J. Aquat. Plant Manage. 34: 57-59

The effect of Increased Water Level on *Isoetes lacustris* L. in Lake Baciver, Spain

E. GACIA[1,3] AND E. BALLESTEROS[2,3]

ABSTRACT

Ten months after flooding lake Baciver, water levels were 5.5 m higher than the previous normal and the area formally occupied by the *Isoetes* population was reduced. All *Isoetes* originally present below 0.6 m died, and only plants standing between 5.8 and 6.1 m (new depth) survived. As irradiance decreased, remaining individuals produced fewer leaves, but their biomass production was higher, as leaf length increased in response to the diminished available irradiance. Because leaf mortality was excessive, regeneration capacity, population performance and dynamics were adversely affected. In 1992, no new production occurred in *Isoetes lacustris* individuals surviving after the winter. We suggest that low surface oxygen levels at the water column under the ice, and total anoxia below 6 m depth, caused the demise of the *I. lacustris* population in Lake Baciver.

Key words: Pyrenees, oxygen, light, leaf primary production, water level fluctuations, anoxia.

INTRODUCTION

Isoetes lacustris L. is a widely distributed macrophyte in Pyrenean high mountain lakes of oligotrophic and soft waters (Gacia et al. 1994). Population structure and dynamics of this species have been extensively studied in lake Baciver (Gacia and Ballesteros 1993; 1995) where beds occupied more than 50% of lake bottom (Ballesteros et al. 1989) prior to October 1991, when the Lake was dammed. As a result of water level increases, significant variation in bathymetric limits and physico-chemistry of the water column after flooding occurred (Gacia and Ballesteros, *in press*). In the present work we describe changes in the *Isoetes lacustris* population structure (e.g., densities, above vs. below ground biomass ratio, size classes), and leaf primary production during the two summers that followed dam construction (1991 and 1992).

MATERIAL AND METHODS

Lake Baciver is located in the Central Pyrenees (42°41'46" N, 0°59'1" E) at an elevation of 2120 m. Lake area was originally 26629 m^2 and maximum depth 7.5 m (Ballesteros et al. 1989). However, after dam construction in the fall of 1990, water levels rose 5.5 m and lake area increased to 51301 m^2 (Gacia and Ballesteros, *in press*).

Fifteen transects were examined during the ice-free period in 1991 and 1992 to evaluate changes in the *Isoetes lacustris* populations resulting from increased water levels. Structural samples (collected in July), and primary production measurements (early July and late October) were taken in 1991 and 1992. Biomass, structure, and density of the population were obtained from 400 cm^2 samples collected by SCUBA. In the laboratory, individuals were sorted into size categories (Gacia and Ballesteros 1993) and number of leaves per shoot and maximum leaf length were determined. Primary production of *Isoetes* was measured by tagging leaves of 96 individuals with copper wire rings to assess leaf production and loss over a one year period (see Gacia and Ballesteros 1991). Leaf biomass production was estimated from leaf growing function (Gacia and Ballesteros 1995) and values of biomass and production were expressed in a dry weight basis (24 h at 105C).

Photon Flux Density (PFD) in the water column was measured with a spherical quantum sensor Licor SPQA coupled to a Licor Li-1000 datalogger. Water samples were collected from the centre of the Lake at one meter intervals with a Ruttner bottle. Temperature was measured *in situ* and oxygen content of the water was determined in the laboratory following the Winkler method modified by Grasshoff et al. 1983.

Voucher specimens of *Isoetes* plants collected are available in CEAB Herbarium (Blanes, Spain).

RESULTS

After flooding, populations of *Isoetes lacustris* previously located at 0.2 to 2.3 m were now at a depth of 5.7 to 7.8 m and underwent substantial reduction (Table 1), only *Isoetes* plants originally living above 0.6 m depth (now 6.1 m) survived.

Biomass of surviving *Isoetes lacustris* populations tended to increase while density decreased from July 1990 to July 1991 (Table 2). Surviving plants also showed some morphological changes: maximum leaf length and biomass (above: below ground ratio) significantly increased (Table 2). Size diversity of initial shallow water populations increased becoming similar to that of the original deep-water population (Figure 1).

Number of leaves per plant produced by *I. lacustris* in summer 1991 was lower, and leaf loss was also unusually high (Table 3). Nevertheless, new above-ground biomass and total biomass production was higher after dam construction (Table 3).

In June 1992, two winters after water levels increased, remaining *I. lacustris* appeared unhealthy (e.g., areas of

[1]Smithsonian Marine Station at Link Port, 5612 Old Dixie Highway, Fort Pierce, Fl. 34946, U.S.A.

[2]Centre d'Estudis Avançats de Blanes (CSIC), Ctra. de Santa Bàrbara s/n, 17300 Blanes, Girona, Spain. Received for publication June 19, 1996 and in revised form July 3, 1996.

[3]Institute of High-Mountain Research, University of Barcelona, Apartat 21, 25530 Vielha, Lleida, Spain.

TABLE 1. AREA (%) OCCUPIED BY AND BIOMASS (G D W M^{-2}) OF THE *ISOETES LACUSTRIS* COMMUNITY IN LAKE BACIVER BEFORE (DATA FROM BALLESTEROS ET AL. 1989) AND AFTER THE DAM.

Before damming (1989)			One year after damming (1991)		
Substratum	Area (%)	Biomass (Kg d.w.)	Substratum	Area (%)	Biomass (Kg d.w.)
Sediment	2.1	—	Sediment	16.73	—
Rocky benthos	12.2	—	Dead macrophytes	27.91	—
Isoetes lacustris	50.4	3462	*Sparganium angustifolium*	2.90	26
Other macrophyte species	35.4	328	*Isoetes* in regression	7.56	410
			Area of recent inundation	47.8	—

TABLE 2. BIOMASS, DENSITY, ABOVE: BELOW GROUND BIOMASS RATIO, LENGTH AND NUMBER OF LEAVES PER INDIVIDUAL FOR *ISOETES LACUSTRIS* BEFORE AND ONE YEAR AFTER DAM CONSTRUCTION. NON-SIGNIFICANT DIFFERENCES ARE CONSIDERED FOR PROBABILITY HIGHER THAN 0.5.

Parameters	July 1989		July 1991		Significance
	X	SD	X	SD	
Biomass g d. w. m^{-2}	121.0	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	0.05
Maximum length (cm)	2.58	0.856	6.97	2.14	0.005
Number of Leaves.ind.$^{-1}$	6.78	2.52	7.63	2.85	—

necrosis in the leaves, lost of turgor) and did not produce any new leaves throughout the following summer (Table 3). By September 1992, the community had completely died off.

Mean annual light extinction coefficient in the water column for the ice-free period (May to November) increased by a factor of 1.5 (0.28 ± 0.033 to 0.418 ± 0.004 m^{-1}) after flooding (t-test, $p<0.0005$). However, water transparency improved substantially by the summer of 1992 (extinction coefficient of 0.328 ± 0.051 m^{-1}), showing no significant differences compared to values recorded in Lake Baciver in 1989 (t-test, $p>0.5$).

Figure 2 shows depth-profiles of temperature and oxygen concentrations in Lake Baciver after damming. Both parameters usually had a similar pattern of distribution except in winter 1991, when the water column had an inverse stratification and oxygen content was depleted below 5 m. No anoxia was recorded in summer 1992.

DISCUSSION

Isoetes lacustris has been reported at depths of 7 m in Pyrenean and Scandinavian lakes (Gacia and Ballesteros, pers. observation; Rørslett 1985a), and therefore it would be expected to survive at greater depths than those experienced after flooding Lake Baciver in October 1991. Light requirements for this species were above the observed compensation point (Sand Jensen 1978, Rørslett 1985b, Gacia and Peñuelas 1991), at all distribution depths, even in 1991 when transparency of the water was the lowest. Hence, the absence of light limitation, together with theoretical deep range tolerance, points to non documented stressful conditions to explain the demise of the deep-water population during the winter of 1990-1991. We hypothesize that temporary anoxia of the water column below 6.1 m depth (Figure 2), caused the *I. lacustris* die off, since this species has been reported to be very sensitive to low oxygen levels (Rørslett and Brettum 1989).

Overall increase in leaf length recorded in the summer of 1991 is related to the decrease in available irradiance, since low light levels enhance leaf length in *Isoetes lacustris* (Gacia and Ballesteros 1993). Longer leaves seem to account for the increase in the above: below ground biomass ratio (Table 2).

The original shallow water *Isoetes lacustris* population in Lake Baciver consisted of small plants, homogenous in maximum leaf length. Strong, shore-related disturbances such as natural water level fluctuations and ice-scour, would damage shallow water individuals preventing size diversity in the plants (Gacia and Ballesteros 1993). With the increase in water level, shallow water disturbances were ameliorated and leaves of *Isoetes* individuals increased in length (stimulated also by low light levels) and developed a greater size diversity similar to the original deep-water population (Gacia and Ballesteros 1993).

Decrease in light availability in summer 1991 could explain the lower number of leaves produced by surviving *Isoetes lacustris* plants. However, major leaf loss in the same period indicates the possibility of other stressful conditions in these individuals. Increase in new leaf biomass, due to longer leaf size, resulted in higher biomass production (Table 3) similar to the original deep-water populations (Gacia and Ballesteros 1995).

The total depletion in oxygen content of the water column down to 6 m in winter 1991-1992 (Figure 2) probably explains the death of the remaining *Isoetes*, and strengthens our hypothesis that deep water *Isoetes* also died from hypoxia the first winter after flooding.

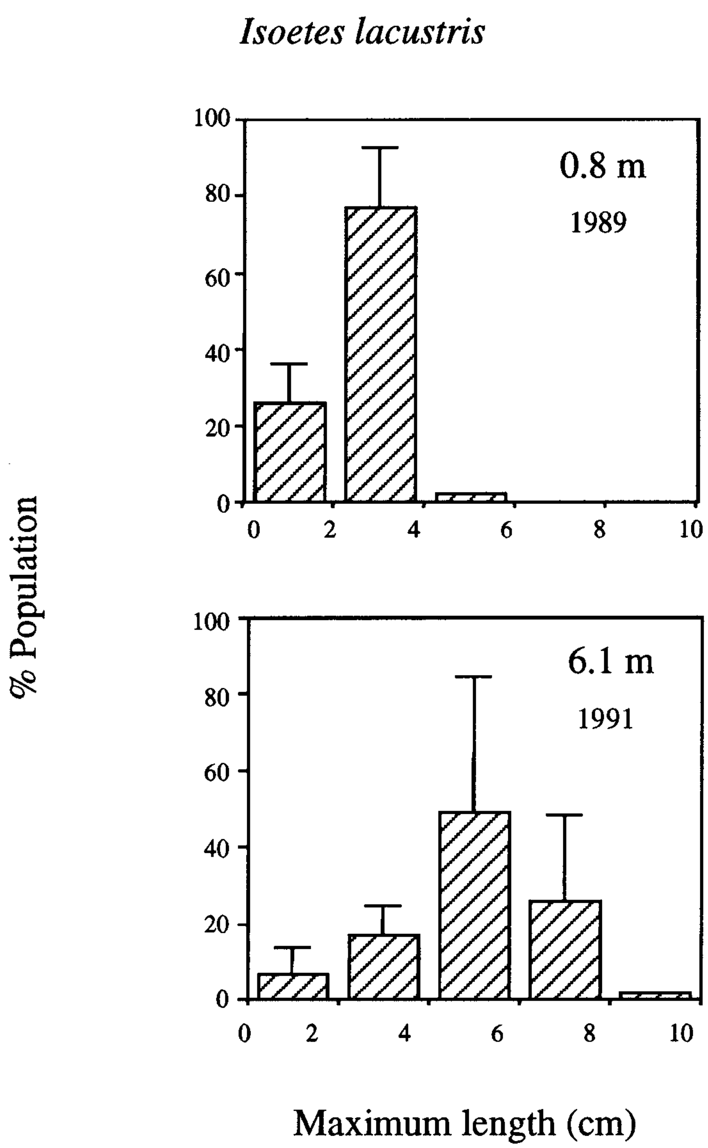

Figure 1. Distribution of *Isoetes lacustris* individuals in relation to maximum leave length before (0.8 m) and after (6.1 m) dam construction in Lake Baciver.

TABLE 3. NUMBER OF LEAVES PRODUCED AND LOST PER YEAR, AND ANNUAL BIOMASS PRODUCTION FOR THE SURVIVING *ISOETES LACUSTRIS* POPULATION AFTER DAM CONSTRUCTION.

Production	Year		
	1989 (0.8 m)	1991 (6.1 m)	1992 (6.1 m)
Number of leaves			
Produced	6.69	6.65	0
Lost	9.90	16.28	all
g dw m^{2}			
Leaves	53.5	111.1	0
Corms	8.0	11.6	—
Roots	14.7	6.8	—
Total	76.3	129.5	—

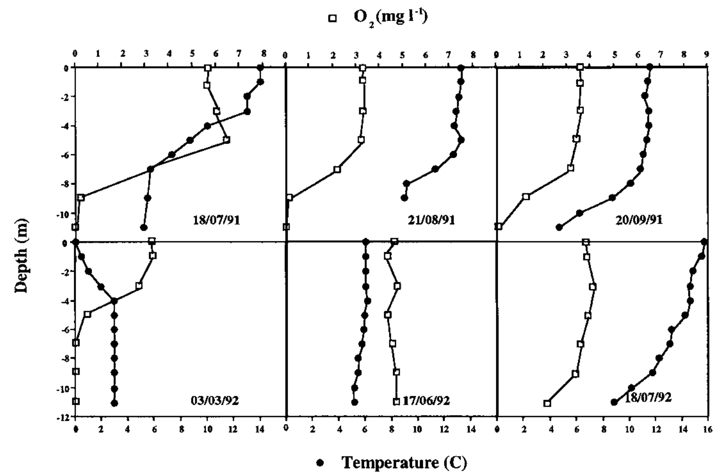

Figure 2. Temperature and oxygen concentration profiles in Lake Baciver from July 1991 to July 1992.

ACKNOWLEDGMENTS

Financial support was provided by a grant from the Caixa de Barcelona to E.G.

REFERENCES

Ballesteros, E., E. Gacia and L. Camarero. 1989. Composition, distribution and biomass of benthic macrophyte communities from Lake Baciver, a Spanish alpine lake in the Central Pyrenes. Ann. Limnol. 25: 177-184.

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

Gacia, E. and E. Ballesteros. 1993. Population and individual variability of *Isoetes lacustris* L. with depth in a Pyrenean lake. Aquat. Bot. 46: 35-47.

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

Gacia, E. and E. Ballesteros. *in press.* Effects of building up of a dam in a shallow mountain lake (Baciver, Central Pyrenees). Oecol. Aquat.

Gacia, E. and J. Peñuelas. 1991. Carbon assimilation of *Isoetes lacustris* L. from Pyrenean lakes. Photosynthetica. 25(1): 97-104.

Gacia, E., E. Ballesteros, L. Camarero, O. Delgado, A. Palau, J. J. Riera and J. Catalan. 1994. Macrophytes from lakes in the eastern Pyrenees: community composition and ordination in relation to environmental factors. Freshw. Biol. 32: 73-81.

Grasshoff, K., M. Ehrhardt and M. Kremling. 1983. Methods of seawater analysis. 2th edition. Verlag Chemie, Weinheim, Germany. 419 pp.

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.

Rørslett, B and P. Brettum. 1989. The genus *Isoetes* in Scandinavia: an ecological review and perspectives. Aquat. Bot. 35: (223-261).

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