Effects of building up a dam in a shallow mountain lake (Baciver, Central Pyrenees)

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SUMMARY

Changes in the water, the sediment, and the structure and dynamics of the submerged macrophyte populations were studied after the building up of a dam in a high mountain Pyrenean lake in late summer 1990. The most outstanding variations in the physical and chemical features were: (a) a 5.5 m rise of the shore level, (b) a decrease in light transmittance into the water column, (c) an oxygen depletion in deep waters, coupled to a pH decrease and a rise in conductivity and cation concentration, (d) an increase in the total dissolved nitrogen (mainly ammonium) and phosphorus concentration in the water column, and (e) an increase in the reduced N-compounds (nitrite and ammonium) in the sediment pore-water of the *Isoetes lacustris* community, coupled to a decrease in nitrate. Changes in the chemical features seem to be related to the decomposition of organic matter provided by the flooded terrestrial subalpine meadows and shrubs, and the lake's submersed vegetation.

Both the area occupied by the submersed vegetation and the number of macrophyte species suffered an important reduction with the daming of Lake Baciver. All the small, non dominant species *(Eleocharis acicularis, Subularia aquatica* and *Isoetes setacea)* dissappeared along the summer 1991. *Sparganium angustifolium* experienced a degradation (low density of shoots, short leaves) in 1991 which lead to its complete die off in spring 1992. The strong attenuation of the light regime could account for these losses. *Isoetes lacustris* individuals originally living below 0.6 m depth were completely dead in summer 1991, probably due to an oxygen depletion in winter time. The only surviving *Isoetes* plants (those originally living above 0.6 m depth which were between 5.8 and 6.1 m depth after the dam) increased its leaf length as a response to the decrease in available irradiance. Although the number of produced leaves was slightly lower in 1991 than it was before the daming, the production of biomass increased, since leaves were longer. However, the lost of leaves was very high, resulting in a global decay of the population. In late spring 1992 surviving *Isoetes lacustris* had the remaining leaves very damaged, probably because of the winter anoxy, and no leaves were produced in summer 1992. This brought a complete dissapearence of the community in the lake.

KEY WORDS: high mountain lakes, reservoirs, benthos, environmental impact.

RESUMEN

Efectos del represamiento de un lago somero de montaña (Baciver, Pirineos centrales). Se estudiaron los cambios en el agua, el sedimento y la estructura y dinámica de las poblaciones de macrófitos sumergidos después del represamiento de un lago de alta montaña de los Pirineos a finales del verano de 1990. Las variaciones más notables de las características físicas y químicas fueron: a) elevación de 5,5 m del nivel del litoral; b) disminución de la transmitancia de la luz en la columna de agua; c) depleción de oxígeno en las aguas profundas, junto a la reducción del pH y al aumento de la conductividad y de la concentración de cationes; d) aumento de la concentración de nitrógeno disuelto total (principalmente amonio) y de fósforo en la columna de agua, y e) aumento de los compuestos de N reducidos (nitrito y amonio) en el agua intersticial de la comunidad de *Isoetes lacustris*, ligada a una disminución del nitrato. Los cambios en las características químicas parecen estar relacionados con la descomposición de la materia orgánica aportada por los prados y matorrales subalpinos terrestres, así como por la vegetación sumergida del lago.

Tanto el área ocupada por la vegetación sumergida como el número de especies de macrófitos experimentaron una importante reducción con el represamiento del lago Baciver. Todas las especies pequeñas, no dominantes *(Eleocharis* *acicularis, Subularia aquatica* e *Isoetes setacea)*, desaparecieron a lo largo del verano de 1991. *Sparganium angustifolium* experimentó un proceso de degradación (baja densidad de pies, hojas cortas) en 1991 que condujo a su completa desaparición en la primavera de 1992. La fuerte atenuación del régimen de iluminación podría explicar dichas pérdidas. Los individuos de *Isoetes lacustris* que originalmente vivían por debajo de los 0,6 m de profundidad estaban completamente muertos en el verano de 1991, probablemente debido a la depleción invernal de oxígeno. Las únicas plantas de *Isoetes* que sobrevivieron (las que originalmente vivían por encima de los 0,6 m de profundidad y que después del represamiento se hallaban entre 5,8 y 6,1 m) aumentaron su longitud foliar como respuesta a la reducción de irradiancia disponible. Aunque el número de hojas producidas fue ligeramente menor en 1991 de lo que era antes del represamiento, la biomasa producida aumentó, pues las hojas eran más largas. Sin embargo, la pérdida de hojas fue muy grande, lo que produjo una reducción global de la población. A finales de la primavera de 1992, los *Isoetes lacustris* supervivientes tenían las hojas restantes muy dañadas, probablemente debido a la anoxia invernal, y no se produjo ninguna hoja nueva en el verano de 1992. Esto condujo a la desaparición total de la comunidad en el lago.

PALABRAS CLAVE: lagos de alta montaña, presas, bentos, impacto ambiental.

INTRODUCTION

High mountain lakes in the Pyrenees have traditionally been exploited for hydroelectric power production and, in to a much lower extent, to provide water for recreative use. Both uses involve the transformation of natural lakes into reservoirs through the construction of dams.

Daming has an outstanding ecological impact in the landscape and the implicated rivers and lakes. Nevertheless, there are no studies on the changes that the limnic communities experience after the daming in Pyrenean lakes since most dams were built up between the 1950's and the 1970's. In this study we focus on the changes undergone by the chemical features of the water column, the sediment, and in the structure and dynamics of the submerged macrophyte communities after the construction of a dam in the pristine Lake Baciver.

Lake Baciver was a model of a valley Pyrenean lake due to its physico-chemical features, and specially for having a high coverage of submersed macrophytic vegetation. For these reasons studies on the physical and biological features of the Lake existed previous to the daming, thus allowing a comparative study of this perturbation (Ballesteros *et al.*, 1989; Camarero & Catalan, 1991; Catalan *et al.*, 1990, 1992; Catalan & Camarero, 1993; Gacia & Ballesteros, 1991, 1993a, 1993b, 1994).

STUDY AREA

Lake Baciver is located in the Central Pyrenees (42° 41' 42"N, 0° 59' 1"E) at 2120 m a. s. l. in a granodioritic basin. Its origin is related to glacial overdeepening and subsequent morainic obstruction. The vegetation of the catchment is dominated by acidophilous shrubs of *Rhododendron ferrugineum* L. with *Pinus uncinata* Miller ex Mirbel, and alpine meadows of *Festuca eskia* Ramond ex D.C. and *Carex curvula* All. The Lake is long and narrow, situated at mid altitude in a valley, and the water renewal is very fast (Camarero & Catalan, 1991). Physico-chemical characteristics of the water column and macrophyte vegetation of Lake Baciver in its natural state were described in Ballesteros *et al.* (1989), Catalan *et al.* (1990), Camarero & Catalan (1991), Catalan & Camarero (1993) and Gacia & Ballesteros (1993a, 1994).

MATERIALS AND METHODS

The dam was built during summer 1990, and at the end of September the Lake was replenished to its new level. Changes in the major physical and chemical factors affecting the water column, the sediment and the macrophyte populations were monitored during the years 1991 and 1992 (Table I). Sampling and analyses of the water column were performed following methods described in Catalan *et al.* (1992). Temperature, conductivity, pH and Photosynthetic Photon Flux Density (PPFD) were measured in situ. Water samples were collected and analyzed in the laboratory for oxygen concentration, alkalinity and dissolved nutrient content (phosphate, nitrate, nitrite and ammonium). Chlorophyll content in the lake water was measured spectrophotometrically and the concentrations were calculated following Jeffrey & Humphrey's (1975) equations.

TABLE I. Sampling calendar and studies conducted at each sampling data. *Calendario de muestreos y estudios realizados en cada fecha de muestreo.*

Sampling	7/91	8/91	9/91	10/91	3/92	6/92	7/92
Water column	x	x	x		x	x	x
Macrophytes	x	x		x			x
Sediment		x					

Sediment samples were collected by SCUBA divers in the area previously occupied by the *Sparganium angustifolium* and the *Isoetes lacustris* communities (Ballesteros *et al.*, 1989). Cores of 12.5 cm of diameter per 20 cm length were collected, carried to the laboratory, sorted into horizons of 3 cm of section and kept frozen until analysis. The interstitial water of the sediment was extracted by the fast frozen technique (Levat *et al.*, 1990). Methods for the analysis of the nutrient content in pore-water were the same than those used for the water column.

Biomass, structure, and density of individuals of the macrophyte communities were obtained from samples of plants and sediment of 400 cm^2 collected by SCUBA diving. The *Sparganium angustifolium* individuals were collected at 6.8 m depth in the eastern area of the lake. The *Isoetes lacustris* community was sampled at 6.1 m depth in the northern part of the lake; individuals were sorted in size classes according to its maximum length as described in Gacia & Ballesteros (1993a). Primary production of the surviving *Isoetes* was also measured by means of a leaf tagging technique (Gacia & Ballesteros, 1991) complemented with the description of the leaf growing function (Gacia & Ballesteros, 1994). Biomass and production values were expressed in a dry weight basis (24 h at 105°C).

RESULTS AND DISCUSSION

Table II contains morphometrical parameters of lake Baciver before and after the daming, notice the shore level rose 5.5 m.

TABLE II. Morphometrical parameters of Lake Baciver before and after the building up of the dam. *Parámetros morfométricos del lago Baciver antes y después de su represamiento.*

	Dam	
	Before	After
Area (m^2)	26629	51301
Maximum length (m)	432	565
Maximum width (m)	115	178
Maximum dipth (m)	7.5	13
Volume (m^3)	51.140	79.390

Water column

Figure 1 shows the vertical profiles of light and temperature in Lake Baciver at the different sampling dates. The transparency of the water decreased in 1991 after the daming (t-test, p<0.0005); (Table III). Turbidity was due to a higher content of suspended particles coming from the decomposition of organic matter of terrestrial and aquatic origin. Mean values of the light extinction coefficient from 1992 do not significantly differ from the ones obtained before the daming (t-test, $p>0.5$), highlighting a fast recovery of the water transparency.

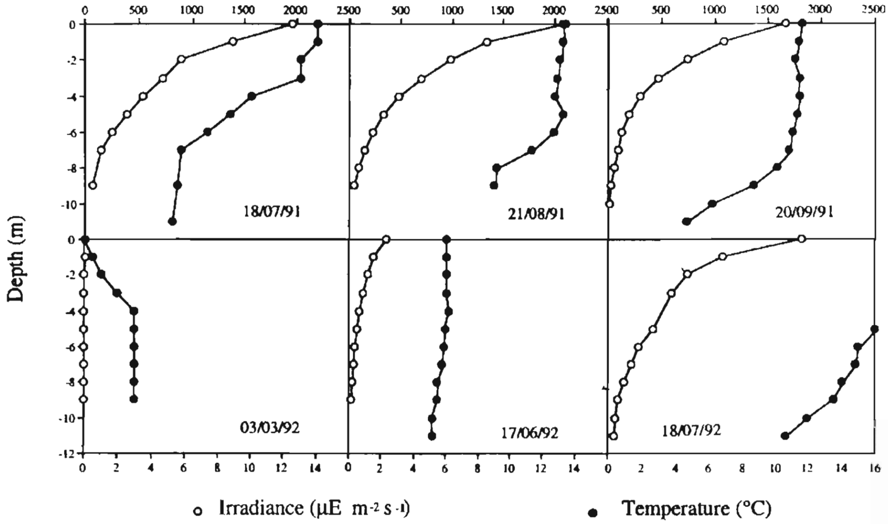

FIG. 1. Temperature and irradiance profiles in the water column at the different sampling dates during the years 1991 and 1992. *Perfiles de temperatura e irradiancia en la columna de agua en las distintas fechas de muestreo durante los años 1991 y 1992.*

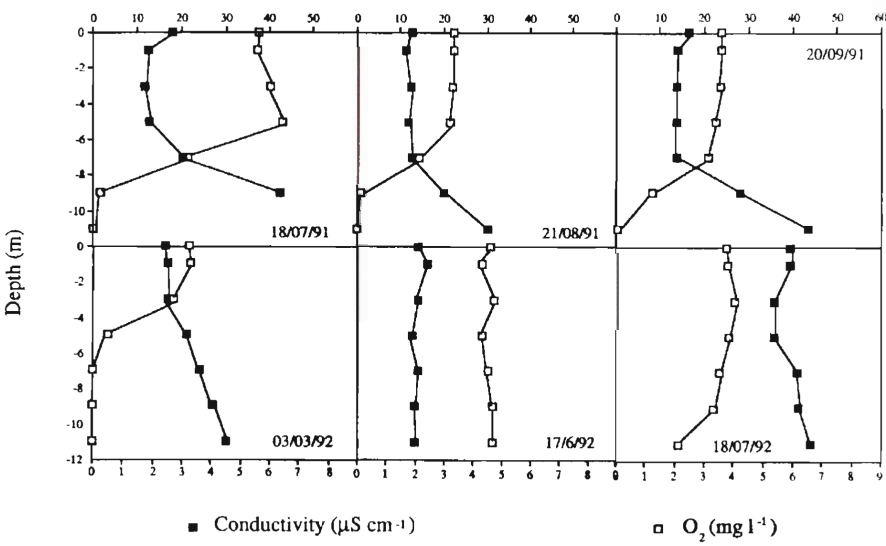

FIG. 2. Conductivity and oxygen concentration profiles in the water column at the different sampling dates along the years 1991 and 1992. *Perfiles de conductividad y concentración de oxígeno en la columna de agua en las distintas fechas de muestreo durante los años 1991 y 1992.*

TABLE III. Mean annual values (not considering the ice-covered period) and standard deviation of the light extinction coeficient in the water column. Year 1989 corresponds to the Lake in its original state, and years 1991 and 1992 concern to the Lake after daming. * Indicates significant differences (t-Student, $p<0.0005$) compared to the original situation. *Valores anuales medios (sin considerar el período en que está cubierto de hielo) y desviación típica del coeficiente de extinción de la luz en la columna de agua. El año 1989 corresponde al lago en su estado original, y los años 1991 y 1992 se refieren al lago después del represamiento. * Indica diferencias significativas (t de Student, p<0.0005) en relación a la situación original.*

Year	Light extinction coeficient m^{-1}	
	X	SD
1989	0.280	0.033
1991	0.418*	0.004
1992	0.328	0.051

The lake was stratified in summer time with a 3 m deep thermocline that progressively sinked. In winter, there was an inverse stratification of the water column due to the influence of the ice and snow cover. The thermical behavior of the water column changed with the increase of the water volume; the higher depth of the lake allowed the formation of a deeper thermocline compared to the lake in its natural state (Camarero & Catalan, 1991).

Respiratory processes dominated in the deepest part of the lake in summer 1991 and brought an oxygen depletion below 9 m depth (Fig. 2). Anoxy had never been documented before in Lake Baciver (see Catalan *et al.*, 1990 for monthly data of an annual survey). At the end of summer the anoxy was restricted to the deepest part of the lake, due to an enhanced water mixing and a higher water exchange in September. The anoxy was even more severe in winter 1992 but it completely dissapeared after the thaw. Water flow (nil in winter time) rather than biological activity (primary production and decomposition) was the determinant of the oxygen concentration increase in the water mass in spring of 1992. At this time of the year the water flow is very strong because of the snow fusion in the catchment.

Conductivity displayed a trend inverse to the oxygen concentration in the water column, increasing significantly in deep waters when the water column was stratified (Fig. 2). A rise in conductivity was coupled to an increase in alkalinity and a pH decrease (Fig. 3). The inverse relationship between oxygen and alkalinity has been previously reported in deep waters from Lake Redó and Lake Baciver (in its natural state; Camarero & Catalan, 1993). According to these authors, this inverse relationship can be explained by a calcium release from the sediment to the water column at low pH levels. In the summer samples of Lake Baciver after the dam, there was also a significant increase in the calcium concentration from the oxic (3 m) to the anoxic (9 m) water layer (Table IV). Together with the increase in the calcium content in deep waters, there was also a major content in other cations (potassium, sodium and magnesium; Table IV) which suggest, in this case, that organic matter coming from the recently inundated soil and from the decomposing terrestrial and aquatic vegetation may be the source of cations instead of the sediment itself. The increase of the cation content of the lake water in two or three orders of magnitude after the construction of the dam is also very noticeable (Table IV).

The inverse relationship between conductivity and oxygen concentration is also explained by the higher cation and proton content in the deepest part of the lake water in anoxic conditions.

Dissolved phosphate, ammonium and nitrite concentration in lake water increased an order of magnitude after the dam, while nitrate decreased (Table V). A rise of the reduced forms of inorganic nitrogen is related to the lowest oxygen levels and more reduced

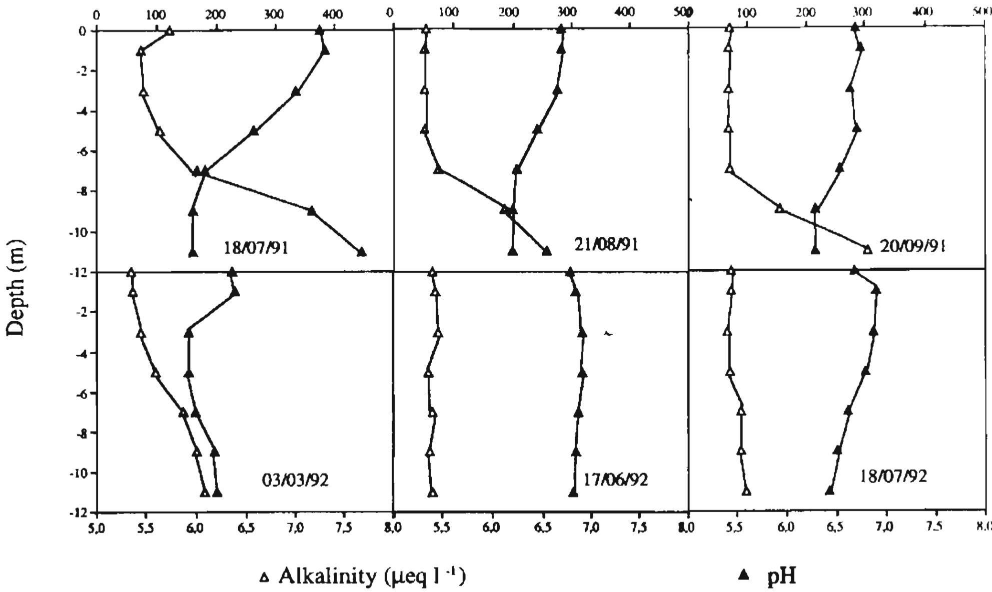

FIG. 3. Alkalinity and pH profiles in the water column at the different sampling dates during the years 1991 and 1992. *Perfiles de alcalinidad y pH en la columna de agua en las distintas fechas de muestreo durante los años 1991 y 1992.*

TABLE IV. Cation concentration (in mg l^{-1}) in shallow and deep waters before (1989) and after (1991) the construction of the dam. *Concentración de cationes (en mg l^{-1}) en las aguas someras y profundas antes (1989) y después (1991) del represamiento.*

Month	Depth	Na^+	K^+	Ca^{++}	Mg^{++}
June 1989	3m	0.0013	0.0010	0.0009	0.0002
	7m	0.0013	0.0010	0.0009	0.0002
August 1989	3m	0.0013	0.0002	0.0009	0.0003
	7m	0.0013	0.0002	0.0010	0.0003
June 1991	3m	0.582	0.272	1.62	0.28
	9m	0.873	0.936	5.26	0.68
August 1991	3m	0.590	0.148	1.47	0.25
	9m	0.771	0.794	4.61	0.65

conditions. Increase in total dissolved nitrogen and phosphate concentration also indicates more eutrophic conditions. The recovery to a more oligotrophic state can be envisaged in 1992, but it is still far from the original situation (Table V).

Chlorophyll content increased in 1991 in agreement with a higher nutrient availability in the water column (Fig. 4; Table V). Chlorophyll depth distribution profiles (Fig. 4) indicate in summer a chlorophyll maximum situated near the thermocline, while in winter chlorophyll concentration was very low and without any appreciable maximum. In September 1991 there was a dominance of chlorophyll *b* over chlorophyll *a* in deep waters, suggesting a more senescent state of the phytoplankton populations (Margalef, 1974).

Sediment porewater

Porewater nutrient concentration in the sediment of the *Isoetes* community changed qualitatively and quantitatively after the daming. Nitrite and ammonium concentration increased while concentration of nitrates and phosphates decreased (Table VI), indicating

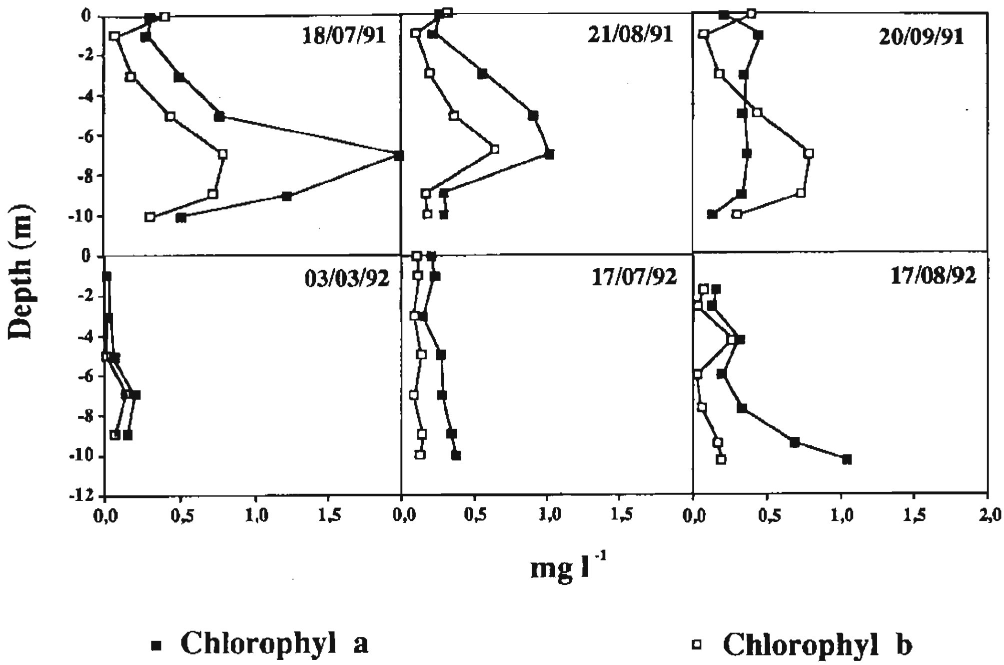

FIG. 4. Profiles of chlorophyll *a* (full squares) and *b* (open squares) in the water column in the different sampling dates during the years 1991 and 1992. *Perfiles de clorofila a (cuadrados negros) y b (cuadradros blancos) en la columna de agua en las distintas fechas de muestreo durante los años 1991 y 1992.*

TABLE V. Annual average, minimum and maximum values of different parameters of the water column at the Lake Baciver in its original state (1989), and after the building up of the dam (1991, 1992). *Valores anuales medios, mínimos y máximos de los diferentes parámetros de la columna de agua del lago Baciver en su estado original (1989), y después de su represamiento (1991, 1992).*

	Year 1989			Year 1991			Year 1992		
	MEAN	MIN	MAX	MEAN	MIN	MAX	MEAN	MIN	MAX
Conductivity (μS/cm)	12.49	8.80	22.90	20.37	11.2	56.8	25.52	12.60	44.1
Alkalinity (μeq/l)	82.36	49.00	156	137.29	52	446	87.24	59.70	180
pH	7.15	5.56	8.51	6.53	5.96	7.3	6.59	5.92	6.91
O_2 (mg/l)	8	5	11.5	3.34	0	8.62	3.26	0	4.71
PO^{3-}_4 (μM)	0.08	0.00*	0.97	0.56	0.33	1.16	0.40	0.04	1.08
NH^+_4 (μM)	1.11	0.02	4.63	1.83	11.1	75.6	10.4	1.64	38.9
NO^-_2	0.03	0	0.18	0.33	0.01	0.67	0.07	0.02	0.43
NO^-_3 (μM)	6.01	0.27	18.22	3.38	0.79	12.67	2.04	0.15	6.43
Chlorophyll (mg/l)	0.37	0.2	0.6	1.53	0.41	2.25	0.38	0.04	1.24

* Below detecion levels

more reduced conditions in the sediment. *Isoetes lacustris* sediment was very oxydized before the daming (Gacia, 1992) due to the high oxygen release by the roots of *Isoetes* (Sand Jensen *et al.*, 1982). In summer 1991, the reduced state of the sediment should be related to the death of *Isoetes*.

An increase in the concentration of ammonia was also noticed in the sediment of *Sparganium angustifolium*, while nitrate and nitrite concentrations did not change (Table VI). This increase was also related to a major organic matter input caused by the death of *Sparganium angustifolium*. In this case, a shift from oxydized to reduced compounds was not observed because healthy *Sparganium* sediment was already hypoxic (Gacia, 1992).

TABLE VI. Mean, minimum and maximum nutrient concentration in pore-water of the sediment of the (a) *Isoetes lacustris* community and (b) *Sparganium angustifolium* community in Lake Baciver before and after the daming. *Valores medios, mínimos y máximos de la concentración de nutrientes en el agua intersticial del sedimento de la comunidad de* Isoetes lacustris *(a) y de* Sparganium angustifolium *(b) en el lago Baciver antes y después del represamiento.*

a) *Isoetes sediment porewater*

	Before daming			After daming		
	Mean	Min	Max	Mean	Min	Max
PO^{3-} (µM)	5.58	1.40	11.32	2.25	0.35	3.90
NH^{+}_{4} (µM)	11.48	9.80	40.00	128.67	40.60	334.60
NO^{-}_{2} (µM)	0.33	0.15	0.51	4.46	1.85	11.80
NO^{-}_{3} (µM)	32.67	2.00	62.00	3.88	2.20	6.28

b) *Sparganium sediment porewater*

	Before daming			After daming		
	Mean	Min	Max	Mean	Min	Max
PO^{3-} (µM)	4.01	2.66	5.43	3.03	0.91	5.50
NH^{+}_{4} (µM)	37.06	9.04	104.40	82.17	44.00	118.00
NO^{-}_{2} (µM)	0.56	0.14	0.73	0.54	0.46	0.64
NO^{-}_{3} (µM)	7.79	2.73	18.11	8.01	2.10	11.20

Macrophyte communities

The area occupied by the submersed vegetation as well as the number of macrophyte species experienced an important reduction with the daming of Lake Baciver (Tables VII, VIII). In the first summer after the dam there was a regression of a 64 % of the area previously occupied by rooted macrophyte species. The only species that survived the daming were *Sparganium angustifolium* and *Isoetes lacustris*, while all the other species that used to grow in the mixed community were dead (Table VIII).

Table VII. Percentage of the area occuppied by the different benthic communities of Lake Baciver before and after daming. The biomass of the surviving macrophyte communities is also indicated. *Porcentaje de la superficie ocupada por las distintas comunidades bentónicas antes y después del represamiento. Se indica asimismo la biomasa de las comunidades de macrófitos supervivientes.*

Before daming			One year after daming		
Communities	% Area	Biomass (Kg d.w.)	Communities	% Area	Biomass (Kg d.w.)
Sediment	2.1	-	Sediment	16.7	-
Rocky benthos	12.2	-	Dead macrophytes	27.9	-
Sparganium	5.6	239	*Sparganium*	2.9	26
Isoetes	50.4	3462	*Isoetes* in regression	7.6	410
Nitella	29.7	89	Area of recent inundation	47.8	-

The rise of the water level accounted for the dissapearance of the small species of the mixed community (*Eleocharis acicularis, Subularia aquatica* and *Isoetes setacea*) since they are typical plants of shallow areas (maximum 2-3 m; Rørslett, 1985a). An increased water level creates a reduction of the incident light that could limit their growth (Chambers & Kalff, 1985; Dale, 1986).

In summer 1991, *Sparganium angustifolium* was growing at 6.8 m in the same areas that it used to before the construction of the dam. Nevertheless, there was a significant reduction of shoot density ($p<0.0005$; Fig. 5) and individual biomass (Fig. 6). Also, both the number of leaves per individual and their maximum length were significantly reduced (Table IX).

TABLE VIII. Specific composition of the different macrophyte communities of the Lake Baciver in its natural state (1989) and after the construction of the dam (1991 and 1992). The mixed community contains both species of the *Sparganium* and *Isoetes* communities. V, dominant, IV, very abundant, III, abundant, II, common, I, rare and r, accidental. *Composición específica de las distintas comunidades de macrófitos del lago Baciver en su estado natural (1989) y después de la construcción de la presa (1991 y 1992). La comunidad mixta contiene a la vez las especies de las comunidades de* Sparganium *e* Isoetes. *V, dominante; IV, muy abundante; III, abundante; II, común; I, rara, y r, accidental.*

	Before daming Communities				One year after daming Communities				Two years after daming Communities			
	Sparganium	mixed	*Isoetes*	*Nitella*	*Sparganium*	mixed	*Isoetes*	*Nitella*	*Sparganium*	mixed	*Isoetes*	*Nitella*
S. angustifolium	V	V	-	-	II	I	-	-	-	-	-	-
E. acicularis	-	II	-	-	-	-	-	-	-	-	-	-
S. aquatica	-	II	-	-	-	-	-	-	-	-	-	-
I. setacea	-	II	-	-	-	-	-	-	-	-	-	-
I. lacustris	-	IV	V	r	-	III	-	-	-	I	-	-
N. gracilis	-	-	-	IV	-	-	-	-	-	-	-	II

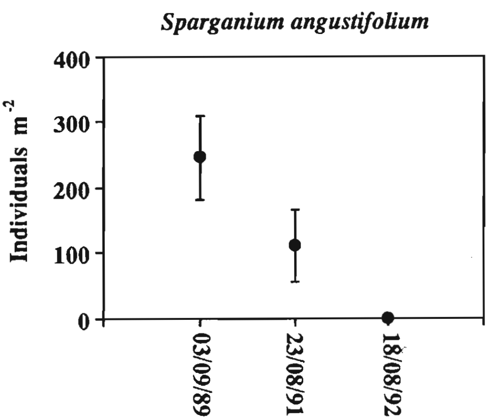

FIG. 5. Variation in the number of individuals per square meter of *Sparganium angustifolium* in the summers of 1989, 1991 and 1992. Notice the decrease after the dam. *Variación en el número de individuos por metro cuadrado de* Sparganium angustifolium *en los veranos de 1989, 1991 and 1992. Adviértase la reducción posterior al represamiento.*

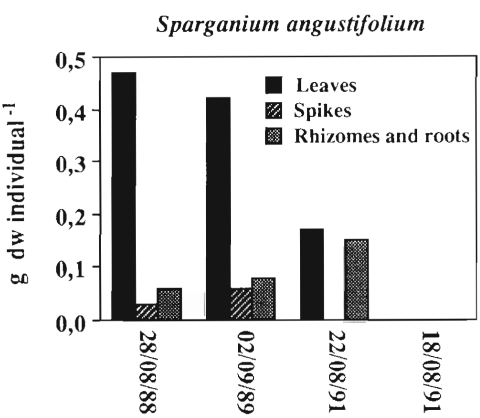

FIG. 6. Biomass of the different parts of *Sparganium angustifolium* during the summers of 1989, 1991 and 1992. Notice the decrease of the aerial biomass after the dam. *Biomasa de las distintas partes de* Sparganium angustifolium *en los veranos de 1989, 1991 and 1992. Adviértase la reducción de la biomasa aérea con posterioridad al represamiento.*

Table IX. Mean values and standard deviation of the number of leaves per individual and maximum length of the leaves of the *Sparganium angustifolium* population before (1989) and after (1990) the dam. Statistical differences (t-Student) are also indicated. *Valores medios y desviación típica del número de hojas por individuo y longitud máxima de las hojas de la población de* Sparganium angustifolium *antes (1989) y después (1990) del represamiento. También se indican las diferencias estadísticas (t de Student).*

	1989		1991		Significance
	Mean	SD	Mean	SD	p<
NUM. of leaves ind.$^{-1}$	5.84	1.30	4.11	1.15	0.0005
Leaves max. length (cm)	5.84	1.30	4.11	1.15	0.0005

The production of the *Sparganium angustifolium* community was much lower after the dam (17.5 g C m^{-2} y^{-1} in 1991 compared to 130.0 g C m^{-2} y^{-1} in 1989; Gacia, 1992) indicating limiting conditions for growth. Many factors might reduce *Sparganium* growth but it seems that the decreased light availability (Table III) could be the main reason for this reduction in primary production. In summer 1992 not any *Sparganium* was found alive and the community had completely dissappeared.

After one year, the daming of Lake Baciver brought a reduction of a 85% of the surface previously occupied by the *Isoetes lacustris* community (Table VII; Ballesteros *et al.*, 1989). *Isoetes* plants originally living below 0.6 m depth were completely dead in summer 1991, and the only surviving individuals were growing at 6.1 m depth.

TABLE X. Biomass, density, aboveground/belowground biomass ratio, length and number of leaves per individual in the *Isoetes lacustris* bed situated at 0.5 meters depth in 1989 and at 6 m depth after the construction of the dam in 1991. Statistical differences (t-Student) are also indicated. *Biomasa, densidad, relación biomasa foliar/biomasa subterránea, longitud y número de hojas por individuo en el prado de* Isoetes lacustris *situado a 0,5 m de profundidad y a 6 m después del represamiento en 1991. También se indican las diferencias estadísticas (t de Student).*

Parameters	July 1989		July 1991		Significance
	X	SD	X	SD	p<
Biomass g d. w. m^{-2}	12.0	66.3	181.0	61.5	-
Density ind. m^{-2}	5520	2840	2980	1350	-
Ratio above/below ground biomass	0.520	0.055	0.757	0.075	0.005
Maximum length (cm)	2.58	0.836	6.97	2.14	0.005
Number of leaves ind^{-1}	6.78	2.52	7.63	2.85	-

The biomass of the *Isoetes lacustris* individuals which survived in 1991 tended to increase and their density to decrease even though the differences between the populations before and after the dam were not statistically significant (Table X; t-test, p>0.5). Nevertheless, the surviving plants displayed some morphological differences as regards to the original population. There was a significant increase in the maximum length of the leaves and also of the aboveground:belowground biomass ratio (Table X). Distribution of individuals in size classes was also more diversified after the dam, showing a size pattern more close to the original deep-water population (Fig. 7; Gacia & Ballesteros, 1993a). The reason for the lengthening of the leaves is related to the decrease in the available irradiance, since low light levels enhance leaves elongation (Gacia & Ballesteros, 1993a).

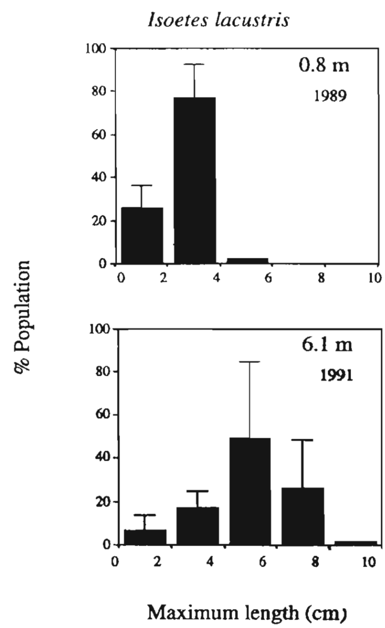

FIG. 7. Distribution of the individuals of the *Isoetes lacustris* community in relation to its maximum length of the leaves before (0.8 m) and after (6.1 m) the building up of the dam. *Distribución de los individuos de la comunidad de* Isoetes lacustris *en relación a la longitud máxima de sus hojas antes (0,8 m) y después (6,1 m) del represamiento.*

We have no data on the causes of the death of all *Isoetes* growing below 6 m depth after the replenishment of the Lake. On the one hand, *Isoetes lacustris* has been reported growing down to 7 m depth in other Pyrenean and Scandinavian lakes (unpublished data of the authors; Rørslett, 1985a), so it could survive, at least, between 6 and 7 meters depth. On the other hand, even in 1991 when the transparency of the water was the lowest (Table III), there was light above the compensation point for this species (Sand Jensen, 1978; Rørslett, 1985b; Gacia & Peñuelas, 1991) at least until the previous lower limit of distribution (8 m after the daming). Therefore, probably non-documented physical stressful conditions occurring in winter 1990-1991, such as a temporary anoxy of the water column below 6 m depth, could explain the complete die off of the deep water population.

The number of leaves produced by the surviving *Isoetes lacustris* in summer 1991 was lower than it used to be before the dam (Table XI). Nevertheless, new aboveground biomass was higher probably due to the lengthening of the leaves, and resulted in a higher production in 1991 compared to the original situation (Table XII).

TABLE XI. Number of produced and lost leaves per year and leaf renovation rate in the *Isoetes lacustris* population growing at 6.1 m depth. *Número de hojas producidas y perdidas por año y tasa de renovación de las hojas en la población de* Isoetes lacustris *situada a 6,1 m de profundidad.*

	1989 (0.8 m)	1991 (6.1 m)	1992 (6.1. m)
Produced leaves. ind^{-1}	6.69	5.65	0
Lost. leaves ind^{-1}	9.90	16.28	all

Remaining *I. lacustris* after winter 1991-1992 offered a very unhealthy aspect in June 1992 and leaf production was nule during summer 1992 (Table XI). As a consequence, at the end of summer time there was a total die off of the community. We have documented anoxy afecting up to 6 m depth in winter 1991-1992 (Fig. 2) which could be the reason for the death of the remaining plants of *Isoetes*. This result strengthens our hypothesis that anoxy killed the deep-water *Isoetes* in the first winter after the construction of the dam.

Table XII. Annual biomass production for the *Isoetes lacustris* population that survived to the dam. *Producción anual de biomasa para la población de* Isoetes lacustris *que sobrevivió al represamiento.*

Production (g dw m^{-2})	Year 1989 (0.8 m)	1991 (6.1 m.)	1992 (6.1 m)
Leaves	53.35	111.1	0
Corms	8.0	11.6	-
Roots	14.7	6.8	-
Total	76.3	129.5	-

In conclusion, our study shows the strong changes in the physico-chemical parameters and biotic components of a high mountain lake after the construction of a dam. Although the water column displayed symptoms of recovery after two years of the daming, benthic communities followed an apparently irreversible degradation, leading to the total die off of macrophyte assemblages.

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REFERENCES

BALLESTEROS, E., GACIA, E. & CAMARERO, L. 1989. Composition, distribution and biomass of benthic macrophyte communities from lake Baciver, a Spanish alpine lake in the central Pyrenees. *Annls. Limnol.*, 25:177-184.

CAMARERO, L. & CATALAN, J. 1991. Horizontal heterogeneity of phytoplankton in a small high mountain lake. *Verh. Intern. Verein. Limnol.*, 24:1005-1010.

CATALAN, J., BALLESTEROS, E., CAMARERO, L. & GACIA, E. 1990. Aspectos generales de la limnología invernal de dos lagos pirenaicos morfológicamente muy distintos (Estany Redó y Estany Baciver). *Scientia Gerundensis*, 16(2):55-68.

CATALAN, J., BALLESTEROS, E., CAMARERO, L., FELIP, M. & GACIA, E. 1992. Limnology in the Pyrenean lakes. *Limnetica,* 8: 7-38.

CATALAN, J. & CAMARERO, L. 1993. Seasonal changes in alkalinity and pH in two Pyrenean lakes of very different water residence time. *Verh. Intern. Verein. Limnol.*, 25:749-753.

CHAMBERS, P.A. & KALFF, J. 1985. Depth distribution and biomass of submersed aquatic macrophyte communities in relation to Secchi Depth. *Can. J. Fish. Aquat. Sci.,* 42:701-709.

DALE, H.M. 1986. Temperature and light: The determining factors in maximum depth distribution of aquatic macrophytes in Ontario, Canada. *Hydrobiologia,* 133:73-77.

GACIA, E. 1992. Ecologia dels macròfits submergits del estanys del Pirineu: estructura i dinàmica de les poblacions de l'estany Baciver. Ph. D.Tesis. University of Barcelona.

GACIA, E. & BALLESTEROS, E. 1991. Two methods to estimate leaf production in *Isoetes lacustris*: A methodological critical assessment. *Verh. Intern. Verein. Limnol.*, 24:2714-2716.

GACIA, E. & BALLESTEROS, E. 1993a. Ecological studies on *Isoetes lacustris* from a Pyrenean lake: population structure and depth limits. *Aquat. Bot.*, 46:35-47.

GACIA, E. & BALLESTEROS, E. 1993b. Diel acid fluctuations in Pyrenean *Isoetes* species: the effects of seasonality and emersion. *Arch. Hydrobiol.*, 128(2):187-196.

GACIA, E. & BALLESTEROS, E. 1994. Production of *Isoetes lacustris* in a Pyrenean lake: seasonality and ecological factors involved in the growing period. *Aquat. Bot.*, 48:77-89.

GACIA, E. & PEÑUELAS, J. 1991. Carbon assimilation of *Isoetes lacustris* L. from Pyrenean lakes. *Photosynthetica*, 25(1) 97-104.

JEFFREY, S.W. & HUMPHREY, G.F. 1975. New spectrophotometric equations for determining chlorophylls a, b, c1 and c2 in higher plants, algae and natural phytoplankton. *Biochem. Physiol. Pflanzen*, 167:191-194.

LEVAT, Y., LASSERRE, P. & LE CORRE, P. 1990. Seasonal changes in pore water concentrations of nutrients and their diffusive fluxes at the sediment-water interface. J. Exp. Mar. Biol. Ecol., 35: 135-160.

MARGALEF, R. 1974. *Ecología*. Omega. Barcelona.

RØRSLETT, B. 1985a. Regulation impact on submerged macrophytes in the oligotrophic lakes of Setesdal, South Norway. *Verh. Int. Verein. Limnol.*, 22:2927-2936.

RØRSLETT, B. 1985b. Death of submerged macrophytes -actual field observations and some implications. *Aquat. Bot.*, 22:7-19.

SAND-JENSEN, K. 1978. Metabolic adaptation and vertical zonation of *Littorella uniflora* (L.) Aschers. and *Isoetes lacustris* L. *Aquat. Bot.*, 4:1-10.

SAND-JENSEN, K., PRAHL, C. & STOCKHOLM, H. 1982. Oxygen release from roots of submerged aquatic macrophytes. *Oikos*, 39:349-354.