

# Responses to a warming trend and “El Niño” events in a tropical lake in western Mexico

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**Abstract** Lakes are sensitive ecosystems to climatic change but in the tropics it is frequently difficult to evaluate as there are few long-term records. In this paper hydrochemistry and phytoplankton data during the 2009–2010 “El Niño” are contrasted with non-“El Niño” conditions (pre- and post- the 2009–2010 event) and with long-term (23 years) meteorological and paleolimnological data from a lake in eastern Mexico. Meteorological data provide evidence of a recent (since year 2000) warming trend, and paleolimnological data show that the diatom assemblage changed at this time to a more diverse association, including low abundances of a small *Cyclotella* species (*C. ocellata*) and a small needle shaped species (*Fragilaria nanana*) to the previously dominant assemblage (*Ulnaria delicatissima*, *Achnanthyidium minutissimum*). Phytoplankton associations during non-“El Niño” are consistent with the paleolimnological record (*U. delicatissima*–*A. minutissimum*, + *Staurastrum* sp.) but they changed at the onset of “El Niño” (May 2009), when N and P co-limitation favoured a *Coelastrum reticulatum*–*C. ocellata* assemblage. During “El Niño” winter (February

2010) colder temperatures led to a longer mixing period and a whole water column deoxygenation event that favoured a particularly low diversity association (*Botryococcus* sp.–*Sphaerocystis* sp.). The low diversity *C. ocellata*-bloom has no precedent for the last 23 years. The previous 1998–1999 “El Niño” had a similar low diversity assemblage but dominated by *U. delicatissima*. The different response of the phytoplankton to the two “El Niño” events is related with the warmer conditions since the year 2000, that lead to more stable stratification periods and more frequent or intense nutrient limitation, particularly during the warmer than average “El Niño” 2009–2010 summer. Under a global warming scenario, minor changes in ecosystem’s base levels determine that even normal climatic variability events can cause unexpected changes in the ecosystem’s diversity and species composition.

**Keywords** Climate change · Global warming · El Niño-ENSO · Tropical lakes · Phytoplankton · Biodiversity

## Introduction

There is currently a consensus that meteorological data indicate a significant increase in surface air temperatures during the last decades in most regions of the world (IPCC 2013). On top of this general climatic trend, inter-annual variability in temperature and precipitation has been associated with shorter-term events such as the recurrent (2–7 years) El Niño–Southern Oscillation (ENSO) phenomenon. ENSO is considered the most important short-term climatic anomaly and the scientific community is particularly concerned about how its impacts, frequency and intensity, will be modulated by the current global warming scenario (Cane 2005).

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Lakes are amongst the most sensitive ecosystems to climatic variations because temperature changes can modify their thermal behavior, affecting the annual phytoplankton succession as well as the structure of the community at higher trophic levels. Several studies report the impact of global warming on high altitude or high latitude lakes (Catalan et al. 2013; Hampton et al. 2008; Katz et al. 2011; Koinig et al. 2002), showing that a reduction in the ice cover season has had important ecological impacts. However, lakes in temperate and tropical locations are also sensitive to global warming and/or to ENSO temperature fluctuations. In general, global warming is causing more superficial thermoclines, longer and more stable stratification periods and reduced vertical mixing which leads to more intense deep-water oxygen depletion, higher nutrient limitation and changes in phytoplankton succession (Shimoda et al. 2011; Winder et al. 2009). These changes can favor smaller, less palatable phytoplankton species, ultimately lowering fish populations and therefore affecting local economies (Catalan et al. 2013; Ndebele Murisa et al. 2010). During “El Niño” years (warm ENSO phase) all these changes can be further aggravated (Katz et al. 2011; Shimoda et al. 2011). In many regions of Mexico it is very difficult to evaluate recent climatic trends and their impact on lacustrine ecosystems given the limited number of long-term limnological data necessary for such correlations. The few available data are consistent with global trends. For example in Alchichica, one of the deepest (ca. 60 m) lakes in central Mexico, a more superficial thermocline, an increase in metalimnetic temperature gradient and changes in phytoplankton succession were recorded during the 1997–1998 “El Niño” (Alcocer and Lugo 2003). Recent ENSO events have also been related to important changes in two shallow (<10 m) lakes: Chapala (Tereshchenko et al. 2002) and Tecocomulco (de la Lanza-Espino et al. 2011), with shallower conditions during “El Niño” and deeper during “La Niña”.

Given the limited number of long-term limnological records in Mexico, a paleolimnological approach can help to contrast modern climatic trends and climatic conditions during ENSO years with longer-term conditions (1988–2011). In this paper, we analyze the effects of warmer years since ca. 2000 on the sediment diatom associations and of extreme meteorological conditions during the 2009–2010 “El Niño” on the water column, hydrochemistry, and phytoplankton community of the lake as well as on its sediment diatoms. We also contrast the effects in the sediment diatoms associations of the 2009–2010 “El Niño” with the previous 1998–1999 “El Niño”.

## Materials and methods

### Study area

The Alberca de Tacambaro (AT, 19°13'30N, 101°27'30W) is a crater lake on the south-western part of the Trans-Mexican Volcanic Belt (TMVB, Fig. 1a). The climate of the region is temperate (mean annual temperature of 19 °C) with the warmest months from April to June (20–22 °C) and the coldest in January (17 °C). Precipitation (1164 mm year<sup>-1</sup>) is concentrated between June and October. Due to its altitude (1460 m asl) this lake is at the ecotone between the tropical climate of the lower altitudes (<~1500 m asl), where tropical deciduous forest is dominant, and the temperate climate of the TMVB highlands, where pine and oak forest is dominant (Rzedowski 1994).

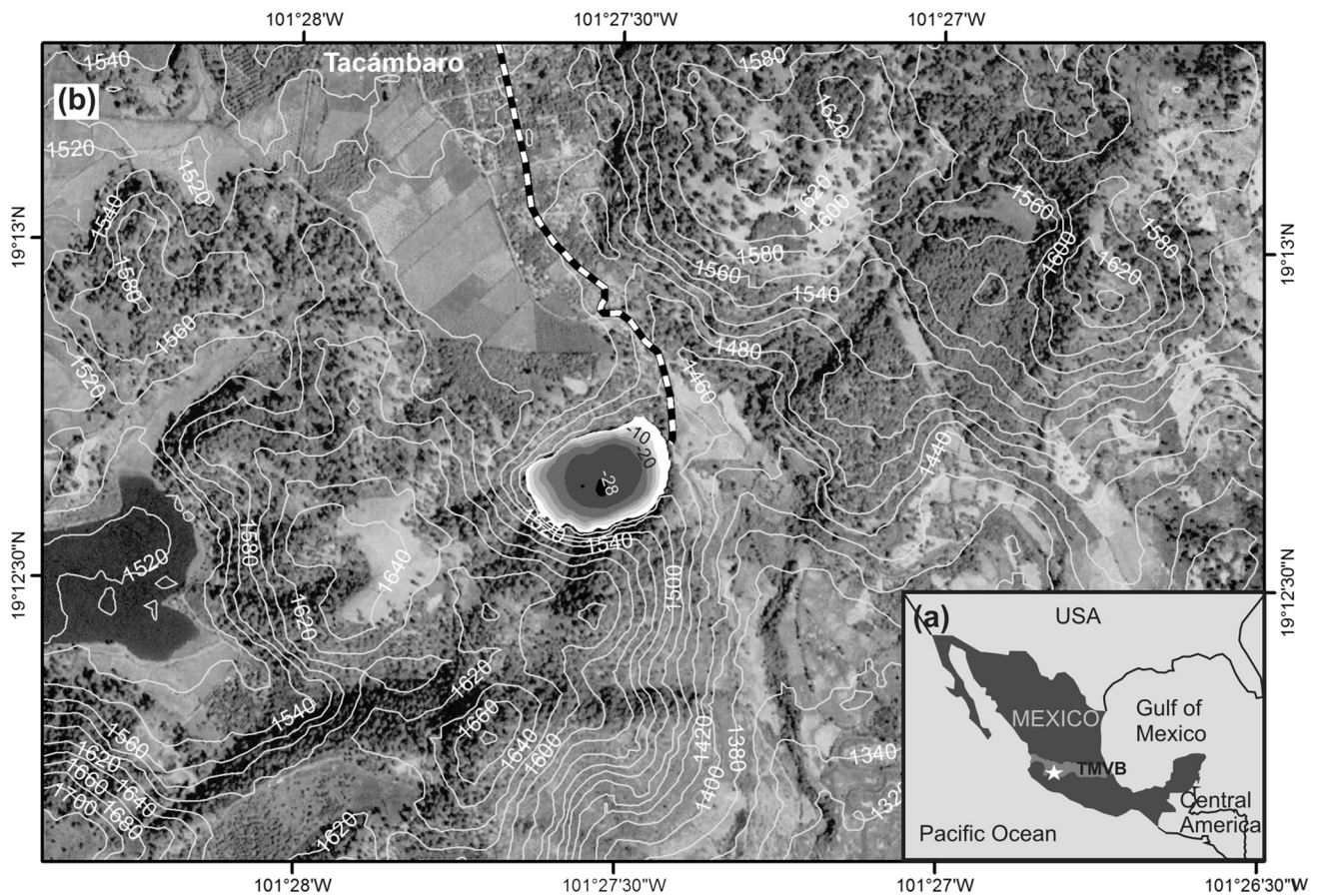
The AT is a small, deep lake (relative depth – maximum depth as a percentage of mean diameter  $\gg 4\%$ ; Fig. 1b) with steep sides and a narrow littoral environment. Its main morphometric characteristics are presented in Table 1. According to temperature and oxygen depth profiles from 2006 (Hernández-Morales 2011; Hernández-Morales et al. 2011) this is a warm monomictic lake (summer metalimnion between 5 and 10 m), with a brief winter mixing and an early stratification starting around February. These last authors report a phytoplankton cell density dominated by: Bacillariophyta [mainly *Synedra (Fragilaria) acus*, winter], Chlorophyta (mainly *Didimocystis* and *Tetraedron*, spring to autumn) and Cyanobacteria (mainly *Microcystis* and *Anabaena*, autumn).

### Meteorological data

The “Servicio Meteorológico Nacional” provided monthly average temperature and total precipitation values between 1930 and 2011 from the closest (<3 km) weather station (SMN16123; 19°14'N, 101°28'W). Temperature and precipitation anomalies to the 1930–2011 mean were calculated for monthly and annual values from 1988 to 2011. Single monthly missing data in this series were interpolated. When two or more successive months were missing that year was discarded from the annual anomalies data. The intensity of ENSO conditions was determined following the Multivariate ENSO Index (MEI) (Wolter and Timlin 1998), which is one of the most comprehensive ENSO indexes (<http://www.esrl.noaa.gov/psd/enso/mei/>).

### Paleolimnology

Surface sediment samples for diatom analysis were collected using an Ekman dredge in August and October 2009,



**Fig. 1** Research area. **a** Location of lake Alberca de Tacámbaro (white star) on western Mexico, shaded area represent the Trans-Mexican Volcanic Belt (TMVB). **b** Topographic map of the research

area including bathymetry of lake Alberca de Tacámbaro, taken from Hernández-Morales (2011)

**Table 1** Morphometric characteristics of lake Alberca de Tacámbaro, western México. Note its particularly high relative depth

Parameter	Units	
Crater major axis	km	0.7
Crater minor axis	km	0.5
Crater (catchment) area	km <sup>2</sup>	0.3
Lake length ( <i>l</i> )	km	0.4
Lake width ( <i>b</i> )	km	0.3
Lake perimeter ( <i>L</i> )	km	1.2
Shoreline development ( <i>D<sub>s</sub></i> )	%	1.2
Lake area ( <i>A</i> )	ha	8.2
Maximum depth ( <i>Z<sub>m</sub></i> )	m	28 <sup>a</sup>
Mean depth ( <i>Z</i> )	m	13
Relative depth ( <i>Z<sub>r</sub></i> )	%	8.6
Lake volume ( <i>V</i> )	m <sup>3</sup> × 10 <sup>6</sup>	1.1 <sup>a</sup>
Catchment area/lake area		4.0

<sup>a</sup> Data from Hernández-Morales et al. (2011)

February 2010 and June 2011. Additionally diatom analyses were performed on each 1 cm slice throughout the top 20 cm of a short core (TAC0106GIII) collected from the center of the lake in 2006 using an Uwitec gravity corer. One sediment sample from this core was sent to a commercial laboratory for radiocarbon age determination (Beta-324552, 126.1 ± 0.5 pMC). This date was calibrated with the CALIBomb program (Hua et al. 2013; Reimer et al. 2013) and used to generate an age-depth model based on a polynomial interpolation between the dated level (34 cm, 1961) and the top of the core (2006), this interpolation model was selected to account for changes in sediment compression towards the top of the core; according to this model the top 20 cm of the core date from ca. AD 1988 to 2006. A composite age sequence was built with the core and the dredge samples.

For diatom analyses, dry sediment samples (0.2–0.5 g) were cleaned using HCl (10 %), H<sub>2</sub>O<sub>2</sub> and HNO<sub>3</sub>.

Permanent slides were prepared with 200  $\mu\text{l}$  of clean material, using Naprax as mounting media. Diatom counts were done using an Olympus BX50 microscope (1000 $\times$ ) with interdifferential phase contrast, minimums of 400 valves were counted. Diatom identification follows specialized literature (Krammer and Lange-Bertalot 1986–1991; Patrick and Reimer 1966). Diatom counts were transformed to concentration (frustules per gram of dry sediment) and later to biovolume ( $\mu\text{m}^3 \text{ gram}^{-1}$  of dry sediment) by approximation to the closest geometrical shapes. Diatom data were handled with the TILIA program (Grimm 2004). A Detrended Correspondence Analysis (DCA) on the sediment (core and dredge) diatom data was done using the PAST program (Hammer et al. 2001) to evaluate the changes in the diatom community through time (Correa Metrio et al. 2014).

### Limnology and phytoplankton

The lake was sampled seven times between November 2008 and June 2011, four of them during the 2009–2010 “El Niño” event (May, August and October 2009 and February 2010). In all occasions visibility was measured with a Secchi disk and depth profiles for temperature and dissolved oxygen were taken from the center of the lake (27 m deep) using a multiparametric probe (Hydrolab Quanta-G). Water samples were collected with a Van Dorn type bottle at different depths for major ions, nutrients, phytoplankton and chlorophyll *a* (Chl*a*) analyses (Table 2). Nutrients and Chl*a* samples were filtered in the field (Whatman GF/C filters). Water samples for major ions and nutrients were stored at 4 °C until analyses were performed, and phosphorus samples were stored in 250-ml glass bottles. Ammonium ( $\text{NH}_4^+$ , Nessler), nitrate ( $\text{NO}_3^-$ , brucine), bicarbonate ( $\text{HCO}_3^-$ ), carbonate ( $\text{CO}_3^{2-}$ ) and total alkalinity as  $\text{CaCO}_3$  (titration with phenolphthalein), chloride ( $\text{Cl}^-$ , titration with  $\text{AgNO}_3$ ), sulfate ( $\text{SO}_4^{2-}$ , turbidimetric technique), total phosphorus (TP, persulfate digestion and ascorbic acid), reactive phosphorus (RP, ascorbic acid) and

silica ( $\text{SiO}_2$ , molybdate) were measured by spectrophotometric techniques (APHA 1998). Calcium ( $\text{Ca}^{2+}$ ) and magnesium ( $\text{Mg}^{2+}$ ) were measured using an atomic absorption spectrophotometer (Shimadzu Mod. AA6501); sodium ( $\text{Na}^+$ ) and potassium ( $\text{K}^+$ ) were measured with a flame photometer (Corning Mod. 410).

For Chl*a* determinations, the filtered material was kept refrigerated in darkness and analyzed within the next 24 h in the laboratory. Chl*a* was extracted with 90 % methanol and measured spectrophotometrically, its concentration ( $\mu\text{g l}^{-1}$ ) was determined through Holden’s equations (Meeks 1974). Unfiltered samples were fixed with Lugol acetate for quantitative analyses of phytoplankton. Phytoplankton cells were counted in sedimentation chambers (2.5–10 ml, 24 h) with an inverted microscope (Hasle 1978). Cell density (cells  $\text{ml}^{-1}$ ) was estimated by counting the total number of individuals per species in the entire bottom area of the sedimentation chamber. Biovolumes ( $\mu\text{m}^3 \text{ ml}^{-1}$ ) were calculated by approximation to the closest geometrical form for each species and multiplying by the species cell density (Hillebrand et al. 1999). Species were identified based on specialized literature (Bourrelly 1970; Komárek and Anagnostidis 1999, 2005; Komárek et al. 1983; Krammer and Lange-Bertalot 1986–1991; Prescott 1962).

Phytoplankton biovolume and physico-chemical variables of the vertical profiles were associated with a Canonical Correspondence Analysis (CCA) with the CANOCO program (v. 4.5) (ter Braak and Šmilauer 2002). Species data were square-root transformed, rare species were scored with low weights in the analysis. The physical and chemical variables were normalized if necessary after an assessment of normality (Shapiro–Wilk’s test) and then standardized by a z-score transformation (mean = 0, standard deviation = 1). Variables with a high colinearity as indicated by high inflation factors (VIF > 10) were discarded. Monte Carlo test (999 permutations) was used to analyze the statistical significance of the identified gradients.

**Table 2** Sampling dates, ENSO conditions, depths collected and types of analysis performed in this study of lake Alberca de Tacambaro, western Mexico

Date	ENSO	Secchi	Depth profiles <sup>a</sup>	Depths collected (m)	Major Ions	Phytoplankton	Nutrients	Chl <i>a</i>
17/November/2008	No	Yes	Yes	0.5, 25	Yes	Yes	No	No
25/January/2009	No	Yes	Yes	0.5, 5, 25	Yes	Yes	Yes	No
29/May/2009	Spring	Yes	Yes	0.5, 5, 8, 10, 25	Yes	Yes	Yes	Yes
1/August/2009	Summer	Yes	Yes	0.5, 5, 8, 10, 15, 20, 25	Yes	Yes	Yes	Yes
4/October/2009	Autumn	Yes	Yes	0.5, 5, 8, 10, 15, 20, 25	Yes	Yes	Yes	Yes
5/February/2010	Winter	Yes	Yes	0.5, 5, 8, 10, 15, 20, 25	Yes	Yes	Yes	Yes
17/June/2011	No	Yes	Yes	0.5, 25	Yes	Yes	Yes	Yes

<sup>a</sup> Depth profiles for temperature and dissolved oxygen were performed in the central region of the lake at 27 m depth, all water samples and other in situ measurements were taken simultaneously

**Diversity indices**

Species diversity for total phytoplankton and for planktonic diatoms at each depth of the water column samples (2009–2011) and also for diatoms in the sediment samples (1988–2011) was respectively analyzed using the numbers equivalents of the diversity indexes (Jost 2007). These estimators form part of the so-called true diversities  ${}^qD$  because they represent the number of equally likely species needed to produce the given value of the diversity index (Jost 2007, 2010). The diversity of order  $q = 2$  ( ${}^2D$ ) is  $1/\lambda$ , where  $\lambda$  is Simpson’s index.  ${}^2D$  is a dominance metric that we used to analyze the species diversity because we focus our objectives on the most common species of the diatom assemblages, and dominant measures are the most appropriate descriptors of species diversity in such studies (Maurer and McGill 2011).  ${}^0D$  is the species richness of a community, and was only used to analyze the phytoplankton, in order to have a more complete description of the recent status of this assemblage.

**Results**

**Meteorological parameters**

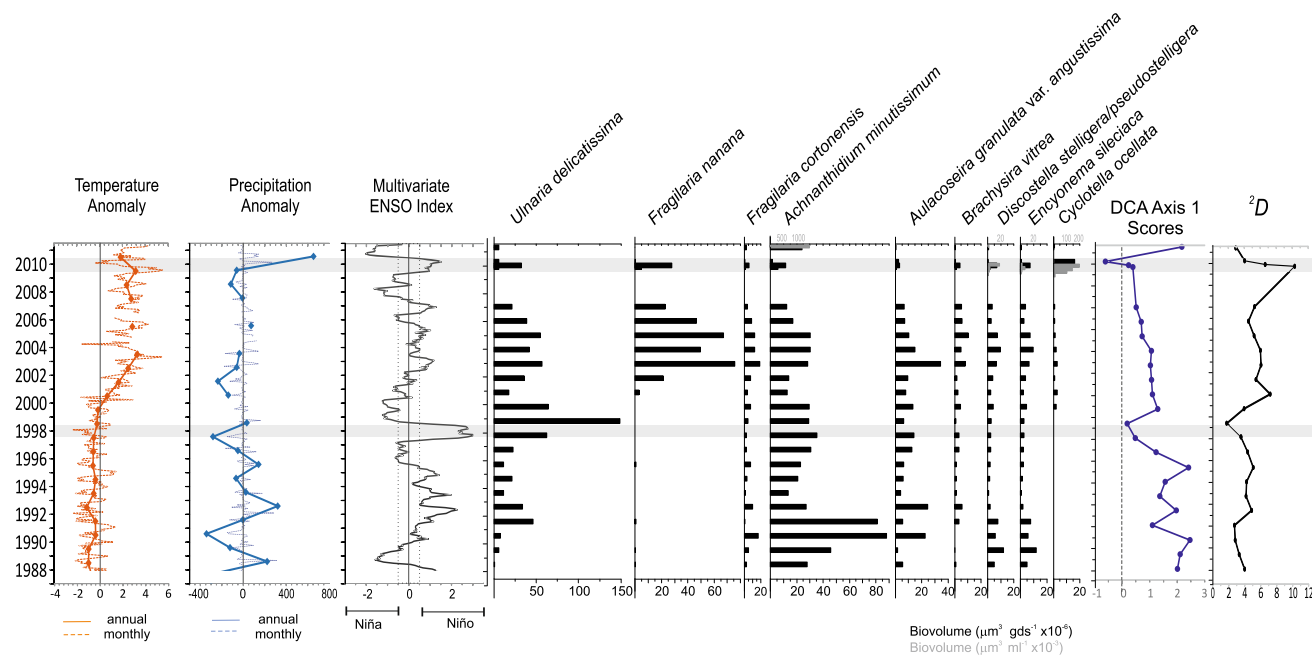
The meteorological data from 1988 to 2011 show positive temperature anomalies since 2000, with higher values

( $\sim 2\text{ }^\circ\text{C}$ ) since 2003 (Fig. 2). During this time the strongest positive ENSO event (MEI  $> 2$ ) was the 1997–1998 “El Niño”, followed by the most recent (MEI  $> 1.5$ ) in 2009–2010, during which the limnological part of this study was conducted; of similar intensity (MEI  $> 1.5$ ) but with shorter temporal extent were the 1991–1992 and 1993 events. Positive ENSO conditions (MEI  $> 0.6$ ) mark the beginning of the 2009–2010 “El Niño” in May 2009 extending until May 2010 (Fig. 2). Negative ENSO conditions (MEI  $< -0.6$ ) were present from July 2010 until April 2011, the strongest “La Niña” since 1988. November 2008, January 2009 and June 2011 had near neutral ENSO conditions (Fig. 2).

**Sedimentary diatoms**

*Ulnaria delicatissima* in association mainly with *Achnanthydium minutissimum* (Fig. 2) have been the dominant diatom species by biovolume in the lake since ca. 1988. *Fragilaria nanana* and *Cyclotella ocellata* appear in the record after ca. 2000; *F. nanana* becomes abundant ( $>10\text{ }\mu\text{m}^3\text{ gds}^{-1}$ ) after ca. 2002. *C. ocellata* on the other hand remains as a rare species in the sediments until February 2010, when it becomes dominant, with a significant reduction in species diversity ( ${}^2D$ ). In June 2011 *C. ocellata* returns to low values.

Negative Axis 1 DCA scores separate the February 2010 sample from the rest of the core, showing that it had a



**Fig. 2** Meteorological and paleolimnological data from 1988 to 2011 from lake Alberca de Tacambaro, western Mexico: temperature and precipitation anomalies, Multivariate Enso Index (MEI), main diatom species by biovolume in the sediments (black bars) and in the

phytoplankton (gray bars), DCA Axis 1 scores and species true diversity ( ${}^2D$ ). Full list of diatom species in the sediments is presented in Table 2, Online Resource 1

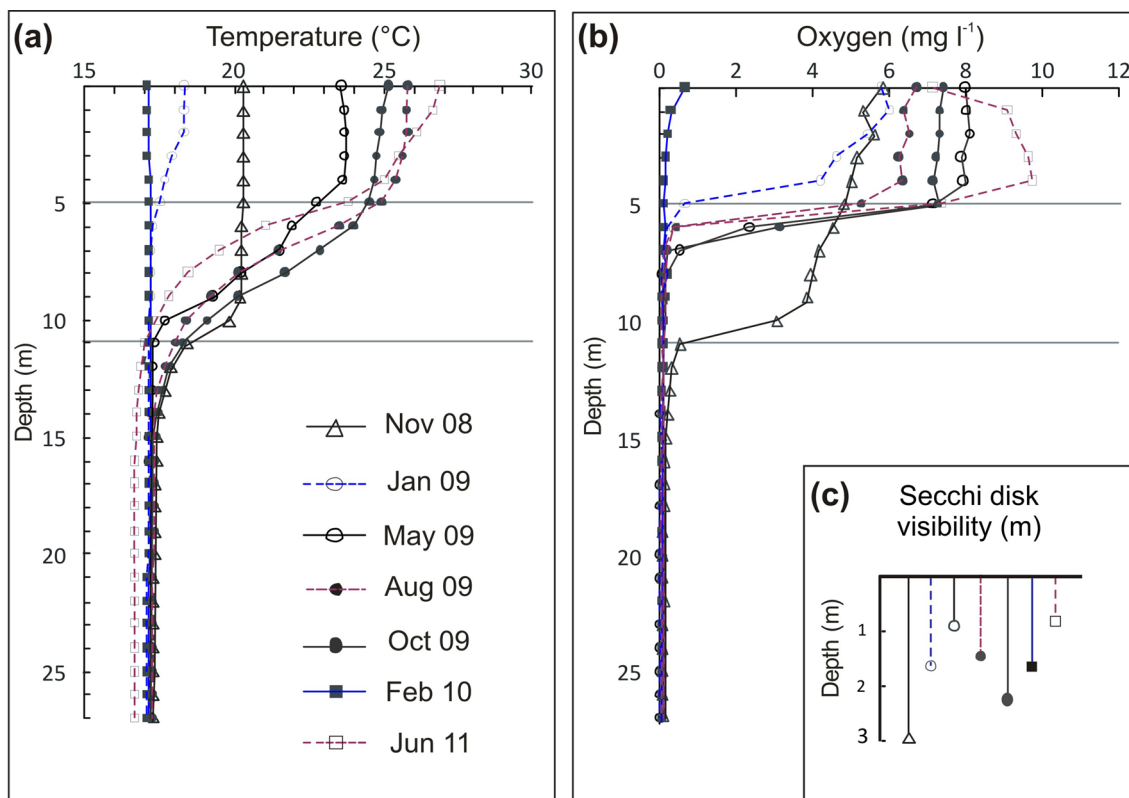
different diatom assemblage from the rest of the sequence (dominated by *C. ocellata*). In the rest of the core high Axis 1 DCA scores ( $>1.5$ ) and relatively low species diversity values ( ${}^2D < 5$ ) are present from ca. 1988 to ca. 1996 and in June 2011, associated to the *U. delicatissima*–*A. minutissimum* assemblage. There is a shift to low DCA Axis 1 scores and minimum species diversity ( ${}^2D = 1.8$ ) by ca. 1998–1999 (“El Niño” year), associated with a particularly high *U. delicatissima* biovolume. Intermediate Axis 1 DCA scores (0.5–1) and generally higher species diversity values ( ${}^2D > 4$ ) are present from ca. 2000 to 2009, when the diatom assemblage included *Fragilaria nanana*, besides *U. delicatissima* and *A. minutissimum*.

### Limnology

Temperature depth profiles (Fig. 3a) show that, except for the winter months (January 2009 and February 2010), the Alberca de Tacambaro was thermally stratified. Clinograde oxygen depth profiles (Fig. 3b) also show a stratified lake, in this case except only for February 2010 when the whole water column was anoxic. The thermocline (metalimnion) was present between 5 and 11 m; metalimnetic temperature difference was on average around 5 °C, reaching up to 8 °C in June 2011. Dissolved oxygen concentrations in the

top 5 m of the water column ranged from anoxia ( $<0.2 \text{ mg l}^{-1}$ ,  $\sim 2 \%$ , February 2010) to 142 % oversaturation ( $9.8 \text{ mg l}^{-1}$ , June 2011); bottom waters ( $>11 \text{ m}$ ) were always anoxic ( $<0.3 \text{ mg l}^{-1}$ ,  $<4 \%$ ). Secchi disk visibility showed its minimum values in early summer (May 2009, June 2011) and its maximum in autumn (November 2008, October 2009) (Fig. 3c).

The lake water was slightly alkaline ( $\text{pH} > 7$ ), with relatively low electric conductivity (Table 3). Ionic composition was dominated by  $[\text{HCO}_3^- + \text{CO}_3^{2-}]$  and  $[\text{Mg}^{2+}] - [\text{Ca}^{2+}] > [\text{Na}^+]$ .  $\text{Mg}^{2+}$  was the dominant ion in surface waters ( $<5 \text{ m}$ ) while  $\text{Ca}^{2+}$  was frequently dominant in deeper waters (Table 2); this situation was also frequent even in surface waters during the 2009–2010 “El Niño”, particularly in February 2010, when  $\text{Mg}^{2+}$  showed its lowest values. Dissolved inorganic nitrogen (DIN) had, in general, lower values in the epilimnion and metalimnion, while the hypolimnion showed the highest (Table 2), the maxima recorded in August and October 2009 (Fig. 4). During the winter months (January 2009, February 2010), DIN was more homogeneously distributed throughout the water column and surface waters ( $<5 \text{ m}$ ) values were the highest (Fig. 4). TP and SRP had more uniform depth profiles with maxima in the hypolimnion in August 2009. DIN/SRP was generally higher than the 16N:1P Redfield



**Fig. 3** Temperature (a) and oxygen (b) depth profiles and Secchi disk visibility (c) from lake Alberca de Tacambaro, western Mexico, from November 2008 to June 2011

**Table 3** Physico-chemical characteristics of lake Alberca de Tacambaro, western Mexico

Tacambaro		Epilimnion (0–5 m)				Metalimnion (5–11 m)				Hypolimnion (11–27 m)			
Variable	Units	Mean	Max.	Min.	SD	Mean	Max.	Min.	SD	Mean	Max.	Min.	SD
Temp.	°C	22.3	26.9	17.1	3.5	19.5	25.0	17.1	2.3	17.2	17.9	16.7	0.2
Oxygen	mg l <sup>-1</sup>	6.0	9.8	0.2	2.7	1.3	7.4	0.1	2.2	0.1	0.3	0.1	0.0
pH		8.7	9.6	7.3	0.7	7.8	9.5	6.9	0.7	7.4	8.4	6.6	0.4
EC	μS cm <sup>-1</sup>	174	204	149	19	190	239	120	29	213	340	181	20
Alk tot	mg l <sup>-1</sup>	98.5	114.6	88.7	9.9	109.5	145.6	77.5	22.0	121.9	138.2	85.2	15.0
CO <sub>3</sub> <sup>2-</sup>	meq l <sup>-1</sup>	10.75	31.25	0.00	12.48	0.14	0.59	0.00	0.19	0.02	0.10	0.00	0.04
HCO <sub>3</sub> <sup>-</sup>	meq l <sup>-1</sup>	1.61	2.17	1.01	0.37	2.05	2.91	1.23	0.53	2.42	2.76	1.70	0.32
Cl <sup>-</sup>	meq l <sup>-1</sup>	0.12	0.18	0.07	0.04	0.12	0.15	0.08	0.02	0.10	0.13	0.07	0.02
SO <sub>4</sub> <sup>2-</sup>	meq l <sup>-1</sup>	0.08	0.11	0.06	0.02	0.07	0.11	0.04	0.02	0.06	0.14	0.02	0.03
Na <sup>+</sup>	meq l <sup>-1</sup>	0.42	0.53	0.33	0.07	0.46	0.51	0.36	0.05	0.43	0.49	0.31	0.07
K <sup>+</sup>	meq l <sup>-1</sup>	0.07	0.08	0.05	0.01	0.06	0.07	0.04	0.01	0.06	0.09	0.04	0.01
Ca <sup>2+</sup>	meq l <sup>-1</sup>	0.75	1.00	0.56	0.16	0.99	2.25	0.37	0.53	0.95	1.03	0.74	0.07
Mg <sup>2+</sup>	meq l <sup>-1</sup>	0.88	1.17	0.37	0.25	0.76	0.98	0.37	0.23	0.81	1.20	0.34	0.24
N-NH <sub>4</sub>	μM	42.1	111.2	0.0	48.7	66.7	139.6	1.7	54.9	167.0	310.1	109.5	66.1
N-NO <sub>3</sub>	μM	3.5	9.3	0.5	3.2	3.7	17.0	0.8	4.8	2.8	9.5	0.9	2.8
DIN	μM	45.7	113.2	0.5	50.7	70.4	143.1	2.5	56.1	169.8	312.8	110.6	67.2
TP	μM	1.40	3.31	0.33	1.0	1.19	2.43	0.46	0.68	3.43	12.98	0.39	3.42
SRP	μM	0.16	0.31	0.02	0.1	0.28	0.87	0.04	0.32	0.81	2.95	0.06	0.81
SiO <sub>2</sub>	μM	733	1116	264	288	891	1085	723	104	835	985	244	190
DIN/RP	Molar ratio	324	719	13	310	533	1117	5	483	535	1788	554	554
Si/RP	Molar ratio	12,251	38,017	1048	14,977	9585	28,285	887	9807	3718	15,511	326	4989
Si/DIN	Molar ratio	410	2085	3	762	76	442	6	129	5	9	2	2
Chla	μg l <sup>-1</sup>	23.0	38.9	9.6	10.9	34.0	123.9	8.5	32.3	19.2	44.0	6.8	11.3
Secchi	m	1.6	3.0	0.7	0.8								

Mean, maximum, minimum and standard deviation (SD) are presented by stratification layers: epilimnion (n = 8), metalimnion (n = 12) and hypolimnion (n = 13)

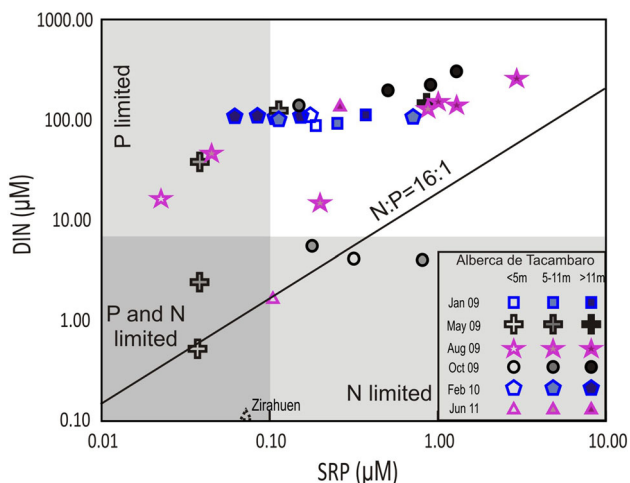
ratio (Redfield 1958) but SRP and DIN were usually above the 0.1 and 7 μM threshold values suggested by Reynolds (1999). Some water samples (<11 m), however, were below these values, suggesting either N (October 2009, July 2011) or P (August, May 2009) limitation, only surface waters (≤5 m) in May 2009 were below these threshold values for both nutrients (Fig. 4). Silica had lower concentrations in January 2009 (244–336 μM) than in the rest (720–1100 μM) of the samples, but Si:DIN and Si:SRP were always above the 1Si:1N and 16Si:1P threshold ratios (Xu et al. 2008).

### Chlorophyll *a* and phytoplankton

Water column average Chla values were high (>25 μg l<sup>-1</sup>) with a deep water (10 m) maximum in August 2009; only in February 2010 low Chla concentrations were recorded (<10 μg l<sup>-1</sup>) (Fig. 5a). Average total biovolume in the water column was low (ca. <4 × 10<sup>6</sup> μm<sup>3</sup> ml<sup>-1</sup>) from

January to October 2009, increasing in February 2010, but the highest values were by far those from June 2011 (Fig. 5b). Except for February 2010 biovolume showed its highest values in the upper 8 m of the water column (Fig. 5b). Chla and biovolume throughout the water column showed no significant correlation ( $r = -0.255$ ,  $p > 0.05$ ) but average surface waters (<5 m) Chla showed negative correlations with biovolume ( $r = -0.9$ ,  $p < 0.03$ ) and with Secchi disk visibility ( $r = -0.8$ ;  $p < 0.03$ ). Chla and DIN/SRP throughout the water column also showed a significant negative correlation ( $r = -0.9$ ;  $p < 0.03$ ).

Chlorophyta always dominated the lake's biovolume (>50 %) mostly in winter (January 2009 and February 2010) (Figs. 5c, 6a–d). Maximum Chlorophyta biovolume was in June 2011 (*Staurastrum* sp.) and February 2010 (*Botryococcus* sp. and *Sphaerocystis* sp.) and minimum was in August 2009. Bacillariophyta (diatoms) were the second most important algal group by biovolume (Figs. 5c,



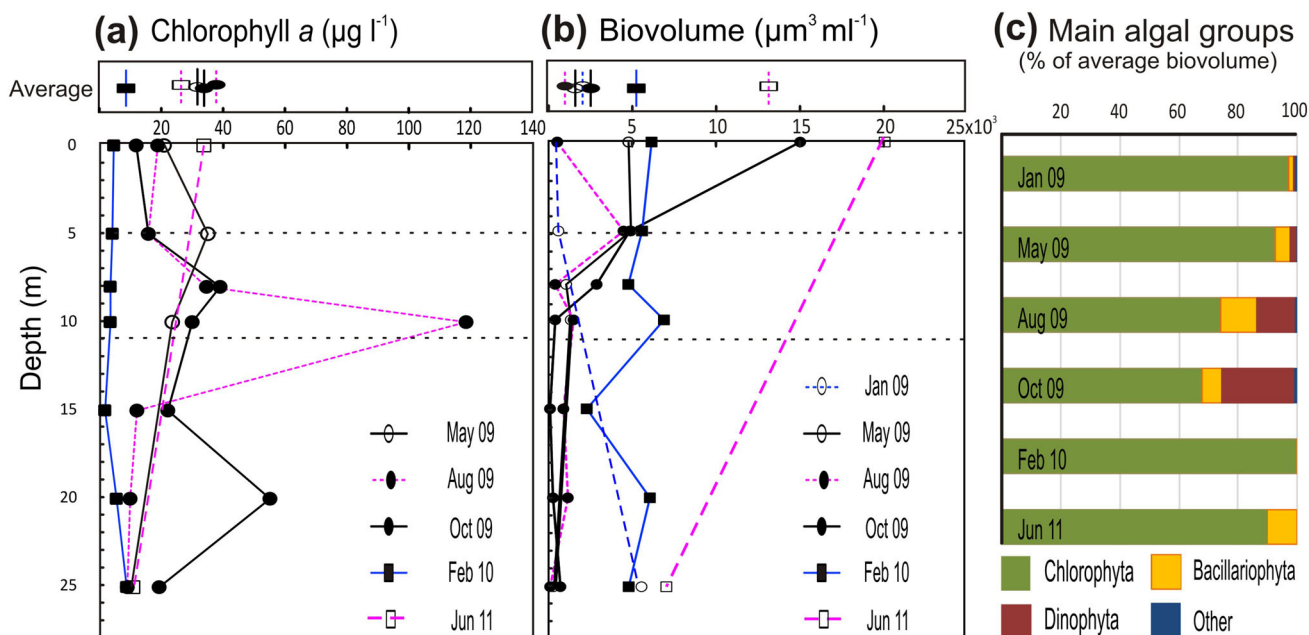
**Fig. 4** Soluble reactive phosphorous (SRP) and dissolved inorganic nitrogen (DIN) in water samples from lake Alberca de Tacambaro, western Mexico, from January 2009 to June 2011. Shaded areas define nutrient limiting values according to Reynolds (1999):  $\text{SRP} < 0.1 \mu\text{M}$  and  $\text{DIN} < 7 \mu\text{M}$

6e–h), with their lowest relative and total abundances in the winter months (January 2009 and February 2010) and their highest in summer and autumn (August, and October 2009, *C. ocellata* and June 2011, *A. minutissimum*). Dinophyceae (*Peridinium* spp.) were also important in August and October 2009 (Figs. 5c, 6i).

The highest true diversity values for richness ( ${}^0D$ ) in the water column phytoplankton community were recorded in January and May 2009 (>15 species) in surface waters

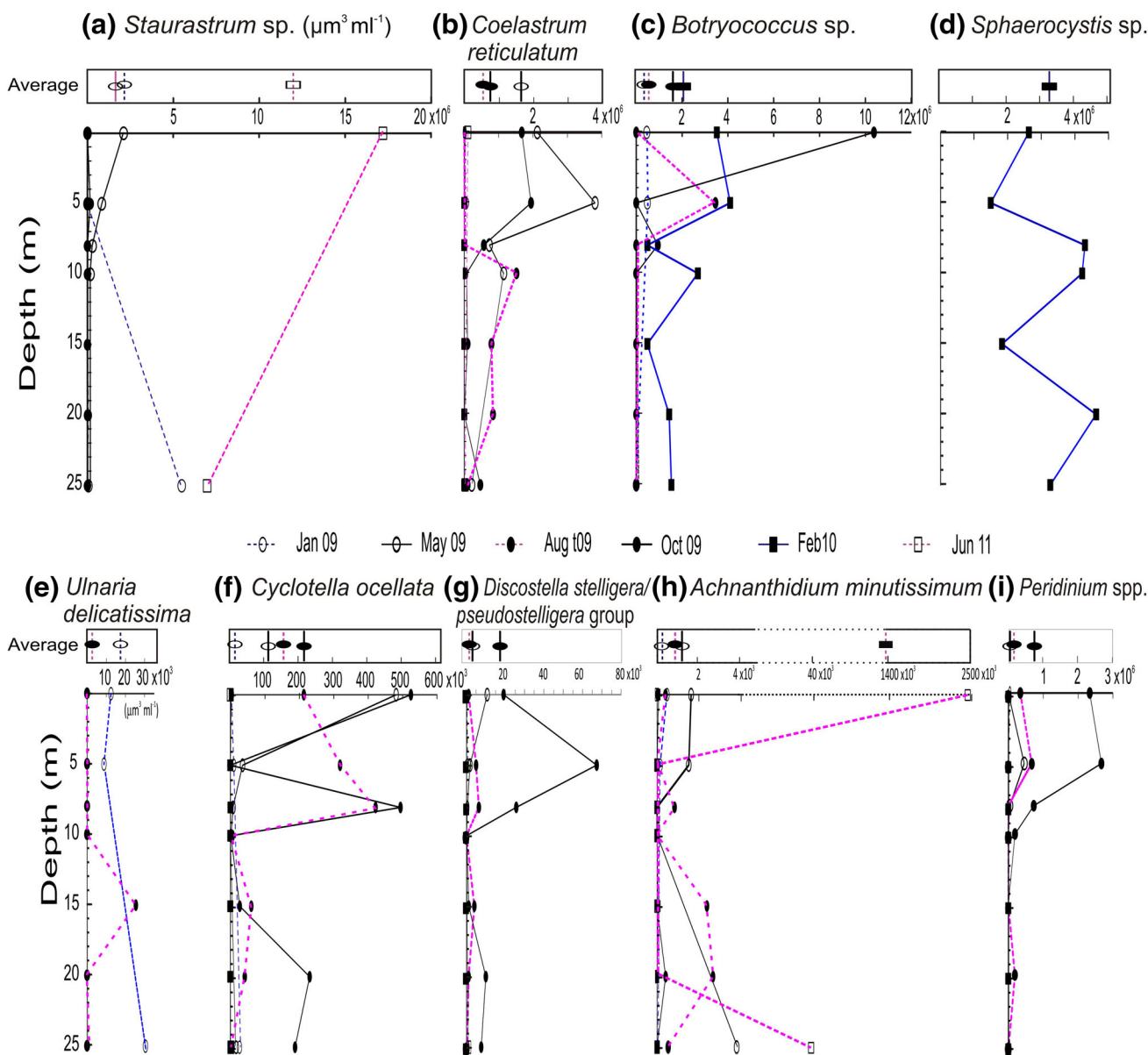
(<5 m), and the lowest in August 2009, February 2010 and June 2011 (<10 species) (Fig. 7a). The highest and lowest  ${}^2D$  diversity values were recorded in the metalimnion in October and August 2009 respectively (Fig. 7b).  ${}^2D$  diversity showed low fluctuations throughout the water column during the other months (Fig. 7b). Considering only the diatoms in the water column, they had the highest species richness ( ${}^0D$ ) and diversity ( ${}^2D$ ) in surface waters during January and May 2009 ( ${}^0D \geq 8$  species) and the lowest in February 2010 ( ${}^0D < 3$  species) (Fig. 7c, d).

With respect to the CCA, the first axis was significant (Monte Carlo test,  $p = 0.002$ ), and axes 1 and 2 accounted for 39 % of the total data variance. The CCA identified  $\text{Mg}^{2+}$ , TP, temperature, DIN/SRP,  $\text{SiO}_2$  and  $\text{SiO}_2/\text{DIN}$  as the main environmental variables explaining the phytoplankton species distribution; DIN/SRP showed a direct correlation while  $\text{Mg}^{2+}$ , TP and  $\text{SiO}_2/\text{DIN}$  showed an inverse correlation with Axis 1.  $\text{SiO}_2$  and temperature correlated with Axis 2 (Fig. 8a). On the CCA Axis 1 versus Axis 2 diagrams four groups of samples can be identified and associated with their characteristic phytoplankton species (Fig. 8a, b). The samples from January 2009 (non ENSO winter) are grouped at the lowest Axis 2 scores (low temperature and  $\text{SiO}_2$  values) and correlate with high values of *U. delicatissima* (Bacillariophyta) (Figs. 6e, 8b). The samples from May, August and October 2009 (ENSO spring, summer and autumn) are located towards the left and center of the diagram (higher temperature and  $\text{SiO}_2$ , low DIN/SRP), and are associated with high values of *Coelastrum reticulatum* (Chlorophyta), *C. ocellata*



**Fig. 5** Chlorophyll a (a) and biovolume (b) depth profiles and main algal groups (c) in water samples from lake Alberca de Tacambaro, western Mexico, from January 2009 to June 2011





**Fig. 6** Biovolume depth profiles of main species in the phytoplankton of lake Alberca de Tacambaro, western Mexico, from January 2009 to June 2011. They are distributed in main algal groups as follows: Chlorophyta (a–d), Bacillariophyta (e–h) and Dinophyta (i)

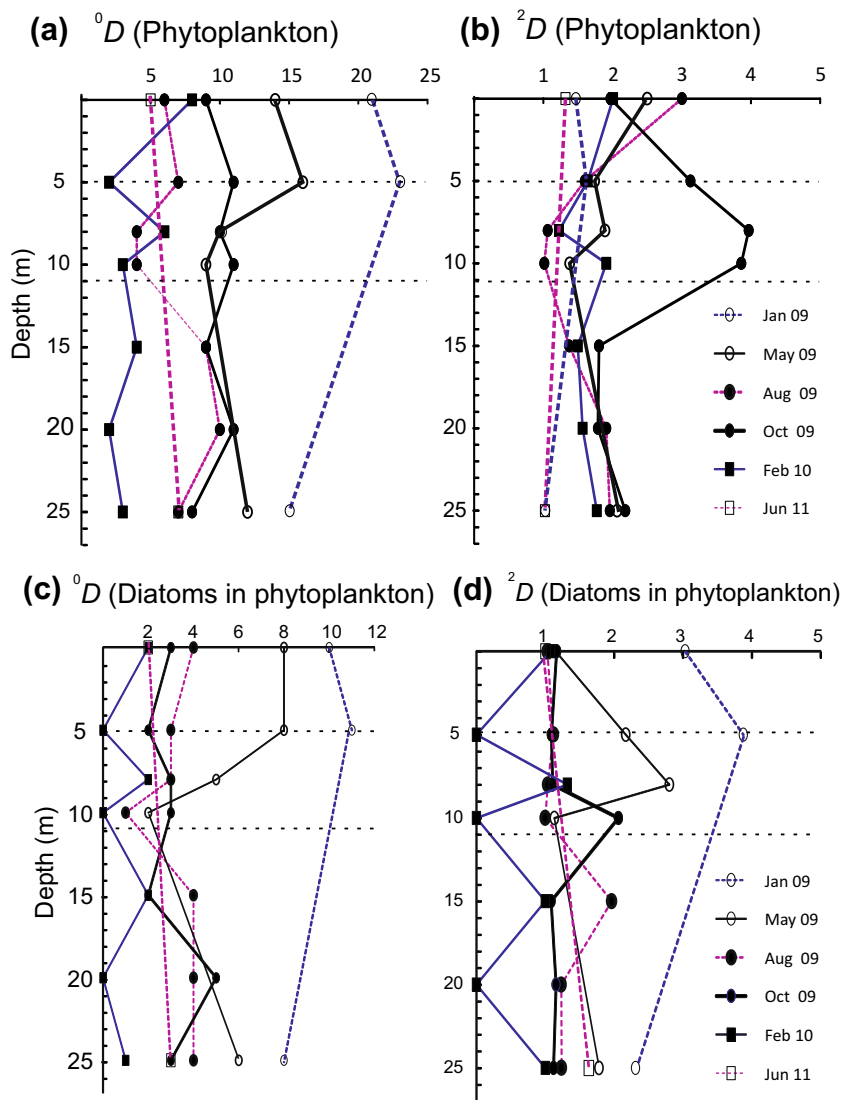
(Bacillariophyta), *Discostella stelligera/pseudostelligera* group (Bacillariophyta) and *Peridinium* spp. (Dinophyta) (Figs. 6b, f, g, i, 8b). The samples from February 2010 (ENSO winter) form a clear group at the extreme right of the diagram (highest DIN/SRP, low temperature and lowest  $\text{Mg}^{2+}$ ), with a species composition dominated by *Botryococcus* sp. (Chlorophyta) and *Sphaerocystis* sp. (Chlorophyta) (Figs. 6c, d, 8b). The June 2011 samples (non ENSO summer) are grouped to the left of the diagram (highest  $\text{Mg}^{2+}$ , high TP, high  $\text{SiO}_2/\text{DIN}$  and lowest DIN/SRP), with high abundance of *Staurastrum* sp. and *A. minutissimum* (Bacillariophyta) (Figs. 6a, h, 8b).

## Discussion

### Limnology of lake Alberca de Tacambaro

The AT is a slightly alkaline,  $[\text{HCO}_3^- + \text{CO}_3^{2-}]$  and  $[\text{Mg}^{2+}] - [\text{Ca}^{2+}] > [\text{Na}^+]$ , eutrophic, freshwater lake with low transparency, high Chl*a* and TP concentrations (OECD 1982). It is a warm-monomictic lake with a brief winter mixing, limited to the coldest weeks of the year (January, 17 °C) when surface waters temperatures reach values similar to those of the hypolimnion. Its protected basin, small area, high relative depth (8.6 %) and low

**Fig. 7** Diversity indices ( ${}^0D$  = species richness,  ${}^2D$  = true diversity) for phytoplankton (**a, b**) and diatoms in phytoplankton (**c, d**) in water samples along depth profiles from Alberca de Tacambaro, western Mexico, from January 2009 to June 2011



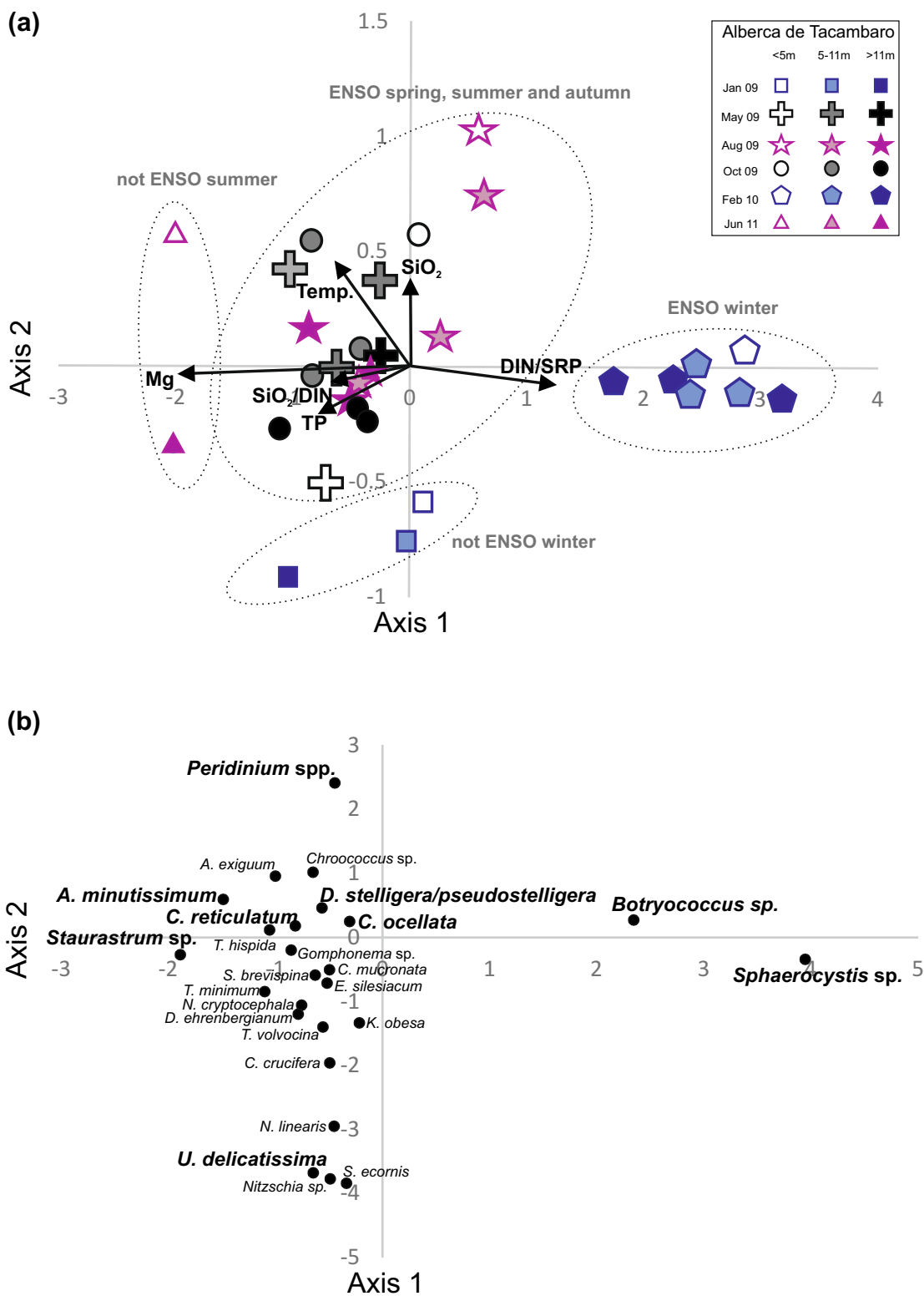
transparency, determines its short winter mixing and thin epilimnion (5 m) compared to other lakes in central Mexico where mixing extends for 2–3 months, hypolimnetic temperatures are similar to those in spring (March–April) and thermoclines are usually deeper (>10 m) (Alcocer et al. 2000; Caballero et al. 2013; Tavera and Martinez Almeida 2005). We consider that density driven mixing is very important in this lake as wind fetch is limited by its morphometric characteristics.

Maximum productivity in AT seems to occur during the warmer (stratified) months of the year, in surface waters (<10 m) and associated with a reduction in surface waters nutrient levels (SRP and/or DIN). High phytoplankton species richness ( ${}^0D$ ) and diversity ( ${}^2D$ ) also occurred during stratification. Chlorophyta and by Bacillariophyta (diatoms) were the dominant algae groups. Even though diatoms had its highest species richness ( ${}^0D$ ) and diversity

( ${}^2D$ ) in January 2009, they had a low winter biovolume. There is no evidence in this lake of a winter mixing diatom bloom similar to that reported for other lakes in the region (Alcocer et al. 2000). This could be related to its relatively short winter mixing and possible whole water column anoxic conditions (see below).

### The 2009–2010 ENSO event

The meteorological data from Tacambaro show a clear trend to warmer than average years since the year 2000 which fits with the warming trend identified in meteorological data at the country level (Englehart and Douglas 2005; Pavia et al. 2009). The 2009–2010 “El Niño” was characterized by a warmer and drier summer and a colder and wetter winter, a pattern that is in accordance with the anomalies identified for “El Niño” years in Mexico (Bravo



**Fig. 8** CCA Axis 1 versus Axis 2 graphs of samples (a) and species (b) from lake Alberca de Tacambaro, western Mexico. In **bold** are the main species in the phytoplankton which correspond with those presented in Fig. 6. Full list of species is presented in Table 1, Online Resource 1

Cabrera et al. 2010; Magaña 2004; Magaña et al. 2003). However, under this warmer than average scenario the “El Niño” 2009 summer represents one of the warmest since 1988 ( $\sim 5$  °C anomaly). On the other hand the “El Niño” winter (February 2010) was one of the coldest since 2003; that year (2010) was also the wettest since 1988 given that both the “El Niño” 2009–2010 winter (February 2010,  $>200$  mm anomaly) and the subsequent “La Niña” 2010 summer ( $>100$  mm anomaly) were unusually wet (Fig. 2).

Our data from AT indicates that during the “El Niño” winter (February 2010), water column mixing was longer, caused by its unusually cold conditions. Given the high organic matter load of this eutrophic lake, this was related to a full water column deoxygenation. This anoxic mixing event was associated with the lowest species (phytoplankton and diatoms) richness ( $^0D$ ) and diatom diversity ( $^2D$ ) and abundance in the water column. It was also related with high DIN levels in surface waters and therefore also high DIN/SRP ratios. Full water column deoxygenation is not an uncommon phenomena in productive tropical lakes (Caballero et al. 2013; Whitmore et al. 1991) and could be a recurrent situation during the short full water column mixing that could help to explain the lack of a winter diatom bloom in this lake.

Phytoplankton associations are related with the environmental conditions during the development of the 2009–2010 “El Niño” event. In January 2009 and June 2011, during non ENSO conditions, the phytoplankton was dominated by *Staurastrum* sp. (January 2009 and June 2011), *U. delicatissima* (January 2009) and *A. minutissimum* (June 2011); these last species are the dominant diatoms in the sediments of this lake since 1988. However, when “El Niño” conditions were established (May 2009), surface waters had the lowest SRP and DIN (N and P co-limitation, Fig. 4) and the dominant species became *C. reticulatum* and *C. ocellata*. This assemblage dominated during the “El Niño” summer and autumn (and was recorded in the sediments after stratification broke in February 2010, gray vs. black bars, Fig. 2). However, during the “El Niño” winter (February 2010) the environmental conditions changed (full water column mixing and deoxygenation, higher DIN and DIN/SRP) and favoured a phytoplankton assemblage with the lowest species richness ( $^0D$ ), dominated by *Botryococcus* sp. and *Sphaerocystis* sp. Even though this assemblage had a relatively high biovolume, it showed the lowest Chl $a$  values, accounting for the negative correlation between these two variables in surface waters. The high biovolume of these species is explained by their colonial, mucilaginous nature, which can be considered a survival strategy to counter the unfavorable conditions (cold and anoxic water column) that, on the other hand, seem to be limiting photosynthetic activity (low Chl $a$ ) (Mecozzi et al. 2008).

## Historical perspective

The paleolimnological data show that since 1988 the diatom associations in AT have been dominated by two diatom species: the long needle shaped *U. delicatissima*, and the smaller *A. minutissimum*. However with the onset of warmer conditions by the year 2000 the diatom assemblage changed, it became more diverse (higher  $^2D$ ), as it included a smaller needle shaped species, *F. nanana* (Fig. 2). The small centric diatom *C. ocellata* also appeared in the record by this time (Fig. 2), but it remained in low numbers until it bloomed during the 2009–2010 “El Niño” (Fig. 2), when diversity values ( $^2D$ ) decreased sharply.

We consider that several factors concurred that favoured *C. ocellata* over the “usual” diatom species in AT at the onset of the 2009–2010 “El Niño” (January–May 2009). These included the low silica values in January 2009 and the low DIN and SRP values leading to N and P co-limitation in surface waters in May 2009. *C. ocellata* is a species that flourishes in similar conditions in lake Zirahuén (Tavera and Martínez Almeida 2005), with P and N co-limitation (Bernal Brooks et al. 2002) and low silica values (Caballero and Vázquez, unpublished data). The deep water chlorophyll maxima in August 2009 and the high abundance of *C. ocellata* in the metalimnion during August and October 2009, indicates that under poorly mixed conditions this species is finding higher nutrient available in the deeper waters as a survival strategy given the low nutrient concentrations in the epilimnion (Davey and Heaney 1989).

During the previous 1997–1998 “El Niño” event this lake seems to have also responded with a shift to a lower diversity ( $^2D$ ) assemblage dominated in this case by *U. delicatissima*. This response seems less intense than in the 2009 event, as the diatom bloom associated with the “El Niño” involved one of the diatoms that were already common in the lake, while in 2009–2010 the assemblage shifted to a species (*C. ocellata*) which was not abundant previously. The response of this lake to the previous “El Niño” events (1991–1992 and 1993) are unclear, this might be because of the lower intensity of these events or due to the chronological uncertainties of the age-depth model which do not allow clear correlations between the climate data and the sedimentary sequence.

In a large number of arctic, alpine and other temperate lakes climate warming has been associated with higher stability in the water column, increased nutrient limitation and changes towards smaller size phytoplankton species, in particular small *Cyclotella* populations (Catalan et al. 2002; Ndebele Murisa et al. 2010; Winder et al. 2009). This seems to be the case in AT where recent warming has favoured a smaller needle shaped diatom and a small *Cyclotella* species and is consistent with the nutrient co-

limitation observed during the 2009–2019 “El Niño” *C. ocellata* bloom. The recent warming trend in AT can therefore explain the different responses, favouring different diatom species, between the 1989–1999 “El Niño”, occurring before the onset of the warming trend and the recent 2009–2010 event, occurring after nearly a decade of warmer years, which possibly increased nutrient limitation in the lake.

Changes in sedimentary diatom assemblages in shallow marine environments in Florida have also been related with extreme climatic conditions associated with large-scale climatic oscillations like ENSO or the Pacific Decadal Oscillation (PDO) events (Wachnicka et al. 2013). In these environments the changes in diatom assemblages have been mostly triggered by the cold phases of these events, and they have been irreversible. In AT the strongest response seems to be to the warm ENSO phase, but the close relationship between the 1998–1999 “El Niño” and the change in diatom association at the onset of the warming trend by ca. 2000 are very closely related and could be an example of a similar situation, when extreme conditions during ENSO can have a longer term consequence in the biological assemblages. However further and continuing research in tropical environments like AT are necessary to fully understand the impact that climatic and environmental changes can have on the diversity and composition of biological associations at all trophic levels and how they can impact other important ecological aspects such as carbon cycling.

## Conclusions

The data from AT shows that this small, deep lake is sensitive to meteorological changes that can alter its thermal behaviour and as a consequence its phytoplankton succession, being a good site for modern and paleo-environmental studies. The trends recorded in this lake related to global warming and ENSO events are in accordance with findings from lakes in other regions of the world, where longer and more stable stratification periods, increased nutrient limitation and changes in phytoplankton succession towards smaller size species have also been recorded. In AT a recent warming trend (after year 2000) was related with an increase in the diversity of the diatom assemblage, while two “El Niño” events (1998–1999 and 2009–2010) were related to a reduction in diversity, with the dominance of one species (1998–1999—*U. delicatissima* and 2009–2010—*C. ocellata*). The difference in the diatom species favoured in each “El Niño” event seems to be related with a change in base level conditions (increase in nutrient limitation) as a response to a warmer climate. The data from this tropical lake suggest that under a

climate change scenario such as global warming, there are minor changes in ecosystem’s base levels which determine how even normal climatic variability events can cause unprecedented changes in ecosystem’s species composition.

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