

Meromixis origin and recent trophic evolution in the Spanish mountain lake La Cruz

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Key words: Lake La Cruz, trophic changes, meromixis, diatoms, cladocera, ostracoda and pollen stratigraphy.

ABSTRACT

A sediment core from a Mediterranean karstic lake was studied through its pollen, diatom, chydorid, ostracod, charcoal and authigenic mineral composition. Information about environmental history recorded in the sediment sequence since the Middle Ages is presented. The main fluctuations of water volume and trophic status of the lake occurred during periods of great change in land management and during climatic cold phases. The synergetic effect of these two factors led to a high water level phase and triggered a rising of the trophic level which produced meromixis. The onset of meromictic conditions at about 1700 AD coincides with the Maunder minimum in the Little Ice Age as well as with a period of increasing human population, woodland clearance and agricultural expansion to the detriment of the nomadic livestock breeding or transhumance (“Mesta”).

Introduction

Anthropogenic activities and climatic changes can produce similar effects in aquatic ecosystems (e.g. increasing eutrophication): it is extremely difficult to determine the cause-effect relationships (Dearing, 1991). Despite this difficulty, lacustrine sediments are an important source of information concerning historical environmental changes (Löffler, 1975; Gaillard et al., 1991; Schmidt and Simola, 1991;

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Niessen et al., 1992; Bradbury and Dean, 1993). Sediments of the karstic Lake La Cruz are especially suitable for study, because the high stability of the water column, due to the relatively great depth of the lake, favours deposition with little disturbance. These sediments record the evolution of a small doline lake, without surface influents or effluents, where water level and trophic status vary in close association with environmental changes.

At present the lake is meromictic and the sediments show a varve sequence reflecting a whiting phenomenon which occurs every summer for a short time (about one week) due to calcium carbonate precipitation (Rodrigo et al., 1993). Meromictic lakes are not very frequent and permanent meromixis is a condition only found in a few lakes (Miracle et al., 1992). Out of seven dissolution lakes of similar morphometry and substratum, which are very close together, Lake La Cruz is the only one with permanent meromixis.

The great diversity of taxonomic groups well preserved in the sediments of Lake La Cruz allows a multidisciplinary approach to the lake's history (Frey, 1964). Sedimentation rates in karstic lakes, such as La Cruz (less than 1 mm/yr), provide a time-integrated record for lake biology, chemistry and deposition processes. This time-integration reduces the impact of short variations in productivity and nutrient availability on sediment composition, thus enabling general tendencies and patterns to be explored.

The level of water in solution lakes is usually highly variable; in fact, recently, La Cruz has undergone fluctuations in water level (of a few metres) in response to seasonal and long-term variations in ground water levels. Can the variation of the water volume in the past be detected from the study of the remains of lacustrine biota in the sediments? Is this correlated with weather conditions and/or historical events inferred from pollen and charcoal analyses?

The aim of this paper is to elucidate the potential effects of land use history and rapid climatic variations on the hydrological balance and trophic evolution of Lake La Cruz, based mainly on the evolution of the lake's biotic composition. The paper describes the main changes in lithology and other features, and shifts in the species composition of the remains of pollen and lacustrine organisms (diatoms, ostracods, cladocerans). Additionally, the palaeoecological perspective enables to propose a hypothesis on the possible causes of the present meromictic conditions.

Site description

La Cruz Lake

La Cruz lake is a funnel-like sinkhole located at 1,000 m altitude in the Iberian Ranges near Cuenca, Spain (39°59'20" North; 01°52'25" West). The region is karstic (Fig. 1), and composed of Cenomanian-Turonian limestones and dolostones. The lake is a doline formed in Cenomanian dolostones that subhorizontally overlie impermeable lower Cenomanian marls which sustain the aquifer feeding the lake. The lake has a negligible catchment area with no connections with running waters, and is mainly fed by lateral sources nowadays located about 4–5 m above the bottom, just over the chemocline layer (Vicente and Miracle, 1988).

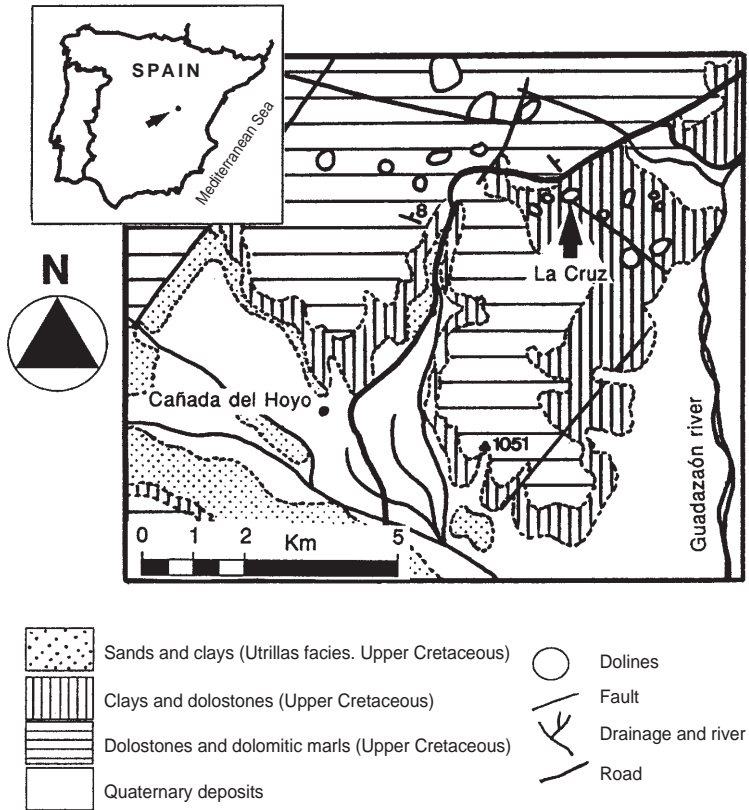


Figure 1. Geological sketch of the surrounding karstic area of Lake La Cruz

At the time of the coring, the water body had a mean diameter of 132 m and a maximum depth of 23.5 m, whereas the steep walls which make up the conical sink stood out 15–20 m above the water surface. The lake shows a biogenic iron meromixis with a permanent anoxic monimolimnion below a depth of 18 m (Vicente and Miracle, 1988). The waters are bicarbonated. Mean annual values of some chemical parameters and ratios in the mixolimnion are as follows: 500 $\mu\text{S}/\text{cm}$, pH 8, alkalinity 5 meq/l, $\text{alk}:\text{Cl}^-:\text{SO}_4^{2-}=125:6.5:1$ and $\text{Mg}^{++}:\text{Ca}^{++}:\text{Na}^+=15:3.5:1$. The littoral zone of the lake is very steep, consisting mainly of exposed, fractured limestones; only a small area of the SE zone supports a sandy overburden. The macrophytic vegetation is extremely poor. Studies based on plankton composition and annual cycle have been published (Dasí and Miracle, 1991; Armengol-Díaz et al., 1993).

Present day climate and vegetation

The region has a continental Mediterranean climate-type. Records from the meteorological station in the nearby town of Cuenca for the last 40 years show that

mean annual precipitation and temperature are respectively 565 mm and 11.7°C. Monthly temperature variations can be quite extreme, e.g. the mean of the minima in January is -2°C and the mean of the maxima in July is 30°C. Differences between day and night are also very important, especially in summer. Frost days average 87 per year distributed between October and May (Roldán, 1988).

The dominant vegetation in the lake area is characterised by associations typical of calcareous karstic soils, corresponding to a continental dry supra-Mediterranean bioclimatic domain consisting mainly of *Pinus nigra* ssp. *salzmanii* and *Juniperus thurifera*.

This arboreal stratum coexists with shrubs of other species of *Juniperus*: *J. communis*, *J. oxycedrus* and *J. phoenicea*, which in the open areas are replaced by xerophyllous bushes of *Erinacea antillis*, *Salvia lavandulifolia*, *Genista scorpius*, *Lavandula latifolia*, *Thymus vulgaris*, *Rosmarinus officinalis*, etc., as well as steppic plants of the genera *Artemisia*, *Astragalus*, *Stipa*, *Pilosella*, etc. This basic type of vegetation is replaced in wetter and shady sites by a mixed forest with deciduous trees such as *Quercus faginea*, *Acer monspessulanus*, *Crataegus monogyna* and also with some *Taxus baccata*. In lower altitudes surrounding the lake area, there are wide open fields of cereals and sunflowers and, in non-cultivated lands, small areas wooded with *Quercus ilex* ssp. *rotundifolia*.

Methods

A 173 cm long core of 6 cm diameter was taken from the lake at its deepest point in June 1994, using a Wright (1980) corer. Coring was stopped at this depth due to the hardness of the bottom. The uppermost 5 cm of the core were extremely wet and the structure of this part of the core was damaged during transportation. It was considered safest to omit this section from the analysis. Consequently, all data presentations for the core start at 5 cm. Magnetic susceptibility was measured using a Bartington meter (MS2). Afterwards, the core was stored in a cool room (2°C) prior to analysis.

The core was split longitudinally for description and sampling. 3 × 2 cm trapezoidal petrographic thin sections (30 µm thick), with an overlapping of 1 cm at each extreme, were obtained after freeze-drying and balsam-hardened. The laminae of the upper part of the core were counted and the thickness of each lamina was measured in several parts under a petrographic microscope with an ocular micrometer. X-ray diffraction analyses of bulk samples were performed. Slices 1 cm thick were cut along the core at intervals of either 5 or 10 cm (depending on the sedimentary structures in the horizons). Slices were then sub-sampled for analysis, using each of the analytical procedures subsequently described.

Pollen and spores were extracted by physico-chemical treatment of about 3 g of dry sediment using the Dricot and Leroy (1989) technique. Between 255 and 479 grains per sample were counted. For calculation of percentages, the basic sum includes all taxa excluding Cyperaceae, *Typha-Sparganium*, *Myriophyllum*-type and monoletete spores. Diatoms from 0.2 g of wet sediment were cleaned with hydrogen peroxide and diluted HCl, and counted at 1000X using an inverted microscope. At least 400 diatom frustules were counted per sample. Other algae remains in these

samples were also quantified. Most samples were studied using scanning electron microscopy as an aid to species identification and in order to estimate the relative proportions of single and bivalve remains. Counts are given as whole individuals. Most diatoms were identified according to Krammer and Lange-Bertalot (1986, 1988, 1991 a and 1991 b). Past ecological conditions inferred from diatoms are based on the general literature, principally using Germain (1981), Patrick and Reimer (1966, 1975), Cholnoky (1968), Margalef (1955), Cleve-Euler (1952, 1955), Hustedt (1937–1939, 1957) and Dasí and Miracle (1991).

Cladoceran microfossils were recovered from sediments using Frey's methods (1979). One ml of fresh sediment was weighed, heated in 10% KOH and then washed in 5% HCl. The residue was sieved through a 30 μm mesh Nylal filter and diluted in distilled water with a few drops of cotton-blue in lactophenol. Several 50 μl subsamples were examined under an inverted microscope until at least 200 fragments of the most abundant chydorid remains were counted. The total number of individuals was estimated as the maximum count of head shields, postabdomens or valves according to the system of Frey (1979). Species and ecological features were identified using Negrea (1983) and Alonso (1996).

For ostracod analysis, 15 ml of wet sediment samples were dried at 60°C and weighed. After treatment with hydrogen peroxide these samples were washed and filtered through a 160 μm -mesh sieve. The remaining sediment and fossils were dried and weighed again. Subsamples were counted at 15–40X in a reticulated (1 cm square) box, using a stereo-microscope. Units are expressed in relation to dry weight. Other remains such as Gasteropoda, Bryozoa and Charales, and the charcoal fragments found in these ostracod samples were also counted.

Results

Lithology and magnetic susceptibility

The La Cruz lacustrine sequence is mainly composed of organic rich mud showing distinct textures and structures. From the base to the sediment surface, four lithological units are differentiated (Fig. 2).

I) 173–115 cm: The mud is mainly composed of clays that contain clasts of dolomite and quartz. Thin laminae formed by detrital grains occur at 1.50 m depth. Above this depth, X-ray diffraction analyses reveal low-magnesian calcite; and below 1.50 m, aragonite and high-magnesian calcite are the most common authigenic minerals.

II) 115–65 cm: In this unit, the mud is richer in sandy detrital content. Thin laminae of dolomite grains are common and some dolomitic pebbles were found. In this level, aragonite and high-magnesian calcite occur as authigenic minerals. The presence of low-magnesian calcite and aragonite in the upper part of this unit could be related to the gastropod remains.

III) 65–24 cm: Organic-rich mud showing fenestral structure due to gas bubbles. Low-magnesian calcite is the main authigenic mineral component.

IV) 24 cm to the top: Very fine couplet white and dark laminae occur. The white laminae are formed by low-magnesian calcite, whereas the dark laminae are organic-rich muds with occasional clasts.

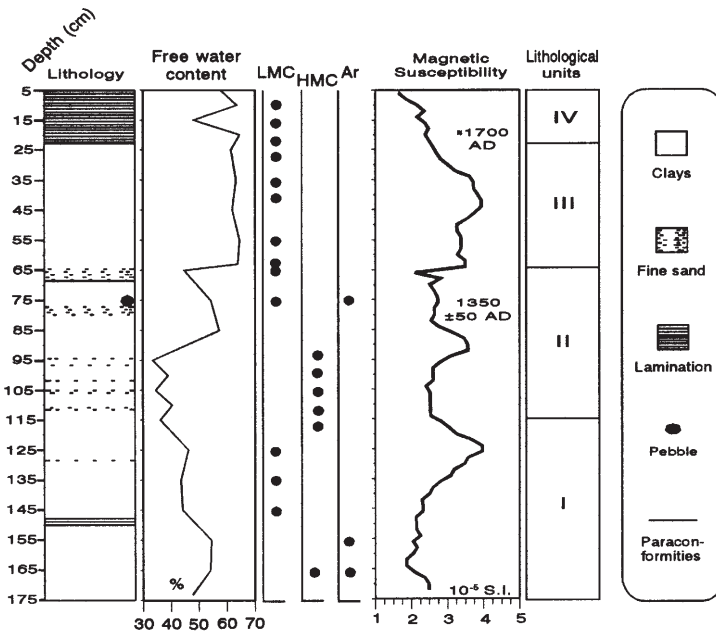


Figure 2. Lithology, free water content (% wet weight), main authigenic mineral composition (LMC: Low-magnesian calcite, HMC: High-magnesian calcite, Ar: Aragonite), magnetic susceptibility and lithological units from the La Cruz sequence

The changes in lithological composition and structures coincide with the main variations in magnetic susceptibility and water content (Fig. 2), suggesting that some sedimentary paraconformities may be associated with these changes. The variation of magnetic susceptibility in Lake La Cruz is mainly connected with the detrital lacustrine input as observed by other authors (Thompson et al., 1975). Nevertheless, the low magnetic susceptibility recorded in the uppermost part of the sequence (unit I) could be interpreted as the result of Fe and Mn release from the sediments due to permanent or seasonal depletion of oxygen and the relatively low pH values (6–6.5) in the bottom water layers.

Core dating

By counting the varves, a time-scale for the uppermost sediment sequence can be calculated. A total of 254 varves were counted in the 18.8 cm of the uppermost part of the available sequence. In consequence, the first varve found at 23.8 cm depth was formed at least 254 yr ago. If a hypothetical homogeneous sedimentation rate for the whole first 23.8 centimetres of the core is supposed, the upper 5 cm lost during the transport would represent at most 68 yr. The extremely wet nature of these last 5 cm of sediments implies a shorter period of time. Consequently, the onset of the varve sequence at 23.8 cm depth was at approximately 1700 yr AD.

Accelerator Mass Spectrometry dating of ¹⁴C of a cf. *Alnus* efflorescence found at 77–78 cm depth gave an uncalibrated age of 640 ± 60 years BP (Livermore labo-

ratory, CAMS-18713). This radiocarbon dating corresponds to a calibrated age of 1350 ± 50 AD with 90% probability. The higher accumulation rate between ^{14}C datation and the first varve with respect to varved sequence is due to the increasing of detritic alloctonous components.

Pollen

One of the most outstanding characteristics of the La Cruz sequence is the continuous presence of pollen taxa relating to agricultural activities, such as *Secale*.

Examination of changes in pollen percentages, pollen concentrations and species composition distinguishes three major vegetational zones (Fig. 3).

Zone 1: 173–90 m. This zone is characterised by the lowest percentages of *Pinus* and the maximum of *Quercus ilex-coccifera*-type, cf. *Juniperus*, Ericaceae, *Artemisia* and Poaceae. Pollen from aquatic plants such as *Myriophyllum* cf. *verticillatum* are abundant. According to percentage changes of major pollen taxa three sub-zones were differentiated: sub-zone 1A: 173–150 cm shows the maximum expansion of evergreen *Quercus* and low values of *Juniperus* and *Myriophyllum*. Sub-zone 1B: 150–120 cm records a progressive regression of evergreen *Quercus* and an expansion of *Juniperus*, *Olea* and *Myriophyllum*. Sub-zone 1C: 120–90 cm records the maximum expansion of *Juniperus*, Ericaceae, *Thymelaea*, Poaceae and crop plants (*Secale*, Cerealia-type, etc).

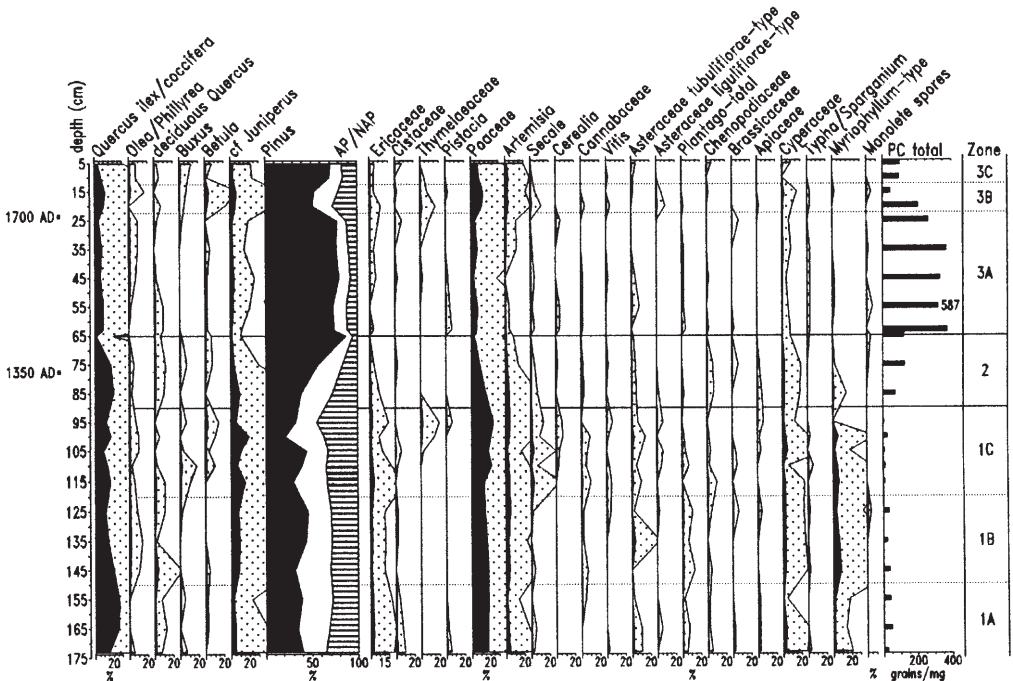


Figure 3. Pollen diagram from the La Cruz sequence. *Pinus* is overlaying the AP (Arboreal Pollen) curve. Dotted pattern represents exaggerated scale 8X

Zone 2: 90–65 cm. This zone is characterised by a progressive increase in arboreal pollen percentages, principally due to the expansion of *Pinus* sp. and a decrease of Poaceae and crop taxa. *Quercus ilex/coccifera* pollen increases and pollen of aquatic plants such as *Myriophyllum* and *Typha* nearly disappear.

Zone 3: 65 cm to the core surface. This zone is characterised by high percentages of arboreal pollen, mainly *Pinus*. *Olea* remains abundant until the most recent core section. Three vegetational sub-zones are indicated by the pollen sequence: Sub-zone 3A: 65–24 cm reveals a relatively stable phase in the pollen sequence, with *Pinus* as the dominant species. Sub-zone 3B: 24–12 cm records an increase in pollen of evergreen oak, *Betula*, *Olea*, cf. *Juniperus* and crops, and a decrease of *Pinus*, producing a sharp fall in the relative proportion of arboreal pollen. Sub-zone 3C: from 12 cm to the sediment surface, shows a recovery of *Pinus* pollen.

Diatoms and other algae

Cyclotella wuethrichiana (Druart and Straub, 1988) was by far the dominant diatom throughout the sequence. *C. distinguenda* (Hustedt) was also recorded but only in particular strata. Both *Cyclotella* species constituted more than 85% of all the counted (two valve) frustules.

Five main zones were distinguished from diatom (Figs. 4 and 5) and other algae (Fig. 6) analyses.

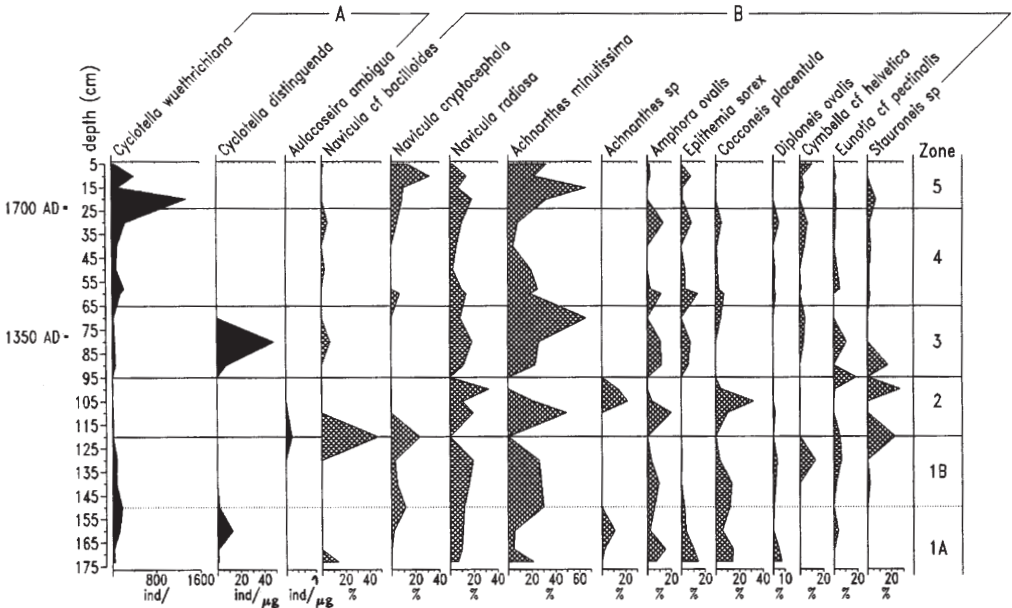


Figure 4. Diatom diagram from the La Cruz sequence: (A) Centric diatoms in absolute abundances: *Cyclotella* spp in number of individuals per μg of dry sediment and *Aulacoseira ambigua* in individuals per μg of dry sediment. (B) Most frequent pennate diatoms in percentages with respect to total sum of this group

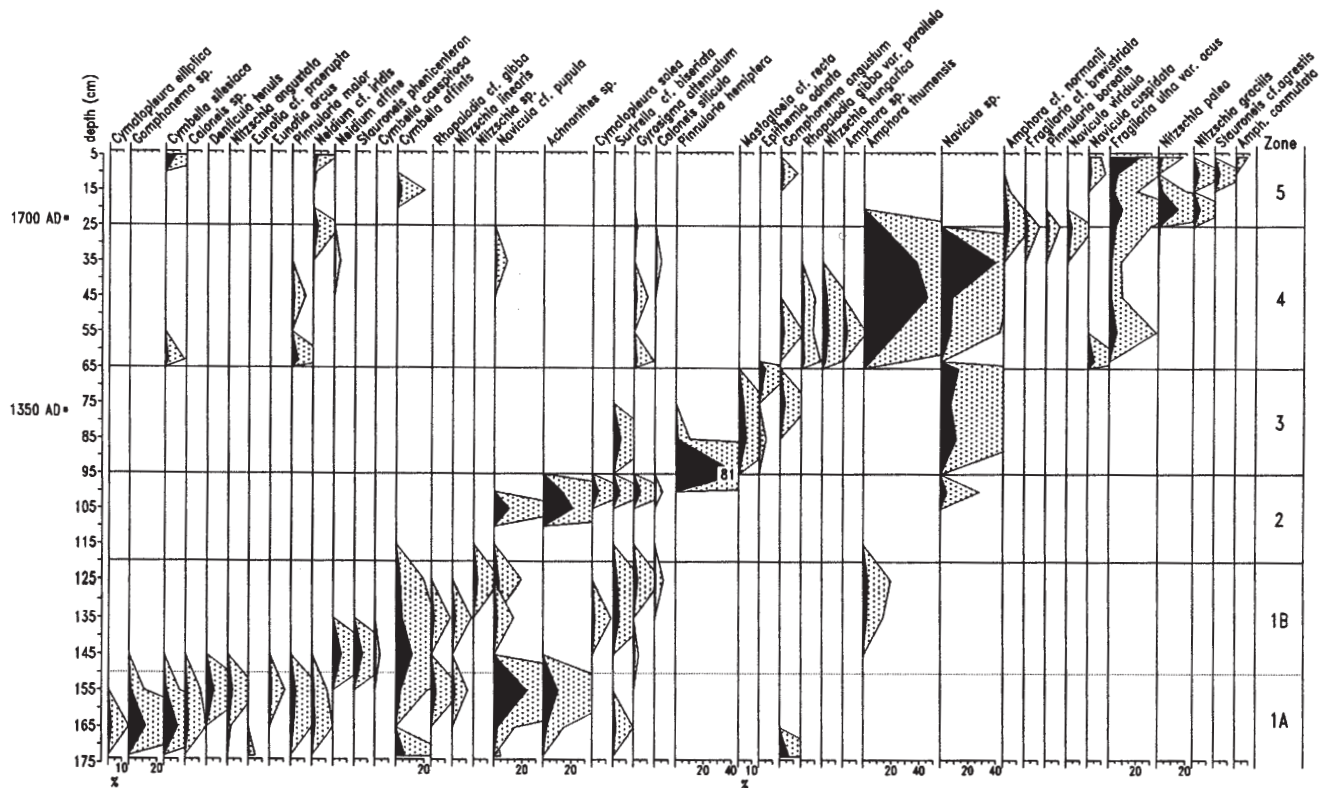


Figure 5. Diagram of pennate diatoms. They are represented in percentages with respect to the total sum of this group. Dotted pattern represents exaggerated scale 6X

Zone 1: 173–120 cm. Subzones *1A*: 173–150 cm and *1B*: 150–120 cm. Subzone *1A*, at the bottom of the sequence, is characterised by a moderate abundance of *C. wuethrichiana*, a notable presence of *C. distinguenda* and a relatively high proportion and diversity (13–17 species identified in the samples) of benthic diatoms. There is also a marked peak of the planktonic chlorophyte *Tetraedron minimum* (Fig. 6). Towards the end of this subzone percentages of both *Cyclotella* species increase, the number of identified species of pennate diatoms per sample which reaches 21, the greatest number recorded in the whole core.

Some replacements between congeneric species are visible in the boundaries between subzones *1A* and *1B*. In sub-zone *1B*, *C. wuethrichiana* peaks (Fig. 4) while *C. distinguenda* decreases until its eventual disappearance. *Nitzschia angustata*, *Navicula* cf. *pupula*, *Cymbella silesiaca*, *Neidium iridis* and *Cymatopleura elliptica* decrease simultaneously to undetectable levels and are respectively replaced by the congeneric partners *Nitzschia linearis*, *Navicula cryptocephala*, *Cymbella affinis*, *Neidium affine* and *Cymatopleura solea*.

Number of pennate diatoms also remains quite high in this sub-zone (15 species) in spite of their representing a low percentage.

Zone 2: 120–95 cm. This zone shows a drastic change. The number of diatom frustules decreases about tenfold, and diversity becomes very low. The number of species recorded in this episode is less than half that found in former episodes. At the beginning of this period the presence of *Aulacoseira ambigua* among the centric

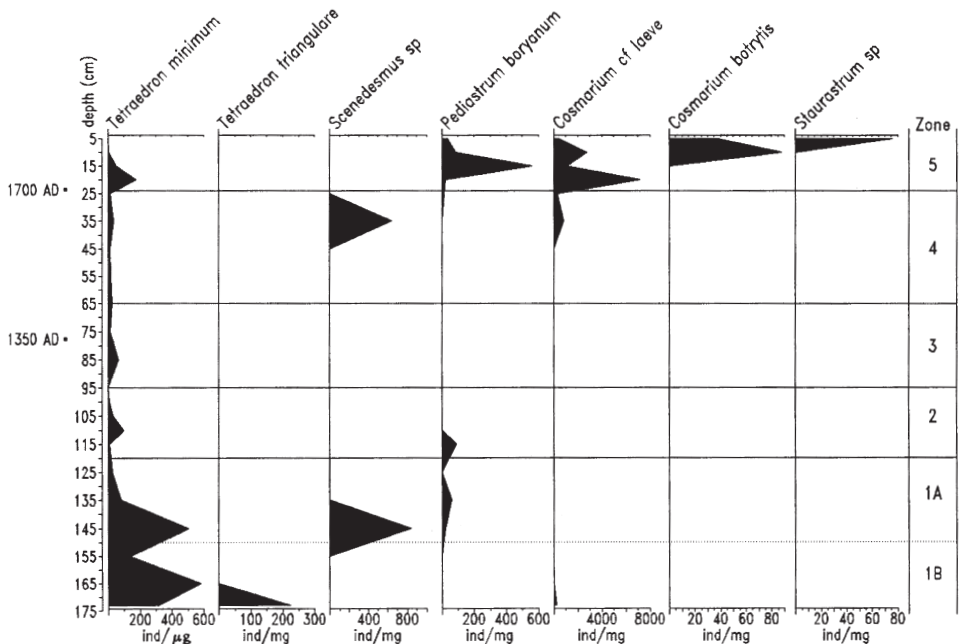


Figure 6. Chlorophytes diagram in absolute abundances. Values are expressed in individuals per mg of dry sediment

diatoms may indicate a rise in Si content (Fritz et al., 1993). This diatom is restricted to the lower part of this zone and does not reappear in the sequence.

Cyclotella wuethrichiana is still the dominant diatom but its abundance, already reduced at the beginning of the period, has fallen almost 100 fold by the end of the episode. The relative proportion of pennate diatoms increases during this period. At 95 cm depth, there is a marked impoverishment of fossil remains; beside *C. wuethrichiana* only *Eunotia pectinalis* and *Pinnularia hemiptera*, both recognised as acidophilous and halophobous species and frequently found in cold mountain waters and springs, are present.

Zone 3: 95–65 cm. Initially, the number of frustules increases again, then gradually decreases to a minimum which coincides with the sample taken in the fine sand layer at 65 cm of core depth. *C. distinguenda* reappears at the start of this zone, then peaks, and afterwards decreases to extinction. A few *Cyclotella glomerata* individuals were found at 85 cm. Pennate diversity increases in this zone but still remains quite low (6–12 species). In this zone the development of *Surirella biseriata*, *Gomphonema angustum*, *Mastogloia recta* and *Epithemia adnata* is also noticeable, the latter two being found exclusively in this zone.

Zone 4: 65–24 cm. The fine sand larger at 65 cm marks an important discontinuity. The abundance of planktonic species increases to a high level, being *C. wuethrichiana* always over 100 frustules/g and *Fragilaria ulna* var. *acus* appearing for the first time and gaining importance in the top of the sequence. The pennate group is characterised by the presence of *Amphora thumensis* which abounds in association with *Rhopalodia gibba* var. *parallela* and *Nitzschia hungarica*, both only found in this episode.

Zone 5: 24 cm-top. An increase to maximum abundance of *C. wuethrichiana* and a peak in *Tetraedron minimum* and *Cosmarium laeve* occur. Several pennate diatoms are exclusive to this zone such as *Nitzschia palea*, an indicator of eutrophic conditions.

Cladocers (Chydorids)

Quantification of cladoceran remains was restricted to Chydorids due to sample preparation. However, some remains of *Daphnia* and of *Diaphanosoma*, which are also the main planktonic species today, were observed.

Sixteen species of chydorids were found with densities up to 3000 ind/mg of dry sediment; the whole sequence is dominated by *Acroperus neglectus*. From the chydorid assemblages the following zones can be distinguished (Fig. 7).

Zone 1: 173–150 cm. This zone is characterised by a great abundance of chydorid remains. Beside *Acroperus neglectus*, the species with higher densities are *Chydorus sphaericus*, *Alona affinis* and *Alona quadrangularis*. Exclusive to this zone are: *Pleuroxus aduncus* and *Leydigia leydigi*.

Zone 2: 150–115 cm. Several species, abundant in the former zone, gradually decrease leading to a drastic reduction in the next zone, especially *A. affinis* and *C. sphaericus*. On the other hand, another group of species increases in abundance: *Pleuroxus laevis*, *Graptoleberis testudinaria* and *Alona guttata*. At the same time *Alona rectangula* appears, a ubiquitous species which is the most frequent in Spanish natural waters (Alonso and Comellas, 1984) and rice fields.

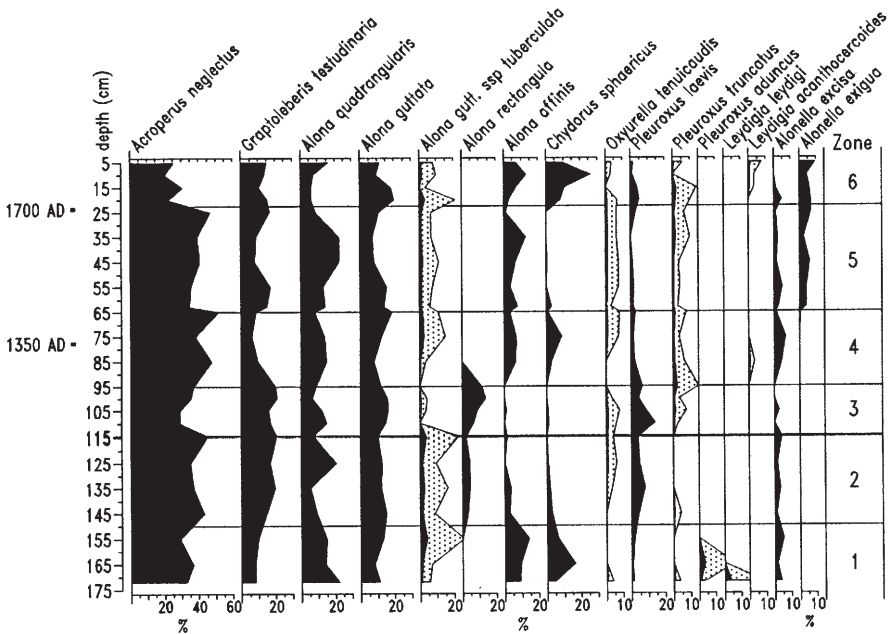


Figure 7. Chydorids diagram of La Cruz sequence. Values are expressed in percentages with respect to the total sum of this group. Dotted pattern represents exaggerated scale 6X

Zone 3: 115–95 cm. This zone is characterised by a drastic decrease in the total number of remains of all species and a high relative abundance of *Alona rectangula*, which reaches its peak. The group of species *P. laevis* – *G. testudinaria* – *A. guttata*, characteristic of zone 2, is also quite common.

Zone 4: 95–65 cm. Densities of all species increase except for *A. rectangula* which disappears. The group of species *C. sphaericus* – *A. affinis* – *A. quadrangularis*, characteristic of zone 1, recovers its dominance in this zone, while the group *P. laevis* – *G. testudinaria* – *A. guttata* declines. *Alonella excisa* shows its maximum relative abundance and *Leydigia acanthocercoides*, a quite rare benthic species, was found only in this zone and zone 6.

Zone 5: 65–24 cm. Maxima of most species occur in this zone except *C. sphaericus* which almost disappears. *Alonella exigua* is found here for the first time and persists until the top layers, while at the same time *Alonella excisa* shows a gradual final decline until its disappearance in zone 6. Two subzones could be created depending on the alternative predominance of the group *P. laevis* – *G. testudinaria* – *A. guttata* (subzone 65–50 cm) or of the group *A. affinis* – *A. quadrangularis* (subz. 50–24 cm).

Zone 6: 24 cm–top. The abundance of most species diminishes in this zone, most notably *A. neglectus*, the most abundant species throughout the sediment profile. In this episode again two subzones could be created, according to the predominance of the group *P. laevis* – *G. testudinaria* – *A. guttata* (subzone 24–12 cm) or the group *C. sphaericus* – *A. affinis* – *A. quadrangularis* (subzone 12–5 cm).

Ostracods

The ostracod assemblage is composed of five species, *Cyclocypris ovum* (Jurine), *Pseudocandona rostrata* Br. et Norm., *Candona candida* (O. F. M.), *Darwinula stevensoni* (Br. et Rob.) and *Limnocythere inopinata* (Baird), which broadly coincides with the present living community (Mezquita et al, 1996). The ostracod assemblage is dominated by *C. ovum* which is euryoic and widely distributed geographically (Löffler and Danielopol, 1978). The density of ostracod shells is highly variable, between 5 and 150 shells per gram of dry sediment.

According to the absolute and relative abundance of ostracod species, five zones are distinguished from the bottom to the top (Fig. 8):

Zone 1: 173–150 cm, shows a high ostracod content of about 100 shells per gram. *C. ovum* species never drops below 85% of total numbers.

Zone 2: 150–95 cm. This zone is characterised by low numbers of ostracods. This decline is mainly due to a sharp drop in *C. ovum*. Some species such as *D. stevensoni*, *C. candida* and *L. inopinata* increase in relative percentages. The latter species is especially important in the lower levels of this zone reaching its maximum relative abundance between 150 and 115 cm depth. In the upper part of this zone, at 93 cm depth, an important peak of *C. candida* occurs.

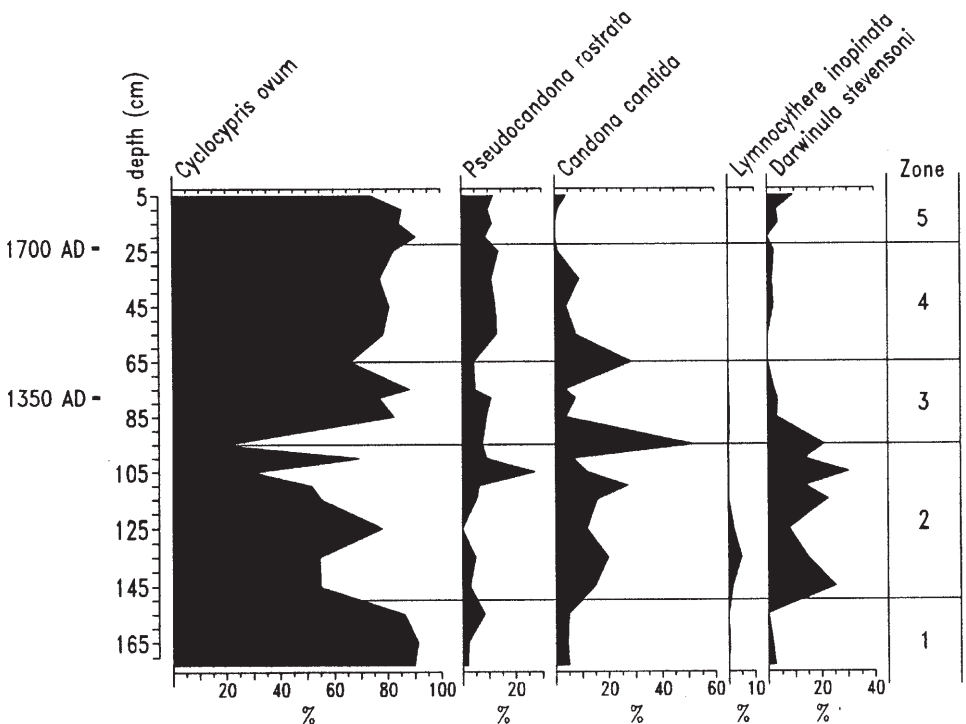


Figure 8. Distribution of ostracod shells in percentages of the La Cruz sequence

Zone 3: 95–65 cm. This zone is characterised by another period of high ostracod numbers where *C. ovum* again dominates the entire assemblage.

Zone 4: 65–24 cm. A general decrease in ostracod content occurs in spite of a moderate peak at 45 cm depth. After this peak the ostracod numbers suffer a drastic decline; the disappearance of *D. stevensoni* and *C. candida* coincides with the end of this zone.

Zone 5: 24 cm-top. At the start of this zone, only two species are present: *C. ovum* and *P. rostrata*. From 15 cm upward there is a general increase in ostracod numbers. *C. candida* and *D. stevensoni* reappear.

Other biological indicators

Total numbers of Gastropoda, Bryozoa and Charales found in the samples prepared for ostracod analysis were also estimated. Individual species within these groups were not identified (Fig. 9). In the samples prepared for Chydorid quantification, mandibles of the diptera larva *Chaoborus* were also found. Their distribution is not plotted because their numbers are too low but their occurrence is clearly more constant and higher in zones 5 and 6.

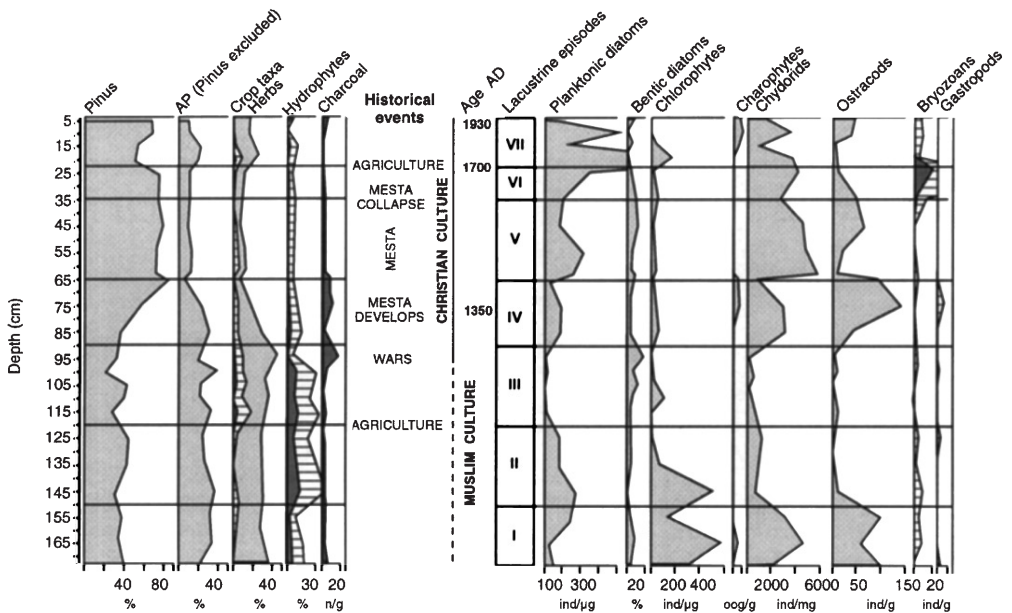


Figure 9. Main lacustrine episodes and history of the socio-economic changes of lake La Cruz deduced from vegetal and faunal assemblages. The main known historical events are located according to sediment dating. (Exaggerated scale: Hydrophytes and crop taxa 3X, Bryozoans 6X, Charophytes and Gastropods 12X). Note the different units used for the dry weight

Discussion

Lacustrine evolution: anthropic and climate interactions

Although geological processes involved in karst may affect lake level changes reinforcing or balancing climatic or anthropic forcings, multiproxy approach, covering regional (as pollen) and local (as diatoms, ostracods, ...) domains, enables to differentiate the spatial and temporal scale of changing processes. Frequent karstic geological processes such as collapses in karst or drainage network modifications causes ecosystem responses at a different time scale easily to recognize in the multiproxy analysis.

The biological (from Fig. 3 to Fig. 8) and mineralogical (Fig. 2) data record seven major environmental episodes in the evolutionary history of the system (Fig. 9). The palaeo-hydrological reconstruction is compared with the history of the socio-economic changes inferred from pollen remains, presence of charcoal and the known historical events corresponding to sediment dating.

EPISODE I (178–150 cm depth)

The results suggest that during this episode there was a small shallow pond with abundance of Charophytes, and where the relative percentage of planktonic as against benthic diatoms was low. The abundance of gastropods (Fig. 9) during this episode also supports evidence for the existence of shallow waters.

During this episode, aragonite occurs in the sediment suggesting a high Mg/Ca ratio and a relatively high mineral content in the water. This suggestion is supported by the presence of diatoms such as *Ephitemia sorex*, *Gomphonema angustum*, *Rhopalodia gibba*, *Surirella biseriata* and *Denticula tenuis* (Fig. 4 and 5), and chydorids like *Pleuroxus aduncus* and *Oxyurella tenuicaudis* (Fig. 7), all of which prefer mineral rich waters. However, the simultaneous presence of *Neidium*, *Pinnularia* and *Eunotia* diatoms, indicators of more acid, colder and less mineralised waters, as well as *Alonella excisa* (Krause-Dellin and Steinberg, 1986) and *A. affinis*, could be interpreted as indicating that sudden changes in water level could occur, and that the lake could fill quite rapidly with waters low in mineral content during cold rainy seasons. Water could then slowly evaporate, triggering higher mineral content during warmer seasons, when conditions would favour the other species of pennate diatoms recorded in the core.

During this phase, the surrounding landscape was dominated by sparse evergreen oak forest with pines.

EPISODE II (150–120 cm depth)

Sediments record a less mineralised freshwater environment, with low-Mg calcite constituting the authigenic mineral phase. This episode records a progressive expansion of planktonic diatoms and a general recession of benthic biota such as ostracods and chydorids. These changes could be related to a progressive increase in water level, as evidenced by a shift from charophytes to *Myriophyllum* dominance (Fig. 9). This interpretation is supported by associated changes in epiphytic diatom and chydorid assemblages. In the ostracod community only cold stenothermal species and those which are more restricted to lakes, such as *Limnocythere*

inopinata and *Darwinula stevensoni* (Fig. 8) maintain or even increase in numbers (Löffler and Danielopol, 1978; Rieradevall and Roca, 1995). Furthermore, thermophilic chydorid species (*Pleuroxus aduncus*) disappear (Fig. 7).

During this episode, the low detrital content in the sediments and the low pollen percentages of *Olea*, *Secale* and Cannabaceae suggest that land management was characterised by small areas of cultivated crops, without excessive modification of the natural vegetation.

Therefore, the dilution of salinity and the rise in water level could have coincided with a possible increase in regional humidity which would have favoured the gentle expansion of the deciduous taxa (Fig. 3).

EPISODE III (120–90 cm)

Magnesium content of the neoformed calcite, the increase in detrital input, and the decrease in planktonic diatoms (*C. wuethrichiana*) suggest a reduction in water volume. La Cruz lake was probably changing from a permanent water body to more ephemeral conditions, when long periods of dry weather could cause shallower and more mineralized waters. Wind detrital supplies and landslides were active. At 95 cm depth, all types of fossils reach a minimum concentration. A drastic drop in hydrophytes occurred at the end of this episode (Fig. 3). A general tendency towards an increase in the proportion of benthic diatoms is observed, culminating at 95 cm depth where pennate diatom communities almost exclusively belong to species of the genus *Pinnularia* and *Eunotia* (Figs. 4 and 5), which are usually found in peat and cold spring habitats (Sabater and Roca, 1990). At this time the lake was fluctuant, with seasonal inflows coming from springs linked to the water-table. Chydorid data support this hypothesis; the presence of *Alona rectangula*, which is an indicator of karstic springs (Dumont, 1987; Amoros, 1984), is limited to this episode, when it replaces *A. affinis* and *C. sphaericus*. In a study of Spanish waters, Alonso and Comelles (1984) characterised *A. rectangula* as most frequent in temporary waters, and *C. sphaericus* and *A. affinis* as the main species in permanent waters.

Furthermore, important peaks of the ostracod *Candona candida* (Fig. 8), considered as typical of spring water fauna (Absolon, 1978), are characteristic of this episode. An explanation of such lake behaviour can be derived from the pollen record: i.e. that a phase of forest clearance for agricultural purposes occurred. This is suggested by a decrease in total arboreal pollen, the expansion of cereal-type taxa and an increase in total non-arboreal pollen. Erodible soil would have been produced, which explains the increase of eolian sediment input into the lake. In addition, the fluctuations in water level which our records suggest would rework the littoral sediments towards the deepest point. Charcoal had also been accumulated at the end of the episode, when Cuenca area became a border zone between fighting Christians and Muslims during the first half of the Middle Ages. The charcoal peak may reflect fires arising from the frequent wars waged during this period.

EPISODE IV (90–65 cm depth)

Sediments record a peak in planktonic diatoms which alternates with peaks in chydorids, ostracods, macrophytes and gastropods. This may indicate cycles of increasing and decreasing water level. The presence of *Surirella biseriata* and

Gomphonema angustum suggests a phase of higher mineral content in the water. Furthermore, *Mastogloia recta* and *Ephitemia adnata* were found exclusively in this episode and are known to prefer high mineral content and calcium-rich waters.

Some of the cultivated areas may have been subsequently abandoned due to the above mentioned wars. The conquest of the town of Cuenca by the Christians (King Alfonso VIII) in 1177 AD coincides with the lower part of this episode. This is corroborated by the ^{14}C date which places the middle of this episode at about the year 1350 AD. Important landslides and detrital input also occurred, both around this date and later, producing a small variation in the chronology expected from the sediment accumulation rate of 0.7–0.9 mm/year estimated for the uppermost varve sediments. An important socio-economic land use change took place in the new Christian territories due to the emergence of the livestock breeding (“Mesta”). The abrupt rise of a second important charcoal peak suggests that fire is now employed in vegetation clearance to increase grassland for pastures. Evidence of the establishment of this new socio-economic structure is supported by the decline in pollen from cultivated plants and by the increase of pine.

EPISODE V (65–35 cm depth)

A similar evolution to that in the previous episode is repeated. From 65 cm depth an increase in the trophic status of the lake is suggested by the appearance of the diatom *Fragillaria ulna* var. *acus* (Fig. 5) and the chydorid *Alonella exigua*, which gradually replaces the oligotrophic indicator *Alonella excisa* (Fig. 7) (Amoros, 1984).

This episode, characterised by higher water level and water dilution, might be explained by changing farming practices, with the full development of nomadic livestock breeding or transhumance (“Mesta”). A sparse vegetation cover would favour the rise of the water level in the lake, due to the decrease of plant evapotranspiration. However, the low detrital content in sediment supports a higher density of herb cover that is reflected by the pollen analysis (only 8%). This could be interpreted as the usual over-representation of pine that distorts herb percentages due to its high pollen production, and dispersion. Pollen from herbs could also be under-represented if herbaceous species were grazed before the main period of pollen production. Historical sources (Klein, 1994) indicate that seasonal transhumance or “Mesta” was widespread all over the Cuenca territory during the XVI century, reaching a maximum between 1500–1550 AD, when more than 3 million head of cattle were recorded.

EPISODE VI (35–24 cm depth)

At 35 cm a period of abrupt changes in biological communities begins, and provides further evidence for the above-mentioned nutrient enrichment, marked by the abrupt development of some chlorophytes (Fig. 6) and a peak in *Plumatella* statoblasts (Crisman et al., 1986). The presence of some diatoms exclusive to this period, such as *Pinnularia borealis*, *Navicula viridula* and species of *Fragilaria*, as well as the restricted species diversity of *Neidium* and higher relative abundance of *A. quadrangularis* and *A. affinis*, may indicate cold climatic conditions.

At this period the “Mesta” declines noticeably and there is a recovery in agriculture.

EPISODE VII (24 cm to the top)

The varve structure proves the meromictic conditions, still persisting today (Miracle *et al.*, 1992, Vicente and Miracle, 1988). A notable increase in *C. wuethrichiana* and the diminution of the percentage of non planktonic diatoms (benthic diatoms in Fig. 9) may mean a rising water level and an increase in trophic level. Furthermore, indications of more eutrophic conditions are suggested by the expansion of the diatoms *Nitzschia palea* and *Fragillaria ulna* var. *acus*, the chlorophytes *Cosmarium laeve*, *Pediastrum boryanum* and the chydorids *Chydorus sphaericus* and *Pleuroxus laevis*.

The ostracod assemblage at 15–20 cm depth (Fig. 8) records an episode marking the expansion of the anoxic hypolimnion as indicated by the disappearance of benthic species with high oxygen requirement such as *Candona candida* (Löffler, 1977) and *Darwinula stevensoni* (Martens and Tudorancea, 1991). The presence of abundant *Chaoborus* remains supports this scenario (Löffler, 1975, 1977). It is noteworthy that species which are well represented at this depth such as *Cyclocypris ovum* (Fig. 8) and *Chydorus sphaericus* (Fig. 7) are very mobile littoral species, able to swim relatively long distances and to find optimal conditions for their survival, avoiding long stays in the more anoxic parts of the lake.

This episode, which starts approximately at the beginning of the 18th century, is characterised by increasing concentrations of crop pollen. At the same time the “Mesta” collapses and a demographic increase occurs. In this most recent agricultural period, arboreal as well as shrubs taxa reach similar percentages to those which occurred in earlier agricultural phases.

Origin of meromixis

La Cruz lake is located in a markedly continental climate and nowadays partially freezes for short periods in winter. This suggests that during colder historical episodes, ice cover on the lake could have lasted for longer periods. During prolonged colder episodes a winter stratification could lead to a summer stratification without a complete spring mixing, originating anoxic conditions in the bottom waters. This fact favours a biogenic increase in dissolved salts liberated from decomposition, specially iron compounds, in this bottom layer. After some years this could develop into a permanent meromixis, without a complete autumn overturn (Hutchinson, 1957). This hypothesis seems applicable to this lake because, on the basis of varve chronology, the change to meromictic conditions coincides with the Maunder minimum of the end of the Little Ice Age (Damon and Jirikowic, 1992), which, in the Iberian Peninsula, corresponds to the Little Ice Age minimum temperatures (Fontana, 1976; Font, 1988). In some of these years the colder winters were followed by warmer summers, thus shortening the potential time for mixing.

In addition, La Cruz lake occupies the bottom of a sheltered and deep doline which greatly inhibits water mixing due to wind action. This fact, together with a possible increase in water volume, further favours meromixis. Fernández *et al.* (1993) studied the dendroclimatology and ring-widths of *Pinus nigra* in the Cuenca Mountains and reported a cold and humid period at the transition between the 17th and the 18th century. The presence of cold water diatom species in the lake sequence corresponding to those years and an abrupt peak in planktonic species suggesting a rise in water level both provide support for this hypothesis.

Another process which possibly influenced to meromixis is woodland clearance for agricultural purposes. The pollen sequence coinciding with the initiation of the varve sequence demonstrates an increase in crop taxa and a decrease in the extent of woodland. Increased soil erosion and associated nutrient input to the lake could also contribute to the eutrophication process. Furthermore, woodland clearance reduces evapotranspiration and could thereby favour an increase in lake volume. All of these processes may together have triggered the onset of meromictic conditions (Frey, 1955; Hutchinson, 1957; Löffler, 1975).

Other cold episodes prior to that of the end of the "Little Ice Age" have also been recorded. For example, for the period around 1530 when the Tajo River was frozen (Fontana, 1976), there is no evidence of meromictic conditions developing in La Cruz. Previous periods of woodland clearance had also occurred (as, for example, in the period around 800 AD) without leading to meromixis in the lake. Meromixis began when a phase of woodland clearance, which might well lead to an increase of water level and nutrient concentration, coincided with a relatively long cold climatic period. The historical evidence suggests a synergetic effect. Further quantification of the precise role of each process in contributing to meromixis in lakes is now required.

ACKNOWLEDGEMENTS

This work received financial support from the European Desertification program (EV5V-CT91-0037), the CICYT (CLI95-1905-CO3-01), and Consejería de Agricultura y Medio Ambiente (JCCM). We are very grateful to K. Kiss for the *Cyclotella* species identification. We are also thankful to E. McGee and S. Giralt for helpful comments, English improvement and technical support. F.B. was granted by Fundación RICH ("Sequía y Desertización" department).

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Received 1 April 1996;

revised manuscript accepted 19 January 1998.