Ecology of Cladocera species from Central America based on subfossil assemblages

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ABSTRACT

Cladocera species composition was analyzed in surface sediments of 29 lakes in Central America (Guatemala, El Salvador and Honduras). The material studied was collected with an Ekman grab in autumn 2013 from lakes located in lowland, highland and mountain regions. The study revealed high variability in qualitative and quantitative composition of subfossil Cladocera. A total of 31 Cladocera species (5 planktonic and 26 littoral) were identified, as well as 4 morphotypes that could not be identified (NRR 1-4). Planktonic Bosminidae and Daphniidae were the most abundant families. Daphniidae were restricted to water bodies in mountain regions, whereas Bosminidae were widely distributed in lakes with different abiotic conditions. Moreover, Bosminidae species also occurred in highly mineralized waters (> 900 µS cm⁻¹). The great majority of the identified Cladocera species belonged to the littoral family Chydoridae. *Chydorus* cf. *sphaericus* was the most common species (found in 20 lakes), which probably reflects its tolerance to a wide spectrum of habitat conditions. Cluster analysis discriminated 6 groups of Cladocera species with a high correlation level within groups (≥0.8), which showed different types of correlation with lake characteristics and environmental variables. Canonical correspondence analysis (CCA) showed that altitude and secondly water electrical conductivity were the most important drivers of Cladocera species composition in the region studied. Furthermore, CCA analysis indicated lowland lakes with low water transparency were also characterized by peculiar species assemblages.

Key words: Subfossil Cladocera; Central America; waterfleas ecology; Guatemala; El Salvador; Honduras.

INTRODUCTION

Cladocera are one of the most important components of zooplankton in lacustrine ecosystems. This group is also well-known to promptly respond to environmental changes (Jeppesen *et al.,* 2001). Previous studies have highlighted that temperature and altitude are among the main factors determining Cladocera communities (Campanelli, Mortari and Henry, 2016; Green, 1995; Padhye *et al.,* 2016; Sweetman, 2010; Zawiska *et al.*, 2015). In addition, these studies have shown comparable sensitivities to changes in lake water trophic state, water depth, conductivity and pH (Korhola and Rautio, 2001). These responses to environmental variables makes Cladocera one of the most powerful paleolimnological indicators and for this reason they have been widely used for the reconstruction of past lacustrine environments (Bjerring, 2007; Kienast *et al.,* 2011; Korosi, 2012; Luoto *et al.,* 2009; Mirosław-Grabowska and Zawisza, 2014; Nováková *et al.,* 2013 Sarmaja-Korjonen and Hyvärinen, 2008; Schmidt, 2000; Szeroczyńska, 1991; Szeroczyńska *et al.,* 2007; Szeoczyńska and Zawisza, 2011 a,b). Subfossil remains of Cladocera are commonly used in paleolimnological studies in Eurasia and America (Bjerring, 2007; Mirosław-Grabowska and Zawisza, 2014; Paterson, 1994; Szeroczyńska *et al.,* 2007). However, only a few paleolimnological studies based on water fleas were conducted in Central America (Cuna *et al.,* 2014; Szeroczyńska *et al.*, 2015; Zawisza *et al.,* 2012, 2014, 2016). So far, the majority of studies focused on the living Cladocera and their taxonomy (Elías-Gutiérrez *et al.,* 1999, 2006, 2008; Sinev, 2015; Sinev and Silva-Briano, 2012; Sinev and Zawisza, 2013).

The knowledge of Cladocera species composition, distribution and ecology in freshwater lakes of Central America is crucial for the development of reliable bioindicators, and for paleolimnological investigations. The main objective of the present study was to analyze and identify subfossil Cladocera species in northern Central America, in particular in Guatemala, El Salvador and Honduras, and to explore their relationship to lake environmental characteristics such as altitude, lake area, depth, pH, transparency, conductivity and dissolved oxygen. The obtained results will provide the basis for the reconstruction of regional and global climatic and envoronemntal changes at long-term scale.

METHODS

Study sites

The study included 29 waterbodies located between 13° and 17° N geographical latitude and from 87° to 91° W longitude in Guatemala, El Salvador and Honduras (Fig. 1). The study area is located in the Central American Bioregion of the American Neotropical Ecozone, which is characterized by two distinct seasons: a dry winter and a moist summer season (Taylor and Alfaro, 2005). The subtropical ridge (belt of high atmospheric pressure) from the northern Atlantic is controlling the climate of the region, whereas the Intertropical Convergence Zone (ITCZ) and polar fronts of mid-latitude origin have a secondary impact (Taylor and Alfaro, 2005). One of the main factors affecting the microclimate of the area is topography (Karmalkar *et al.,* 2011; Taylor and Alfaro, 2005). The considerable differences in

mean annual temperature and precipitation which characterize the entire region mainly depend on altitude. The Guatemalan lowlands are characterized by a mean annual temperature of 25-28°C, whereas temperatures in highland and mountain regions are around 12-15°C (Atlas Climatologico for 1928-2003, the National Institute for Seismology, Volcanology, Meteorology and Hydrology of Guatemala; www.insivumeh.gob.gt). Annual precipitation in the area varies considerably during the year and ranges from <1000 mm in the plains to >2500 mm in the mountains (Taylor and Alfaro, 2005).

The lakes studied are located at altitudes ranging from sea level (El Muchacho at 3 m asl) to high altitude lakes (Magdalena and Chicabal at 2863 and 2726 m asl, respectively, Tab. 1). Lake area and depth also were quite variable. The largest lake were Atitlán and Yojoa (125 and ~79 km², respectively, Tab. 1), while several lakes have an area <0.10 km², such as Madre Vieja (0.10 km²), Verde

Fig. 1. Map of the study area showing the location of lakes sampled in Central America, i.e. Guatemala, Honduras and El Salvador. Numbers indicate the names of the lakes: 1, Atitlán; 2, Calderas; 3, Chicabal; 4, Comandador; 5, El Muchacho; 6, El Pino; 7, El Rosario; 8, Grande; 9, Ipala; 10, Lachuá; 11, Las Pozas; 12, Magdalena; 13, Sacnab; 14, Salpetén; 15, Quexil; 16, Chiligatoro; 17, Jucutuma; 18, Madre Vieja; 19, Ticamaya; 20, Yojoa; 21, Apastepeque; 22, Aramuaca; 23, Chanmico; 24, El Espino; 25, Jocotal; 26, Los Negritos; 27, Metapan; 28, Olomega; 29, Verde.

(0.10 km²), Chiligatoro (0.04 km²), El Rosario (0.02 km²), Magdalena (0.01 km²) (Tab. 1). The study covered both very shallow (≤3 m depth, such as Comandador, El Muchacho, El Rosario, Grande, Magdalena, Jucutuma, Ticamaya, Jocotal, Los Negritos, Olomega), and very deep lakes (>300 m), such as Lachuá (a 378 m deep karstic lake), Atitlán (a 340 m deep crater lake) and Chicabal (330 m, Tab. 1).

Sampling and analyses

Sediments were collected in autumn 2013 using an Ekman sediment sampler. The geographical location of the lakes was determined by a handheld navigator (GPSmap 60c). Water transparency was determined using a Secchi disk, and the maximum lake depth was identified using a portable depth sounder (Echosounder Eagle Mach 1). Physical and chemical parameters of the surface waters (*i.e.*, pH, conductivity, dissolved oxygen) were measured with a WTW multi set 350i multiparametric probe. The area of each lake (Tab. 1) was calculated by the measure tool of Google Earth. Lake sediment samples were collected both from the littoral as well as from the open-water (pelagic) zone. In eight shallow lakes, where there was no pelagic zone (*i.e.*, Comandador, El Muchacho, El Rosario, Grande, Jucutuma, Ticamaya, Jocotal, Los Negritos), samples were collected only from the littoral zone (Tab. 1). Lakes El Pino, Ipala, Quexil, Madre Vieja, Chanmico, El Espino, Metapan and Verde, were sampled only in the profundal zone due to the shape of the lake basin. Crater lake Aramuaca (107 m depth) was sampled only in the littoral zone (Tab. 1).

Tab. 1. Location, morphometry and selected limnological variables measured at water surface at the waterbodies sampled in Central America.

ID	Name	Country	Geographic coordinates		Altitude	Area	Samples		Z_{max}	Secchi	pH	Conductivity	O_2	HCl
			N	W	(m asl)	(km²)	L	P	(m)	(m)	-	(μS cm⁻¹)	(mgL⁻¹)	
1	Atitlán	Guatemala	14.6837	91.2239	1556	125.00	+	+	340	4.2	8.9	442	5.7	+
2	Calderas		14.4117	90.5913	1790	0.35	+	+	26	2.9	9.2	100	4.9	-
3	Chicabal		14.7875	91.6561	2726	0.21	+	+	330	1.6	9.0	12	5.4	-
4	Comandador		13.9600	90.2544	20	0.65	+		1.7	0.5	7.4	251	5.6	-
5	El Muchacho		13.8892	90.1918	3	0.36	+		2	0.4	9.1	439	5.9	-
6	El Pino		14.3447	90.3941	1038	0.64		+	18	2.8	8.3	100	2.0	-
7	El Rosario		16.5255	90.1601	126	0.02	+		3	0.2	7.2	987	1.7	+
8	Grande		13.8903	90.1703	5	0.95	+		2	0.2	7.4	110	3.7	-
9	Ipala		14.5571	89.6394	1495	0.56		+	25	3.6	8.0	100	2.8	-
10	Lachuá		15.9184	90.6732	170	4.00	+		378	4.4	7.9	906	4.8	+
11	Las Pozas		16.3432	90.1660	152	2.16	+	+	35	3.1	8.3	277	5.4	+
12	Magdalena		15.5426	91.3956	2863	0.01	+	+	3	2.8	8.8	331	6.2	+
13	Sacnab		17.0583	89.3725	170	4.28	+	+	9	1.8	9.0	412	6.1	+
14	Salpetén		16.9815	89.6755	105	2.77	+	+	32	1.7	7.0	4520	5.8	+
15	Quexil		16.9231	89.8099	120	2.20		+	32	2.7	8.5	204	4.5	-
16	Chiligatoro	Honduras	14.3756	88.1830	1925	0.04	+	+	5.5	0.9	7.4	100	1.9	-
17	Jucutuma		15.5123	87.9028	27	4.34	+		2	2.0	7.3	100	1.0	-
18	Madre Vieja		14.3569	88.1376	1866	0.10		+	3.4	0.9	8.5	100	2.7	-
19	Ticamaya		15.5506	87.8897	17	2.91	+		2	0.8	7.2	100	1.6	-
20	Yojoa		14.8606	87.9847	639	79.70	+	+	22	3.3	8.3	100	2.7	-
21	Apastepeque	Salvador	13.6925	88.7448	509	0.38	+	+	47	6.1	8.6	100	2.8	-
22	Aramuaca		13.4294	88.1065	76	0.40	+		107	6.7	8.4	100	4.1	-
23	Chanmico		13.7786	89.3541	477	0.78		+	51	0.9	9.2	100	3.4	+
24	El Espino		13.9530	89.8652	689	0.99		+	5.5	0.4	8.5	85	6.6	-
25	Jocotal		13.3371	88.2519	26	8.70	+		3	1.5	8.0	595	3.0	-
26	Los Negritos		13.2831	87.9370	102	0.69	+		2	0.3	9.2	40	5.2	-
27	Metapan		14.3094	89.4655	450	16.00		+	6	0.2	8.4	255	3.1	-
28	Olomega		13.3072	88.0551	66	25.20	+	+	2.5	0.9	7.7	105	2.5	-
29	Verde		13.8915	89.7872	1609	0.10		+	12	2.7	7.5	83	4.5	-

L, littoral zone; P, pelagic zone; Z_{max}, maximum lake depth; HCl, reaction with acid during preparation. The World Geodetic System of 1984 (WGS84) datum was used for the Cladocera samples.

Sediment samples were placed in plastic bottles (100 mL) immediately after collection, and stored under refrigeration. Samples were then transported to the Paleolimnology Laboratory of Universidad National Autonomous de Mexico (UNAM), where subsamples for subfossil Cladocera analysis were obtained and preserved in cooling condition.

Subfossil Cladocera were analyzed at the Bioindicator Laboratory at the Warsaw Research Center of the Institute of Geological Sciences, the Polish Academy of Sciences. Each sample consisting of 1 cm^3 of wet sediment was prepared according to standard methods (Frey, 1986). Sediments were treated with 10% HCl to eliminate carbonate and then heated in 10% KOH for 30 min. The residue was centrifuged and sieved through a 38 μm sieve, transferred into a test tube and filled up to 5 cm^3 with distilled water. Samples were stained with safranin. Three to four slides obtained from of 0.1 cm^3 liquid suspension each were examined at the microscope for each sample. The identification of Cladocera taxa followed Elías-Gutiérrez *et al.* (2006, 2008), Hudec (2000), Kotov (2009), Kotov *et al.* (2003), Rajapaksa and Fernando (1987), Rey and Vasquez (1986), Sinev (1998, 2001, 2015a, 2015b), Sinev and Dumont (2016), Sinev and Zawisza (2013), Van Damme *et al.* (2011). The Cladocera relative abundance diagram was prepared using the C2 program (Juggins 2005, 2007).

In order to determine the relation between species distribution and lake characteristics (area, altitude, maximum depth) and water variables (pH, Secchi transparency, dissolved oxygen), cluster analysis and canonical correspondence analysis (CCA; ter Braak, 1986) were performed. Cluster analysis is based on the similarity measure performed on qualitative data (Hammer *et al.*, 2011), while CCA is a combination of mutual averaging algorithm with a multiple regression (ter Braak, 1986) which performed on combined quatitative Cladocera and environmental data. Statistical analyses were conducted using the PAST software (Hammer *et al.,* 2001).

RESULTS

Environmental variables

In general, the surveyed lakes were characterized by relatively low water transparency, with exception of lakes Aramuaca and Apastepeque, which showed Secchi depth >6 m (Tab. 1). Secchi depth values ranging between 2.7-4.4 m were measured in 10 lakes, *i.e.* Lachuá, Atitlán, Ipala, Yojoa , Las Pozas , Calderas, El Pino, Magdalena, Quexil and Verde (Tab. 1). The waters of Lake Jucutuma (2.0 m depth) were characterized by visibility reaching the bottom, while four lakes were characterized by clarity of 1.5-1.8 m (Sacnab, Salpetén, Chicabal, Jocotal). The other lakes (Comandador, El Muchacho, El Rosario, Grande, Chiligatoro, Madre Vieja, Ticamaya, Chanmico, El Espino, Los Negritos, Metapan, Olomega) were characterized by Secchi disk visibility <1.0 m (Tab. 1).

The lakes investigated did not show considerable differences in pH values, which ranged from neutral (7.0 in Lake Salpetén) to alkaline (9.2 in Lake Chanmico and Lake Los Negritos, Tab. 1). Circumneutral water pH was recorded for lakes El Rosario, Ticamaya, Jucutuma, Comandador, Chiligatoro, Grande, Olomega, Verde and Lachuá. Waters of five lakes were strongly alkaline (pH ≥9.0), *i.e.*, Sacnab, El Muchacho, Calderas, Los Negritos, and Chanmico. The other 14 lakes were characterized by slightly alkaline waters, with pH values ranging from 8.0 to 9.0 (Tab. 1). Electric conductivity ranged from 12 μS cm^{-1}, measured at Lake Chicabal, to 4520 μS cm^{-1} in Lake Salpetén (Tab. 1). High conductivity was recorded in the waters of El Rosario and Lachuá (Tab. 1). Values between ~400 and 600 μS cm^{-1} were determined in lakes Jocotal, Atitlan, El Muchacho, and Sacnab (Tab. 1). In the remaining lakes this parameter was <350 μS cm^{-1} (Tab. 1). Ten of the sampled lakes were characterized by the dissolved oxygen content of over 5.0 mg L^{-1}, *i.e.*, El Espino, Magdalena, Sacnab, El Muchacho, Salpetén, Atitlán, Comandador, Las Pozas, Chicabal and Los Negritos (Tab. 1). The amount of dissolved oxygen in nineteen lakes ranged from 1.0 mg L^{-1} (Jucutuma) to 4.9 mg L^{-1} (Calderas). The lowest dissolved oxygen concentration (<2.0 mg L^{-1}) were recorded in lakes Chiligatoro, El Rosario, Ticamaya and Jucutuma (Tab. 1).

Subfossil Cladocera

A total of 31 Cladocera taxa belonging to three families – Daphniidae, Bosminidae and Chydoridae – were found in the sediments of the lakes studied. Some Cladocera remains that could not be identified to species level belong to four different morphotypes and were referred to as "Not Recognized Remains" (NRR) 1, 2, 3 and 4, respectively (Fig. 2). Species relative abundances are presented in Fig. 3. Frequency (n), mean and maximum relative abundance of each Cladocera species are collated in Tab. 2.

The species richness per lake ranged from one in Lake Calderas to 12 species (lakes Atitlán and Verde), and included both planktonic and littoral forms. Only in the sediments of the deep Aramuaca crater lake no subfossil cladocerans remains were found. Planktonic species were represented by five taxa, *i.e.*, *Bosmina longirostris* (O.F.Müller, 1785), *Bosmina (E.) longispina* (Leydig, 1860), *Bosmina (E.) coregoni* (Baird, 1857), group of *Daphnia longispina* (O.F. Müller, 1785), group of *Daphnia pulex* (Leydig, 1860), which occurred in 17 lakes (Fig. 3). Cladocera communities from lakes El Rosario and Calderas were entirely dominated by planktonic species (Fig. 3), while the share of Bosminidae and/or

Daphniidae exceeded 90% in lakes Ipala, El Pino and Apastepeque (Fig. 3). Pelagic species were dominant (60-88% of total Cladocera abundance) in lakes Salpetén, Yojoa, El Espino, Atitlán, Sacnab, Chicabal, Lachuá (Fig. 3).

The remaining lakes (16) were dominated by littoral species of Chydoridae, which also represented the most species-rich group. In fact, 26 littoral Cladocera species and four NRR (Fig. 3 and Tab. 2) were identified in the sediments studied, with the NRR most likely belonging to also to littoral Chydoridae. *Chydorus* cf. *sphaericus* (O.F. Müller, 1776) (20 lakes), *Alona glabra* (Sars, 1901) (*Ovalona glabra*, following Sinev, 2015a) (13 lakes) and Cladocera comparable to (13 lakes) and *Alona quadrangularis type* (O.F. Müller, 1776) (12 lakes) were the most common taxa (Fig. 3 and Tab. 2). In five lakes (Las Pozas, Quexil, Verde, Chiligatoro, Magdalena), both littoral and planktonic species were present. The share of littoral species ranged from 60% to 80% in lakes Las Pozas,

Quexil, Verde and Chiligatoro. In the sediments of lakes Las Pozas and Quexil, eight and nine littoral species were identified, respectively, and two planktonic species were detected. In Las Pozas, *Alona ossiani* (Sinev, 1998), was the most abundant littoral species (approx. 20%), whereas in Quexil – *Chydorus* cf. *sphaericus* (ca. 15%) and *Alona quadrangularis* type (ca. 15%, Fig. 3) were dominant. Lake Verde and Lake Chiligatoro were characterized by the presence of 12 and 6 species, respectively. *Chydorus* cf. *sphaericus* (ca. 25%) and group of *Anthalona verrucosa* (Sars, 1901) (ca. 15%) were the dominant species of the littoral zone in Lake Verde, while *Alona ossiani* (ca. 35%) and *Simocephalus* sp. (Schoedler, 1858) (ca. 20%) were the most abundant species in Lake Chiligatoro (Fig. 3 and Tab. 2). In Lake Magdalena, the deep-water species accounted for a minor portion of cladocerans, and *Chydorus* cf. *sphaericus* was the dominant species (ca. 90%). Planktonic taxa were completely absent in the sediments
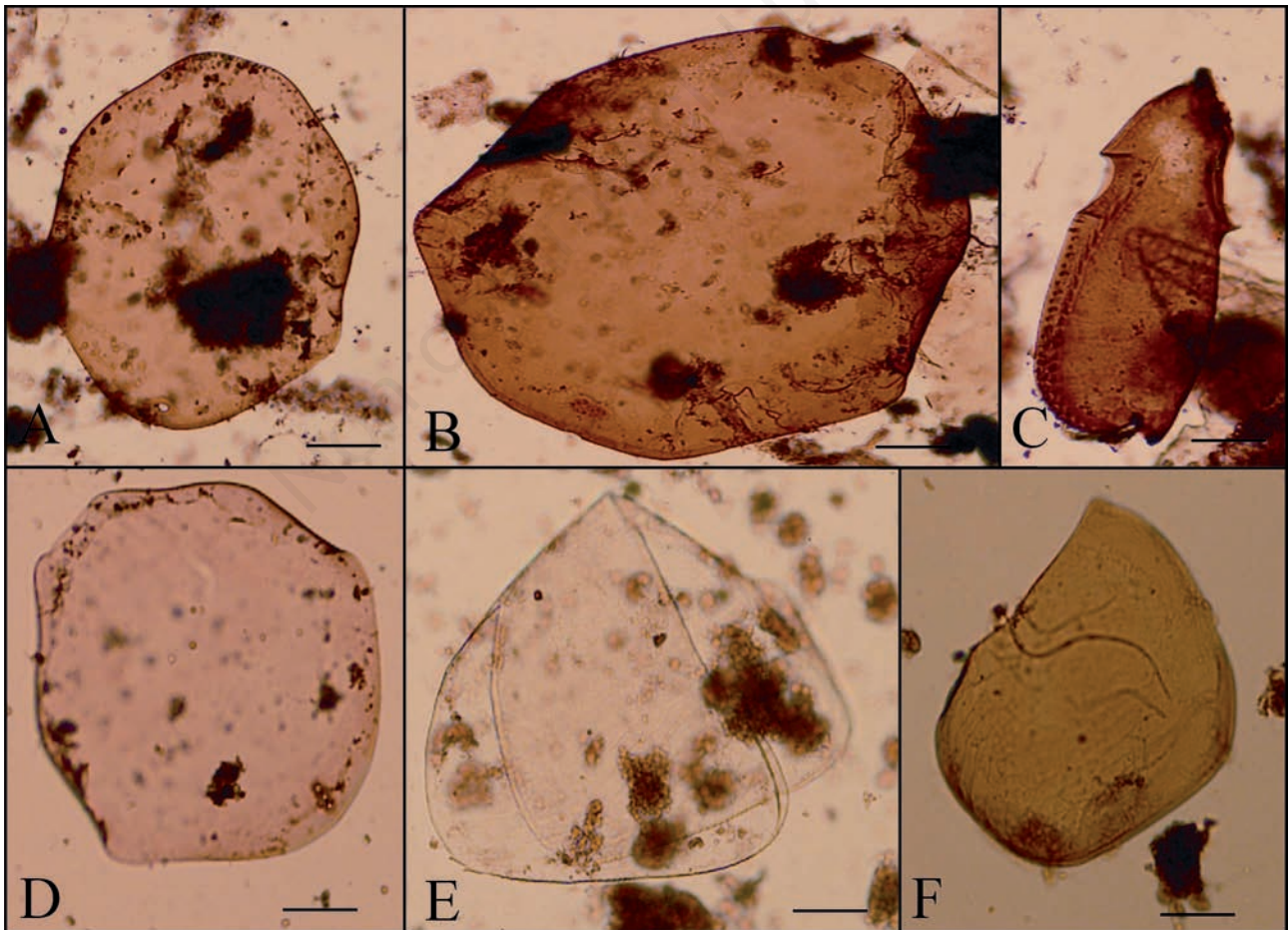

Fig. 2. Unidentified subfossil remains (NRR) of Cladocera. A) Probably headshield of *Euryalona* sp. B) Headshield NRR1. C) Postabdomen of *Leydigiopsis ornata*. D) Probably headshield of *Leberis* sp. E) NRR3, probably shell of Cladocera from group of *Coronatella monacantha*. F) shell NRR4. Scale bars: 500 μm.

of eleven lakes (Fig. 3). Lakes Comandador, Los Negritos, Ticamaya and Jocotal were dominated by *Chydorus* cf. *sphaericus*, which represented from 36% to 50% of the Cladocera communities. This taxon was also common in Madre Vieja (15%), Metapan (23%) and Olomega (16%). In Lake Madre Vieja, *Alona ossiani* was the most abundant species (ca. 42%), *Camptocercus dadayi* (Stingelin, 1913) was the dominant species in Metapan (ca. 31%), and NRR1 (ca. 32%) (Figs. 2 and 3) were dominant in Olomega. In Lake Jucutuma, *Acroperus* sp. (Baird, 1843) (ca. 22%) and *Camptocercus dadayi* (ca. 22%) were dominant, whereas *Alona quadrangularis type* (ca. 43%) and *Alona glabra* (ca. 29%) dominated in Lake Grande. Lake El Muchacho and Lake Chanmico were characterized by low species diversity (3) and low frequency of individuals. Group of *Leydigia acanthocercoides* (Fischer, 1854) was dominant in Lake El Muchacho (ca. 52%), whereas *Leberis* sp. (Smirnov, 1989) was the most prominent species in Lake Chanmico (50%, Fig. 3). The largest number of subfossil Cladocera remains was determined for Lakes Sacnab (22,000 ind. cm^{-3}) and Ipala (21,000 ind. cm^{-3}), where open-water species dominated. The maximum number of water fleas in the waterbodies dominated by littoral forms was ca. 10,000-11,000 ind. cm^{-3}, as recorded in Madre Vieja, Quexil and Verde.

Statistical analysis

The "cophenetic coefficient" in the cluster analysis was 0.8009 and well reflected the similarities within the data. The dendrogram shown in Fig. 4 (see also Tab. 3) defined six Cladocera groups. The highest correlation coefficient between species was determined for *Alona rustica* (Scott, 1895) (group of *Flavalona rustica*, following Sinev and Dumont, 2016) and *Simocephalus* sp. (0.99, Group 6), and for *Daphnia pulex*-group and *Bosmina longirostris* (0.94, Group 1, Fig. 4a and Tab. 3). The species *Bosmina (E.) coregoni*, *Bosmina (E.) longispina*, *Alona quadrangularis*
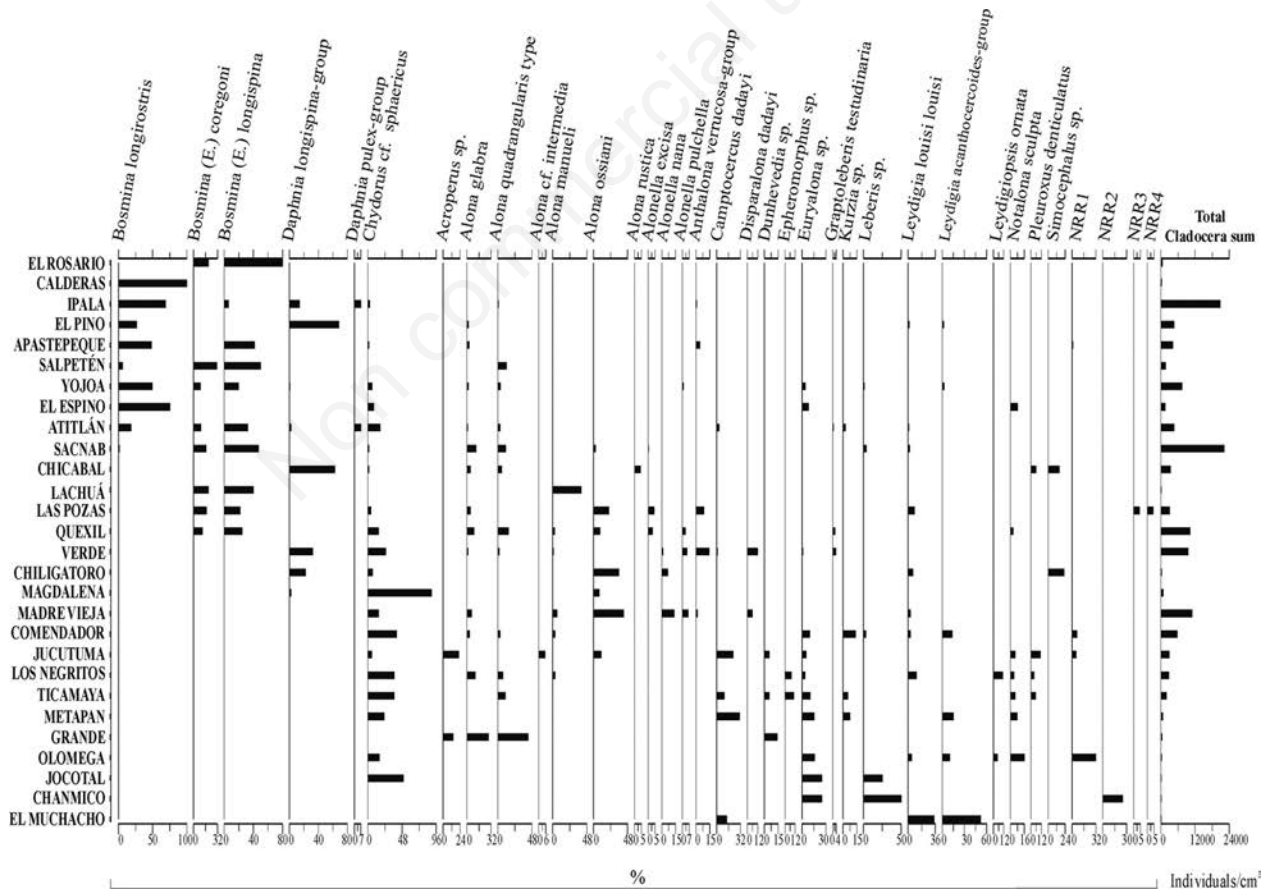

Fig. 3. Relative abundances (%) diagram for the subfossil Cladocera species identified in surface sediments from freshwater ecosystems of Central America. Lakes are ordered by decreasing contribution of planktonic forms. NRR1, unidentified remains type 1; NRR2, unidentified remains type 2, probably headshield of *Leberis* sp.; NRR3, unidentified remains type 3, probably of *Coronatella of monacantha*-group); NRR4, unidentified remains type 4.

type, *Alona glabra* and *Leberis sp.* (Group 2) resulted to be correlated at the similarity level of 0.92. In the three other groups the correlation coefficient between species ranges between 0.8 and 0.86 (Fig. 4a).

The CCA analysis was conducted using the species included the six distinguished clusters and an additional set of other Cladocera species that were not included in any cluster. Due to their rarity and low contribution to total Cladocera remains, NRR were not included in the analysis. The CCA ordination biplot is presented in Fig. 4b. Arrows show environmental variables, and their length and direction indicate the strength and direction of their influence on the species composition (ter Braak, 1986).

Axis 1 and 2 explained almost 80% of the variability (axis 1=49.98%, axis 2=29.29%). Altitude, transparency, pH and the maximum depth were positively correlated with axis 1, while conductivity and lake area were negatively correlated with the first canonical axis (Fig. 4b). The location of Group 1 in quadrant I, and of Group 3, Group 6 and the *Daphnia longispina*-group in quadrant IV underlines the positive correlation of the abundances of these species groups with altitude and negative correlation with conductivity. Moreover, the occurrence of *Graptoleberis testudinaria* (Fischer, 1848) and Group 1 also seem to be strongly determined by the Secchi disk visibility (Fig. 4b). Species and groups of Cladocera located in quadrants II and III were correlated negatively with altitude (Fig. 4b) and positively with conductivity and lake area (Fig. 4b and Tab. 3). Group 2 and *Alonella excisa* (Fischer, 1854) were placed in the 2nd quarter. Species of Group 4 and 5 and *Epheromorphus* sp. (Frey, 1982), *Leydigia louisi louisi* (Jenkin, 1934), *Leydigiopsis ornata* (Daday, 1905), *Notalona sculpta* (Sars, 1901) were located in the 3rd quarter. According to Fig. 4b, these species dominated in lowlands and in the waters with low visibility (negative correlation with Secchi disk visibility and altitude). *Chydorus* cf. *sphaericus* was located between quadrants III and IV, which may indicate a weak relation with all of the considered environmental variables.

DISCUSSION

Thirty-one Cladocera species were identified in surface sediments of the lakes studied. The number of species found in individual lakes was generally small. In fact, the maximum number of species found in lakes Atitlán and Verde was only 12. Compared to European lakes, which are normally inhabited by over 30 species (Dumont, 1994), the species diversity of Cladocera was low in the considered region of Central America. These findings seems to confirm that the number of Cladocera species found in one waterbody in the Neotropics is in general low and usually ranges from several to over a dozen species (Cuna *et al.*, 2014; Peréz *et al.*, 2013; Zawisza *et al.*, 2012). The differences in the number of cladoceran species between the con-

tinents may result from species competition (Feniova *et al.*, 2011; Shurin, 2000), fish or invertebrate predation (Korhola and Rautio, 2001), as well as from different geological history of the area (Korhola and Rautio, 2001).

The identified Cladocera included both littoral and pelagic species. Planktonic species of Daphniidae and Bosminidae were the most abundant. Remains of the *Daphnia pulex*-group and the *Daphnia longispina*-group were mainly associated to lakes located at altitudes above

Tab. 2. Number of occurrences, maximum and mean percentage contribution of cladoceran species identified in the sediments of the surveyed waterbodies.

Group or species	n	Max (%)	Mean (%)
Bosmina longirostris	9	100.0	43.8
Bosmina (E.) coregoni	8	31.3	17.0
Bosmina (E.) longispina	10	80.0	36.2
Daphnia longispina-group	8	67.9	25.6
Daphnia pulex-group	2	7.0	7.0
Chydorus cf. *sphaericus*	20	89.5	19.7
Acroperus sp.	3	22.2	12.2
Alona glabra	13	28.6	6.7
Alona quadrangularis type	12	42.9	10.7
Alona cf. *intermedia*	1	5.6	-
Alona manueli	6	40.0	9.6
Alona ossiani	8	42.4	16.4
Alona rustica	1	4.3	-
Alonella excisa	3	4.3	2.5
Alonella nana	3	13.6	7.1
Alonella pulchella	4	6.1	3.7
Anthalona verrucosa-group	5	14.3	5.9
Camptocercus dadayi	6	30.8	13.7
Disparalona dadayi	2	11.9	9.0
Dunhevedia sp.	3	14.3	8.4
Ephemeroporus sp.	2	10.5	9.0
Euryalona sp.	11	25.0	11.3
Graptoleberis testudinaria	3	3.6	2.5
Kurzia sp.	4	13.3	7.2
Leberis sp.	5	50.0	16.6
Leydigia louisi louisi	10	34.4	7.8
Leydigia acanthocercoides-group	6	51.7	15.9
Leydigiopsis ornata	2	11.1	8.1
Notalona sculpta	7	15.9	7.1
Pleuroxus denticulatus	4	11.1	6.4
Simocephalus sp.	2	22.4	19.0
NRR1	4	31.8	11.4
NRR2	1	25.0	-
NRR3	1	4.3	-
NRR4	1	4.3	-

n, occurrence; NRR1-4, not recognize remains type 1 to 4; NRR2, probably headshield of *Leberis* sp.; NRR3, probably *Coronatella monacantha* (Sars 1901) group.
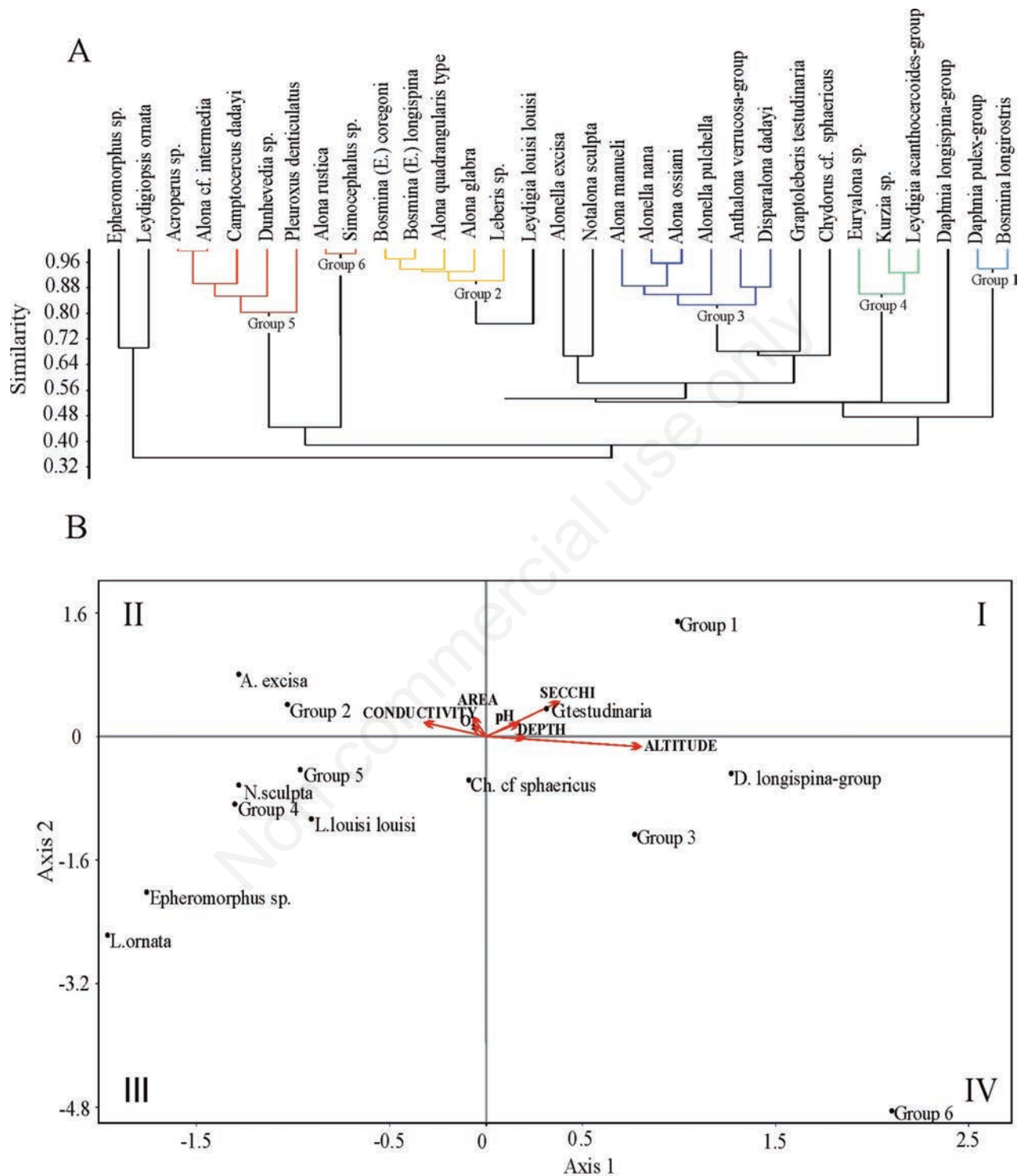
Fig. 4. Results of multivariate statistical analysis applied to qualitative and quantitative results of species composition of subfossil Cladocera, and environmental variables. A) Cluster analysis showing species grouping according to reciprocal correlation level; the groups were distinguished for species that showed a high level of similarity >0.8; species composition of each group is presented in Tab. 3; B) Canonical correspondence analysis (CCA) for species relative abundances and environmental variables; length and direction of arrows show respectively the strength and direction of a certain environmental variable.

1000 m asl. CCA analysis showed the preference of the *Daphnia pulex*-group for clear waters, such as lakes Atitlán and Ipala, that showed transparency of 4.2 m and 3.6 m, respectively. Moreover, the contribution of Daphniidae was negatively correlated with conductivity and was higher in waters with conductivity ≤100 μS cm⁻¹. The results show the preference of Daphniidae for highlands and mountain areas and clean, low-mineralized and nutrient-poor waters. Similar environmental preferences by Daphniidae were also suggest by Hart (2004) and by Mergeay *et al.* (2005) for African lakes. The occurrence of Daphniidae species in lakes of Central American highlands was also observed by Peréz *et al.* (2013).

Bosminidae species were observed along the whole altitudinal gradient of the lake studied, from lowland, to highland and mountain lakes. CCA analysis revealed a negative correlation of *Eubosmina* (*Bosmina (E.) coregoni, Bosmina (E.) longispina*) and a positive correlation of *Bosmina longirostris* with altitude. *Eubosmina* was found in six lowland lakes, but also in two lakes located at >1000 m asl (Atitlán and Ipala), in Lake Yojoa (639 m asl) and in Lake Apastepeque (509 m asl). This suggests that even though *Eubosmina* prefered lakes located at a lower altitude, this is probably not the main factor determining the distribution of this genus. On the other hand, *Eubosmina* mainly occurred in waters with high conductivity. These species were dominant in highly mineralized (4520 μS cm⁻¹) and brackish (salinity=2.5‰) waters of Lakes Salpetén, as well as in El Rosario and Lachuá, which showed conductivity values >900 μS cm⁻¹. The presence of *Eubosmina,* along with *Bosmina longirostris* in Lake Salpetén, confirms the tolerance of Bosminidae to waters with high mineral content and/or salinity (Aladin, 1991). The obtained results also confirm the wide distribution of planktonic Daphniidae and Bosminidae in Central America (Elías-Gutiérrez *et al.,* 1999; Korovchinsky, 2006).

Chydoridae was the most species rich group of Cladocera in the sediment studied. *Chydorus* cf. *sphaericus* was the most common species, as it was present in 20 out of the 29 surveyed lakes located both in lowland and mountain areas. The relative abundance of *Chydorus* cf. *sphaericus* in the lake located at the highest altitude (Lake Magdalena, 2863 m asl) was almost 90%. CCA analysis showed that none of the measured environmental factors had a significant effect on the distribution of the species in the region studied of Central America. This confirmed the ubiquity of *Chydorus* cf. *sphaericus* and its wide range of tolerance to environmental and ecological conditions (Flössner, 2000; Fryer, 1968; Korhola and Rautio, 2001; Zawisza and Szeroczyńska, 2011).

The genus *Alona* was mostly represented by *Alona glabra* and the *Alona quadrangularis* type. These species were found in 13 and 12 lakes, respectively, which were characterized by different conductivity, oxygenation, water visibility and altitude. The *Alona quadrangularis type* was the unique littoral species found in Lake Salpetén, which may indicate its tolerance to waters with higher mineralization. The genus *Alona* was also represented by *Alona manueli* (Sinev and Zawisza, 2013) and *Alona ossiani*, which, based on the cluster analysis, were grouped together, along with *Alonella nana* (Baird, 1843), *Alonella pulchella* (Herrick, 1884), the *Anthalona verrucosa*-group and *Disparalona dadayi* (Birge, 1910). The multivariate analysis showed a negative correlation between Group 3 and lake conductivity, which most likely resulted from the presence of species included in Group 3 in lakes with conductivity ≤100 μS cm⁻¹ and with medium conductivity (204-331 μS cm⁻¹). Lake Sacnab (412 μS cm⁻¹) and Lake Lachuá (906 μS/cm) are exceptions, and two species from Group 3 (*i.e.*, *Alona ossiani* and *Alona manueli*, respectively) were present.

Sinev (1998) showed that *Alona ossiani* belongs to the *Alona affinis complex,* which is considered an oligotrophic species in Eurasia (Kamenik *et al.*, 2007; Korhola and Rautio, 2001). On the other hand, *Alona manueli* (an endemic species of Central America) and *Alonella pulchella* were identified in oligotrophic lakes in Mexico (Cuna *et al.,* 2014; Sinev and Zawisza, 2013). Moreover, this studied provided the first record of *Alonella pulchella* in the tropical region, as previously this species was recorded only in Canada (Korosi and Smol, 2012). The obtained results seem to confirm the preference of these species for waters of low trophic status. The negative correlation of Group 3 with the lake area may indicate the preference of these species for smaller lakes with well-developed littoral zone. In particular, *Alonella*

Tab. 3. Groups of species correlated with each other at the minimum level of 0.8 and distinguished based on the cluster analysis.

Group	Species composition
1	*Daphnia pulex*-group, *Bosmina longirostris*
2	*Bosmina* (*E.*) *coregoni*, *Bosmina* (*E.*) *longispina*, *Alona glabra*, *Alona quadrangularis* type, *Leberis* sp.
3	*Alona manueli*, *Alona ossiani*, *Alonella nana*, *Alonella pulchella*, *Anthalona verrucosa*-group, *Disparalona dadayi*
4	*Euryalona* sp., *Kurzia* sp., *Leydigia acanthocercoides*-group
5	*Acroperus* sp., *Alona* cf. *intermedia*, *Camptocercus dadayi*, *Dunhevedia* sp., *Pleuroxus denticulatus*
6	*Alona rustica*, *Simocephalus* sp.

nana, was present in only three small lakes with area ≤0.1 km². This suggests that, similarly to what observe in Europe, *Alonella nana* may prefer small lakes (Fryer, 1968; Korosi and Smol, 2012). Furthermore, the presence of *Alona ossiani* in mountain lakes may indicate a pronounced tolerance toward the harsher climatic conditions determined by altitude. The Eurasian species *Alona affinis*, is considered to tolerate lower temperatures (Kamenik *et al.,* 2007; Locke and Sprules, 2000) and the results of the present study indicated that *Allona ossiani* shows similar characteristics in Central America.

Leydigia louisi louisi and *Leydigia acanthocercoides*-group played a significant role in Lake El Muchacho (almost 90%), which was characterized by a water transparency of only 0.4 m. Moreover, these species were relatively abundant (>10%) in other lakes with water transparency below 0.9 m. The CCA analysis confirmed the preference of these species for waters with lower Secchi visibility. The presence of a species characteristic of Central America such as *Leydigiopsis ornata*, which is a typical benthic species (Van Damme and Dumont, 2010), was recorded only in 2 shallow (<2.5 m water depth) and scarcely transparent lakes, which were characterized (Secchi depth <1 m). *Graptoleberis testudinaria*, which was recorded in the sediments of Lakes Atitlán, Quexil and Verde, preferred waters with higher Secchi visibility (≥2.7 m), as showed also by the CCA analysis. However, the results of the multivariate statistical analysis are highly controversial, because *Garptoleberis testudinaria* is commonly considered to be associated with aquatic vegetation (Fryer, 1968; Rybak and Błędzki, 2016). This suggests that other factors not included in our analysis control the distribution of this species.

Pleuroxus denticulatus (Birge, 1879) remains were identified in the sediments from four lakes (Chicabal, Jucutuma, Ticamaya, Los Negritos) and its maximum contribution to the Cladocera communities did not exceed 12% (average=6.4%). The presence of only one *Pleuroxus* species in the lakes of the study area and its local distribution confirms the rarity of this Cladocera group in the tropical region (Korovchinsky, 2006).

Canonical correspondence analysis outlined altitude as a key driver of the cladoceran fauna of in Central America. Other significant environmental factors affecting the Cladocera distribution were water transparency and conductivity. Among the environmental variables considered in this study, the less significant in affecting the waterflea population in the study area was the concentration of dissolved oxygen.

CONCLUSIONS

This study showed a relatively typical distribution of Cladocera in lakes of the Neotropic region. In summary, our results indicate that: i) the most common Cladocera species of the study area was *Chydorus* cf. *sphaericus*, likely in relation to the ability of this species to adapt to different ecological conditions; ii) planktonic species of Daphniidae and Bosminidae were the most abundant; iii) Daphniidae species were recorded primarily in highland lakes; iv) *Eubosmina* and the *Alona quadrangularis* type showed pronounced tolerance to waters with high mineralizativon level; e) *Alona ossiani*, *Alona manueli, Alonella nana* and *Alonella pulchella* were negatively correlated with water conductivity; vi) the presence of *Alonella nana* was restricted to lakes with a smaller surface area; vii) *Alona ossiani* was an important subdominant species in shallow lakes located at high altitudes; viii) among the environmental variables considered, altitude was a key driving factor for distribution of the Cladocera fauna whereas dissolved water oxygenation was almost insignificant.

These results provide basic information on Cladocera communities in freshwater ecosystems of Central America, a region where research carried out so far is insufficient to provide robust taxonomical and ecological information.

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