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Distribution, diversity and ecology of modern freshwater ostracodes (Crustacea), and hydrochemical characteristics of Lago Petén Itzá, Guatemala

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ABSTRACT

We analyzed modern ostracode species assemblages and water column physico-chemical characteristics in Lago Péten Itzá, Guatemala. Lake waters are dominated by sulfate, bicarbonate, calcium and magnesium and display a total ion concentration of ~11 meq L^{-1}. Eleven extant ostracode species were identified. We found higher abundances of living ostracodes, as well as relatively higher species richness (eight species) and biodiversity (H of 1.6) between the littoral zone and a water depth of 20 m. At water depths >40 m, these variables all decreased. The thermocline is located at a water depth of ~20-40 m. Cluster analysis revealed three water depth ranges in the lake of importance to ostracode distribution: 1) littoral zone (0.1-3 m), 2) water depths from the base of the littoral zone to the base of the thermocline (3-40 m), and 3) water depths below the thermocline (40-160 m). The assemblage "Darwinula-Heterocypris-Pseudocandona-Strandesia" *is characteristic of waters <15 m. The* "Cypridopsis-Cytheridella-Limnocythere" *assemblage characterizes waters <40 m and* "Physocypria" *indicates waters >40 m. Ostracode taxa from Lago Petén Itzá show specific ecological preferences related to water depth and associated physico-chemical characteristics, thus illustrating the potential of ostracodes as indicators of lake level changes and hydrodynamics.*

Key words: freshwater ostracodes, ecology, Lago Petén Itzá, Guatemala, hydrochemistry, water depth

1. INTRODUCTION

Ostracodes are microscopic bivalved crustaceans that are often used for paleolimnological and paleoclimate reconstruction owing to their high abundance, wide distribution, good preservation in lake sediments, and their sensitivity to many environmental factors. Their utility in some regions is limited, especially where little is known about their modern ecological preferences. Investigation of the modern ostracode fauna and species ecologies in Lago Petén Itzá, Guatemala, became a priority when the lake was selected for paleolimnological study by the International Continental Scientific Drilling Program (ICDP). One objective was to use microfossils in sediment cores as proxies for past climatic and environmental changes in the lowland Neotropics.

Ostracodes, also called "mussel shrimps," are generally 0.7-1.0 mm long, but their size ranges between 0.3 and 5.0 mm in freshwater systems. Their valves are composed of low-Mg calcite (Bridgwater *et al*. 1999; Dole-Olivier *et al*. 2000; Griffiths & Holmes 2000; Brenner *et al*. 2002; Horne *et al*. 2002; Schwalb 2003; Scharf 2005). They are distributed worldwide and live in almost all aquatic environments, including lakes, rivers, groundwaters, estuaries, and oceans. Previous research has shown that ostracodes are sensitive to changes in water variables such as temperature, conductivity, pH, and depth, as well as substrate type, aquatic macrophyte cover and energy level of the environment (Smith 1993; Mourguiart & Carbonel 1994; Holmes 1996; Horne *et al*. 2002; Smith & Horne 2002; Viehberg 2005; Frenzel *et al*. 2006; Mischke *et al*. 2007). Ostracodes from water bodies in the Petén Lake District, Guatemala, were shown to be useful for paleoclimate reconstructions in the region (Goulden 1966; Curtis *et al*. 1996; Leyden *et al*. 1996; Whitmore *et al*. 1996; Curtis *et al*. 1998; Brenner *et al*. 2002; Rosenmeier *et al*. 2002a, b; Hillesheim *et al*. 2005; Hodell *et al*. 2005; Escobar *et al*. 2009). For instance, Holocene $\delta^{18}O$ records from ostracode valves provided evidence that the terminal Classic Maya collapse in the 9th Century AD was related to drought in the lowland Neotropics (Hodell *et al*. 1995).

Tropical regions, including the Neotropics, serve as "heat engines", and as such, are critical areas for understanding past climate changes. The Yucatán Península of southern Mexico, northern Guatemala and Belize, is located in the northernmost Neotropics and consists of a karst platform with an altitude ranging between about 0 and 300 m a.s.l. (Ibarra-Manríquez *et al*. 2002; Perry *et al*. 2003; Rosenfeld 2002; Rosenmeier *et al*. 2002a; Schmitter-Soto *et al*. 2002; Suárez-Morales 2003). Lago Petén Itzá (N 17°00', W 89°51'), in the southern portion of the Yucatán Península, is part of the central Petén Lake District, Guatemala. Table 1 presents selected morphometric and limnological characteristics of this lake, which is a meso-oligotrophic karst water body, and

Tab. 1. Principal morphometric and limnological characteristics of Lago Petén Itzá gathered from MARN-AMPI (2008), INSIVUMEH (personal communication), and this study. Reported data are from 2005 if not indicated otherwise. [1)] From 1990-2003; [2)] Determined in November 2005.

Morphometric and limnological characteristics		Physico-chemical variables from surface waters above the deepest point (160 m)[2)]	
Longitude	N 17°00'	Dissolved oxygen	8.9 mg L^{-1}
Latitude	W 89°51'	pH	8.5
Altitude	120 m a.s.l	Conductivity	533 µS cm^{-1}
Watershed area	~1064 km^2	Ca^{2+}	2.9 meq L^{-1}
Lake area	~112 km^2	Mg^{2+}	1.5 meq L^{-1}
Lake volume	8.5 km^3	Na^+	0.5 meq L^{-1}
Mean water depth	76.2 m	K^+	0.1 meq L^{-1}
Maximum water depth	160 m	SO_4^{2-}	3.3 meq L^{-1}
Water transparency	7.5 m	HCO_3^-	1.9 meq L^{-1}
Lake trophic status	meso-oligotrophic	Cl^-	0.4 meq L^{-1}
Location of thermocline	~20-40 m	Total ionic composition	10.6 meq L^{-1}
Averaged annual air temperature range[1)]	23.8-27.7 °C	Total phosphorus	9 µg L^{-1}
Averaged annual air temperature	27.2 °C	Water temperature	27.6 °C
Averaged annual precipitation	~1665 mm	$\delta^{18}O$ lake water	+2.9‰
Annual averaged relative humidity	67.3%	$\delta^{13}C$ lake water	-5.2‰

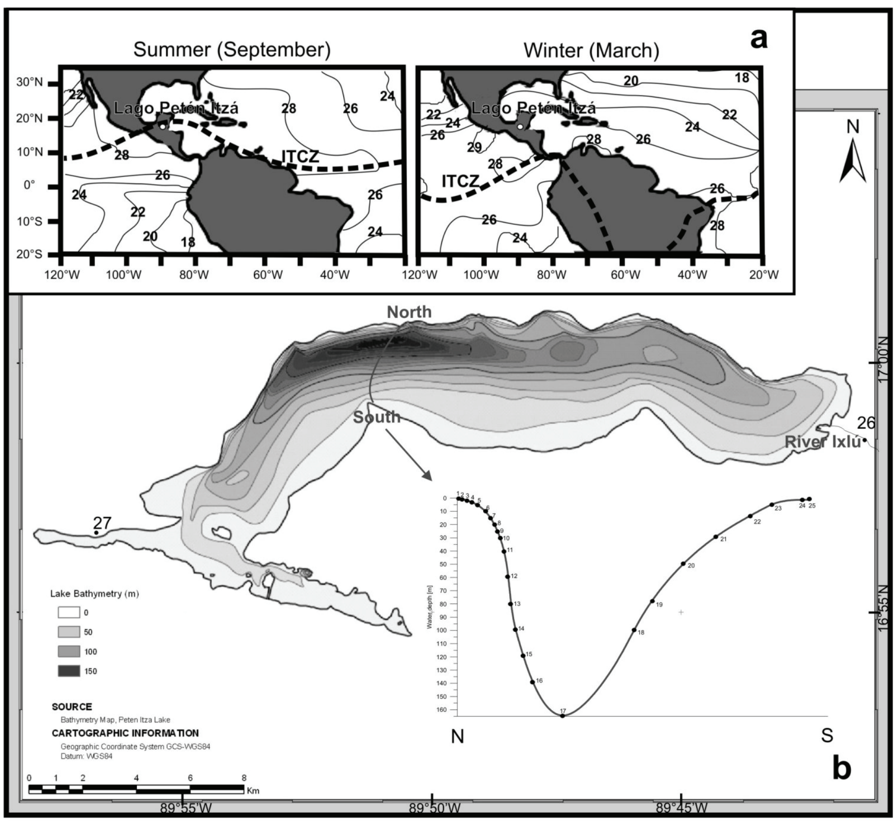


Fig. 1. **a**. Position of the Intertropical Convergence Zone (ITCZ) over the South American Continent. Dashed lines indicate the seasonal variation in the mean position of the ITCZ in summer and winter (modified from Haug *et al*. 2003). **b**. Study area, Lago Petén Itzá, located in northern Guatemala, showing the 27 sampling sites where surface sediment samples were retrieved.

the deepest in the Central American lowlands. Lago Petén Itzá, is ~160 m deep and ~100 km^2 in area (Fig. 1b). The watershed covers an area of ~1064 km^2 (MARN-AMPI 2008). Owing to its great depth, Lago Petén Itzá, unlike most lakes on the Yucatán Península, never dried out during the last Glacial and deglacial, and has consequently yielded a complete sediment record spanning those time periods. Drilling operations in 2006 recovered cores spanning the past >85 kyrs (Hodell *et al*. 2006, 2008).

The region is characterized by relatively humid tropical climate. The minimum monthly mean air temperature in Flores, Petén, occurs in January (22.3 °C) and the maximum temperature is reached in May (29.8 °C). Temperatures start to decrease in June, with the onset of seasonal summer rains. Evaporation is very low during the months of December and January (MARN-AMPI 2008). Precipitation in the region depends on the seasonal migration of the Intertropical Convergence Zone (Haug *et al*. 2003, Fig. 1a) and ranges from 450 mm y^{-1} on the northwest coast, to 2000 mm y^{-1} on the southeastern part of the Yucatán Península (Schmitter-Soto *et al*. 2002). Total annual rainfall in Flores in 2005 was ~1665 mm. The rainy season typically lasts from late May to December. Precipitation is highest in the months of June and September, averaging ~215 mm (Pérez *et al*. 2008), but can be influenced strongly by individual tropical storms or hurricanes.

Overland inflow to Lago Petén Itzá is low due to fast infiltration of precipitation into ubiquitous calcrete aquifer layers (Perry *et al*. 2003). Remains of both ancient and 20^{th} Century construction in shallow waters near the present shoreline of Lago Petén Itzá illustrate that this lake experienced significant lake level changes, and that it responds rapidly to climate change.

Lakes in the region vary in their water chemistry as a result of climate, geology, topography and anthropogenic impact. Petén Itzá lake waters are dominated by calcium, bicarbonate, magnesium and sulfate, as it is typical of many karst lakes. Physical and chemical variables were measured in the lake in 1969 (Brezonik & Fox 1974), 1976 (Deevey *et al*. 1980), 1985 (Basterrechea 1988), and 1993 (Curtis *et al*. 1998). There was an increase in ionic concentration over this sampling period. The volume of the lake and its water chemistry are sensitive to changes in precipitation and evaporation ratios that vary on seasonal to decadal timescales. Hillesheim *et al*. (2005) analyzed the oxygen isotopic composition of lake waters and precipitation in August 2002. Mean $\delta^{18}O$ of lake waters was about +2.9‰ and about -4.0‰ for precipitation, indicating the strong influence of evaporation on the oxygen isotope signature of the lake water.

In conjunction with the drilling effort, a sampling campaign was carried out in Lago Petén Itzá and other lakes of the Yucatán Península in November 2005 and February 2008 to collect modern ostracode assemblages and limnological data. Our objective was to gather ecological information on modern ostracode species for a better interpretation of fossil assemblages from Petén Itzá sediment cores.

2. METHODS

2.1. *Collection and analysis of surface sediments, ostracodes and water samples*

The spatial distribution of ostracodes was studied along a north-south water depth transect across Lago Petén Itzá. In the northern part of the main basin of the lake, surface sediment samples were retrieved from the littoral zone (0.5, 2, 3 m) down to a depth of 160 m. Samples were collected at intervals of 5 m to a water depth of 30 m, and at 20 m intervals from 40 m to a depth of 160 m. In the southern part of the main basin, samples were collected from the littoral zone (0.1, 0.7 m), and at water depths of 5, 15, 30, 50, 80 and 100 m (Fig. 1b). Twenty-seven surface sediment samples were collected at the end of the rainy season in November 2005. In February 2008, a littoral zone in the west and the Río Ixlú tributary in the east, were also sampled. Surface sediment samples along the N-S transect were retrieved with an Ekman grab attached to a 170 m long cable on an UWITEC hand winch. Littoral samples were taken in macrophyte beds with a special hand net (mesh size 250 µm). Sediment samples for ostracode analyses were preserved by adding 96% ethanol to reach a final concentration in surface sediments of ~70%. Water samples were collected with a Ruttner sampler at a site located over the deepest part of the lake. Samples were taken from the surface, at 5 m intervals to 20 m, and at 20 m intervals down to a depth of 160 m. Water transparency was measured with a Secchi Disc. Water samples for geochemical analyses were filtered with cellulose acetate (CA) membrane filters (0.2 µm), and then refrigerated. Lake waters were measured in situ for temperature, conductivity, pH and dissolved oxygen using a WTW Multi Set 350i. Bicarbonate (HCO_3^-) was titrated immediately in the field with 0.1N HCl and the endpoint (pH 4.3) was read using methyl orange indicator. Duplicate water samples were collected for later analysis of elemental composition in the laboratory. Samples for cation measurement were preserved with HNO_3^-. Both analyses for anions (F^-, Cl^-, Br^-, NO_3^-, SO_4^{-2}) and cations (Sr^{+2}, Ca^{+2}, K^+, Mg^{+2}, Na^+) took place in the Institute of Environmental Geology (IUG), University of Braunschweig. Anions and cations were determined, respectively, using Ion Chromatography with a 761 Compact IC Metrohm, and Inductively Coupled Plasma Optical Emission with an ICP-OES Jobin Yvon JY 50 P. Total phosphorus from samples conditioned with H_2SO_4 was determined in the Leibniz Institute of Freshwater Ecology and Inland Fisheries, Berlin. Water samples preserved with $CuSO_4$ (500 mg L^{-1}) were analyzed for carbon and oxygen isotopes in the Department of Geological Sciences and Land Use and Environmental Change Institute (LUECI), University of Florida. Water samples for $\delta^{18}O$ were measured using a VG/Micromass (now GV Instruments) PRISM Series II isotope ratio mass spectrometer. Oxygen isotopic results for waters are reported in delta notation relative to Standard Mean Ocean Water (VSMOW). Carbon isotopic ratios of DIC (Dissolved Inorganic Carbon) were measured with a Finnigan-MAT DeltaPlus XL isotope ratio mass spectrometer with a GasBench II universal on-line gas preparation device. Loss-on-ignition from surface sediments was determined after Heiri *et al*. (2001) at 550 °C and 950 °C, for the estimation of organic matter content and carbonate, respectively. Big shells of gastropods were removed from sediment samples to avoid their influence on carbonate content determination. Measurements were carried out in the IUG.

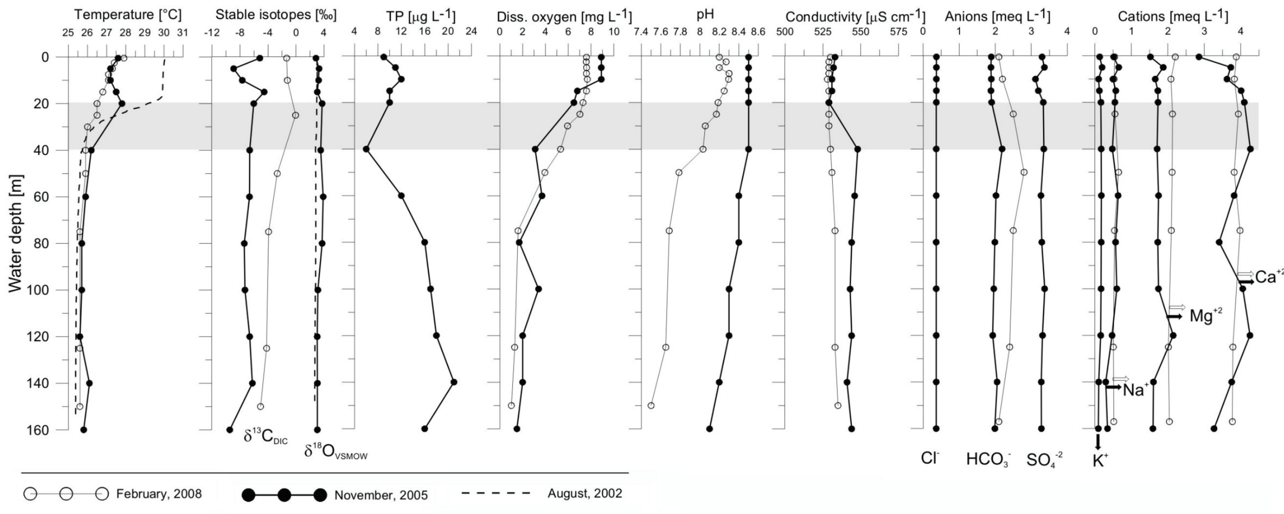


Fig. 2. Physical and chemical variables determined in a vertical water column profile at the deepest point of Lago Petén Itzá, Guatemala (November, 2005 and February, 2008). Grey bar at 20-40 m water depth indicates the location of the thermocline. Dashed lines show temperatures and $\delta^{18}O$ values reported by Hillesheim *et al*. (2005) for August 2002.

2.2. Ostracode distribution analysis

For ecological analysis and interpretation, we used adult ostracodes with well-preserved valves and soft parts. We also distinguished between living individuals (carapaces with soft parts) and dead specimens (carapaces without soft parts). Ostracodes collected in 2005 were separated from sediment samples with fine brushes. Adult ostracode recovery was facilitated by wet-sieving surface samples with a 250 µm mesh size, which removed clay and silts from samples. At least 5 mL of wet sediment was analyzed from each sample. Samples with <100 valves were analyzed completely. Species relative abundances were calculated as percentages in 50 mL of wet surface sediment. Ostracode species were identified using the taxonomic works of Brehm (1939), Furtos (1933, 1936a, b), Deevey *et al.* (1980), Pérez *et al*. (2009).

2.3. Biodiversity indices, cluster analyses and correlations

The Shannon Wiener Index "H" (Krebs 1989) was determined for the ostracode assemblages at each water depth to compare diversities, and the evenness index "E" (Magurran 1988) was calculated to evaluate the uniformity of species distributions in samples from different water depths. If the E value is 1, then individuals are evenly distributed among species in the sample. We used Renkonen's percent similarity index (Renkonen 1938), which is based on species relative abundance, to determine the similarity between samples. Surface samples with <100 valves in 50 mL of wet sediment, collected at 80 and 95 m water depth in the northern segment and at 80 m in the southern segment of the transect, and samples with low abundances of *Cypretta brevisaepta*?, and *Candonocypris serratomarginata*?, were excluded from the multivariate analyses on normalized data. Normalization of the data was achieved by dividing the mean by the standard deviation (x-mean/stdev). Cluster analysis (Ward's method, Euclidean distance) was used to define groups of water depths and of ostracode species based on their abundances. Ostracode species abundances were correlated with water depth, dissolved oxygen, and water temperature using Spearman's correlation. Other physico-chemical variables displayed only slight changes throughout the water column and thus were left out of this analysis. All analyses were done with the program PAST, version 1.89.

3. RESULTS

3.1. Hydrochemistry

Water transparency in Lago Petén Itzá was 7.5 m in November 2005, and 6.6 m in February 2008. Lake waters had an average total phosphorus (TP) concentration of ~13 µg L^{-1} in November. Water column data (Fig. 2) from the deepest site in the lake suggest it is meso-oligotrophic. Water temperatures at 15 m water depth in November were ~1 °C higher than those measured in February. The vertical temperature profile reported by Hillesheim *et al*. (2005) for August 2002 shows higher epilimnetic temperatures, and a total decrease of 4.5 °C in the metalimnion. Temperatures in August ranged from 30 to 25.4 °C. The temperature range in November and February was smaller, from about 27.9 to 25.6 °C. In both November and February, the thermocline was located between 20 and 40 m water depth, and temperatures in the hypolimnion ranged from 25.6 to 26.0 °C. In November, water at 5 and 10 m depth had slightly lower temperatures (27.2 °C) than water at the surface and 20 m depth (27.8 °C). The carbon isotopic composition ($\delta^{13}C$) of the water column was more negative in November than in February. $\delta^{13}C$

of dissolved inorganic carbon (DIC) ranged from -9.5 to -4.6‰ in November, and from -5.1 to -0.1‰ in February. $\delta^{13}C$ values from 5 and 10 m water depth were more negative (-8.9 and -7.7‰) in November than values at the surface and at 20 m (-6‰). $\delta^{18}O$ values in the water column displayed similar values top to bottom and were fairly stable across seasons. The oxygen isotopic composition in November 2005 averaged +3.3‰, ranging only from +2.9 to +3.9‰, and in August 2002, averaged +2.9‰ (+2.7 to +3.0‰). Total phosphorus concentrations in the vertical profile ranged from 6 to 21 $\mu g\ L^{-1}$, with highest values in the hypolimnion.

Dissolved oxygen concentration in surface waters was 8.9 mg L^{-1} in November, while bottom waters contained only ~1.25 mg L^{-1}. Surface waters displayed a pH range of 8.2-8.5. The lowest value (7.5) was measured in February 2008 in deep waters of the lake (~150 m), and probably reflects the presence of abundant respiratory CO_2. Conductivity in November ranged from 529 to 544 $\mu S\ cm^{-1}$, and 528 to 535 $\mu S\ cm^{-1}$ in February. Conductivity increased slightly with water depth. Salinity was 0.2‰. The total ion concentration at the surface was ~10.6 meq L^{-1}. Sulfate and bicarbonate were the dominant anions, and calcium and magnesium were the dominant cations. Concentrations of cations were very similar in November 2005 and February 2008. Cl^-, Na^+, and K^+ were present in relatively low concentrations (<0.7 meq L^{-1}). Chloride concentration in all water samples was 0.4 meq L^{-1}. Sulfate concentration ranged between 3.1 and 3.4 meq L^{-1} and HCO_3^- between 1.9 and 2.2 meq L^{-1}. Maximum concentrations of cations occurred in November 2005: calcium (4.3 meq L^{-1}), potassium (0.2 meq L^{-1}), magnesium (2.1 meq L^{-1}), and sodium (0.7 meq L^{-1}). The minimum concentrations in that year were: calcium (2.9 meq L^{-1}), potassium (0.1 meq L^{-1}), magnesium (1.5 meq L^{-1}), and sodium (0.3 meq L^{-1}).

3.2. Ostracode species assemblages of Lago Petén Itzá across the north-south water depth transect

Eleven ostracode species were identified in surface sediments from the N-S transect, the littoral zone in the west of Lago Petén Itzá, and in the Río Ixlú tributary (Tab. 2). For details regarding taxonomy, Scanning Electron Microscope (SEM) and Light Microscope photographs of taxa, see Pérez *et al*. (2009).

3.2.1. Species richness, diversity and abundances

Figure 3 shows species assemblages, species relative abundances, and biodiversity indices along the north-south transect in Lago Petén Itzá. Relative abundances (%) of carapaces with and without soft parts, and valves from adult ostracodes are presented. Maximum species richness on the south end of the transect was eight, and on the north end seven. The Shannon Wiener Index ranged in the northern transect segment from 0.24 to 1.59, and in the southern transect segment from 0.74 to 1.84 (Fig. 3). The highest diversities were found at water depths of 0.7 m (1.63) and 30 m (1.84) in the southern part of the lake, and the lowest at 2 m (0.24) in the northern part of the lake. The Evenness Index ranged on the northern transect segment from 0.13 to 0.98 and on the southern segment from 0.27 to 0.95. The lowest Evenness Index was determined on samples taken at a water depth of 50 m in the south and at 2 m in the north. The Renkonen similarity percentage correlates well with the dominance of *P. globula*. The lowest Renkonen percentage in the northern transect segment was 30.4%, corresponding to a water depth of 100 m, and 34.5% at 5 m. The lowest percentage in the south was 31.5% at a water depth of 50 m. The highest percentages (91.7 and 90.4%) were found at 30 and 20 m water depth, respectively, on the northern transect.

The dominant species in the lake are *P. globula* and *C. okeechobei*, followed by *L. opesta*, *C. ilosvayi* and *Pseudocandona* sp. *Strandesia intrepida*, *H. punctata*, and *D. stevensoni* are less common. *Cypridopsis okeechobei* showed the highest number of living ostracodes (502 individuals at 3 m water depth on the northern transect), followed by *L. opesta* (214 individuals in the littoral zone of the northern transect) and *P. globula* (101 individuals at 5 m on the southern transect). *Cytheridella ilosvayi*, *D. stevensoni*, and *Pseudocandona* sp. were generally represented by valves rather than living specimens.

Tab. 2. Modern ostracode fauna of Lago Petén Itzá, Guatemala.

Crustacea
Ostracoda
Candonidae Kaufmann, 1900
Physocypria globula Furtos, 1933
Pseudocandona sp.
Cyprididae Baird, 1845
Candonocypris serratomarginata? (Furtos, 1936)
Cypretta brevisaepta? Furtos, 1934
Cypridopsis okeechobei Furtos, 1936
Heterocypris punctata Keyser, 1976
Stenocypris major (Baird, 1859)
Strandesia intrepida Furtos, 1936
Darwinulidae Brady & Norman, 1889
Darwinula stevensoni (Brady & Robertson, 1870)
Limnocytheridae Klie, 1938
Cytheridella ilosvayi Daday, 1905
Limnocythere opesta Brehm, 1939

3.2.2. Grouping of ostracode assemblages based on species assemblages at various water depth ranges

Analysis of the ostracode distribution, diversity, and abundance allowed classification of three main water depth ranges in Lago Petén Itzá: littoral zone (0.1-3 m), above and at the thermocline (≤40 m), and below the thermocline (>40 m). Two dendrograms (Figs 4a, b) show the relationship between ostracode abundances and water depth. Figure 4a classifies all sampled water depths into 5 groups and three main water depth ranges:

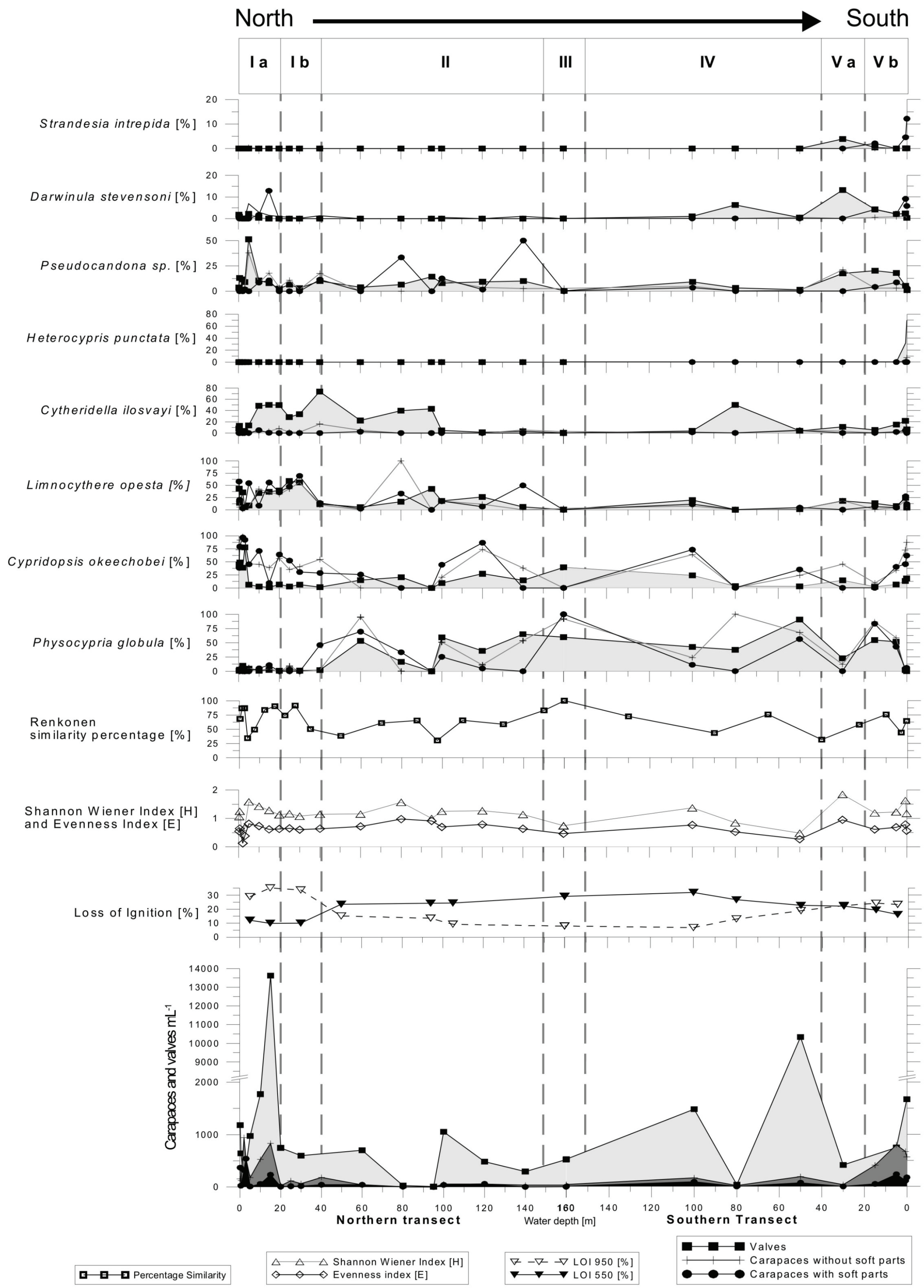


Fig. 3. Modern ostracode species assemblages (adult valves, carapaces with and without soft parts) from surface sediments collected in 2005 across a north-south transect in Lago Petén Itzá. Species relative abundance, biodiversity indices, and loss on ignition are shown. The light grey shading in the bottom graph indicates the number of valves; grey, carapaces without soft parts; and black, carapaces with soft parts in 50 mL of wet sediment.

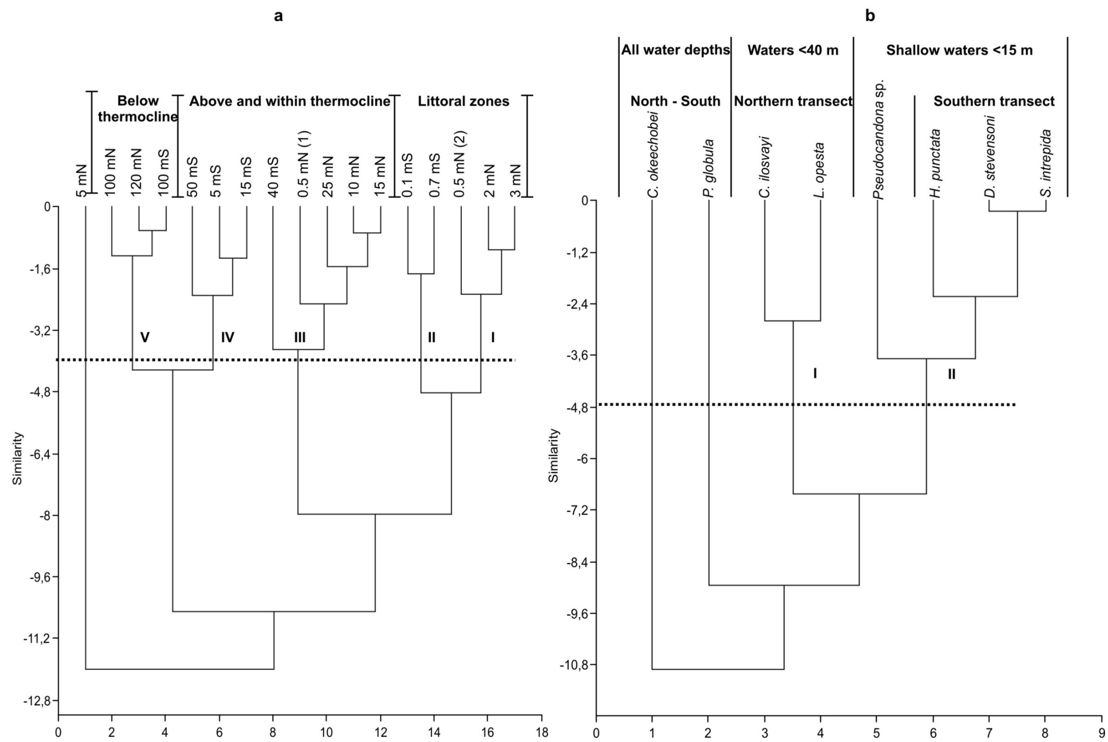


Fig. 4. Dendrograms of two cluster analyses using Ward's method. Dashed line shows the cut-off criterion for cluster partitioning. **a**. Cluster analysis based on water depths in a north-south transect, indicating the three groups of water depths based on species relative abundances in Lago Petén Itzá (1) littoral zones, (2) depths above, at the thermocline, and (3) below the thermocline; **b**. Cluster analysis showing species three main associations and ostracode water-depth preferences: (1) water depths <40 m, (2) shallow waters <15 m, (3) and water depths >40 m.

(1) Littoral zone (0.1-3 m)

Groups I and II in the cluster analysis (Fig. 4a) consist only of depths in the littoral zone from 0.1 to 3 m, where temperature (27.6 °C) and the dissolved oxygen concentration (8.9 mg L^{-1}) reach maxima. There, macrophyte cover, consisting mainly of *Typha domingensis*, *Vallinesneria americana* and *Potamogeton* sp., was higher than at other water depths. Ostracode carapaces were more abundant from the littoral zone to a water depth of 20 m (Sections Ia, and Vb, Fig. 3). Carapaces lacking soft parts were most abundant (943 carapaces 50 mL^{-1}) at a water depth of 2 m along the northern shore of the lake, and carapaces containing well preserved soft parts (541 carapaces 50 mL^{-1}) were mostly collected at 3 m water depth, also in the north (Section Ia, Fig. 3).

(2) Above and at the thermocline (≤40m)

Groups III and IV (Fig. 4a) comprise water depths from the littoral zone to 40-50 m, i.e. from the base of the littoral zone to the base of the thermocline. Compared with surface waters, these deeper water depths are characterized by decreases in dissolved oxygen concentration of ~5 mg L^{-1} and a temperature reduction of ~1.7 °C. From 20 to 40 m (Sections Ib, Va, Fig. 3) abundances decreased. These depths, i.e. 20-40 m, define the position of the thermocline (Fig. 2). The highest number of valves in the N-S transect (13,623 valves 50 mL^{-1}) was found at a water depth of 15 m near the northern shore of the lake (Section Ia, Fig. 3). There, *C. ilosvayi* and *L. opesta* were the dominant species.

(3) Below the thermocline (>40 m)

Group V (Fig. 4a) includes depths from 100-160 m, well below the thermocline. Here, conductivity is only slightly higher (544 µS cm^{-1}) than in shallower water depths (533 µS cm^{-1}), but oxygen content is low (1 mg L^{-1}) and temperatures reach minimum values (25.6 °C). Fewer carapaces with and without soft parts were usually found below 40 m depth (Sections II, III, IV, Fig. 3), but the highest number of valves along the southern part of the transect (10,845 valves 50 mL^{-1}) was found at 50 m water depth (Section IV, Fig. 3).

The second dendrogram of the cluster analysis (Fig. 4b) classifies the species into two groups and three species associations based on their spatial distribution: 1) *Cytheridella-Limnocythere-Cypridopsis* (Group I): *Cytheridella ilosvayi* and *Limnocythere opesta* are benthic species that live at a maximum water depth of ~40 m and are more abundant in shallow waters (<20 m) of the northern transect segment. Living specimens of *L. opesta* dominated primarily in waters <40 m, and specimens of *C. ilosvayi* were scarce in the lake. *Cypri-*

Tab. 3. Spearman's correlation between species abundance, dissolved oxygen and temperature in lake waters. Variables with a high correlation (+/- 0.7-1.0) are shown in bold underlined numbers. Bold numbers indicate a correlation between 0.6-0.7. Correlation values are shown in the lower triangle and the probabilities in the upper triangle of the matrix. Diss. O: Dissolved oxygen; Cond.: Conductivity; Temp.: Temperature; C. okee: *C. okeechobei*; C. ilos: *C. ilosvayi*; D. stev: *D. stevensoni*; Pseudo. sp.: *Pseudocandona* sp.; H. punc: *Heterocypris punctata*; L. opes: *L. opesta*; P. glo: *P. globula*; S. intre: *S. intrepida.*

	Depth	Diss. O	Temp.	C. okee	C. ilos	D. stev	Pseudo. sp.	H. punc	L. opes	P. glo	S. intre
Depth		0.00	0.00	0.07	0.60	0.13	0.72	0.03	0.69	0.00	0.00
Diss. O	**-0.96**		0.00	0.09	0.56	0.10	0.96	0.12	0.73	0.00	0.00
Temp.	**-0.89**	**0.84**		0.24	0.37	0.14	0.51	0.10	0.50	0.00	0.00
C. okee	-0.39	0.36	0.26		0.00	0.12	0.12	0.23	0.25	0.07	0.10
C. ilos	-0.12	0.13	0.20	-0.59		0.02	0.11	0.80	0.00	0.24	0.89
D. stev	-0.32	0.35	0.32	-0.33	0.49		0.00	0.30	0.25	0.93	0.04
Pseudo. sp	0.08	-0.01	-0.14	-0.33	0.34	**0.68**		0.19	0.26	0.29	0.15
H. punc	-0.44	0.34	0.35	0.26	-0.06	0.23	-0.28		0.71	0.23	0.20
L. opes	-0.09	0.08	0.15	-0.25	0.57	0.25	0.24	-0.08		0.05	0.99
P. glob	**0.65**	-0.60	**-0.71**	-0.39	-0.25	-0.02	0.23	-0.26	-0.42		0.07
S. intre	**-0.73**	**0.71**	**0.61**	0.35	-0.03	0.44	0.31	0.28	0.00	-0.38	

dopsis okeechobei is nektobenthonic and is the dominant species in the littoral zone where there is abundant vegetation; 2) *Pseudocandona-Heterocypris-Darwinula-Strandesia* (Group II): *Pseudocandona* sp., *H. punctata*, *D. stevensoni* and *S. intrepida* inhabit primarily shallow waters (≤15 m). *Pseudocandona* sp. prefers water depths between 5 and 15 m in the northern segment of the transect. Few living specimens of *Pseudocandona* sp. and *D. stevensoni* were found in water depths <15 m. *D. stevensoni* and *S. intrepida* were more abundant in the southern transect segment and were also abundant at a water depth of 15 m. *H. punctata* was found at a maximum water depth of ~1 m in the southern transect; 3) *Physocypria*: Unlike other species, *P. globula* was found at almost all water depths. Living specimens of *P. globula* were the dominant taxon at water depths between 50 and 60 m.

3.3. Ostracode abundances related to water depth and associated variables

The number of ostracodes correlates positively with the carbonate concentration in sediments. Carbonate content in the sediment displays highest concentrations in the lake littoral zone (23.3%), down to a water depth of 20 m (35.2%, Fig. 3). Organic matter concentration in sediment increases at ~20 m (22%) and reaches highest values at 100 m (31.9%) and 160 m (29.1%). Few ostracodes were encountered in these organic-rich deposits. Shallow waters down to 20 m depth are characterized by low amounts of clay and high quantities of silt. Sediments from deeper waters are composed of higher amounts of clay and lower amounts of silt.

We used simple correlation to explore relationships among ostracode abundances, water depth, temperature, and oxygen concentration (Tab. 3). Water depth is negatively correlated with oxygen concentration (r = -0.96), temperature (r = -0.89), and with the abundance of *Strandesia intrepida* (r = -0.73). *Physocypria globula* displays a positive correlation with water depth (r = 0.65). Dissolved oxygen showed a relatively strong positive correlation with temperature (r = 0.84) and with the abundance of *S. intrepida* (r = 0.71). Water temperature is negatively correlated with abundance of *Physocypria globula* (r = -0.71) and positively correlated with abundance of *S. intrepida* (r = 0.61). *Darwinula stevensoni* showed a positive correlation of 0.68 with *Pseudocandona* sp.

4. DISCUSSION

An understanding of modern physico-chemical requirements of ostracode species is important for interpreting the paleoenvironmental significance of ostracode fossil assemblages. This study provides some of the first ecological information necessary for using ostracodes as indicators of past climate and environmental changes in the lowland Neotropics.

4.1. Physical and chemical characteristics of lake waters

Lago Petén Itzá was thermally stratified at the end of the rainy season in 2005 (November), and during the dry season in 2008 (February). Stable stratification was also reported from July 1969 (Brezonik & Fox 1974), and August 2002 (Hillesheim *et al.* 2005). The thermocline is located between ~20 and ~40 m water depth (Brezonik & Fox 1974; Basterrechea 1988; Hillesheim *et al.* 2005). Brezonik & Fox (1974), and Basterrechea (1988) attribute the stable stratification in Lago Petén Itzá to the large density difference per degree change in temperature in warm waters, lake basin morphometry, and high relief along the north shore, which provides wind protection. Thermal profiles measured in 1980 (Brenner & Binford, unpublished data) close to the north-shore village of San Andrés (~40 m water depth), showed the thermocline located between 10 and 20 m water depth from June to August. This highlights the importance of measuring vertical temperature profiles at different water depths throughout the lake.

$\delta^{13}C$ values of DIC were more negative in November 2005 than in February 2008, suggesting less primary productivity and lower phytoplankton concentrations in November than in February. Secchi disc transparency in November was greater (7.5 m) than in February (6.6 m), suggesting lower plankton concentrations in November. Secchi disc transparency in November and February was ~2-2.5 m greater than values reported by Brezonik & Fox (1974) and Basterrechea (1988). Water transparency in the lake is determined largely by turbidity, which is mostly associated with plankton density. Temperatures in June and July are higher than in November and February and nutrient concentrations are probably higher in the rainy season. Thus, plankton concentrations in summer are higher and Secchi disc transparency is lower. Turbidity may also increase during the rainy season (May-December) because of higher surface runoff, which carries abundant suspended material. Although evaporation is normally lower in November than in August, higher input of precipitation in August with more negative isotopic values (δ^{18}OSMOW: -4.0‰, Hillesheim *et al.* 2005), might explain why the mean δ^{18}O value (3.3‰) of waters we collected in November 2005 was higher than those reported for August (2.9‰) by Hillesheim *et al.* (2005).

The dominant cation in lake waters is calcium and the dominant anion is sulfate. Basterrechea (1988) pointed out that magnesium concentrations in the lake decreased after 1974 and suggested that an increase of calcium could be related to a reduction in groundwater outflow, also leading to higher lake levels. Lago Petén Itzá, however, still lacks a quantitative hydrologic budget.

4.2. Ostracode distribution and diversity along a water depth gradient

The distribution and abundance of ostracode species in Lago Petén Itzá is related to water depth and associated variables temperature, dissolved oxygen, carbonate and organic matter content in the sediments, and sediment type. The carbonate content in sediments is positively correlated with the abundance of ostracodes in part because we did not remove ostracode valves from sediments. Only large gastropod shells were removed. Külköylüoğlu (2005) and Yılmaz & Külköylüoğlu (2006) reported temperature and dissolved oxygen as the most important influences on ostracode species assemblages. Other critical variables that can affect ostracode distribution are altitude, air temperature, degree of organic pollution, water flow velocity, water chemical composition, and water depth (King *et al.* 1996; Mezquita *et al.* 1996, 1999; Frenzel *et al.* 2009). Ostracodes are not directly influenced by water depth (Wrozyna *et al.* 2009). Instead, changes in physical and chemical variables and type of substrate associated with water depth influence the ostracode species composition. Temperature, pH, dissolved oxygen concentration, species richness and abundances all decrease in the metalimnion (20-40 m). Ostracodes mostly inhabit waters <20 m because deeper waters (>75 m) are low in oxygen, and sediments are rich in organic matter and poor in carbonates. Waters <20 m depth contain more plants, which provide ostracodes with protection against predation. Plant epiphyton provides ostracodes with food. Müller *et al.* (2009) identified a "shallow-water zone" in Lago Petén Itzá extending to 23 m water depth, with a high abundance and diversity of gastropods. They also defined a "deep-water zone" (23-160 m), characterized by few gastropods. Gastropod and ostracode distribution and diversity are controlled mainly by the position of the thermocline in the lake and lithologic composition of the sediment, thus accounting for the correlation between species abundances and water depth.

Ostracodes are more abundant on the northern side of the lake, but species richness is slightly higher in the south, perhaps reflecting differences in lake morphology. The northern basin is very steep, causing sediment resuspension and redeposition, while the southern basin is much shallower, and possesses seasonal swamps at the edge (Hillesheim *et al.* 2005). The southern part of the lake is characterized by more extensive macrophyte cover and calmer waters. Species preferring such environments are *D. stevensoni*, *S. intrepida* and *H. punctata*. *Cytheridella ilosvayi*, *C. okeechobei* and *L. opesta* prefer environments in the northern segment of the transect. *Physocypria globula* has a wide distribution in Lago Petén Itzá. According to Deevey *et al.* (1980), this species is one of the few non-marine planktonic ostracode species in the world. In their study, they discovered that this species is actually part of the zooplankton and thus truly planktonic. We only analyzed surface sediments and did not retrieve Schindler-trap samples for zooplankton as did Deevey *et al.* (1980). We occasionally found ostracode carapaces of "living" specimens in deep waters (50-60 m). This might indicate that the species tolerates low oxygen concentrations (~3 mg L^{-1}) in waters, or that ostracodes that inhabit more oxygenated waters may have died and been carried to deep sites by currents. In such cases, physico-chemical variables at the collection site may not be truly indicative of the ostracode's preferred environment. Ability to reside in deep waters may be a means to avoid predation by fish (Deevey *et al.* 1980). In a study of vertical migration of *P. globula* (which they mistakenly identified as *Cypria petenensis*) in Laguna de Yaxhá (~25 m water depth), Deevey *et al.* (1980) found that adult specimens avoided the upper ~2 m of the water column during daylight hours, but could be found at depths with little dissolved oxygen, consistent with our observations. Our results show a positive correlation between *P. globula* and organic matter concentration (Fig. 3). As noted above, we sometimes found carapaces with soft parts of *P. globula* in deep waters, which probably corresponded to ostracodes that were transported to these deep-water, organic-rich sediments after death. *Strandesia intrepida* showed a relatively strong negative correlation with water depth (r = -0.73) and positive correlations with temperature (r = 0.61) and dissolved oxygen (r = 0.71). This indicates that the distribution of this species is probably determined by a combination of these related factors. It requires warm temperatures (>27 °C) and high concentrations of dissolved oxygen (>7 mg L^{-1}).

We determined the number of whole carapaces at each sampling site, as this might be indicative of post-mortem transportation. High numbers of intact carapaces would indicate low or no post-mortem transport and rapid burial (Whatley 1988), which is the case in the littoral zone and waters <15 m of Lago Petén Itzá. The amount of carapaces, however, might also depend on the type of hinge, or solution used when preserving ostracodes, i.e. alcohol. We found the highest number of valves across the N-S transect at a water depth of 15 m on the northern side of the lake. *Cytheridella ilosvayi* and *L. opesta* were the dominant species there. Nevertheless, close to this sampling site, at 2 m water depth, fewer valves were encountered. The Renkonen similarity index, which compares ostracode abundances among samples, yielded a low value for samples from 2 and 15 m water depth, which is related to low abundance of valves in 2 m of water. We suspect that valves 2 m water depth were transported to the site at 15 m. The Renkonen index was also low (30.3%) when we compared ostracode abundances from samples retrieved at 95 and 100 m. The number of valves in samples from these water depths was very low (<44 valves), and we again suspect that valves from these water depths were transported from these areas to even deeper sites. Other sediment redeposition sites were identified at 50 and 100 m water depth in the southern part of the lake, where ostracode valve concentrations were relatively high. Anselmetti *et al*. (2006) indicated that at water depths from 20 to 35 m in the metalimnion erosion/non-deposition processes occur, perhaps related to currents. Ostracode analyses of this sort have been used to provide evidence of sediment redeposition (Whatley 1988; Frenzel & Boomer 2005). In our study, the highest numbers of living adult ostracodes, i.e. carapaces with soft parts, corresponded to *L. opesta* and *C. okeechobei*. It is possible that other species were experiencing recruitment when we sampled in November and February, and that juveniles were more abundant than adults during those months. This highlights the importance of collecting ostracodes during different seasons, so that it is possible to assess adult/juvenile ratios, and understand taphonomic features and reproductive patterns (Cohen & Morin 1990; Palacios-Fest *et al*. 2001; Parker *et al*. 2003). There is still a need to study ostracode life histories in Lago Petén Itzá and determine which environmental variables (e.g., changes in precipitation, salinity, etc.) trigger hatching (De Deckker 1983). Additional studies about ostracode communities will provide a better understanding of ostracode ecology. No living specimens and only single valves from *Cypretta brevisaepta*? were collected at a water depth of 15 m on the northern part of the transect, indicating their presence in the lake. This species may be largely restricted to areas we did not sample, and future studies should attempt to collect specimens in other parts of the lake. We sampled only three littoral locations (north, south and west) at two times (November and February). More intensive spatial and temporal sampling might yield species we failed to collect.

4.3. *Ostracode ecological preferences and implications for paleoenvironmental reconstructions*

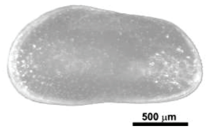
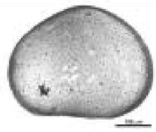
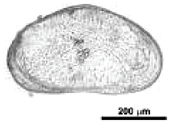
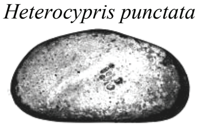
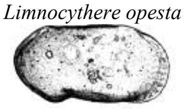
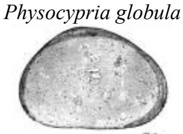
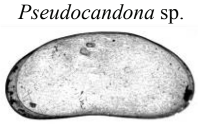
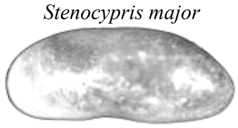
The most important ecological preferences of each species and their implications for paleoenvironmental reconstructions are listed in table 4. Species that primarily live in shallow waters (<1 m) are: *Candonocypris serratomarginata*?, *Heterocypris punctata*, and *Stenocypris major*. *Strandesia intrepida* lives from the littoral zone to a water depth of 15 m. *S. intrepida* and *H. punctata* inhabit only the littoral zone, living among abundant aquatic macrophytes. Species living at a maximum water depth of 20 m are *Cypretta brevisaepta*?, *Cytheridella ilosvayi*, *Darwinula stevensoni*, and *Pseudocandona* sp. Living specimens of *Limnocythere opesta* were found from the littoral zone to a maximum water depth of 40 m. *Cypridopsis okeechobei* and *Physocypria globula* were found at almost all water depths. *Cypridopsis okeechobei* is a nektobenthonic species and is more abundant in the littoral zone. *Physocypria globula* is planktonic and the dominant species in deeper water depths (50-60 m). One important implication for paleoenvironmental reconstruction is that *L. opesta* appears to mark the position of the thermocline. *Physocypria globula* indicates deep waters. *Cypridopsis okeechobei* and *P. globula* display broad hydrochemical tolerance, and their exclusive presence in a sediment sample could indicate environments that are stressful for other species.

5. CONCLUSIONS

Our study shows that the distribution of ostracodes in Lago Petén Itzá, Guatemala, is influenced by the physico-chemical characteristics of the water column and surface sediments. Characteristics such as water depth, temperature, dissolved oxygen concentration, and sediment type, influence the distribution and abundance of eleven ostracode species in the lake. Ostracodes from Lago Petén Itzá sediment cores thus have high potential as indicators of lake level changes. Highest abundance and diversity are found in the littoral zone and in shallow waters down to a depth of 20 m. The thermocline is located between 20 and 40 m water depth, and deeper waters (>40 m) hosted few living ostracodes.

Ostracodes from Lago Petén Itzá can be used for the reconstruction of lake level changes because their distribution can be grouped by depth:

Tab. 4. Most important ecological preferences of Lago Petén Itzá's ostracodes and their application for paleoreconstructions.

Species	Ecological preferences	Application for paleoreconstructions
Candonocypris serratomarginata? 	Nektobenthonic. Prefers running shallow waters (1 m).	Indicator of shallow running waters.
Cypretta brevisaepta? 	Nektobenthonic. Single valves found at 15 m water depth.	Indicator of warm waters, and water depths above thermocline (?).
Cypridopsis okeechobei 	Nektobenthonic. Displays a high hydrochemical tolerance, and prefers calm waters. Valves were collected at all water depths. Living specimens collected no deeper than 40 m. More dominant in the littoral zones with rich vegetation.	If one of the dominant species in the species assemblage, could indicate stressful environment for other species and waters no deeper than 40 m.
Cytheridella ilosvayi 	Benthic. Living specimens found primarily at 10-15 m water depth, distributed only in the Neotropics. Prefers warm waters (>20 °C). Collected at a maximum water depth of 40 m.	Indicator of warm shallow waters (<40 m).
Darwinula stevensoni 	Benthic. Inhabits maximum water depths of 15 m. Prefers aquatic environments with slow currents.	Indicator of shallow waters.
Heterocypris punctata 	Nektobenthonic. Inhabits lake waters not deeper than 1 m. Lives among abundant aquatic macrophytes.	Indicator of littoral zone.
Limnocythere opesta 	Benthic. Abundant in littoral zones with macrophytes. Living specimens found from the littoral zone to a water depth of 40 m.	Indicator of a water depth from the littoral zone to 40 m. Marks the approximate position of the thermocline, and the base of the metalimnion
Physocypria globula 	Planktonic. Tolerates low concentrations of oxygen, to ~3 mg L^{-1}. Abundant at a water depth of 50-60 m. Displays a high hydrochemical tolerance.	If one of the dominant species, could indicate deep waters, ~50-60 m, i.e. below the thermocline and beginning of hypolimnion. Could also indicate stressful environments for other species.
Pseudocandona sp. 	Benthic. Display a high hydrochemical tolerance. Prefers shallow waters (<15 m), but some living specimens were also collected at 40 m.	Could indicate extreme environments, high conductivities. Indicator of shallow waters.
Stenocypris major 	Nektobenthonic. Inhabits waters with conductivities <1025 µS cm^{-1}. Was collected only in river Ixlú (water depth 0.5 m) among aquatic plants such as *Salvinia* sp.	Indicator of shallow running waters.
Strandesia intrepida 	Nektobenthonic. Inhabits shallow waters of 15 m water depth. Typical of littoral zones. Very sensitive to changes in physical and chemical variables.	Indicator of shallow waters, high concentrations of dissolved oxygen and temperatures.

(1) littoral zone (*Heterocypris punctata*, *Strandesia intrepida*), (2) water depths from the littoral zone to the base of the thermocline (*Cypretta brevisaepta*?, *Cytheridella ilosvayi*, *Darwinula stevensoni*, *Limnocythere opesta*, *Pseudocandona* sp.), and (3) water depths below the thermocline (*Physocypria globula*). *Candonocypris serratomarginata*? and *Stenocypris major* are indicative of shallow running waters. *Limnocythere opesta* and *C. ilosvayi* are benthic species marking the location of the thermocline. Our results showed that the distribution of *C. okeechobei* and *P. globula* are not correlated with changes in physicochemical variables, indicating their broad hydrochemical tolerance. To make more effective use of ostracodes as proxies for environmental reconstructions in Lago Petén Itzá, studies are needed in which ostracode juvenile instars are included. This approach might reveal if species collected were actually living at the sampling location, or were transported to the sampling site by water currents. Understanding ostracode ecology is difficult because seasonal (temporal) and spatially-related environmental factors, as well as life-history characteristics, influence the sampled assemblages. More studies on ostracode communities, with respect to seasonal variation, vertical migration, spatial distribution, and hydrochemical and substrate analyses, are required to better understand ostracode ecology.

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