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# Hydrochemistry, ostracods and diatoms in a deep, tropical, crater lake in Western Mexico

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*ABSTRACT*

*Crater lakes are sensitive to natural and anthropogenic environmental changes and it is important to define and understand their current status in order to evaluate past changes related to climate variability and future ones associated with modern global change. We sampled lake waters, surface sediments and sediment trap samples (dry* vs *wet season) in lake Santa Maria del Oro (SMO), Western Mexico (21°22'58"N, 104°34'48"W, 750 m asl). Its present condition was assessed in terms of: i) thermal and oxygen stratification patterns, ii) hydrochemistry and nutrient status, iii) carbonate precipitation (dry* vs *wet season), and iv) spatial (depth) and seasonal (dry* vs *wet season) distribution of ostracod and diatom communities. Our results indicate that this 65-m deep lake is warm monomicitic, with a stable thermal stratification for most of the year (thermocline 16-24 m, metalimnetic gradient up to 7ºC). The water column is thermally homogeneous from late January to early March. Dissolved oxygen is vertically homogeneous only in January, when deoxygenation occurs throughout the water column. This is the first report of such a situation in a Mexican lake. Santa Maria del Oro has slightly alkaline, [$HCO_3^-$]-[$Cl^-$] and [$Na^+$]>[$Mg^{2+}$]>>[$Ca^{2+}$] waters. Although it is a freshwater system, total dissolved solids, electrical conductivity (EC) and [$Cl^-$] indicate that the lake has undergone evaporative concentration. Aragonite precipitation, occurring during the wet and warm part of the year, favours $Ca^{2+}$ depletion and $Cl^-$ enrichment of lake waters. This is a mesotrophic lake with relatively high soluble reactive phosphorus and silica levels. Nitrogen reaches its highest values during winter mixing (January), but becomes the limiting nutrient during stratification. Ostracod and diatom assemblages differ in specific regions of the lake. Ostracods are more diverse and abundant in littoral areas with dense vegetation, where the community is mainly formed by* Potamocypris variegata*,* Cypridopsis vidua *and* Darwinula stevensoni*. Diatoms show high diversity and low dominance in the littoral areas, where benthic, periphytic species (*Amphora coffeaeformis*,* Planothidium delicatulum *and* Hippodonta lunemburgensis*) are dominant. Deeper (>10 m) areas show low diversity and high dominance, and sediment trap data indicate a diatom bloom during winter mixing, dominated by* Aulacoseria ganulata *and* Nitzschia amphibia*.*

*Key words: hydrochemistry, ostracods, diatoms, tropical lake, crater lake.*

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## INTRODUCTION

Central Mexico is characterised by intense Neogene volcanism centered on the trans-Mexican volcanic belt (TMVB), a volcano-tectonic chain that crosses Central Mexico in an East-West transect at about 21-19ºN. As a consequence of this recent volcanism, the TMVB has several crater lakes; these cluster in two main areas, at Los Tuxtlas, Veracruz (Vazquez *et al.*, 2004), and in the Oriental basin, Puebla (Vilaclara *et al.,* 1993*)* (Fig. 1), but there are several others along the TMVB (Armienta *et al.,* 2008). Most are small (<1 km$^2$), with depths ranging from a few metres (2 to 4 m) up to about 60 m. Santa María del Oro (SMO), Nayarit, in the western sector of the TMVB, is one of the largest and deepest of these lakes, with a ~2 km diameter and 65.5 m maximum depth (Serrano *et al.,* 2002).

The hydrology of several of these lakes, mostly those in the less humid climates, has reflected recent human impact by a marked reduction in lake levels (Alcocer *et al.,* 2000b; Kienel *et al.,* 2009) or by an increase in turbidity and trophic status as a result of changes in land use (Caballero *et al.,* 2006). These alterations show how sensitive these systems are to changes in environmental conditions, whether they are driven by human activities or by natural environmental variability. These lakes are therefore potentially good environmental archives recording not only lake evolution but also changes in the basin, vegetation and climate (Caballero *et al.,* 2006; Kienel *et al.,* 2009). In particular, SMO was selected for palaeoenvironmental research because it is considered to be sensitive to long-term climatic changes due to its geographical location, close to the arid frontier of Mesoamerica and the vegetation ecotone between tropical deciduous forests and subtopical deserts (Peinado *et al.,* 2011), in a region whose climate is controlled mainly by the intensity of the Mexican monsoon.

Documentation of modern conditions of these lakes provides a reference (base line) against which past and/or future changes can be contrasted. Limnological characterisation of SMO is also advisable since its increasing use as a tourist destination may lead to rapid changes in the system. With these objectives in mind, we investigated the lake's stratification pattern, chemistry and sedimentation, as well as diatoms and ostracods.

### Research area

Santa María del Oro lies at the western end of the TMVB (21°22'58''N, 104°34'48''W, 750 m asl) on the Tepic-Zacoalco rift, near the southern extreme of the Sierra Madre Occidental (Ferrari *et al.*, 2003) (Fig. 1). This lake is 65 km from the Pacific ocean coast, at the border between a higher plain (900 m asl) and a lower valley (660 m asl) that drains towards the Rio Grande de Santiago. The area has an Eocene andesitic basement covered by Miocene volcanic rocks (21.3 Ma) and Pleistocene basaltic flows. The lake is inside a crater which is possibly of Pleistocene age (Vázquez-Castro *et al.,* 2008).

The climate of the area is tropical, sub-humid, characterised by a long dry season that extends for 7 to 8 months (October to May). Mean annual precipitation is 1214 mm $yr^{-1}$, mean annual evaporation reaches 1708 mm $yr^{-1}$, and mean annual temperature is 21°C. June is the warmest month of the year (25°C) and January is the coldest (16.5°C).

The distribution of precipitation favours the presence of a tropical deciduous forest, a highly diverse plant community in which arboreal elements lose their leaves during the long dry season. Today, the natural vegetation in the southern and western parts of the SMO crater has been replaced by cultigens such as *Zea mays* L. and *Agave tequilana* Web. Natural vegetation is better preserved in the rest of the crater owing to the steeper slopes.

The SMO crater is oval with very steep slopes, with an altitudinal drop of about 450 m between the highest point of the crater's rim (~1200 m asl) and the lake's surface (750 m asl). The crater rim is lower on the North-East side, with an area called El Desagüe, now above the lake level, but where an artificial channel formerly drained towards the eastern valley (Fig. 1). Currently, SMO receives water from precipitation, surface run-off and underground flow, and loses water through evaporation and seepage.

The lake is squarish, with steep sides and a scant littoral zone. The lake drops to a nearly flat bottom with a maximum depth of 65.5 m according to Serrano *et al.* (2002), even though in the present study the maximum depth recorded was 59 m. There is a small bay (Agua Caliente) with shallower waters (depth <20 m) on the south-western side of the lake (Fig. 1). Main morphometric characteristics are presented in Tab. 1.

## METHODS

The lake was sampled on 11 occasions between November 2002 and December 2007, on average twice a year (mixing and stratification). Secchi disk visibility and depth profiles [temperature, pH, dissolved oxygen and specific conductivity (SC)] were collected from the deepest part of the lake (C56 station, ~56-58 m) using a multiparametric Hydrolab Datasonde 3. Depth profiles were also collected from the shallower Agua Caliente bay (AC10 station, ~10-12 m) between October 2003 and December 2007 (9 occasions). On every occasion, water samples for major ions, total dissolved solids (TDS) and $SiO_2$ determinations were collected at each station from the surface (0.1 m below lake

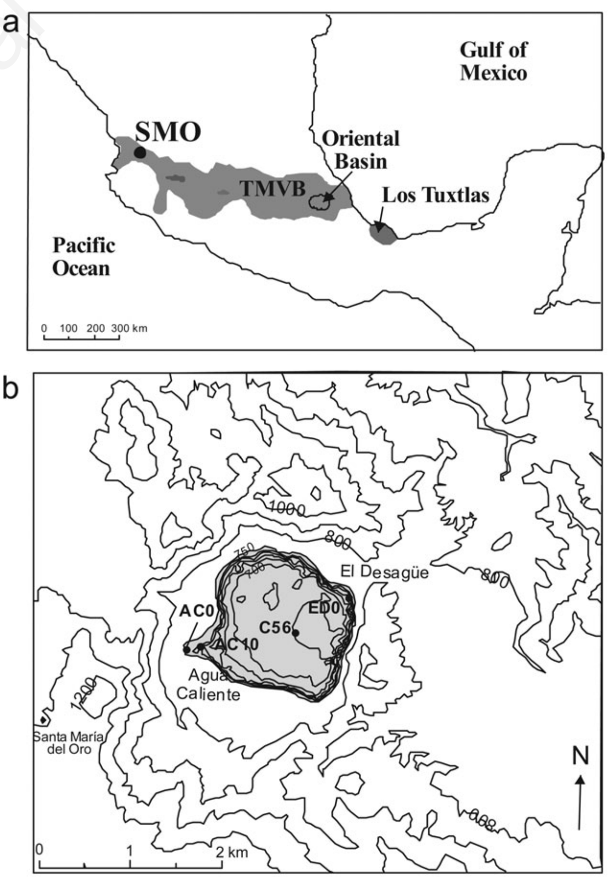


**Fig. 1.** Lake Santa Maria del Oro (SMO): (a) on the western end of the trans-Mexican volcanic belt (TMVB), Central Mexico; (b) the lake and its basin, including lake bathymetry [modified from Serrano *et al.* (2002)].

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surface) and bottom (1 m above sediment) in a Van Dorn type sampler. Samples for total alkalinity, major ions ($CO_3^{2}$, $HCO_3^-$, $Cl^-$, $SO_4^{2-}$, $Na^+$, $Mg^{2+}$ and $Ca^{2+}$), TDS and Si-$SiO_2$ determinations were transported in a cool container and analysed by standard techniques (APHA, 2005; Armienta *et al.*, 2008) in the analytical chemistry laboratory of the Institute of Geophysics, *Universidad Nacional Autónoma de México*. Dissolved nutrients were determined only in surface water samples from each station collected between January 2004 and October 2005 (5 occasions). These samples were filtered through 0.45 and 0.22 µm (Millipore™ type HA; Millipore, Billerica, MA, USA) nitrocellulose membranes, with two drops of chloroform added, and then stored frozen in 30 mL polypropylene containers until analysis (within 48 h). Soluble reactive phosphorus (SRP), $NH_4^+$ (Solórzano, 1969), $NO_3^-$ and $NO_2^-$ (Strickland and Parsons, 1972) were determined on a Skalar San-plus segmented-flow continuous autoanalyser in the aquatic biogeochemistry laboratory in the Marine Science and Limnology Institute, *Universidad Nacional Autónoma de México*.

Surface sediment samples for ostracod and diatom analysis were collected in January and October 2004 and in April and October 2005 along a transect with four stations that covered different areas of the lake: the littoral area in the Agua Caliente bay (AC0 station, 0.5 m), the relatively shallow Agua Caliente bay (AC10 station, 10-12 m), the deep main lake (C56 station, 56-58 m) and the littoral area near El Desagüe (ED0 station, 0.5 m) (Fig. 1). Bottom sediment was recovered with an Ekman dredge, taking care to collect only the top 1 cm of sediment in plastic jars. The littoral samples were collected directly with the sampling jar. Ostracod samples were preserved in 70% ethanol in order to preserve soft body parts. Ostracods and diatoms were also analysed in two sediment trap samples. The sediment traps (8.5 cm inner diameter×84 cm height) were placed at the C56 station, about 2 m above the sediment surface, and left from April to October 2005 (TAO05), representing the wet season, and from October 2005 to April 2006 (TOA06), representing the dry season, thereby covering a full year cycle. Total dry sediment weight captured in each trap was measured, and total inorganic carbon (TIC) was determined by coulometry, evolving $CO_2$ with HCl (UIC 5030). These data are expressed as percentage of dry weight and also as the equivalent $CaCO_3$ concentration, considering that pure $CaCO_3$ has a TIC value of 12%. Bulk mineralogy of sample TAO05 was identified by X-ray diffraction (XRD) analysis using a Philips 1130/96 X-ray diffractometer with digital data collection (Philips, Amsterdam, The Netherlands).

For ostracod analysis, 6 g freeze-dried sediment was soaked in 250 mL deionised water with 0.3 g baking soda for several days. Once the sample had been completely disaggregated, it was slowly wet-sieved through a 63 µm mesh. All the ostracod carapaces with soft parts (living individuals) were picked from the sample under an Olympus SZX12 stereomicroscope (Olympus, Tokyo, Japan) and stored in micropalaeontological slides. The ostracod counts are expressed as valves per gram of dry sediment (v $gds^{-1}$).

For diatom analysis, 0.5 g dry sediment was cleaned successively with HCl (10%), $H_2O_2$ and $HNO_3$. Permanent slides were made with 200 µL of clean material, with Naphrax as mounting medium. Minimum counts of 400 valves were undertaken with an Olympus BX50 microscope with interdifferential phase contrast at 1000× (Olympus). Species composition is reported as relative abundance (%), and total abundance is reported as valves per gram of dry sediment (v $gds^{-1}$). Ostracod and diatom diagrams were prepared with Tilia software (Grimm, 2011).

Species richness (S), Shannon's diversity index (H) and Dominance (D) were calculated for each of the samples in the biological data sets (ostracod and diatom). The non-parametric Kruskal-Wallis test was used to find statistical differences between the data ($P<0.05$), in each case: i) between the physicochemical data (AC10 and C56, surface and bottom), ii) the nutrient and Secchi disk data (AC10 and C56, surface) or iii) between each of the biological data sets (ostracod or diatom in AC0, AC10, C56, ED0, TAO05 and TOA06). The PAST programme (Hammer *et al.*, 2001) was used for these analyses.

**Tab. 1.** Morphometric characteristics of lake Santa Maria del Oro.

| Parameter | Value |
|---|---|
| Crater major axis (km) | 5 |
| Crater minor axis (km) | 3 |
| Crater (catchment) area ($km^2$) | 11.8 |
| Lake length (km) | 2.3 |
| Lake width (km) | 2.2 |
| Lake perimeter (km) | 7 |
| Shoreline developement (%) | 1.03 |
| Lake area ($km^2$) | 3.7 |
| Maximum depth* (m) | 65.5 |
| Mean depth (m) | 46 |
| Relative depth (%) | 3.27 |
| Lake volume* ($km^3$) | 0.17 |
| Basin area:lake area | 3.19 |

**Data from Serrano* et al. *(2002).*

## RESULTS

### Temperature and oxygen depth profiles

Profiles for the C56 station (Fig. 2) show that the lake was fully stratified during the warm months of the year. Only the profiles taken in January and March showed no temperature stratification, and only in January there was no DO stratification. The thermocline was present between 16 (occasionally 10 m) to 24 m, and the oxycline between 13 to 20 m (occasionally 30 m). Average temperature in the epilimnion (top 16 m) was 28.8±0.9°C and in the hypolimnion (30 to 60 m) was 22.4±0.2°C. Metalimnetic temperature differences ranged from 1.6 (April) to 7.3ºC (October). Dissolved oxygen concentrations in the epilimnion ranged from 9.4 mg $L^{-1}$ (oversaturation, 143%) in April to anoxia (<1 mg $L^{-1}$) in January. The hypolimnion was always anoxic, except for March 2004 (1.9 mg $L^{-1}$, undersaturation of 22%).

The water column in the shallower AC10 station had temperature and DO profiles that were relatively straight lines during most of the months that it was sampled, ranging from 22.5 to 30.0°C, and from 0.5 to 9.0 mg $L^{-1}$ DO. As in the main lake, a fully anoxic water column was also recorded in January; only in March did DO show a stratified profile with values ranging from 3-4 mg $L^{-1}$ in bottom waters to 7-10 mg $L^{-1}$ at the surface.

**Water chemistry: salinity and main ions**

Lake water was slightly alkaline (pH>8), with a ionic composition dominated by $[HCO_3^-]$-$[Cl^-]$ and $[Na^+]$>$[Mg^{2+}]$>>$[Ca^{2+}]$ (Tab. 2). Specific conductivity, TDS and $[Cl^-]$ were relatively high for a freshwater lake, falling within the mesohalobus range (500-3000 mg $L^{-1}$) in Kolbe's halobium spectrum, which is frequently used as a reference in the description of the ecological distribution of diatom species (Lowe, 1974).

No differences were found (Kruskal-Wallis, P>0.05) in the physicochemical characteristics of the Agua Caliente bay water column (AC10 station, surface and bottom) and the main lake surface waters (C56 surface). The deep water from the main lake (C56 bottom) did have distinctive characteristics that defined the hypolimnion, with lower temperature, DO, pH and $[CO_3^{2-}]$, and higher $[Si\text{-}SiO_2]$, total alkalinity, $[HCO_3^-]$ and $[Ca^{2+}]$ (Kruskal-Wallis, P<0.05).

**Secchi disk visibility and nutrients**

Secchi disk visibility fluctuated between 1.3 m (Mar04) to 12 m (Oct06). In general, values recorded during mixing (January and March) were lower (<5 m) than during stratification (>7 m, April-November). If the calculated euphotic zone ($Z_{eu}$) is considered to be approximately 1.7 times the Secchi disk visibility (Idso and Gilbert, 1974), then $Z_{eu}$ in SMO had an average value of 10.5±5.5 m, ranging between 2.2 and 20.2 m (Tab. 3). Following the OECD criteria based on Secchi disk visibility (OECD 1982), SMO is classified as a mesotrophic lake.

Soluble reactive phosphorus, dissolved inorganic nitrogen (DIN=N-$NH_4$+N-$NO_2$+N-$NO_3$) and silica (Si-$SO_2$) values in surface waters showed no differences between the C56 and the AC10 stations (Kruskal-Wallis, P>0.05). P-$PO_4$ and DIN were highly variable (Tab. 3), SRP ranged from 0.6 (Oct05) to 9.0 µM $L^{-1}$ (Mar04), and DIN ranged

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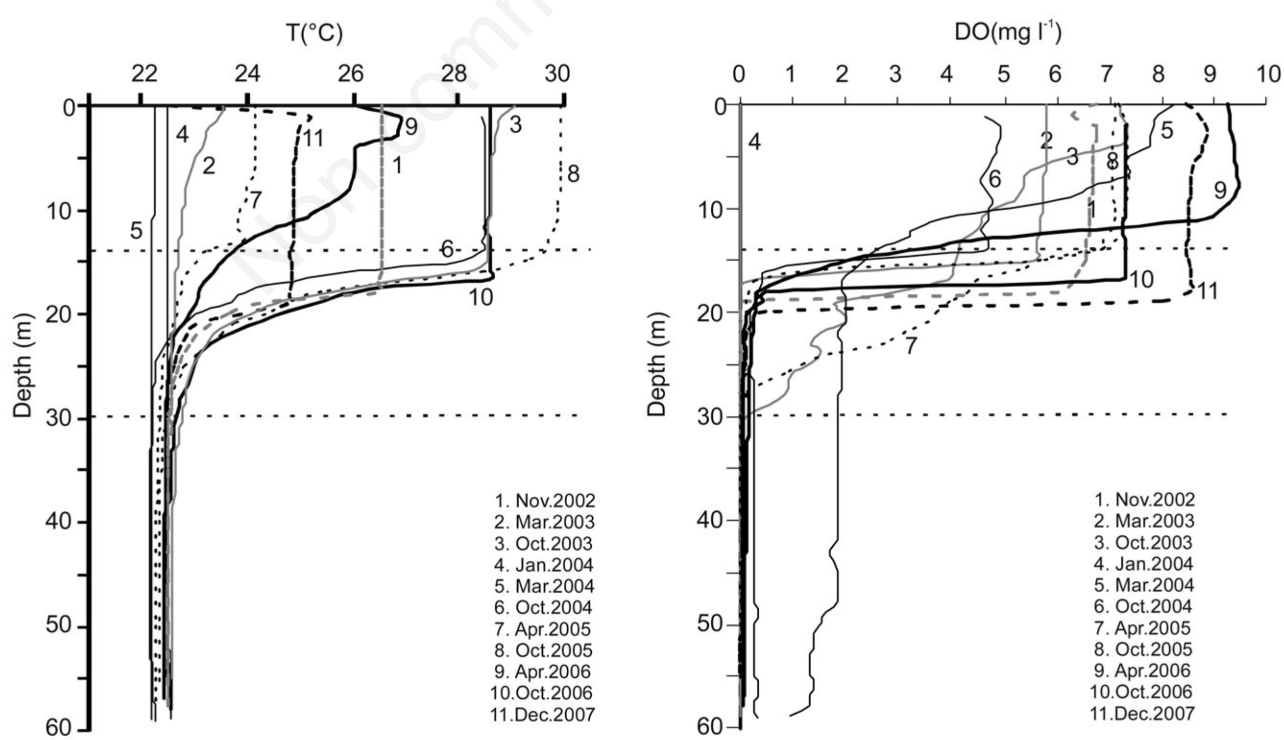


**Fig. 2.** Temperature and dissolved oxygen (DO) profiles from Central (C56) station between November 2002 and December 2007 at lake Santa Maria del Oro.

from 0.9 (Apr05) to 41.0 μM $L^{-1}$ (Jan04) with $N$-$NH_4$ as the most abundant form. Silica concentrations were more uniform, ranging from 300 (Oct05) to 416 μM $L^{-1}$ (Mar04). DIN:SRP ratio was always below the 16N:1P Redfield ratio (Redfield, 1958).

## Total inorganic carbon and X-ray diffraction in sediment trap samples

Total sediment accumulation was slightly higher during the dry season (TAO06), but sediment composition was very different between the wet and the dry seasons (Tab. 4), with TIC, and therefore carbonates, having much higher values in the sediment collected during the wet season (TOA05). According to the XRD analysis, the carbonate-rich TAO05 sample is dominated by aragonite and minor amounts of quartz.

## Ostracods

A total of six ostracod species living in this lake were recorded. Species richness ranged from 1 in the AC0 station to 6 in C56 and ED0. Shannon's diversity was lower than 2 in all the sites, especially in AC0, where only one species was recorded. In each sample except for AC0, dominance was lower than 0.5 (Fig. 3).

Ostracod abundance was lower than 10 valves $g^{-1}$ in the Agua Caliente bay samples (AC0 and AC10); the highest values were recorded in ED0 (954 valves $g^{-1}$). The Agua Caliente bay (AC0 and AC10) also differed in species com-

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**Tab. 2.** Physicochemical data (n=11 for C56 and n=9 for AC10) of surface and bottom waters from deeper Central (C56) and shallower Agua Caliente (AC10) stations.

| | Central (C56) | | | | Agua Caliente (AC10) | | | |
|---|---|---|---|---|---|---|---|---|
| | Surface | | Bottom | | Surface | | Bottom | |
| Variable | Mean | SD | Mean | SD | Mean | SD | Mean | SD |
| Depth (m) | 0 | 0 | 57.4 | ±1.6 | 0 | 0 | 11.88 | ±1.17 |
| Temperature (°C) | 26.1 | ±2.7 | 22.4* | ±0.1 | 26.7 | ±2.8 | 26.1 | ±2.9 |
| pH | 8.6 | ±0.3 | 7.4* | ±0.3 | 8.6 | ±0.3 | 8.6 | ±0.3 |
| Conductivity (μS $cm^{-1}$) | 1366 | ±140 | 1437 | ±106 | 1389 | ±134 | 1386 | ±139 |
| Oxygen (mg $L^{-1}$) | 6.5 | ±2.5 | 0.2* | ±0.3 | 6.8 | ±2.6 | 6.1 | ±2.2 |
| TDS (mg $L^{-1}$) | 805 | ±38 | 827 | ±33 | 814 | ±44 | 810 | ±36 |
| Alkalinity (meq $L^{-1}$) | 8.44 | ±0.34 | 8.81 | ±0.47 | 8.51 | ±0.29 | 8.49 | ±0.28 |
| $CO_3^{2-}$ (meq $L^{-1}$) | 1.82 | ±0.66 | 0.98* | ±0.75 | 1.83 | ±0.76 | 1.81 | ±0.70 |
| $HCO^{3-}$ (meq $L^{-1}$) | 6.63 | ±0.64 | 7.84* | ±1.10 | 6.69 | ±0.65 | 6.69 | ±0.63 |
| $SO_4^{2-}$ (meq $L^{-1}$) | 0.03 | ±0.05 | 0.02 | ±0.03 | 0.03 | ±0.05 | 0.02 | ±0.04 |
| $Cl^-$ (meq $L^{-1}$) | 6.72 | ±0.44 | 6.79 | ±0.29 | 7.00 | ±0.28 | 7.03 | ±0.26 |
| $Na^+$ (meq $L^{-1}$) | 8.16 | ±0.73 | 8.06 | ±0.56 | 8.24 | ±0.55 | 8.16 | ±0.57 |
| $K^+$ (meq $L^{-1}$) | 0.48 | ±0.02 | 0.47 | ±0.02 | 0.47 | ±0.02 | 0.47 | ±0.02 |
| $Ca^{2+}$ (meq $L^{-1}$) | 1.07 | ±0.29 | 1.5* | ±0.33 | 1.02 | ±0.30 | 1.05 | ±0.32 |
| $Mg^{2+}$ (meq $L^{-1}$) | 5.63 | ±0.18 | 5.65 | ±0.18 | 5.69 | ±0.20 | 5.63 | ±0.29 |

*SD, standard deviation; TDS, total dissolved solids. *Significant differences between samples (Kruskal-Wallis test, P<0.05).*

**Tab. 3.** Secchi disk visibility (n=10 for C56 and n=8 for AC10) and nutrient concentrations (n=5 for both stations) in surface waters from deeper Central (C56) and shallower Agua Caliente (AC10) stations.

| | Central (C56) | | | | Agua Caliente (AC10) | | | |
|---|---|---|---|---|---|---|---|---|
| | Surface | | Bottom | | Surface | | Bottom | |
| Variable | Mean | SD | Mean | SD | Mean | SD | Mean | SD |
| Secchi (m) | 6.1 | ±3.3 | 1.7 | 12.0 | 6.8 | ±2.9 | 1.3 | 9.4 |
| $N$-$NH_4$ (μM $L^{-1}$) | 7.8 | ±11.7 | 0.8 | 28.6 | 7.7 | ±9.6 | 2.3 | 24.7 |
| $N$-$NO_2$ (μM $L^{-1}$) | 0.1 | ±0.07 | 0.1 | 0.2 | 0.1 | ±0.02 | 0.1 | 0.2 |
| $N$-$NO_3$ (μM $L^{-1}$) | 5.0 | ±6.0 | 0.0 | 12.3 | 2.5 | ±2.7 | 0.2 | 6.8 |
| DIN (μM $L^{-1}$) | 12.9 | ±16.4 | 0.9 | 41.0 | 10.3 | ±8.7 | 2.7 | 25.3 |
| SRP (μM $L^{-1}$) | 3.0 | ±3.5 | 0.6 | 9.1 | 2.9 | ±2.7 | 0.6 | 7.6 |
| $Si$-$SiO_2$ (μM $L^{-1}$) | 356 | ±42 | 300 | 416 | 353 | ±32 | 316 | 399 |
| N:P | 7.2 | ±6.7 | 0.5 | 14.9 | 4.6 | ±2.9 | 0.9 | 9.0 |
| Si:P | 250 | ±191 | 46 | 535 | 213 | ±178 | 53 | 514 |
| Si:N | 118 | ±161 | 9 | 399 | 55 | ±39 | 14 | 118 |

*SD, standard deviation; DIN, dissolved inorganic nitrogen; SRP, soluble reactive phosphorus.*

**Tab. 4.** Sediment flux, total inorganic carbon, carbonate, diatom abundance and diatom flux in sediment trap samples from wet (TAO05) and dry (TOA06) seasons, from lake Santa Maria del Oro.

| | TAO05 | TOA06 |
|---|---|---|
| Season | Wet | Dry |
| Days (n) | 174 | 203 |
| Sediment flux (g $m^{-1}$ $d^{-1}$) | 2.3 | 2.8 |
| TIC (%) | 9.0 | 0.6 |
| Carbonate (%) | 75 | 5 |
| Diatom abundance (v $gds^{-1}$×$10^6$) | 64 | 175 |
| Diatom flux (v $m^{-2}$ $d^{-1}$×$10^6$) | 148 | 491 |

*TIC, total inorganic carbon; v $gds^{-1}$, valves per gram of dry sediment; v $m^{-2}$ $d^{-1}$, frustules per square meter per day.*

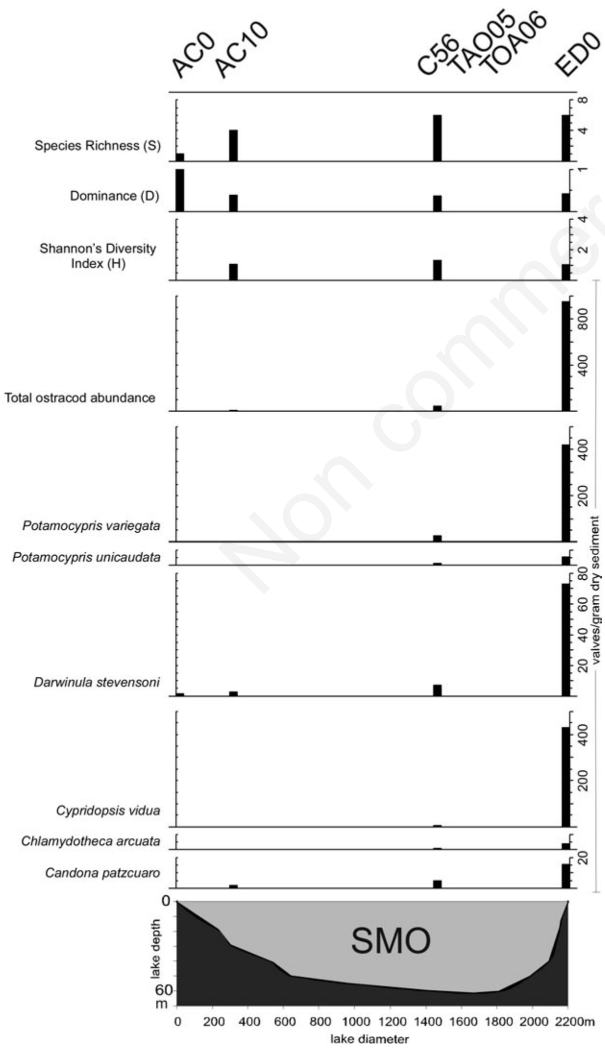


**Fig. 3.** Ostracod species richness, dominance, diversity and composition along a transect in lake Santa Maria del Oro (SMO).

position from the C56 and ED0 samples (Kruskal-Wallis, P<0.05). In the Agua Caliente bay samples, *Darwinula stevensoni* Brady & Robertson was nearly the only ostracod species present, while in the main lake (C56), and especially in the littoral area El Desagüe (ED0), a richer ostracod community was recorded, with *Potamocypris variegata* Brady & Norman, *Cypridopsis vidua* Müller and *D. stevensoni* as the main taxa (Fig. 4). No ostracod valves were observed in the sediment trap samples.

### Diatoms

In total, 38 diatom taxa had higher than 1% abundance in at least one site, of which only 16 had abundances higher than 5% (Fig. 4). The littoral sites (AC0 and ED0) showed higher S and diversity (H>2) with very low dominance (D<0.2), while the deeper water samples (AC10 and C56) had the opposite trend (Fig. 4).

Total diatom abundances were higher in the lake samples (AC10 and C56 stations) than in the littoral sites; the highest value was recorded in C56 (284×$10^6$ v $gds^{-1}$) and the lowest in AC0 (2×$10^6$ v $gds^{-1}$). The lake samples differed from the littoral samples in species composition (Kruskal-Wallis, P<0.05), being dominated by *Aulacoseira granulata* (Eherenberg) Simonsen (>70%). In C56 *A. granulata* was associated (>5%) with *Nitzschia amphibia* Grunow, and in AC10 with *N. amphibia, Hippodonta lunemburgensis* (Grunow) Lange-Bertalot, Metzeltin & Witkowski and *Tryblionella granulata* (Grunow) Mann. At the littoral sites, assemblages were formed mainly (>10%) by *Amphora coffeaeformis* (Agardh) Kützing, *Planothidium delicatulum* (Kützing) Round & Bukhtiyarova and *H. lunemburgensis;* the ED0 assemblage also included 7 other species at abundances between 10 and 5% (Fig. 4).

Diatom valves were abundant in the sediment trap samples, their assemblages showing low species richness (S<4), low diversity (D<2) and high dominance (H≥0.5), similar to the C56 site (Fig. 4). Abundance in each trap was lower than at C56, but higher than at any of the other stations, and if summed (full year cycle) they reach values comparable to those at C56. The diatom assemblage was the same as in C56, dominated by *A. granulata* and *N. amphibia* (Fig. 4). During the dry season (TOA06), percentages of *N. amphibia* (Fig 4), total diatom abundance and diatom flux to the bottom of the lake (Tab. 4) were higher than during the wet season (TAO05). Total annual diatom flux is around 122,000×$10^6$ v $m^{-2}$ $y^{-1}$ (equivalent to 61,000 ×$10^6$ frustules $m^{-2}$ $y^{-1}$ as one frustule is formed by two valves), 82% of which corresponds to the dry season.

## DISCUSSION

### Stratification

Santa María del Oro is a warm monomictic lake which stratifies during the warmer months and briefly mixes dur-

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ing winter. This is the characteristic mixing pattern of deep (>10-12 m) lakes in tropical latitudes (Lewis, 2000), and has been recorded in other deep crater lakes in central Mexico (*e.g.* Alchichica, Oriental basin; Alcocer *et al.,* 2000b). The metalimnetic thermal gradient in SMO reaches values of up to 7°C, which agrees with the maximum of 1°C/m reported by Serrano *et al*. (2002). Given the higher changes in water density per degree in warmer waters (Wetzel, 2001) this metalimnetic temperature gradient implies that the stratification in this lake is very stable. Serrano *et al.* (2002) identified SMO as a lake that remains thermally stratified during most of the year, mixing only in February and March. Our results show that even when the water column was thermally homogeneous (January-March), it could still show a clinograde DO profile; only once (January 2004) did the lake have a well mixed water column, with the disappearance of both the thermocline and the oxycline. This indicates that a complete vertical mixing of the water column in SMO is probably confined to the coldest month (January) during the annual cycle. Serrano *et al.* suggested that this strong stratification probably hinders the vertical transfer of substances in this lake. The epilimnion is, however, well mixed as a result of a daily change in breeze direction (Serrano *et al.,* 2002); SMO is characterised by a valley breeze circulation that is westerly at night and easterly in the afternoon, which generates internal seiches and drift currents of up to 20 cm $s^{-1}$.

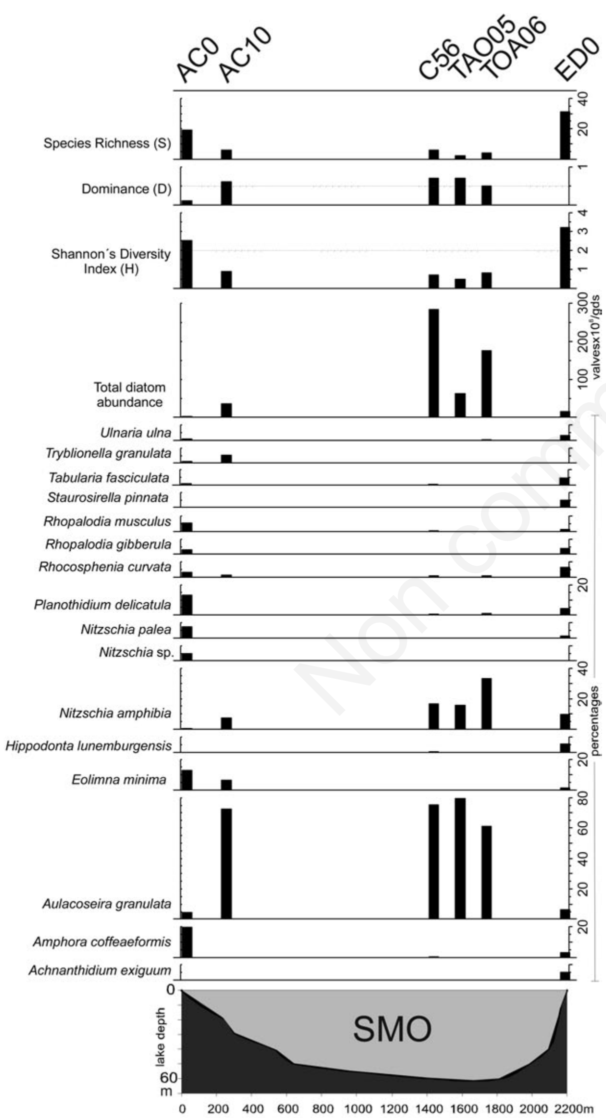


**Fig. 4.** Diatom species (>5%) abundance, diversity, dominance and species richness along a transect in lake Santa Maria del Oro (SMO).

Hypolimnetic temperatures in SMO are very stable throughout the year (22.4±0.2ºC) and correspond closely to the local average air temperatures of the months when stratification is wholly established (April, 21.4ºC) rather than to the colder temperatures of the winter months (January, 16ºC). Hypolimnetic temperatures in the morphometrically very similar lake Alchichica (2.5 $km^2$ and 62 m deep; Alcocer *et al.,* 2000b) are cooler (14.7±0.2ºC) because of its higher altitude (2380 *vs* 750 m asl), but they also correspond to the average air temperature of April (15.4°C) rather than January (10°C).

Thermal stratification in SMO is coupled with an intense DO stratification (Fig. 2). Dissolved oxygen depletion in the water column is so intense that when the lake mixed in January 2004 the water column became wholly anoxic. On the other hand, the deep waters (30 to 65 m) were almost always anoxic; only once were slightly higher DO concentrations (1.9 mg/L, undersaturation of 22%) recorded (March 2004), most likely as a consequence of the complete mixing of the water column during previous January. The intense oxygen depletion in SMO is explained by its high temperature (therefore low oxygen solubility), high relative depth (>2%) and its mesotrophic status. The nearly permanent hypolimnetic anoxia in SMO indicates that winter mixing does not transport enough oxygen to the bottom waters of this relatively deep, mesotrophic lake to compensate for oxygen consumption (respiration, oxidation). Similar oxygen depletion of a whole water column during winter mixing has been recorded in a few productive tropical lakes in Africa (lake Pawlo; Baxter *et al.,* 1965) and Florida (Johnson pond; Whitmore *et al.*, 1991). In tropical lakes, hypolimnetic anoxia due to oxidation of phytoplankton has been recorded even in oligotrophic systems such as lake Alchichica (Adame *et al.,* 2007); in that cooler, oligotrophic lake, however, bottom waters are replenished with DO during the winter mixing. To our knowledge, the case of SMO is the first formal report of full water column

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deoxygenation during winter mixing in a Mexican lake. Nevertheless, as suggested by Whitmore *et al.* (1991), this situation could be more common, maybe even the rule rather than the exception in mesotrophic to eutrophic, deep, tropical lakes. Data from at least two other Mexican crater lakes confirm this approach (Tacambaro, Caballero and Vázquez, unpublished data; Aljojuca, Vilaclara and Alcocer, unpublished data) which is further supported by the common observation amongst Mexican fishermen that during winter fish usually are swimming with their mouths open near the lake surface, a behaviour they call *boqueando*. This raises concerns since the current trend for many tropical lakes is an anthropogenic increase in nutrient loads (Caballero *et al.,* 2006; Vázquez and Caballero, 2013), and most likely an increase in water temperatures due to global warming, which will further lower oxygen solubilities. In this scenario, whole-column oxygen depletion would become more intense and frequent, leading to adverse effects on the biota of these lakes, such as massive fish kills [*e.g.* lake Victoria (Ochumba, 1990) or lake Rio Cuarto (Gocke *et al.,* 1987)].

Physicochemical and nutrient data from the shallower Agua Caliente bay indicate that this area is undifferentiated from the rest of the lake. Temperature and oxygen depth profiles show that its water column corresponds mostly to the epilimnion, as the thermocline and oxycline are usually below the bottom of this shallower area (~12 m). Hypolimnetic anoxic waters could, however, occupy the deeper areas in this bay (>15 m) during early stratification (April), when the thermocline is shallower or occasionally due to thermocline depth fluctuations (*e.g.* tilting) associated with internal seiches. In this area, light can reach the bottom sediment during the stratification period (April-December), but turbidity is higher during mixing, preventing light penetration. These characteristics can be relevant for biota, such as benthic diatoms and osctracods (see below), and it can be of importance for the palaeolimnological interpretation of records recovered from this area (Vázquez-Castro *et al.,* 2008) providing evidence of periods of shallower conditions with light, oxygenated bottom environments or on the contrary deeper intervals with dimmer, anoxic bottom environments.

## Hydrochemistry

Although SMO is a freshwater lake, it has relatively high salinity (0.8 g $L^{-1}$ TDS), electrical conductivity (EC) and [$Cl^-$], close to the advisable limits for drinking water, according to the World Health Organization (TDS=1 g $L^{-1}$, [$Cl^-$]=250 mg $L^{-1}$). This suggests that SMO has experienced periods of evaporative concentration in the past, a situation that is consistent with the high evaporation (1707 mm $y^{-1}$) characteristic of its climate. Evaporative concentration is coupled with aragonite precipitation, and TIC values in the sediment trap samples indicate that this occurs mostly during the wet season. The wet season includes also the hottest months in the year, which are the most favourable for carbonate precipitation (Gierlowski-Kordesch and Kelts, 1994). Carbonate precipitation during the hot season might also be favoured by algal blooms, mainly cyanobacteria, which were observed during field work. Aragonite forms thin white laminae that were observed in the sediment trap and which are characteristic of the laminated sediments of this lake (Sosa-Nájera *et al.,* 2010). Even though salinity and evaporation are not necessarily linearly related during solute evolution (Ito and Forester, 2008), carbonate precipitation in SMO is associated with [$Ca^{2+}$] depletion and [$Cl^-$] enrichment (Path IIIA; Eugster and Hardie, 1978). Lake Alchichica, lying in a drier climate than SMO (399 *vs* 1214 mm annual precipitation), is at a more advanced stage of brine evolution, for it is already a saline lake (~9 g $L^{-1}$) with a ionic composition dominated by [$Cl^-$]>[$HCO_3^-$+$CO_3^{2-}$] and [$Na^+$]-[$Mg^{2+}$], with a near absence of [$Ca^{2+}$] (Armienta *et al.,* 2008; Vilaclara *et al.* 1993). An even more extreme case in the TMVB is Rincón de Parangueo, a crater lake in the state of Guanajuato that has undergone severe desiccation due to a marked drop in phreatic level (Alcocer *et al.,* 2000a) and has become a [$Ca^{2+}$]- and [$Mg^{2+}$]-depleted brine with very high salinity (EC>140 mS $cm^{-1}$) and alkalinity (>1500 meq $L^{-1}$; Armienta *et al.,* 2008).

## Nutrients

In SMO, the DIN:SRP ratio was always below the 16N:1P Redfield ratio (Redfield, 1958), suggesting that DIN, rather than SRP, is the limiting nutrient in this lake (Tab. 3). This is further supported by the relatively high SRP concentration, always above the limiting value of 0.1 μM $L^{-1}$ suggested by Reynolds (1999). On the other hand, DIN values, which were highest during mixing (January), occasionally fell below the limiting value of 6 to 7 μM $L^{-1}$ suggested by the same author (Fig. 5a). Nitrogen limitation, which is more frequent in tropical lakes (Lewis, 2000), has also been reported at other crater lakes in central Mexico (*e.g.* Alchichica; Ardiles *et al.,* 2011); Manantiales, Los Tuxtlas (Vázquez and Caballero, 2013). Si:SRP and Si:DIN ratios were always above the limiting values for diatom growth (Si:P<16, Si:N<1; Xu *et al.,* 2008), indicating that silica availability is not a limiting factor in this lake (Fig. 5b).

Given that nutrient status classifications such as the OECD (1982) are based mostly on data from phosphorus-limited temperate lakes, classification of tropical lakes is best based on criteria other than phosphorus concentrations, *e.g.* Secchi disk visibility (Vázquez and Caballero, 2013). According to this criterion (OECD, 1982), SMO corresponds to a mesotrophic lake.

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## Ostracods

Ostracod populations in SMO have low abundances (<10 valves $g^{-1}$), low species richness (S≤6), low diversity (H<2) and in general low dominance (D<0.5). The Agua Caliente bay (AC10) had a distinctive ostracod assemblage dominated by *Darwinula stevensoni* and *Candona patzcuaro,* both benthic species indicative of silty-sandy sediments with high organic content, usually found at 12-15 m (Meisch, 2000; Tressler, 1954). The littoral area of Agua Caliente bay (AC0) is not a favourable habitat for ostracods because it has a high sediment supply and it is mostly urbanised, with almost no natural (unaltered) habitats.

The ostracod species characteristic of the main lake were *Potamocypris variegata*, *Cypridopsis vidua* and *D. stevensoni*. Given that ostracod valves were not found in the sediment traps, we assume that the valves found in the surface sediment from the centre of the lake (C56) were transported from littoral sites. The El Desagüe station (ED0), with a lower sediment supply and denser littoral vegetation, had the highest ostracod abundance. This site was more representative of the natural littoral environment of the lake and was the best location for ostracod population assessment. With this information we can infer that an increase in ostracod abundance and diversity in the sedimentary record from the Agua Caliente bay would be indicative of shallower conditions, more abundant vegetation and a low sediment input to the lake. Deeper intervals, on the contrary, would lead to lower oxygen bottom conditions and lower ostracod abundance.

The ecology of the ostracod species at El Desagüe is consistent with the limnological characteristics of this lake. *Potamocypris variegata* and *C. vidua* are nektic species indicative of littoral environments with dense aquatic vegetation and spring-groundwater influence (Curry and Delorme, 2003; Meisch, 2000). *Darwuinula stevensoni* and *C. vidua* are known to tolerate relatively high salinity (Holmes, 1992; Meisch, 2000). *Chlamydotheca arcuata,* even though present at very low abundance, is indicative of water temperature above 20ºC (Smith *et al.*, 2003) throughout the year.

## Diatoms

Deeper-water (AC10 and C56) and littoral (AC0 and ED0) sites could be distinguished by their diatom communities. In the deeper-water samples, diatoms showed low species richness (S<10) and high dominance (D>0.5), while diversity was highest (H>2) at the littoral sites. Diatom abundance was higher at the deeper-water sites, with the top values in the centre of the lake, suggesting a low dilution effect by sediment accumulation at this site compared with the Agua Caliente bay. The deeper-water samples (AC10 and C56) had the same diatom assemblage found in the sediment traps, with *Aulacosira granulata* and *Nitszchia amphibia* as the characteristic planktonic diatom taxa. The Agua Caliente bay community also included *Tryblionella granulata* and *Hippodonta lunemburgensis*. This last one is a mesohalobous, benthic species (Lange-Bertalot, 2001) that can survive in this shallower area (~12 m) because during stratification it lies within

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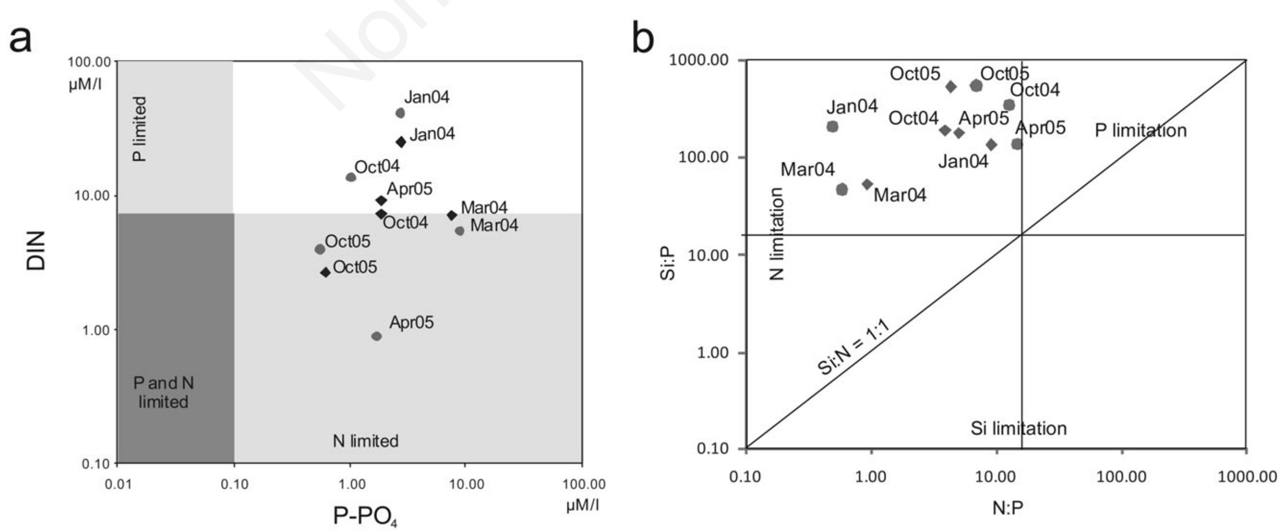


**Fig. 5.** Nutrients in surface waters from AC10 (diamonds) and C56 (circles) stations from lake Santa Maria del Oro. a) P-$PO_4$-DIN diagram, shaded areas define nutrient limiting values [P-$PO_4$<0.1 μM $L^{-1}$, DIN<7 μM $L^{-1}$ according to Reynolds (1999)]; b) nutrient molar ratios showing areas of Si, N or P limitation according to Xu *et al.* (2008).

the euphotic zone. *Tryblionella granulata* is a littoral, marine species (Gasse, 1986; Moreno *et al.*, 1996) and its presence in this lake was surprising; this report extends its ecological range to fresh waters, albeit with relatively high [$Cl^-$]. The littoral samples (AC0 and ED0) were more diverse and richer in periphytic taxa, such as *Amphora coffeaeformis, Planothidium delicatulum* or *H. lunemburgensis*. The presence of these species in the sedimentary record from the Agua Caliente bay would be therefore indicative of shallower water conditions in the past, during which a lower precipitation/evaporation ratio would favour evaporative concentration leading to the present relatively high salinity characteristic of this freshwater lake. Deeper intervals, on the contrary, would lead to dimmer environments not favourable for the development of benthic diatom taxa.

The higher diatom abundance in the dry-season sediment trap, which includes the short mixing period of the lake, together with the low Secchi disk visibility recorded during the winter months (mostly March), are indicative that SMO has a winter diatom bloom. Diatom frustule fluxes to the bottom of the lake suggest that about 80% of the diatom productivity is concentrated during this period. Diatom blooms during winter mixing are relatively common in tropical monomictic lakes; for example, this is the case in lake Alchichica (Oliva *et al.,* 2001). Alchichica is a nitrogen-limited lake but, unlike SMO, it is also limited by silica (Ardiles *et al.,* 2011). Not surprisingly, in that oligotrophic, silica-limited lake, total annual diatom flux is lower than at SMO ($15{,}000\times10^6$ *vs* $61{,}000\times10^6$ frustules $m^{-2}$ $y^{-1}$).

*Aulacoseria granulata* and *Nitzschia amphibia* are the main species during the winter diatom bloom. These species were, however, also abundant during the wet season, suggesting that they are present in the phytoplankton during the full annual cycle. *Aulacoseira granulata* is frequently present in eutrophic lakes because it has high silica and phosphorus requirements (Kilham *et al.,* 1986; Stoermer *et al.,* 1996), which are fulfilled in SMO (Fig. 3). This heavily silicified, meroplanktonic species needs turbulence to remain suspended in the water column (Lund, 1954; Wang *et al.,* 2012); therefore, its dominance in SMO relies on the relatively deep and well mixed epilimnion in this lake (Serrano *et al.,* 2002). *Nitzschia amphibia* is a species with wide ecological tolerances; it is considered eurihalobous (tolerant of a wide range of salinities) and has been reported as planktonic or periphytic (Gasse, 1986). It is also known to be a facultative nitrogen heterotrophic taxon (Van Dam *et al.,* 1994), a metabolic path that would be of advantage in this nitrogen-limited lake.

## CONCLUSIONS

First, SMO is a deep (~60 m), warm monomictic lake that shows a very stable stratification over 9 to 10 months of the year. The water column is thermally homogeneous only from late January to early March. Dissolved oxygen is vertically homogeneous only for a short period in late January, when deoxygenation of the whole water column occurs. Lake mixing brings nutrients to surface waters and high DIN values are recorded; this favours a diatom bloom during winter mixing. By March, the lake shows a well established DO stratification, with a suboxic hypolimnion. Deep waters (>30 m) remain anoxic the rest of the year (11 months). Thermal stratification is established in April with a relatively shallow thermocline (~10) that becomes deeper during well-structured stratification (October), when the metalimnetic temperature gradient reaches 7ºC (1ºC/m) and thermocline and oxycline are at about 16 to 24 m depth. The prevalence of high water column stability and hypolimnetic anoxia are favourable for the formation and preservation of laminated sediments and in general for proxy preservation.

Second, SMO is a freshwater lake with slightly alkaline, [$HCO_3^-$]-[$Cl^-$], and [$Na^+$]>[$Mg^{2+}$]>>[$Ca^{2+}$] waters. The ionic composition and its slightly high salinity (mesohalobus) suggest that the lake has undergone evaporative concentration in the past. Total inorganic carbon contents and XRD analysis in sediment traps indicate that aragonite precipitates when the lake is stratified, during the wet season, which includes the hottest months of the year, producing the thin carbonate layers that are characteristic of the sediments of this lake (Sosa-Nájera *et al.,* 2010). Carbonate precipitation favours [$Ca^{2+}$] depletion and [$Cl^-$] enrichment of the lake waters, a condition not easily found in continental waters with salinities under 1 g $L^{-1}$ as in SMO.

Third, nutrient concentrations and molar ratios indicate that SMO is not limited by SRP or silica. On the other hand, DIN values, which are higher during mixing (January), can fall to limiting values in the mixing layer during stratification. The water column shows higher turbidity during the mixing months, when diatom productivity is higher. The calculated $Z_{eu}$ ranged between 2.2 and 20 m. Based on Secchi disk visibility, SMO is classified as a mesotrophic lake.

Fourth, ostracods showed low diversity and abundance, and their assemblages differed between the Agua Caliente bay (*Darwinula stevensoni* and *Candona patzcuaro*) and the main lake area (*Potamocypris variegata*, *Cypridopsis vidua* and *D. stevensoni*). Highest abundance and diversity were recorded at the El Desagüe station (ED0), which is considered to be representative of the littoral environment of this lake, where ostracod populations are mostly concentrated. Higher ostracod diversity and abundance in the sediments from Agua Caliente bay would be indicative of shallower conditions, more abundant littoral vegetation and low sediment supply.

Last, diatom assemblages point to a significant differ-

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ence between the littoral and the deeper (>10 m) areas of the lake. Littoral environments showed lower abundance, higher diversity and lower dominance than the deep-water sites, with the presence of characteristic benthic or periphytic species, whose presence in the sedimentary samples from the Agua Caliente bay could be indicative of shallower water conditions in the past. Deeper-water sites were dominated mostly by two planktonic diatoms: *Aulacoseira granulata* and *Nitzschia amphibia.* Sediment traps allowed the identification of a diatom bloom during winter mixing which accounts for about 80% of diatom productivity in the lake.

To conclude, the data presented in this paper define the present conditions of SMO as an important step for the evaluation of past and/or future changes in this climatically and ecologically sensitive site which, as most tropical areas, is currently under the effect of stressors such as global warming, increased agriculture and cultural eutrophication. Its relatively high salinity for a freshwater lake and its ionic composition are already giving evidence that the lake has undergone periods of higher evaporative stress sometime during the past. Furthermore, the data presented in this paper provide valuable information for a better understating of tropical limnology; they confirm that tropical lakes with high relative depth (>2%) develop very stable stratification, reflected in both temperature and oxygen depth profiles, which only fully break briefly (one or two months) during winter. Given the lower oxygen solubility due to their higher water temperatures, oxygen depletion in the bottom waters of tropical lakes is frequent even in relatively low nutrient level systems (oligotrophic or mesotrophic). Our data further suggest that deoxygenation of the whole water column during the brief winter mixing can be a relatively common phenomenon in mesotrophic to eutrophic, deep tropical lakes.

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## REFERENCES

Adame MF, Alcocer J, Escobar E, 2007. Size-fractionated phytoplankton biomass and its implications for the dynamics of an oligotrophic tropical lake. Freshwater Biol. 53:22-31.

Alcocer J, Escobar E, Lugo A, 2000a. Water use (and abuse) and its effects on the crater-lakes of Valle de Santiago, Mexico. Lakes Reservoirs Res. Manage. 5:145-149.

Alcocer J, Lugo A, Escobar E, Sánchez MR, Vilaclara G, 2000b. Water column stratification and its implications in the tropical warm monomictic Lake Alchichica, Puebla, Mexico. Verh. Internat. Verein. Theor. Angew. Limnol. 27:3166-3169.

APHA, 2005. Standard methods for the examination of water and wastewater. American Public Health Association ed., Washington, DC.

Ardiles V, Alcocer J, Vilaclara G, Oseguera LA, Velasco L, 2011. Diatom fluxes in a tropical, oligotrophic lake dominated by large-sized phytoplankton. Hydrobiologia 679:77-90.

Armienta MA, Vilaclara G, De la Cruz-Reyna S, Ramos S, Ceniceros N, Cruz O, Aguayo A, Arcega-Cabrera F, 2008. Water chemistry of lakes related to active and inactive Mexican volcanoes. J. Volcanol. Geoth. Res. 178:249-258.

Baxter R, Prosser M, Talling J, Wood R, 1965. Stratificationin tropical African lakes at moderate altitudes (1,500 to 2,000 m). Limnol. Oceanogr. 10:510-520.

Caballero M, Vázquez G, Lozano-García S, Rodríguez A, Sosa-Nájera S, Ruiz-Fernández AC, Ortega B, 2006. Present limnological conditions and recent (ca. 340 yr) palaeolimnology of a tropical lake in the Sierra de Los Tuxtlas, Eastern Mexico. J. Paleolimnol. 35:83-97.

Curry BB, Delorme LD, 2003. Ostracode-based reconstruction from 23,300 to about 20,250 cal yr BP of climate, and paleohydrology of a groundwater-fed pond near St Louis, Missouri. J. Paleolimnol. 29:199-207.

Eugster PH, Hardie LA, 1978. Saline lakes, p. 237-293. In: A. Lerman (ed.), Lakes: chemistry, geology, physics. Springer.

Ferrari L, Petrone CM, Francalanci L, Tagami T, Eguchi M, Conticelli S, Manetti P, Venegas-Salgado S, 2003. Geology of the San Pedro-Ceboruco Graben, western Trans-Mexican volcanic belt. Rev. Mex. Cienc. Geol. 20:165-181.

Gasse F, 1986. East African diatoms, taxonomy, ecological distribution. Gebruder Borntraeger Verlagsbuchhandlung Publ., Berlin: 201 pp.

Gierlowski-Kordesch E, Kelts K, 1994. Global geological record of lake basins. Cambridge University Press, Cambridge: 464 pp.

Gocke K, Bussing W, Cortés J, 1987. Morphometric and basic limnological properties of the Laguna de Río Cuarto, Costa Rica. Rev. Biol. Trop. 35:277-285.

Grimm E, 2011. Tilia program. Illinois State Museum ed., Springfield. Available from: http://intra.museum.state.il.us/pub/grimm/tilia/

Hammer Ø, Harper DAT, Ryan PD, 2001. PAST. Paleontological statistics software package for education and data analysis. Palaeontol Electron 4:1-9. Available from: http://palaeo-electronica.org/2001_1/past/past.pdf

Holmes JA, 1992. Nonmarine ostracods as Quaternary palaeoenvironmental indicators. Prog. Phys. Geogr. 16:405-431.

Idso B, Gilbert RG, 1974. On the Universality of the Poole and Atkins Secchi Disk-Light Extinction Equation. J. Appl. Ecol. 11:399-401.

Non commercial use only

Ito E, Forester RM, 2008. Changes in continental ostracode shell chemistry; uncertainty of cause. Hydrobiologia 620:1-15.

Kienel U, Bowen SW, Byrne R, Park J, Bohnel H, Dulski P, Luhr JF, Siebert L, Haug GH, Negendank JFW, 2009. First lacustrine varve chronologies from Mexico: impact of droughts, ENSO and human activity since AD 1840 as recorded in maar sediments from Valle de Santiago. J. Paleolimnol. 42:587-609.

Kilham P, Kilham SS, Hecky RE, 1986. Hypothesized resource relationships among African planktonic diatoms. Limnol. Oceanogr. 31:1169-1181.

Lange-Bertalot H, 2001. Navicula sensu stricto 10 genera separated from Navicula sensu lato Frustulia. Gantner Verlag, Königstein: 526 pp.

Lewis WM, 2000. Basis for the protection and management of tropical lakes. Lakes Reservoirs Res. Manage. 5:35-48.

Lowe RL, 1974. Environmnetal requirements and pollution tolerance of freshwater diatoms. United States Environment Protection Agency ed., Philadelphia: 333 pp.

Lund JWG, 1954. The seasonal cycle of the plankton diatom Melosira italica (Ehr.) Kutz. subsp. subarctica O. Müll. J. Ecol. 42:151-179.

Meisch C, 2000. Freshwater Ostracoda of Western and Central Europe. Spektrum Akademischer Verlag, Heidelberg: 522 pp.

Moreno JL, Licea S, Santoyo H, 1996. [Diatomeas del Golfo de California]. [Book in Spanish]. Universidad Autonoma de Baja California Sur (UABCS) ed., Mexico City: 272 pp.

Ochumba PBO, 1990. Massive fish kills within the Nyanza Gulf of Lake Victoria, Kenya. Hydrobiologia 208:93-99.

OECD, 1982. Eutrophication of waters. Monitoring, assessment and control. Organization for Economic Cooperation and Development, Paris: 154 pp.

Oliva G, Lugo A, Alcocer J, Peralta L, Sánchez MR, 2001. Phytoplankton dynamics in a deep, tropical, hyposaline lake. Hydrobiologia 466:299-306.

Peinado M, Macías MÁ, Ocaña-Peinado FM, Aguirre JL, Delgadillo J, 2011. Bioclimates and vegetation along the Pacific basin of Northwestern Mexico. Plant Ecol. 212:263-281.

Redfield AC, 1958. The biological control of chemical factors in the environment. Am. Sci. 64:205-221.

Reynolds CS, 1999. Non-determinism to probability, or N:P in the community ecology of phytoplankton nutrient ratios. Arch. Hydrobiol. 146:23-35.

Serrano D, Filonov A, Tereshchenko I, 2002. Dynamic response to valley breeze circulation in Santa Maria del Oro, a volcanic lake in Mexico. Geophys. Res. Lett. 29:27-31.

Smith AJ, Davis JW, Palmer DF, Forester RM, 2003. Ostracodes as hydrologic indicators in springs, streams and wetlands: a tool for environmental and paleoenvironmental assessment, p. 203-222. In: L.E.P.A.J. Smith (ed.), Bridging the gap: trends in the Ostracode biological and geological sciences. Yale University Press.

Solórzano L, 1969. Determination of ammonium in natural waters byphenol-hypoclorite method. Limnol. Oceanogr. 14:799-801.

Sosa-Nájera S, Lozano-García S, Roy PD, Caballero M, 2010. [Registro de sequías históricas en el occidente de México con base en el análisis elemental de sedimentos lacustres: el caso del lago de Santa María del Oro]. [Article in Spanish]. Boletín de la Sociedad Geológica Mexicana 62:437-451. Available from: http://boletinsgm.igeolcu.unam.mx/bsgm/vols/epoca04/6203/(8)Sosa-Najera.pdf

Stoermer EF, Emmert G, Julius ML, Schelske CL, 1996. Paleolimnologic evidence of rapid recent change in Lake Erie's trophic status. Can. J. Fish. Aquat. Sci. 53:1451-1458.

Strickland JHD, Parsons TR, 1972. A practical handbook of seawater analysis. B. Fish. Res. Board Can. 167:1-130.

Tressler WL, 1954. Fresh-water Ostracoda from Texas and Mexico. J. Wash. Acad. Sci. 46:333-336.

Van Dam H, Mertens A, Sinkeldam J, 1994. A coded checklist and ecological indicator values of freshwater diatoms from the Netherlands. Aquat. Ecol. 28:117-133.

Vázquez G, Caballero M, 2013. The structure and species composition of the diatom communities in tropical volcanic lakes of eastern Mexico. Diatom Res. 28:77-91.

Vazquez G, Favila ME, Madrigal R, del Olmo CM, Baltanas A, Bravo MA, 2004. Limnology of crater lakes in Los Tuxtlas, Mexico. Hydrobiologia 523:59-70.

Vázquez-Castro G, Ortega-Guerrero B, Rodríguez A, Caballero M, Lozano-García S, 2008. [Mineralogía magnética como indicador de sequía en los sedimentos lacustres de los últimos ca. 2,600 años de Santa María del Oro, occidente de México]. [Article in Spanish]. Rev. Mex. Cienc. Geol. 25:21-38.

Vilaclara G, Chavez M, Lugo A, Gonzalez H, Gaytan M, 1993. Comparative description of crater-lakes basic chemistry in Puebla-State, Mexico. Verh. Internat. Verein. Theor. Angew. Limnol. 25:435-440.

Wang L, Rioual P, Panizzo VN, Lu H, Gu Z, Chu G, Yang D, Han J, Liu J, Mackay AW, 2012. A 1000-yr record of environmental change in NE China indicated by diatom assemblages from maar lake Erlongwan. Quaternary Res. 78:24-34.

Wetzel RG, 2001. Limnology. Lake and river ecosystems. Academic Press, San Diego: 1006 pp.

Whitmore TJ, Brenner M, Rood BE, Japy KE, 1991. Deoxygenation of a Floriad lake during winter mixing. Limnol. Oceanogr. 36:577-585.

Xu J, Ho AY, Yin K, Yuan X, Anderson DM, Lee JH, Harrison PJ, 2008. Temporal and spatial variations in nutrient stoichiometry and regulation of phytoplankton biomass in Hong Kong waters: influence of the Pearl River outflow and sewage inputs. Mar. Pollut. Bull. 57:335-348.

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