LIMNOLOGY IN THE PYRENEAN LAKES

J. Catalan [1 2], E. Ballesteros [3 2], L. Camarero [1 2], M. Felip [1 2] and E. Gacia [1 2]

1. Department of Ecology. University of Barcelona. Diagonal 645. 08028 Barcelona. Spain.
2. Institute of High-Mountain Research. University of Barcelona. Apartat 21. 25530 Vielha. Lleida. Spain.
3. Centre of Advanced Studies. CSIC. Carretera de St. Barbara sn. 17300 Blanes. Girona. Spain.

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ABSTRACT

The Pyrenees hold more than 1,000 lakes, which provide valuable sites for limnological research. Since 1983 the Institute of High-Mountain Research of the University of Barcelona is carrying out studies on biogeochemistry, plankton ecology, and physiology and ecology of macrophytes. Between November and December all lakes freeze and remain covered in ice and snow for 4 to 7 months, especial attention is paid to this winter period. This paper presents the main results obtained to date, and the outlines of the ongoing studies.

INTRODUCTION

The Pyrenees hold the main freshwater lake district in Spain. Because of the severe weather and abrupt landscape, the Pyrenean lakes are still pristine aquatic ecosystems, which provide valuable sites for fundamental research and as reference for studies of man-influenced systems (MARGALEF, 1985; CATALAN, 1986; CATALAN, 1989b; CATALAN, in press). Yet these lakes cannot escape global and regional influences, so that they serve as sensors of global change, both past and future, for their sediments hold a record of the last 40,000 years (VILAPLANA *et al.*, 1989).

DELEBECQUE & RITTERO (1898) provided the first data on the biota of lakes on the French slopes of the Pyrenees. In the 20's some German naturalists contributed with invertebrate studies of Spanish valleys (ARDNT, 1926; BOFILL & HAAS, 1920; VIETS, 1930). LOZANO REY (1935) in his study of fish in Spanish rivers included some data on Pyrenean lakes. MARGALEF (1948, 1949, 1952, 1953, 1956) extended our knowledge of the biota of Pyrenean lakes, especially algae, and started an ecological approach that was followed in the 70's by an extensive study of chemistry, phytoplankton and zooplankton (MARGALEF *et al.* 1975; VILASECA, 1978; MIRACLE, 1978a, 1978b; CAMPAS & VILASECA, 1979). Detailed studies of the primary production, zooplankton and benthos have only been carried out in the Neouvielle range, especially in the Porth-Bielh lake, as part of the International Biological Program (CAPBLANCQ & LAVILLE, 1983). Since 1983, limnological studies have been carried out by a working group of the Institute of High-Mountain Research of the University of Barcelona (fig. 1) with the broad aim of understanding the patterns and causes of variability from the atmospheric input to the sediment record through the lake ecosystem dynamics. In this paper we summarize the present state of knowledge on the lakes and describe ongoing research aims. Most information comes from the studies carried out in a deep cirque lake, Lake Redó, since 1984 (42º 38' 34" N, 0º 46' 13" E), a shallow valley lake, Lake Bacivér, since 1987 (42º 41' 46" N, 0º 59' 1" E), and from a survey of 102 lakes carried out from July to September 1987. This research was in the fields of physical and biogeochemical limnology, and plankton and macrophyte ecology; but much basic information is still lacking for the Pyrenean lakes, especially for benthos (CAPBLANCQ & LAVILLE, 1983: CATALAN, 1989b).

PHYSICAL LIMNOLOGY

The lakes of the Pyrenees are deep for their modest surface area (fig. 2). As in other ranges with glacial erosion, the lakes can be broadly classified into cirque and valley lakes. Even then, most shallow valley lakes show dimictic behaviour, with mixing periods after thaw in June and during autumn from October to December (CATALAN *et*

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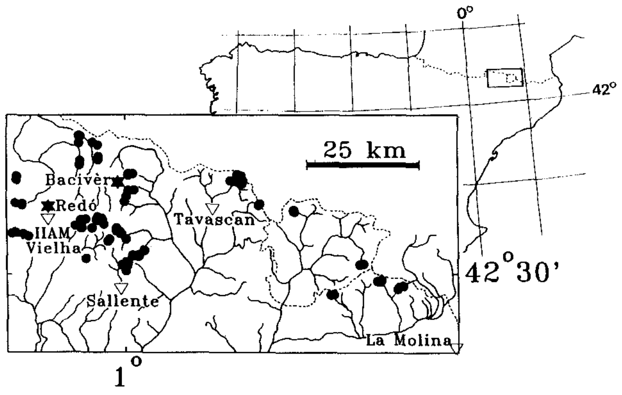


Figure 1. Map of the area covered by the limnological studies of the Institute of High Mountain Research of the University of Barcelona. Circles represent lakes or groups of lakes covered in extensive regional studies. Stars show our main locations (Lake Baciver and Lake Redó) for process-oriented studies. Inverted triangles show precipitation sampling stations.

al., 1990). Deep lakes show sharp thermoclines during summer between 10 and 15 m deep. Especially interesting is mixing in the hypolimnion in lakes without summer inflow. In a vertical profile in Lake Redó, apparent diffusivities are higher between 5 to 10 m below the thermocline (CATALAN, 1988). Microstructure studies have shown that there is turbulent mixing in this zone although it is highly stratified, and this is related with significant boundary mixing close to the shore (IMBERGER, pers. comm.).

Until recently little information has been published on winter conditions. Between November and December all the lakes freeze and remain covered in ice and snow for 4 to 7 months. Some differences between these covers and those of the lakes at higher latitudes are remarkable (fig. 3). Except in very unusual years, there is a short period between lake freezing and accumulation of a large amount of snow. This determines that black ice thickness rarely exceeds 30 to 40 cm, whereas total cover thickness ranges between 2 and 5 m. Melting and refreezing of the snow and new snowfalls produces a complex layered structure in the cover, which is further modified by water flooding from the lake. Initially, the black ice supports the weight of the snow, but as this increases, water rises from below until a hydrostatic equilibrium is reached. In Lake Redó, this water accounts for more than 50% of the water equivalent of the cover and the amount is proportional to the accumulated precipitation (CATALAN, 1989a). This flooding of the cover with water from the lake deepens the base of the ice, often leading to scouring of the shallow aquatic macrophytes, and diverting stream flow through the snow cover above the ice, instead of through the lake (CATALAN *et* al., 1990). The main hydrological event in the lakes is spring thaw. About 30 to 50% of the annual precipitation falls while the lakes are covered by ice, then most of this water circulates through the lake in about one month. For small lakes this means water renewal in the whole lake. Autumn vertical isothermy is longer than spring isothermy (CAPBLANCQ & LAVILLE, 1983; CATALAN, 1988). The duration and intensity of the spring mixing may be closely related to the duration of the ice cover, so that we may expect summer productivity to be negatively correlated to winter precipitation.

There are a few data on annual heat budgets, which lie between 15,000 and 20,000 cal cm^{-2}, from 25 to 50 % corresponding to heat for melting the snow and ice cover. During summer, surface temperature rarely exceeds 15°C, and only in very small ponds.

During the ice-free season, light penetration is very high, the photic zone always being deeper than the thermocline during the stratified period and usually reaching the bottom in lakes less than 20 m deep. When lakes freeze, the accumulation of snow on the surface of the lake reduces underwater irradiance to compensatory levels; this condition may last several months.

BIOGEOCHEMICAL LIMNOLOGY

Pyrenean lakes have several features of interest to general biogeochemistry: a) catchments are usually of non-sedi-

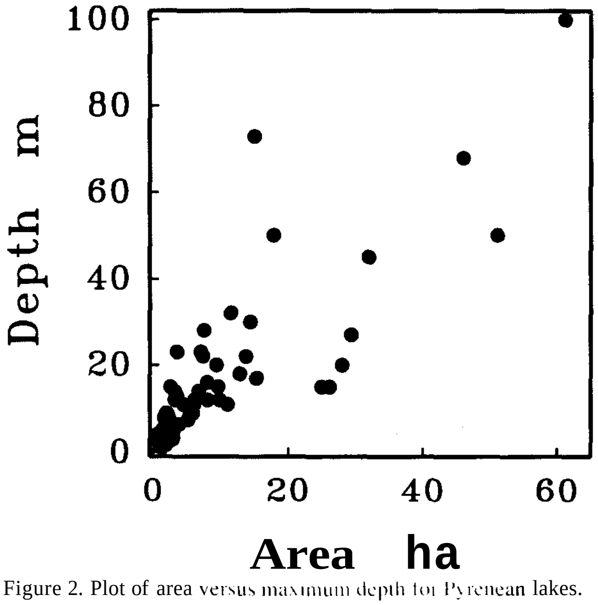


Figure 2. Plot of area versus maximum depth for Pyrenean lakes.

mentary bedrock, thus, water reflects the first phases of weathering and organisms match particular features of each rock type; b) since vegetation cover is sparse, catchments are small, and igneous rocks present low weathering; rainfall composition influences the chemistry of lakes in a significant way; c) organism activity strongly influences the water composition because of the low concentration of most biogenic compounds.

Bulk precipitation in the Central and Eastern Pyrenees is more alkaline than precipitation in the Alps. This is due to the higher calcium concentrations and the lower pollution levels of sulphate and nitrate (CAMARERO & CATALAN, *in press*), although nitrogen compounds seem to be increasing significantly (CATALAN & CAMARERO, *in* press b). The rainfall has a positive mean alkalinity but 30 % of rains are acid. The chemical characteristics of the rain differ significantly depending on its geographical origin. Rains coming from South and South-East (Mediterranean) are alkaline, while those from North-West (Atlantic) are more acidic. The location and particular orography of each lake catchment determine the amount of precipitation received from each direction and, therefore, the chemical features of each location.

The alkalinity of the lakes in the Pyrenees is low (< 300 ueq l^{-1}) but there is no regional acidification (CATALAN & CAMARERO, 1988; CATALAN *et* al., 1990; CATALAN & CAMARERO, *in press* a; CATALAN *et* al., submitted). Most chemical variation is related to the nature of the bedrock. Lakes on Devonian, Cambro-Ordovician, Silurian or granodioritic batholites are easily distinguished (table 1). There are also clear differences between certain granodiorite batholites.

Most variability at seasonal scales in the lakes of the Pyrenees is related with the freezing of the lakes. Winter is

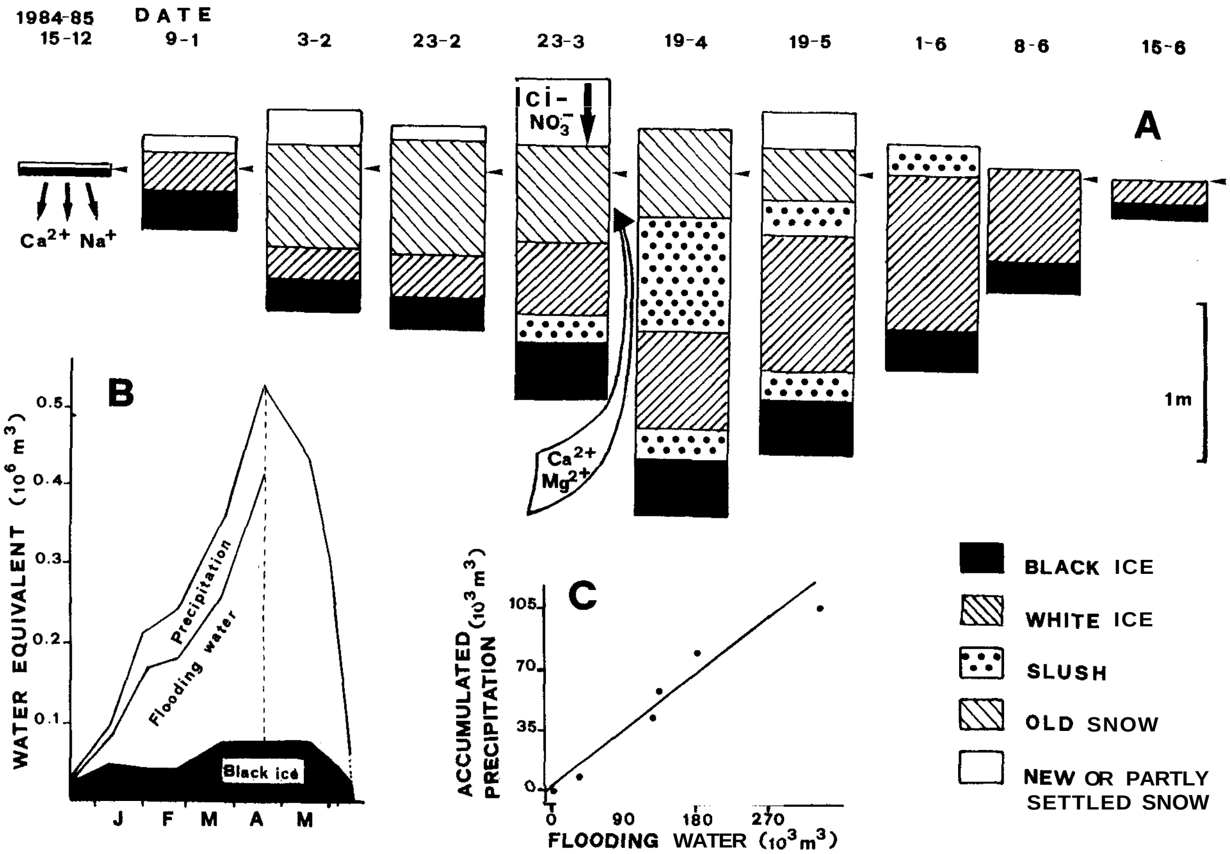


Figure 3. Scheme of the dynamics of the ice and snow cover in Lake Redo during the winter 1984-85. A) Evolution of the structure of the snow and ice cover. Arrows show water level at hydrostatic equilibrium. When black ice forms there is a exclusion of salts. The chemistry of the different layers is determined by original snow composition, differential downward elution of salts and water flooding from the Iake to the cover. B) Evolution of water equivalent content in the cover distinguishing precipitation, black ice and water flooding from the lake. C) Relationship between accumulated precipitation and accumulated flooding water ($r2 = 0.96$, $p < 0.001$).

Table 1. Mean chemical composition of lakes in different bedrocks; sampling carried out during summer 1987

		Granodioritic batholites				Cambro-Ordovician schists	Devoian limestones	Silurian slates
		Maladeta	Bassiers	Marimanha	Andorra Montiluis			
Conductivity	µS cm^{-1}	21.6	4.7	20.2	27.7	11.1	44.2	40.9
pH		7.04	5.80	6.95	6.98	6.17	7.24	4.5
Alkalinity	µeq l^{-1}	155	31	140	249	42	333	<0
SO_2^{2-}	—	38	21	26	47	47	53	236
CI-	—	11	7	11	13	10	22	11
NO_3^-	—	8.57	3.65	10.48	15.60	14.88	10.94	5.32
NO;	—	0.11	0.06	0.14	0.15	0.09	0.21	0.03
NH_4^+	—	1.42	0.86	1.60	1.55	1.34	3.20	2.31
Ca^{2+}	—	168	21	150	206	55	353	44
Mg^{2+}	—	10	5	13	27	11	31	28
Na^+	—	23	11	29	42	20	23	28
K^+	—	7	2	6	9	5	19	3
TP	µmol l^{-1}	0.29	0.18	0.27	0.40	0.15	1.47	0.14

the least studied period in the biogeochemistry of mountain lakes for obvious reasons of sampling difficulty. While the lake is covered by a thick snowpack, there is a linear decrease in the oxygen content of the water column, but only some lakes reach very low values of oxygen saturation in the deepest layers. In Lake Redó, it has been estimated that 60 % of the respiration takes place in the water column. Variation in the oxygen consumption rate in different strata of the water column have been related to the ratio between the surface of sediment and the volume of this stratum (CATALAN, *in press).*

In Lake Redó, as the phytoplankton sedimentation rate has been found to be similar to the decay rate of seston (particulate carbon, particulate nitrogen and particulate phosphorus), it is concluded that most of the particulate organic matter disappeared from the system during winter by sedimentation. The estimated settling velocity is very low (0.14 m d^{-1}) but agrees with the small size of the cells. Fluxes of matter to the sediment are similar to those of Arctic lakes.

As mentioned above, during the ice-covered period there is a flow of water from the lake to the cover to compensate for the hydrostatic imbalance produced by snow accumulation. This means a more homogenous chemical composition of the different snow layers of the cover (CATALAN, 1989a) and also an inoculation of organisms. There is some evidence that there is also a transport of substances towards the lake from the slush layers of the cover which are richer in salts (CATALAN, *in press*). These exchanges between cover and lake merit further research.

In Lake Redó, below 30 m, the trend of variables influenced by biological processes is sustained throughout the winter, and includes a predominance of catabolic processes with both oxygen and pH decreasing. Phosphorus and nitrate increase noticeable during winter near the bottom. Nitrate rise deserves more investigation because it can originate either from a direct flux from the sediment or from a strong bacteria1 nitrification activity using ammonium released from the sediment.

The most significant changes in the chemistry of the lakes take place during thaw. The duration of the melting of the cover depends both on the size of the lake and the catchment, but in any case it takes several weeks. When the snow melts there are some ions (nitrate, sulphate, ammonium) that are eluted faster than others (chloride) providing a sequential change in the chemical composition of the water entering the lakes. Because strong anions move faster than most cations, initial water is more acidic, usually with negative alkalinity. The last melting water is very poor in salts and produces a significant dilution of the lake water.

PLANKTON ECOLOGY

Small coccoid species and flagellates predominate in the phytoplankton of the Pyrenean lakes. Chrysophyceae are quite common (e.g. genera Chromulina, *Ochromonas*, Dinohryon, Bitrichia, Chrysolykos, Pseudokephyrion). and many of them show phagotrophy. Synurophyceae are much less common, no large population has been reported and there seems to be little specific variety in the Pyrenees. Diatoms appear during mixing periods in colonial forms (Melosira, Tahellaria), and some heliophilous *Cyclotella* subsist in the epilimnion during the summer stratification. Desmids are rare, although some very small Cosmarium can reach a relevant biomass in some lakes. Chlorococcales (*Distyosphae-*riun, Monoraphidium, Sphaerocystis, etc.) and species from other groups with similar organization (e.g., the chrysophyte *Stichogloea*) constitute most of the biomass during large periods of the year. Chlorophytes persist longer under ice than Chrysophytes. Cryptophytes are frequent throughout the year, sometimes peaking soon after melting. Small Dinoflagellates, some of them colourless, are also common throughout the year but larger forms (Per-idinium) are restricted to summer, and Ceratium has not been reported.

Small zooplankton is rather diverse throughout the year. Colourless flagellates (*Oicomonas*, *Spumella*, *Monosiga*, etc.) increase in biomass and diversity throughout winter. Ciliates show a great variety (*Strombidium*, Halteria, etc.), especially in late winter when unusual ciliates in the plankton can be found (*Dileptus*, Lacrymaria, etc.). Rotifers constitute from 2 to 10 % of summer zooplankton biomass, and during winter when they can represent most of its biomass if Daphnia is absent. More than sixty species have been found in the Pyrenean lakes; the most common are Ascomorpha ecaudis, *Asplanchna* priodonta, Polyarthra spp. and the boreo-alpine species, Kellicottia *longispina*. This latter reaches its maximum biomass in mid winter, under ice (Catalan, unpubl.).

Large zooplankton consist of few species. *Cyclops abyssorum* can be found in most lakes, individuals survive during winter in a resting stage in the sediment, but a small percentage of copepodites persist in a free-swimming form. Daphnia *longispina* is also very common, but with a less predictable seasonal pattern. Other planktonic Cladocera (*Scapholeberis* mucronata, *Holopedium gibberum*, Daphnia obtusa, D. pulicar-ia and Polyphemus pediculus) can occasionally be found. Diaptomids have a biogeographic interest in the Pyrenees because of the absence of the two most common species in the Alps. There are two large diaptomids, *Diaptomus* cyaneus and D. castaneti, and two small diaptomids, *Mixodiaptomus laciniatus* and *Eudiaptomus vulgaris*. There is size segregation; the two large species or the two small species do not coexist in any lake (MIRACLE,1978a, 1978b).

As yet there are no measurements of bacteria1 activity available for these lakes. However, indirect evidence, through changes in dissolved organic compounds, suggest significant activity even during the large periods when water temperature is below 3° C (CATALAN, in press).

According to the total phosphorus (TP) levels, more than 70 % of the lakes are oligotrophic (TP < 0.3 umol l^{-1}), 25 %

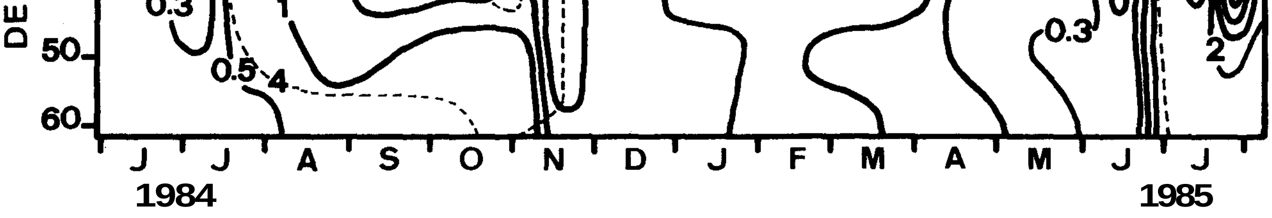


Figure 4. Isopleth diagram for temperature (°C, dashed lines) and chlorophyll (mg Chl m^{-3}) in Lake Redó from June 1984 to Auguat 1985

are mesotrophic ($0.3 < TP < 1$ umol l^{-1}), and only a few very shallow lakes, without a permanent outlet and rich in macrophytes and littoral vegetation, are eutrophic (TP > 3 umol l^{-1}). These lakes present much higher values of ammonium, nitrite, chloride and potassium, which relates the eutrophication to the presence of cattle (CATALAN *et al.*, submitted).

There is no significant statistical relation between any single regional, morphometric or physiographic factor and mesotrophy. However a) lakes on Andorra-Montlluís granodioritic batholite are all mesotrophic, although they include lakes at different altitude and with different morphometric characteristics. b) Although globally there is no correlation between TP and depth, the lakes with the highest TP values inside each cirque or basin were usually shallow (< 5 m deep). c) Most deep lakes with high TP are large and experience level fluctuations because of hydroelectrical exploitation. Globally, however, there is no clear distinction either in chemistry or in trophic status between lakes which have suffered modification to increase hydroelectrical power resources and undisturbed lakes, except for specific extreme cases (CATALAN *et* al., submitted).

Seston composition reflects the scarcity of phosphorus, Lake Redó presents C:N:P ratios about 345:34:1 by atoms throughout the year. Productive periods are linked to the increase in phosphorus diffusion from the sediments by mixing in the water column (fig. 4). After a quick increase

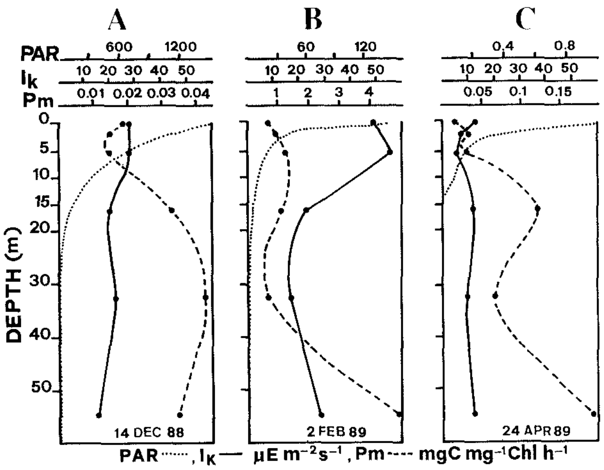


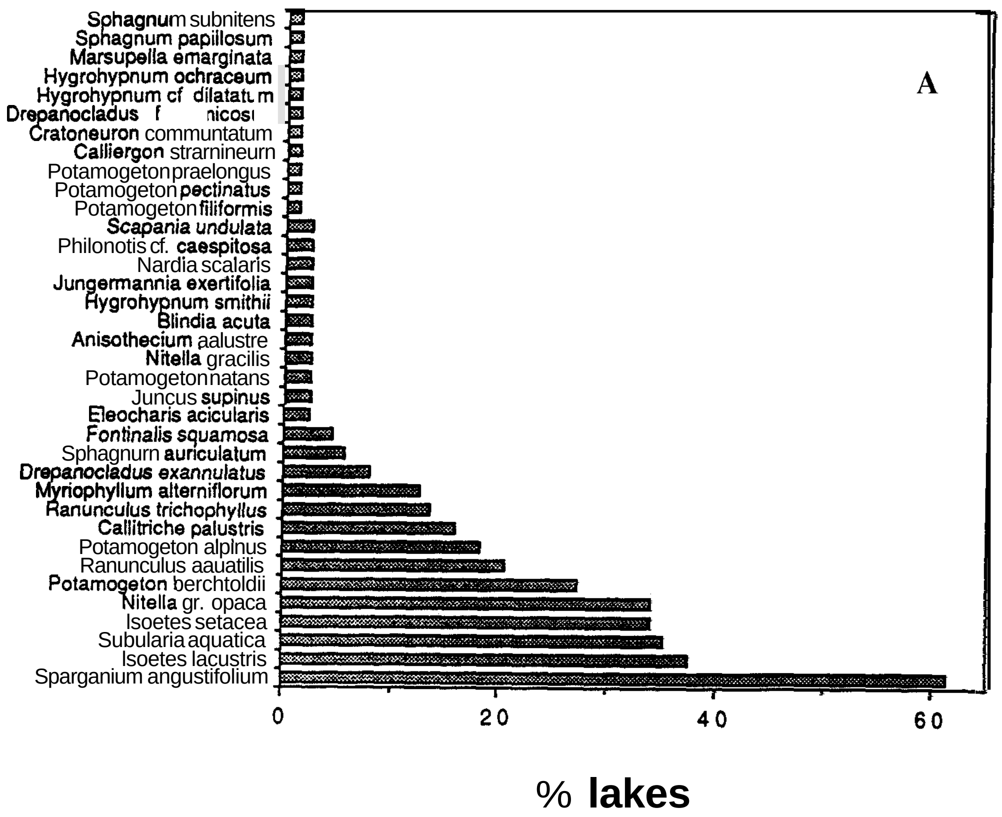
Figure 5. Photoadaptation in Lake Redó (Pyrenees) during 1988-89 winter. During the ice-free period (A) vertical mixing did not allow Ik differentiation, and phytoplankton was adapted to mean depth irradiance. During the ice-covered period with little snow (B) Ik variability followed light values, time of mixing was longer than time of adaptation. When more snow was accumulated in the cover (C), phytoplankton was not able to adapt its Ik to the very low irradiance.

during these periods, chlorophyll decrease very slowly over long periods in deep lakes, either in the hypolimnion during summer, where a deep chlorophyll maximum appears, or under ice during winter (CATALAN & CAMARERO, 1991). In situ recycling seems to play a significant role in maintaining the planktonic community, although fertilizing mechanisms related with boundary mixing and lateral intrusions may be also important.

Mountain lakes are particularly interesting sites in which to investigate scales of photoadaptation in oligotrophic systems. High transparency in summer combines with very low levels during winter below the snow and ice cover. For instance, the transition from autumn overturn to mid winter in Lake Redó is a good illustration of the relationship between mixing and light regimes, and photosynthetic adaptations (CATALAN, 1991). During overturn, phytoplankton distribution is rather homogeneous. Yet, there is a significant differentiation in a (the slope of the photosynthesis vs. irradiance curves) and Pmax (maximum production at light saturation) between surface and deep (>15 m) layers. However I_k (lower light intensity to reach Pmax, which is equal to Pmax/α), which requires a longer adaptation time because it represents a change in the size of the photosynthetic units (HARDING *et* al., 1987) is quite similar for phytoplankton populations at any depth, and its value corresponds to mid-depth light intensity (25 m). This means that during autumn overturn in Lake Redó the mixing time of phytoplankton is shorter than the time of I_k adaptation and longer than the time of a adaptation, and Pmax changes parallel to *a*. During overturn, the mixing time of heat has been estimated to be less than an hour (CATALAN, 1988). For phytoplankton it is likely to be longer, but less than a day. However, when ice forms on the lake surface, turbulent mixing is markedly reduced and, as a consequence, phytoplankton populations are subjected to a determinate light level during longer periods, then I_k adaptation to each level is possible (fig. 5). Finally, when snowpack is thick, available light falls to very low levels. I_k becomes very low but it does not reach the values of light in the water column and so it seems impossible for these algae to adapt fully to such low light levels.

MACROPHYTE ECOLOGY

Nearly 65 % of the ca. 1000 lakes in the Pyrenees have submerged aquatic macrophytes. Species richness (fig. 6) of these lakes is higher than that of the lakes from other European chains (BRAUN BLANQUET, 1948). Quillworts,



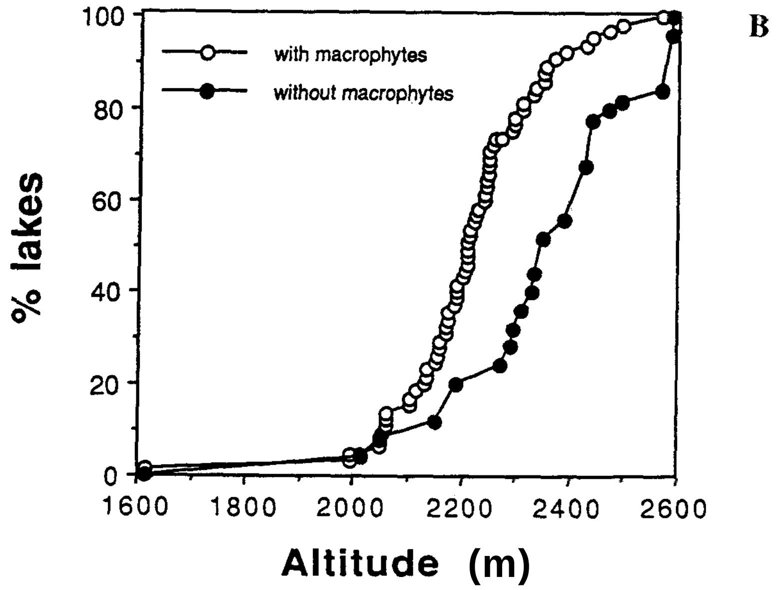


Figure 6. Percentage of presence of the main submerged macrophytes in Pyrenean lakes with macrophytic vegetation (A). Cumulative percentage of lakes with and without macrophyte development in relation to lake altitude in the Pyrenees (B).

aquatic phanerogams and algae of the genus Nitella are the main constituents of the submerged vegetation of natural lakes and pools. Mosses are only common in very soft-water lakes (Sphagnum), in shallow ponds (*Drepanocladus*) or in lakes without cormophytic vegetation. Macrophytic vegetation mainly appears between the lowest limit of occurrence of Pyrenean lakes (usually at 2000-2100 m) and 2400 m above sea level (fig. 6). The upper limit is related to mean

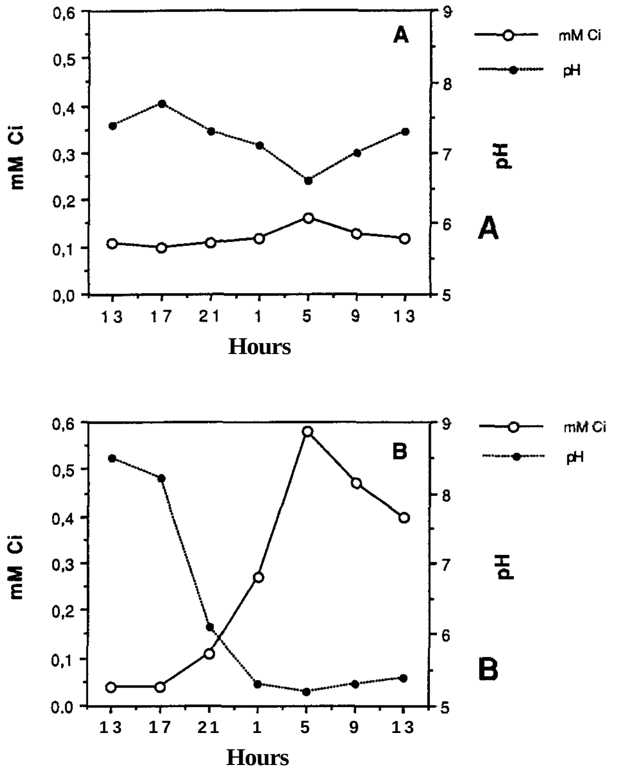


Figure 7. Daily changes in dissolved inorganic carbon and pH in the water near the 1.8 m population of *Isoetes lacustris* in the lake Baciver (A) and in a shallow pond with a *Isoetes* setacea population (B) (12-13/9/90). Notice the different pattern between the sunny first day and the rainy second day.

summer water temperature (above 12ºC) and the ice-free period of the year (6 months or more). If the shore of the lake is not rocky, there is usually a well-defined pattern of zonation between the alpine meadows or subalpine forests and shrubs surrounding the lake and the submerged aquatic vegetation. The alpine or subalpine dominant communities change into a boreo-alpine peat fen mainly dominated by Cyperaceae and Juncaceae (Caricetum *nigrae* Braun Blanquet, 1915) and peat-moss bogs dominated by Sphagnum subnitens. Sometimes, there is an helophytic belt of *Carex* and *Eriophorum* (Caricetum *rostrato-vesicariae* Koch, 1926) in shallow waters of some parts of the lakes.

Five types of Pyrenean lakes can be distinguished attending to their submerged aquatic vegetation: 1) lakes with Isoetes *lacustris* as the commonest species, along with *Subularia* aquatica and sometimes *I.* setacea; 2) lakes with species of Potamogeton (P. *berchtoldii*, P. alpinus and others) and Ranunculus (R. *trichophyllus*, R. aquatilis; 3) lakes with a mixture of the species of types 1 and 2 plus Myriophyllum *alterniflorum*; 4) lakes with Callitriche palustris; and 5) lakes with mosses (Fontinalis *squamosa*, Anisothecium palustris, *Blindia acuta*, etc). Large populations of *Sparganium angustifolium* usually accompany the first four types.

Differences in the trophic status and the water chemistry of the lakes help explain the differences in vegetation between lakes (BALLESTEROS & GACIA, 1990, 1992). Small ponds influenced by cattle contain eutrophied waters, characterized by the dominance of *C.palustris* and S. angus*tifolium*. *Isoetes*-lakes have very low water conductivities (mean 14 µS cm-'), while *Potamogeton*-lakes have higher (mean 36 µS cm-'). Potamogeton and Isoetes species coexist in lakes with intermediate conductivity. Differences in conductivity are mainly associated with differences in alkalinity (BALLESTEROS & GACIA, 1992). Mosses and liverworts that usually grow in rocks are the only macrophytic vegetation in some high altitude lakes.

The low alkalinities of Pyrenean lakes, during periods of low mixing, can produce a CO_2 limitation of photosynthesis. Daily changes in dissolved CO_2 are small even in small lakes (fig. 7) and mean values are close to the CO_2 saturation points calculated for Isoetes lacustris from the lake Baciver (GACIA & PEÑUELAS, 1991). Nevertheless, CO_2 limitation might occur taking into account the CO, consumption at the diffusive boundary layer level (MADSEN & SAND-JENSEN, 1991). In shallow ponds, rich in organic detritus and with a dense coverage of macrophytes, changes of 3.5 pH units have been detected, together with a strong simultaneous decrease in dissolved inorganic carbon (fig. 7).

Submerged aquatic macrophytes have developed different physiological mechanisms to avoid CO_2 limitation. The clusters of species that appear in the different lakes are arranged in relation to water alkalinity, and present different adaptive mechanisms. Isoetids can hardly take up HCO_3^- (GACIA & PEÑUELAS, 1991). However, they are provided with other mechanisms to improve inorganic carbon assimilation, such as CO_2 uptake through the roots (RICHARDSON *et* al., 1984) and crassulacean acid meta-

Table 2. Primary production of the three different macrophyte communities present in lake Baciver (Central Pyrenees).

Community	Depth intervals m	Primary Production g dw m^{-2} y^{-1}	Primary Production g C m^{-2} y^{-1}
Isoetes lacustris	0.5-2.3	43.7-52.1	16.2-19.3
Sparganium angustifolium	0.3-1.2	155.0	64.5
Nitella gracilis	2.5-7.0	11.0-20.0	4.6-8.3

bolism (CAM) (KEELEY, 1982). In contrast, elodeids (e.g. *Potamogeton* plants) can use HCO_3^- as an extra source of inorganic carbon and grow in waters with higher alkalinity. In the lakes where isoetids and elodeids coexist, elodeids live in flowing waters or occupy the places with higher water turbulence (BALLESTEROS, 1989).

CAM of *I. setacea* inhabiting a small shallow water pond and of *I. lacustris* from lake Baciver (BALLESTEROS *et al.*, 1989) were measured in July 1990. A daily cycle of titrable acidity in leaves was measured and a nighttime acidification and a daytime deacidification was demonstrated. Acidity values and acidification/deacidification pattern recorded in Pyrenean *I. lacustris* were similar to values recorded in Scandinavian plants (MADSEN, 1987). However, *I. setacea* plants exhibit steeper daily variations in titrable acidity, which supports the hypothesis of a higher carbon dioxide limitation of photosynthesis in shallow stagnant waters.

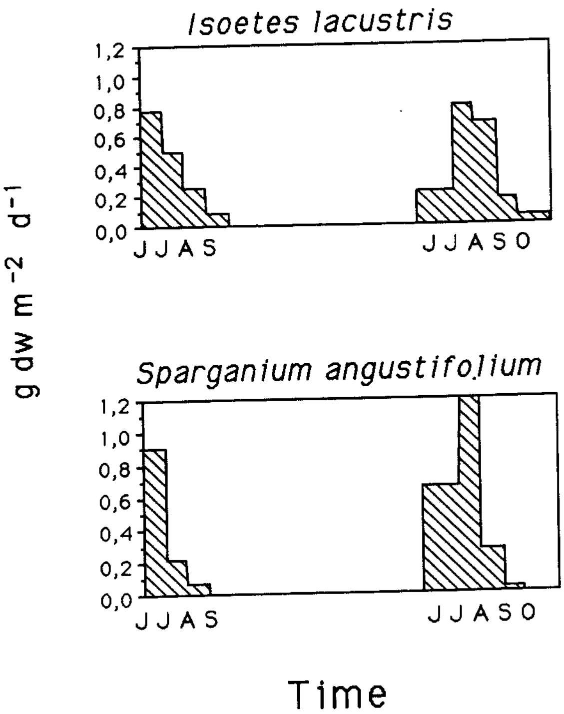


Figure 8. Seasonality of leaves biomass production in *Isoetes lacustris* at 1.8 m depth and in the *Sparganium angustifolium* at 0.8 m depth in the lake Baciver.

The low dissolved nutrient concentration of most Pyrenean lakes (CATALAN et al., submitted) determines the low phytoplankton biomass and productivity of these high mountain lakes (CAPBLANCQ & LAVILLE, 1983; CATALAN, 1987; CATALAN & CAMARERO, 1991). Thus, submerged macrophytes when present are the main primary producers (CAPBLANCQ, 1973; GACIA & BALLESTEROS, *in press*). Growth of the Pyrenean benthic macrophytes is highly seasonal and only occurs between June and October (fig. 8). Values depend on the community (table 2) but they are in the lower range of aquatic communities without light limitation, as has been reported in similar communities from boreal lakes (SOLANDER, 1983). Factors affecting the annual pattern of growth and production change according to each species and population. In *I. lacustris* from the lake Baciver maximum growth rates are obtained at the end of July in coincidence with the highest annual temperatures and underwater irradiances. Experiments in the laboratory has demonstrated that low temperatures strongly reduce growth.

Nutrient availability for macrophyte growth is very low in most Pyrenean lakes if only the water column is considered. Seasonal changes in N and P content in tissues have been demonstrated in *I. lacustris* from the Pyrenees, which suggested that production could be nutrient-limited in summer. In situ nutrient enrichment of the sediment enhanced production and confirmed the nutrient limitation of growth in summertime. Macrophyte communities also affect sediment features. Redox profiles from *S. angustifolium* sediments are completely different from those under *I. lacustris* as indicated by changes in nitrate and ammonium concentrations (CATALAN et al., submitted). The highly oxidized sediments from the *I. lacustris* community are related to the oxygen release from the *Isoetes* roots (SAND JENSEN *et al.*, 1982).

ONGOING RESEARCH

Research in Lake Redó and Lake Baciver is still being carried out. In lake Redó a dual approach to lake ecosystem is intended through the evaluation of carbon, nitrogen and phosphorus cycles together with the study of the life-histories of the plankton organisms. Assuming hydrodynamics as main driving force of the changes in the lake system, we study how life mediates biogeochemical changes. Each season provides interesting aspects. The following aspects are under current research during winter: 1) inoculation of organisms from the lake to the snow and ice cover and biological activity in the slush layer; 2) changes in the function and structure of the plankton induced by the sudden freezing of the lake surface; 3) microbial succession during winter; and sediment-water interaction during winter inverse stratification. Summer investigation is concentrated in the study of the fertilizing and maintenance mechanisms of the deep chlorophyll maximum and production in the hypolimnion.

In Lake Baciver we are evaluating the ecological changes after the construction of a dam that has raised the water level by 7 m. Emphasis is placed on the effects on macrophyte development and growth. Further investigation is being carried out on the relative importance of P and N in the sediment interstitial waters in the limitation of the primary production of *Isoetes* primary production; the control of primary production in *Potamogeton-lakes;* factors controlling macrophyte distribution patterns; and detailed studies in the maintenance of CAM metabolism in emergent *Isoetes setacea* plants.

Future research includes palaeolimnology, studying changes during the industrial period and, at longer time scales, during the last 40.000 years in connection with another research group in the Institute of High-Mountain Research (VILAPLANA *et al.,* 1983; MONTSERRAT & VILAPLANA, 1987; VILAPLANA *et al.,* 1989; VILAPLANA & BORDONAU, 1989).

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