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500 YEARS OF ECOLOGICAL CHANGES RECORDED IN SUBFOSSIL CLADOCERA IN A HIGH-ALTITUDE, TROPICAL LAKE LAGO DE LA LUNA, CENTRAL MEXICO

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Abstract

We present the last 500 years of history of a high-altitude tropical lake Lago de la Luna located at Nevado de Toluca crater, Central Mexico, based on subfossil Cladocera analysis. Through the studied sedimentary sequence only five Cladocera species were present. Cladocera community was dominated by littoral species (4) and among them one (*Ilyocryptus nevadensis*) is endemic. The detailed analysis of the sediments (every 1 cm) allowed us to track contemporary climatic and anthropogenic changes. Our results showed that Lago de la Luna is a very sensitive ecosystem and has strong response to climatic changes. The most remarkable change in the Cladocera community was observed between 1683–1780 yr, which was well correlated with the Little Ice Age. PCA results implied that modern state of the lake Lago de la Luna is very similar to one 400–500 yr ago. Only one period was identified when human impact was of importance. This period seemed to correlate with changes in the lake ecosystem due to fish introduction in the 1950s.

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Key words: subfossil Cladocera, crater Nevado de Toluca, lake sediment

INTRODUCTION

Lakes constitute very responsive ecosystems, alterations of which are recorded in their sediments. Lake sediments are therefore natural archives, and their study has become a basis for the reconstruction of events occurring in the past. Information of the past can also improve understanding of contemporary events and improve forecasts for the future. So far many lacustrine sediments around the world have been studied, but high-altitude tropical lakes are relatively rare, and the literature about their behavior and past changes is somewhat limited. High altitude tropical lakes are located above 3500 m a.s.l. and they are considered to be cold, oligotrophic and polymictic (Loffler 1964, Lewis 1996). Because of their isolated location in the high-elevation areas, those lakes are also called "sky islands" (Warshall 1994, McCormack *et al.* 2009). Sky island habitats are almost untouched by human activity as compared to lowlands lakes and, therefore, they are perfect objects for studying past climatic and environmental changes. Their sediments may contain valid indicators for environmental change, especially the remains of Cladocera (Hofmann 2000, Kamenik *et al.* 2007). Up to now only few Cladocera records for tropical high-altitude lakes are available. Some high Andes lakes were studied by Aguilera *et al.* (2006) and Coronel *et al.* (2007) in Bolivia and by Kotov *et al.* (2010) in Chile. Van Damme and Eggermont (2011) studied lakes located in Rwenzori Mountains in Uganda and D. R. Congo.

Our study lake, Lago de la Luna, is one of the two tropical and high altitude lakes in Mexico. The lake is located in the Nevado de Toluca volcano crater, in central Mexico (Fig. 1). The unique location of the lake and the fact that it has never been subjected to palaeolimnological analyses, inspired us to undertake studies on the history of its development during the last 500 years. This lake has been so far studied in terms of its hydrochemistry (Gonzalez 1984, Alcocer *et al.* 2004), and the composition of zooplankton (Sarma *et al.* 1996, Elias-Guterez *et al.* 1997, Cervantez-Martinez *et al.* 2000, and Dimaz-Flores 2005). These studies have revealed that zooplankton is largely dominated by Rotifera species (29). These authors also recorded the presence of 2 Copepoda and 3 Cladocera species (namely *Alona cf. setulosa* Megard, 1967; *Biapertura intermedia* Sars, 1862; *Ilyocryptus nevadensis;* Cervantes-Martinez *et al.* 2000).

The aim of this study was to trace ecological changes in the recent sediments (last 500 yr) of Lago de la Luna. In this paper we present the first results of this study based on subfossil Cladocera analysis. Because of its isolation, the evolution of Lago de la Luna should be mostly affected by natural (climatic) factors. With a detailed analysis of the sediments we expected to be able to track even small scale climatic and anthropogenic changes.

Another very significant aspect of our study was to determine subfossil Cladocera fauna composition at Lago de la Luna. Species composition of Cladocera occurring in high-altitude tropical lakes is, so far, not well studied. Due to the

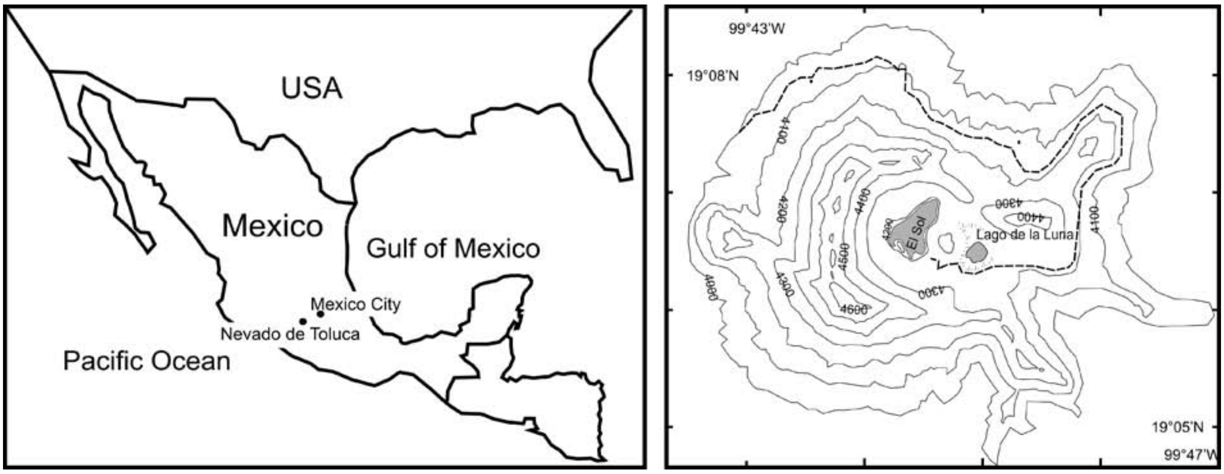

Fig. 1. Geographical location of the study site Lake Lago de la Luna.

unique location of this lake (tropical climate, high altitude, isolation) we expected to find endemic species among the zooplankton.

STUDY AREA

Lago de la Luna (Lake of the Moon) is located in central Mexico, approximately 90 km southwest of Mexico City, in the Nevado de Toluca volcano crater (19°06'13"N, 99°45'20" W, 4620 m a.s.l) (Fig. 1). The Nevado de Toluca is a stratovolcano build mainly by dacitic lava flows. The crater of the volcano contains two lakes: Lago de la Luna and Lago del Sol. The crater developed 11,600 years ago, when the volcano was active for the last time. The lakes located in the crater probably developed soon after this event (Bloomfield, Valastro 1979, Armienta *et al.* 2000). The Nevado de Toluca is a protected National Park since 1936.

The modern climate at the summit of Nevado de Toluca is cold, with a summer raining season. Mean annual temperature is 4°C, with a maximum in May (15°C) and a minimum in January (–7°C) (Mexican Meteorology Service). Mean annual precipitation is 1250 mm. The vegetation surrounding the lakes is mainly composed of several species of "fascicle" growing grasses. In the lower part of the mountain, below the tree line (4000 m a.s.l.), the vegetation consists of *Pinus hartwegii* and *Abies religiosa* forests (Gonzalez 1984, Rzedowski 1981, Caballero 1996).

Surface area of Lago de la Luna is approximately 2.5 ha. The maximum depth of the lake is 8 m, the average pH is around 4.9 and water conductivity is between 17 and 20 μS cm^{-1}. The lake water is very clear and cold, temperature is quite similar throughout the year, fluctuating between 8 and 11°C. Secchi disk visibility usually reaches the bottom of the lake (Caballero 1996, Armienta *et al.* 2000, Alcocer *et al.* 2004, Dimaz-Flores 2005).

MATERIALS AND METHODS

A short (38.5 cm) sediment core was recovered from Lago de la Luna by means of gravity corer at the depth of 8 m in 2003. The core was sealed in the plastic tube and moved to laboratory where its lithology was described and it was subsampled at 1 cm intervals for biological proxies, including subfossil Cladocera. The cladoceran remains were prepared for analysis according to standard method proposed by Frey (1986). Each 1 cm^3 sample, was boiled in 10% solution of KOH, and later left for a half an hour in a magnetic stirrer to eliminate organic matter. The residue was washed with distilled water and sieved using a 38-μm mesh. The final residue was taken to 5 ml using distilled water. For every microscope slide 0.1 ml of final solution was used and identification of remains was made at 100×, 200×, and 400× using OLYMPUS BX50 light microscope. Two to four slides (minimum of 200 remains) from each sample were counted. All cladoceran remains were counted (headshields, shells, ephippia, postabdomens). The identification of cladoceran remains was based on Cervantes-Martinez *et al.* (2000) and Elias-Guterez *et al.* (2008). Results were plotted as absolute and relative abundance diagrams using the C2 software (Juggins 2005, 2007).

The chronology is based on 210-Pb analysis. The analysis was conducted in the Laboratory of Isotopic Geochemistry and Geochronology, Institute of Marine Sciences and Limnology, UNAM, Mexico. 210-Pb activities were obtained by measuring its daughter product 210-Po assuming secular equilibrium between the two isotopes. Aliquots of 0.3 g of sediments were spiked with 209-Po as yield tracer, and were digested in SavillexTM PFA containers, in a 5:4:1 mixture of HNO_3+HCl+HF on a hotplate (~180°C) overnight. The residue was converted to a chloride salt by repeated evaporation with 12 M HCl, then dissolved in 0.5 M HCl with 2.5 g of H_3BO_4, and 0.2 g of ascorbic acid were added to the solution. Po isotopes were deposited on Ag discs at room temperature overnight on an orbital shaker; and the activity was measured by α-spectrometry using ORTEC silicon surface barrier detectors coupled to a PC running under Maestro™ data acquisition software. Blanks were run in parallel to correct for any contamination. The mean sediment accumulation rate (SAR, in cm $year^{-1}$) was obtained by using the CFCS (constant flux, constant sedimentation) model (Sanchez-Cabeza, Ruiz-Fernández 2012).

Numerical analysis was performed using total abundance of Cladocera species in fresh sediment. Due to constant sedimentation rate and uniform lithology of the studied

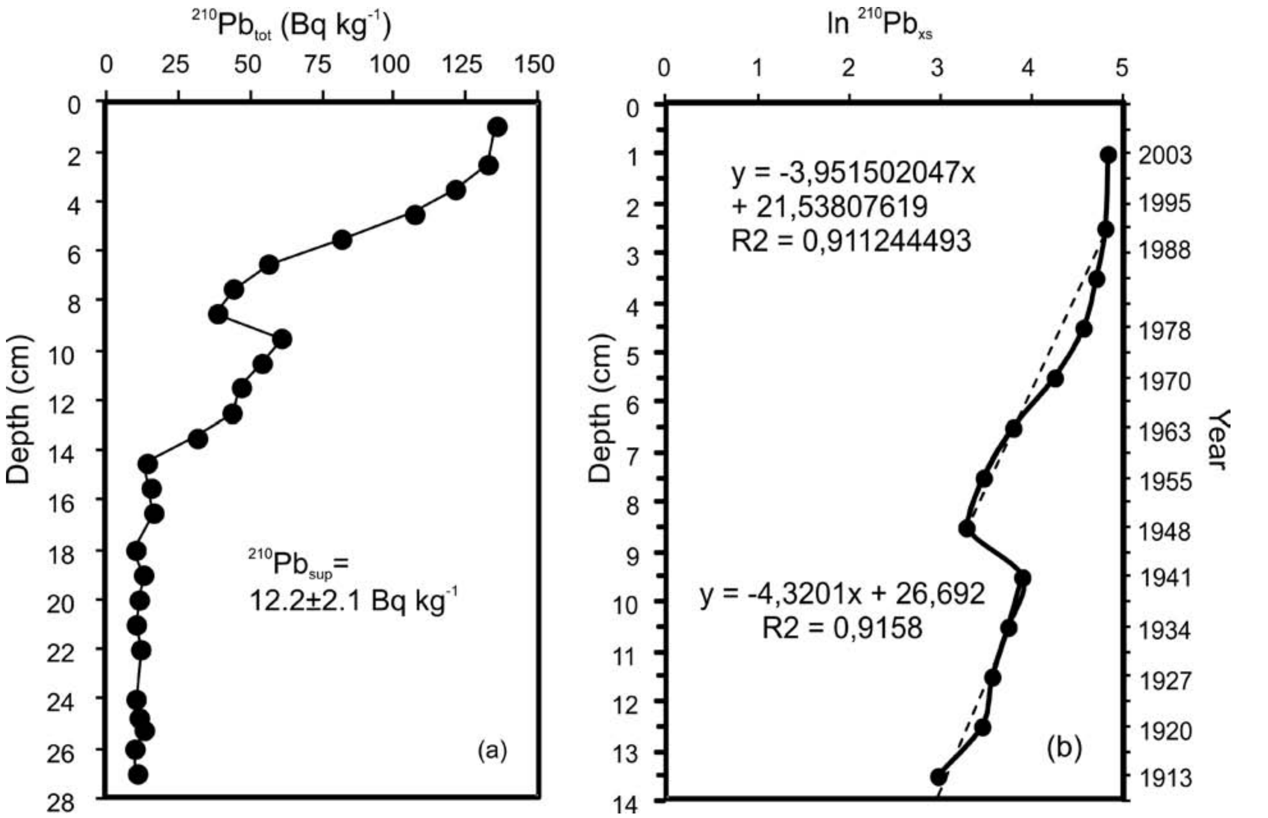

Fig. 2. 210-Pb activities depth profile from Lake Lago de la Luna sediment core. (**a**) Total 210-Pb activities; the discontinuous line represents the supported 210-Pb activities. (**b**) Logarithmic values of excess 210-Pb activities and 210-Pb-derived sediment accumulation rates.

sediment sequence it was possible to use total abundance of Cladocera to perform the statistical analysis. Detrended correspondence analysis (DCA) showed a short gradient length (axis 1 = 1.183 and axis 2 = 0.773 SD), which suggested that PCA (principal component analysis) technique can be used for further analysis (Hill, Gauch 1980). The ordinations were performed by means of CANOCO 4.5 (Ter Braak, Smilauer 2002).

RESULTS

Lithology and chronology

The top most 38.5 cm of the sediments of Lago de la Luna was mostly dark gray silt gyttja. In all the length of the core clastic material up to 3 mm was present. The highest concentration of coarse sediment was between the depths of 23 and 27 cm. Bottom sediments (38.5–36.8 cm) were slightly sandy.

The sediment chronologies, based on excess 210-Pb (210-Pbxs) were performed by using the CFCS model (constant flux and constant sedimentation; Krishnaswamy *et al.* 1971, Sánchez-Cabeza, Ruiz-Fernández 2012), which assumes a constant 210-Pb atmospheric flux and a constant sediment accumulation rate (SAR). The validity of both CFCS model assumptions depends on if a significant linear correlation is found between the logarithm of 210-Pbxs activities and the depth of the sediment core. Significant linear correlations (t-Student's test, P.05) were found between the ln 210-Pbxs and depth in the sediment cores collected in lake Lago de la Luna (Fig. 2), thus confirming the validity of the CFCS hypotheses for the 210-Pb chronology. The ln 210-Pbxs depth profiles obtained from Lago de la Luna showed two regression lines which indicate small changes of SAR with time (Sánchez-Cabeza, Ruiz-Fernández 2012). The SARs obtained for core Luna were 0.14±0.02 cm year^{-1} (from surface to the depth of 9 cm) and 0.15±0.03 cm year^{-1} (from 9 to 14 cm depth); the time elapsed since deposition of sediments at 14 cm depth was determined to be 97±7 years.

Subfossil Cladocera analysis

Remains of only five Cladocera species belonging to three families, Daphniidae, Chydoridae, Ilyocryptidae, were recorded in the sediments of Lago de la Luna. Through the studied sedimentary sequence only one planktonic species, belonging to the *Daphnia longispina* group Muller 1785, was present. Cladocera community was dominated by littoral species. Among them one (*Ilyocryptus nevadensis*; Cervantez-Martinez *et al.* 2000) is endemic, until now it has been recorded only at the Nevado de Toluca. Habitat of *Ilyocryptus nevadensis* is quite unusual. This species, like all Ilyocryptinae, is a bottom dweller, but living on the sandy substrate instead of muddy (Cervantes-Martinez *et al.* 2000). We also found remains of *Alona* sp. which, according to preliminary data, belongs to a new, not yet described species. Population of this species from the neighboring lake Lago del Sol was referred to as *A. intermedia* Sars 1962 by Elias-Guterez *et al.* (1997), but it clearly differs from European *A. intermedia* by the morphology of headshield and postabdomen.

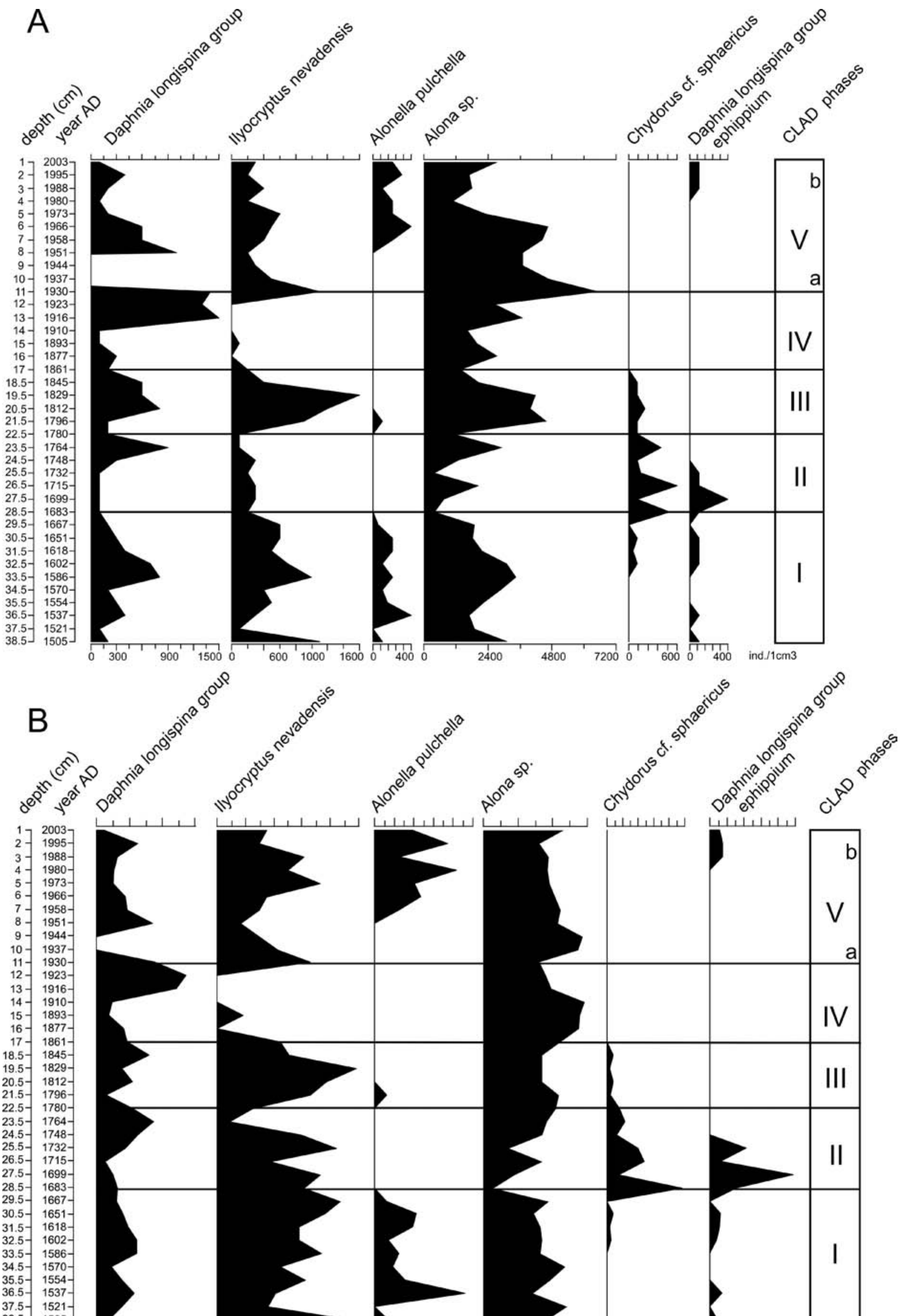

Fig. 3. **A**) Diagram showing the absolute abundance of cladocerans in Lake Lago de la Luna through the last 500 years; **B**) Diagram showing the relative abundance Cladocera in Lake Lago de la Luna through the last 500 years.

The results of the subfossil Cladocera analysis are presented in the diagrams of absolute frequency and relative abundances (Fig. 3). According to visual inspection five Cladocera phases were identified.

CLAD I (1505–1683 AD): all five Cladocera species were present, the most numerous were endemic species *Ilyocryptus nevadensis*, *Alona* sp., and pelagic *Daphnia longispina* group. *Alonella pulchella* Herrick 1884 was also present and it reached its highest frequency in the core. *Chydorus* cf. *sphaericus* was noted only in the youngest part but at low frequency. In this phase, in addition to claws, ephippia of *Daphnia longispina* group were also present.

CLAD II (1683–1780 AD): the total frequency of almost all species decreased (*Alona* sp., *Ilyocryptus nevadensis*, *Daphnia longispina* group) except for *Chydorus* cf. *sphaericus* which, together with ephippia of *Daphnia longispina* group, were the most numerous species, reaching their highest frequency in the core. During this phase *Alonella pulchella* totally disappeared.

CLAD III (1780–1861 AD): the frequencies of dominant species *Alona* sp., *Ilyocryptus nevadensis* and *Daphnia longispina* group increased again. *Chydorus* cf. *sphaericus* was present but its frequency was significantly lower than in the previous phase.

CLAD IV (1861–1930 AD): only three Cladocera species were present and their frequencies were low. The most abundant species was *Alona* sp. The lower part of this phase was characterized by a significant decrease of *Daphnia longispina* group and *Ilyocryptus nevadensis*. In the upper part remains of *Ilyocryptus nevadensis* totally disappeared whereas *Daphnia longispina* group considerably increased its abundance, reaching its highest frequency in the core.

CLAD V (1930–2003 AD): the total frequency of all the littoral species increased again. Remains of *Alona* sp. increased significantly and became predominant. In the beginning of this phase (CLAD Va) *Ilyocryptus nevadensis* reappeared. Very unusual during this time was the temporary (1937–1951AD) disappearance of *Daphnia longispina* group. In the upper part of this phase (CLAD Vb) *Alonella pulchella* and *ephippia* of *Daphnia longispina* group were again present.

Results of PCA analysis

In the principal component analysis (PCA), performed for the sediment samples-Cladocera taxa matrix, the first two axis explained 68.6% of the total variance in the cladoceran assemblage in the core sequence (axes 1 $\lambda = 0.36$ and 2 $\lambda = 0.326$; Fig. 4).

Axis 1 clearly set apart the CLAD phases I and V from phases II, III and IV. A species with the strongest positive correlation with axis1 was *Alonella pulchella*. The results also showed that environmental gradient associated with axis 2 was an important element differentiating samples from Lago de la Luna. Species with a positive correlation with axis 2 were *Chydorus* cf. *sphaericus* and the ephippia of *Daphnia longispina* group, and with a negative correlation, *Alona* sp. In the PCA biplot the sediment samples from the different Cladocera zones were clearly differentiated (Fig. 4). The oldest and the youngest samples (phase I and Vb) were grouped

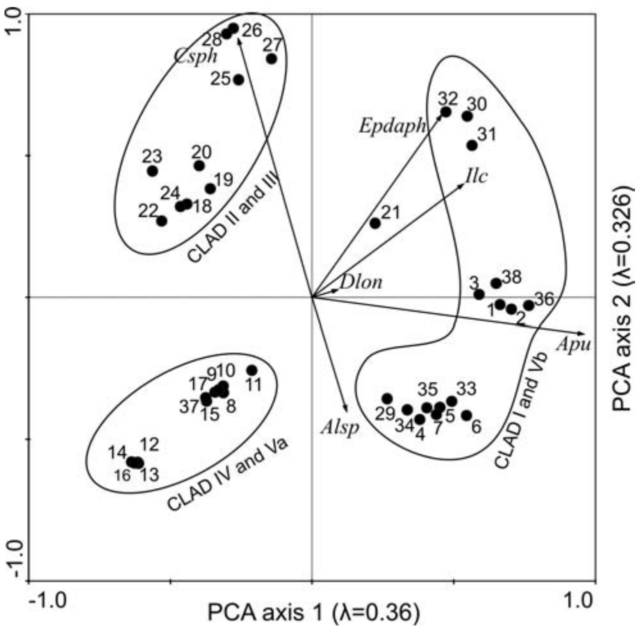

Fig. 4. Principal component analysis (PCA) for the cladoceran community in the sediments of Lake Lago de la Luna. Explanations of the Cladocera species acronyms used in the PCA biplot: Alsp – *Alona* sp., Apu – *Alonella pulchella*, Csph – *Chydorus* cf. *sphaericus*, Dlon – *Daphnia longispina* group, Ilc – *Ilyocryptus nevadensis*, Epdaph – ephippia of *Daphnia longispina* group. Numbers of the biplot refer to depths of the sediment samples.

in the right part of the biplot and the species mostly connected with them were *Alonella pulchella* and *Ilyocryptus nevadensis*. In the lower left part of the PCA biplot are samples from Cladocera phases IV and Va, and in the upper left part samples from Cladocera phases II and III, strongly correlated with *Chydorus* cf. *sphaericus*.

DISCUSSION AND CONCLUSIONS

In the studied sediment core from Lago de la Luna several ecological changes were noted during the last 500 years (Figs 3 and 4). The reconstructed trophic state through all the sedimentary sequence, based on the species composition of Cladocera indicated oligotrophy. In the oldest phase (CLAD I, 1505–1683 AD) littoral species associated with plant and sandy bottom were dominant, particularly *Alonella pulchella*, *Alona* sp. and *Ilyocryptus nevadensis*. These species are known for their resistance to unfavorable environmental conditions, especially low nutrient concentration and low pH values. At that time planktonic species belonging to *Daphnia longispina* group were also present, both as claws and ephippia. Cladocera species composition suggested that the littoral zone was partly covered by plants. Increasing numbers of ephippia in the sediments is associated with seasonal or periodic environmental stress (Jeppesen *et al.* 2003, Johansson *et al.* 2005, Kultti *et al.* 2011). The oldest samples (CLAD I) had positive correlation with environmental factor associated with axis 1 (Fig. 4).

Over the time (phase CLAD II, 1683–1780 AD) the ecological conditions of the lake changed. The frequency of planktonic species (*Daphnia longispina* group) and macrophyte-sediment associated species decreased and the frequency of *Daphnia* ephippium and very tolerant species *Chydorus* cf. *sphaericus* (Fig. 3) increased. This is indicative of unfavorable environmental conditions (environmental stress). The changes in the Cladocera species composition were well correlated with the Little Ice Age (LIA) (Lozano-Garcia *et al.* 2007, Metcalfe, Davies 2007). According to paleoecological data during the second part of the 17th century and 18th century the mean annual temperature was ca. 2°C lower than today. LIA was characterized not only by lower air temperature but also by lower precipitation and longer and colder winters (Haug *et al.* 2003, Metcalfe, Davies 2007), which strongly impacted the Cladocera community. During longer and colder winters the lake stayed ice covered for a longer period of time than usually, and it may have been directly responsible for low oxygen concentration in the littoral zone and a reduction of Cladocera population (Nevalainen *et al.* 2011). Lower annual precipitation was liable for lower water level in the lake, which was manifested by decreasing frequency of plant-sediment associated species. Climate conditions (long winter, cold and dry) favored increasing numbers of *Daphnia* ephippia and the frequency of *Chydorus* cf. *sphaericus*. *Chydorus* cf. *sphaericus* is one of the most tolerant species to unfavorable climate conditions, especially cold water and low level of biogenic substance (Bos, Cumming 2003, Sweetman, Smol 2006). Sometimes this species is even called "arctic species" (Whiteside 1970).

In the end of the 18th century (phase CLAD III, 1780–1861 AD) the next remarkable change in Cladocera community was observed (Fig. 3). One more time plant-sediment associated species became very numerous, particularly *Ilyocryptus nevadensis* and *Alona* sp. The abundance of pelagic species (*Daphnia longispina* group) also increased. Noted changes, specially the increasing frequency of Cladocera and the disappearance of *Daphnia* ephippia in the sediments, are probably an evidence of the improvement of edaphic and climatic conditions after LIA. However as PCA data suggest (axis 2 in Fig. 4) during phase III some environmental factors which were present also during LIA were still present and had influence on Cladocera community.

Since the second half of the 19th century (CLAD IV, 1861–1930 AD) only three cladoceran species were present in the sediments and their frequencies were very low. It is highly probable that the studied lake was slightly deeper and more oligotrophic at that time. In the upper part of this phase, increased frequency of pelagic species (*Daphnia longispina* group) and macrophyte-sediment associated species (*Alona* sp.), suggest nutrients supply from the catchment to the lake, which might be an effect of climate warming after LIA.

In the beginning of the CLAD V (subphase Va, 1937–1951 AD) a temporary lack of the remains of *Daphnia longispina* group was noted in the sediment. This sudden disappearance of *Daphnia* can be correlated with the introduction of fish to the lake. According to historical data in the 1950s there were several attempts to introduce fish in Lago del Sol (Dimas-Flores *et al.* 2008). It is highly probable that this introduction was also made in Lago de la Luna. The appearance of fish in a lake ecosystem has strong influence on the Cladocera community, especially on planktonic species. Pelagic species, particularly Daphniidae, are favorite food for planktivorous fish (Fryer 1985, Adamowicz 2002). Fish predation pressure on planktonic Cladocera can be strong enough to cause their disappearance. In the most recent sediments (subphase CLAD Vb) once more all five Cladocera species were present. Species composition, especially the re-emergence of *Alonella pulchella* and *Daphnia* ephippium, as well as the results of the PCA analysis showed that the ecological conditions of the lake nowadays are very similar to those nearly 500 years ago (Fig. 4).

In summary, the results of subfossil Cladocera analysis from core sediments of Lago de la Luna, showed that the studied lake has developed mostly by natural (climatic) factors. As suggested by our data this kind of lakes (isolated by distance and altitude) are very sensitive ecosystems and they have strong response to climatic changes. During the last 500 years the ecosystem of Lago de la Luna intensely reacted to changes in temperature and precipitation, which were well expressed by changes in the Cladocera community. The results of PCA implied that the modern state of the Lago de la Luna is very similar to one 400–500 yr ago. Within the last 500 years, only one period was identified, when human impact was of importance. Fish introduction in the 1950s was clearly reflected in the subfossil Cladocera community.

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