	0.48	17.3	11
4	Llarg d'Engorgs	2470	2.6	2	7.32	31.7	0.37	14.2	7
5	Guils	2250	2.6	5	6.27	18.4	0.43	5.3	6
6	Malniu	2240	6.7	5	6.69	21.2	0.48	0.9	10
7	Sec	2105	1.9	5	6.52	29.0	0.98	4.3	11
8	Gran de la Pera	2335	2.9	4	6.78	15.9	0.39	18.1	6
9	Petit de la Pera	2295	1.6	4	6.72	18.2	0.20	14.1	7
10	Redó de Bohí	2105	6.0	2	6.91	9.1	0.15	10.6	3
11	Llong de Bohí	1995	8.0	5	7.17	19.3	0.19	9.6	5
12	Llebreta	1615	11.0	7	7.23	32.3	0.29	14.8	11
14	Romedo de Dalt	2114	14.4	4	5.92	4.8	0.20	4.7	3
16	Senó	2137	5.1	4	5.78	5.1	0.15	4.0	2
17	Colatx	2215	2.2	4	5.79	5.2	0.07	8.7	3
18	Aguiló de Dalt	2250	1.0	2	5.66	4.4	0.33	0.4	2
20	Aguiló de Baix	2060	1.3	4	5.80	4.4	0.21	2.4	2
28	Colomina	2430	3.2	1	7.33	23.1	0.22	7.0	10
31	Liat	2160	3.2	4	6.81	12.2	0.18	5.3	3
34	Mangades	2390	9.6	3	7.07	17.7	0.32	53.0	6
36	Travessany	2250	11.5	3	7.20	21.2	0.40	57.0	6
37	Xic	2240	1.3	3	7.27	23.6	0.28	4.0	3
44	Negre de Bohí	2130	9.3	4	6.93	18.6	0.25	12.2	6
47	Munyidera	2355	2.5	4	6.80	13.4	0.23	3.4	4
49	Estanyola de Ratera	2175	0.7	4	6.78	17.2	0.28	5.3	7
50	Ratera	2185	2.9	4	6.94	16.6	0.20	10.9	8
54	Bassa Llastra	2495	0.3	3	7.19	26.0	0.36	bol	9
59	Trescuro de Baix	2055	0.6	5	7.20	38.8	0.15	13.5	6
60	Clòto de Baix	2150	1.6	5	7.01	19.6	0.25	1.1	3
61	Cloto de Naut	2155	1.6	5	7.24	31.0	0.28	2.0	7
62	Long de Colomères	2170	3.8	4	6.94	16.6	0.75	6.6	4
63	Redón de Colomères	2175	1.0	4	6.82	18.2	0.19	7.0	6
65	Cabidornats	2200	5.4	4	6.98	15.1	0.76	bol	4
68	Truites	2310	1.0	2	7.68	73.2	0.10	3.7	5
69	Bassa de Varradós	2170	1.0	3	7.48	78.2	0.16	5.4	11
70	Pessó de Dalt	2370	1.9	2	7.28	33.5	0.17	4.6	14
71	Pessó de Mig	2350	1.6	4	7.17	28.6	0.19	3.7	5
72	Pessó de Baix	2290	2.2	5	7.19	27.1	0.17	81.5	6
76	d'Ès Cròssos	2250	0.6	2	7.46	34.6	0.47	16.5	1
80	Marimanha de Baish	2255	2.2	4	6.86	14.7	0.05	17.6	3
81	Uelhs de Marimanha	2190	0.3	4	6.72	14.1	0.06	11.3	3
82	Muntanyó d'Arreu	2210	5.8	6	7.64	55.8	0.09	5.1	4
83	Podu	2220	0.6	6	6.39	10.0	1.51	8.9	16
84	Garcés	2060	0.3	2	6.40	15.8	8.28	21.6	43
88	Mauberné	2295	0.5	2	5.97	5.5	0.11	5.6	7
91	Còth de Tòro	2215	3.2	3	7.42	33.0	0.10	6.5	6
93	Garguils de Naut	2210	0.6	4	6.97	18.5	0.14	6.2	7
94	Garguils de Baish	2210	1.6	4	6.93	17.6	0.09	10.8	6
95	Mòrt	2225	4.5	4	7.07	20.0	0.14	4.0	6
96	Garrabeia	1995	4.8	4	6.96	15.1	0.16	2.7	4
97	Rosari d'Arreu	2158	9.6	5	7.05	19.5	0.17	4.6	5
98	Cap de Riueno	2190	1.6	2	7.20	34.8	0.24	7.0	31
99	Fe	2190	1.6	2	7.24	31.2	0.14	16.2	18
101	Mig d'Anglós	2230	2.2	3	7.41	35.6	0.48	7.0	5

Table 2 Macrophytes from the analysed lakes: 1, presence; 0, absence. Sang, *Sparganium angustifolium*; Iset, *Isoetes setacea*; Ilac, *Isoetes lacustris*; Saqu, *Subularia aquatica*; Raqu, *Ranunculus aquatilis*; Malt, *Myriophyllum alterniflorum*; Palp, *Potamogeton alpinus*; Pber, *Potamogeton berchtoldii*; Cpal, *Callitriche palustris*; Rtric, *Ranunculus trichophyllus*; Ppra, *Potamogeton praelongus*; Pper, *Potamogeton perfoliatus*; Pnat, *Potamogeton natans*; Jbul, *Juncus bulbosus*; Nit, *Nitella* spp.; Sphag, *Sphagnum denticulatum*; Warn, *Warnstorfia exannulata*

Lake	Sang	Iset	Ilac	Saqu	Raqu	Malt	Palp	Pber	Cpal	Rtric	Ppra	Pper	Pnat	Jbul	Nit	Sphag	Warn
Redó d'Engorgs	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Llarg d'Engorgs	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Guils	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Malniu	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Sec	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Gran de la Pera	1	1	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Petit de la Pera	1	1	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Redó de Boí	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Llong de Boí	1	0	0	0	0	1	1	1	0	0	0	0	0	1	1	0	0
Llebreta	1	0	0	1	1	1	0	1	1	0	0	0	0	1	1	0	0
Romedo de Dalt	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Senó	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Colatx	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1
Aguiló de Dalt	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1
Aguiló de Baix	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Colomina	0	1	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0
Liat	1	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0
Mangades	0	0	1	0	0	0	0	1	0	1	0	0	0	0	1	0	0
Travessany	0	0	0	0	0	1	1	1	0	1	0	0	0	0	1	0	0
Xic	1	0	1	1	1	1	1	1	0	0	0	0	0	0	1	0	0
Negre de Boí	1	0	0	1	1	0	1	1	0	1	0	0	0	0	1	0	0
Munyidera	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Estanyola de Ratera	1	0	0	1	1	0	0	0	1	0	0	0	0	0	0	0	0
Ratera	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0
Bassa Llastra	1	1	0	1	1	0	0	1	0	0	0	0	0	0	0	0	0
Trescuro de Baix	1	1	0	1	1	1	0	1	0	0	0	0	0	0	1	0	0
Cloto de Baix	1	1	1	1	1	1	0	0	0	0	0	0	0	0	1	0	0
Cloto de Dalt	1	1	1	1	1	1	0	0	0	0	0	0	0	0	1	0	0
Llong de Colomères	1	1	1	1	1	0	0	0	0	0	0	0	0	0	1	0	0
Redon de Colomères	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0
Cabidornats	0	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0
Truites	1	1	0	1	1	0	0	1	0	1	0	0	0	0	0	0	0
Bassa de Varradós	0	0	0	0	0	0	1	1	0	1	0	0	0	0	1	0	0
Pessó de dalt	1	1	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0
Pessó de mig	1	1	1	1	1	0	1	1	0	0	0	0	0	0	0	0	0
Pessó de Baix	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
dels Crossos	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Baix de Marimanha	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Guells de Marimanha	1	1	0	1	1	0	0	0	1	0	0	0	0	0	0	0	0
Muntanyó d'Arreu	0	0	0	0	0	0	1	1	0	0	1	1	0	0	0	0	0
Pedó	1	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0
Garces	1	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0
Maubermé	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Coll de Toro	0	0	0	1	1	0	1	0	0	1	0	0	0	0	0	0	0
Garguils superior	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0
Garguils inferior	1	1	1	1	1	0	0	0	1	0	0	0	0	0	1	0	0
Mort	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0
Garrabeia	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0
Rosari d'Arreu	1	1	1	1	1	0	0	1	1	0	0	0	0	0	1	0	0
Cap de Riveno	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Fe	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0
Mig d'Anglós	1	0	0	0	0	0	1	1	0	1	0	0	0	0	1	0	0

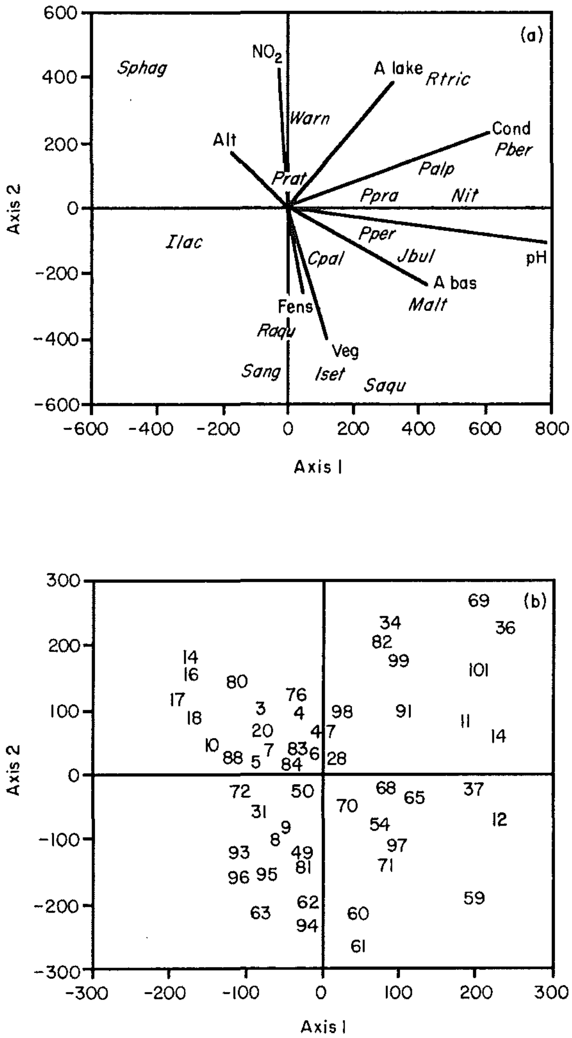

Fig. 4 Ordination diagram of the species and the environmental factors (a), and the lakes (b) over the space defined by the first and second redundancy analysis axes. Abbreviations of species names are as follows: Sang, *Sparganium angustifolium*; Iset, *Isoetes setacea*; Ilac, *Isoetes lacustris*; Saqu, *Subularia aquatica*; Raqu, *Ranunculus aquatilis*; Malt, *Myriophyllum alterniflorum*; Palp, *Potamogeton alpinus*; Pber, *Potamogeton berchtoldii*; Cpal, *Callitriche palustris*; Rtric, *Ranunculus trichophyllus* ssp. *eradicatus*; Ppra, *Potamogeton praelongus*; Pper, *Potamogeton perfoliatus*; Pnat, *Potamogeton natans*; Jbul, *Juncus bulbosus*; Nit, *Nitella* spp.; Sphag, *Sphagnum denticulatum*; Warn, *Warnstorfia exannulata*. Abbreviations of environmental factors are as follows: Alt, altitude; A bas, basin area; A lake, lake area; Veg, vegetation coverage of the basin; Fens, fen coverage surrounding the lake; Cond, conductivity; PT, total phosphorus; NO_2, nitrites; NO_3, nitrates; SO_4, sulphates; Na, sodium; K, potassium. For lake numbers see Table 1.

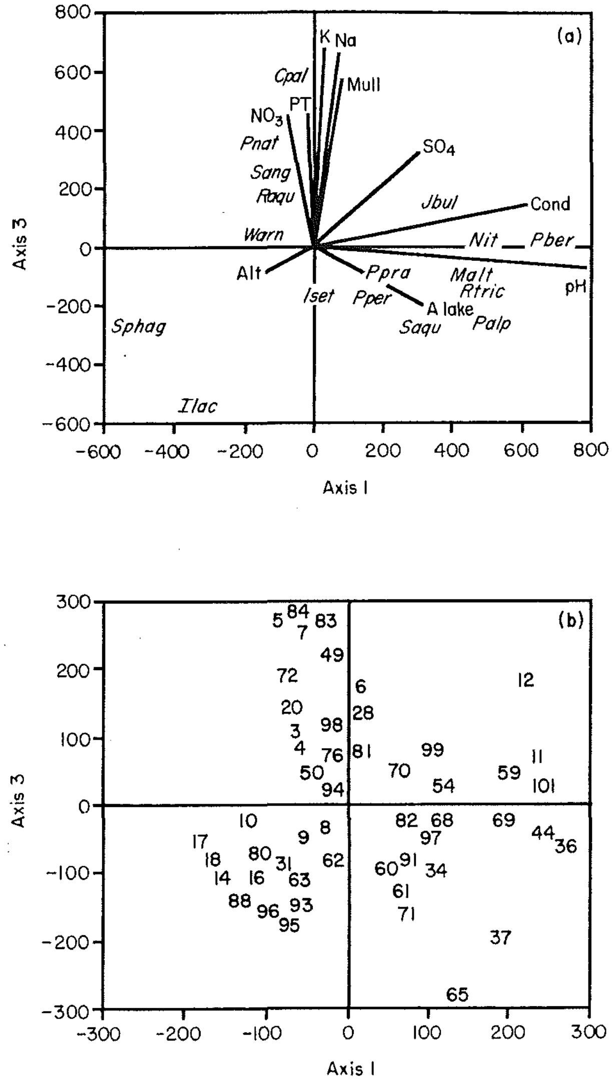

Fig. 5 Ordination diagram of the species and the environmental factors (a), and the lakes (b) over the space defined by the first and third redundancy analysis axes. Abbreviations as in Fig. 4 and Table 1.

of precipitation, but they are more common in dammed lakes.

The macrophytic vegetation of the Pyrenean lakes is dominated by isoetids (*Isoetes lacustris, Subularia aquatica, Isoetes setacea*; Hutchinson, 1975), which characteristically have low growth rates and are adapted to oligotrophic soft waters (Farmer & Spence, 1986; Kautsky, 1988; Boston, Adams & Madsen, 1989). Nevertheless, the most ubiquitous macrophyte in Pyrenean lakes is *Sparganium angustifolium*, a natopotamid with floating leaves, which appears in a broad spectrum of lakes.

According to our results, the main environmental variables that affect the distribution of aquatic plants and determine the kind of macrophyte communities inhabiting the Pyrenean lakes are: (i) ionic content of the water; (ii) vegetation coverage of the catchment and altitude; and (iii) nutrient content (PT and nitrates). In agreement with the results obtained by other authors in other areas of the world (Fraser & Morton, 1983; Catling *et al.*, 1985; Arts & Leuven, 1988), the ionic content of the water and related factors (pH, alkalinity, calcium) are of major importance in establishing the macrophyte composition of Pyrenean lakes. The vegetation coverage of the catchment and altitude are related factors (Braun Blanquet, 1964), which may also implicate temperature as a further environmental variable regulating macrophyte composition in Pyrenean lakes. Finally, total phosphorus and nitrate concentration in the water have also been recognized as relevant variables determining the specific composition of macrophyte communities in lakes (Lohammar, 1965; Arts & Leuven, 1988).

All the species collected are generally characteristic of oligotrophic and softwater conditions (e.g. Lohammar, 1965). However, in the particular Pyrenean context some species are representative of particular environmental conditions—*Potamogeton natans*: relatively eutrophic waters; *Isoetes lacustris*: oligotrophic waters; *Sphagnum denticulatum*: extremely low ionic content as has previously been reported in other areas (Roelofs, Schurkes & Smits, 1984; Wetzel, Brammer & Forsberg, 1984; Raven, 1988; Arts & Leuven, 1988), or *Potamogeton* spp.: relatively high salt content. Other species appear in a wider range of lakes, even though they exhibit some preference for certain environmental conditions. As examples, *Isoetes setacea* is more often found in soft, oligotrophic lakes at low altitude, while *Sparganium angustifolium* is more widespread in lakes situated at low altitudes with a relatively increased nutrient content.

Some lakes are characterized by their low dissolved ionic content and extreme oligotrophy, which favours *Isoetes lacustris* and *Sphagnum* spp. Lakes situated at low altitudes, in vegetated basins and with waters with a low to intermediate salt content and nutrient availability, are suitable for the development of the *Isoeto-Sparganietum angustifolii* association (Braun Blanquet, 1948), with species such as *Isoetes* spp., *Subularia aquatica* and *Sparganium angustifolium*. Lakes with a relatively high ionic content show a development of the *Ranunculo-Potametum alpini* association (Ballesteros & Gacia, 1991), with different species of *Potamogeton*, *Ranunculus trichophyllus* ssp. *eradicatus* and, sometimes, deep-water populations of *Nitella* gr. *opaca*. Finally, the most eutrophic lakes have populations of *Callitriche palustris* and *Sparganium angustifolium*, sometimes with *Potamogeton natans*, while the most oligotrophic lakes are characterized by populations of *Isoetes lacustris* alone.

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