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Diatom fluxes in a tropical, oligotrophic lake dominated by large-sized phytoplankton

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Abstract Alchichica is a warm-monomictic, oligotrophic lake whose phytoplanktonic biomass is dominated by large size (average ca. 55 μm) diatoms. The fast sinking phytoplankton leads to silica, and other nutrient exportation out of the productive zone of the lake. The aim of the present study was to identify and measure the sedimentation fluxes of the diatom species and their temporal dynamics to better understand the magnitude of silica and carbon fluxes.

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Sediment-traps were exposed at three different depths and collected monthly. A total of 13 diatom species were observed in the traps. The maximum diatom flux was in February (304×10^6 cells m^{-2} day^{-1}) related to the winter diatom bloom. The diatom silica (DSi) fluxes varied from 2.2 to 2,997 mg m^{-2} day^{-1} and the diatom carbon (DC) fluxes from 1.2 to 2,918 mg m^{-2} d^{-1}. *Cyclotella alchichicana* was the main contributor (>98%) to the total DSi and DC fluxes. The annual diatom (15×10^9 cells m^{-2} year^{-1}), DSi (147 g m^{-2} year^{-1}) and DC (92 g m^{-2} year^{-1}) fluxes are higher than in other aquatic ecosystems of similar or even higher trophic conditions. Our findings in Alchichica are indicative of the relevance of the phytoplankton type and size in understanding the role tropical and oligotrophic lakes play regarding silica and carbon fluxes. In addition, our results support previous findings suggesting that inland aquatic ecosystems are more important than formerly thought in processing carbon, and can, therefore, affect regional carbon balances.

Keywords Diatom flux · Silica flux · Carbon flux · Sediment-traps · Tropical lake · Lake Alchichica · Mexico

Introduction

Sedimentation is one of the most important processes of phytoplankton loss out from the euphotic zone

(Andreassen & Wassmann, 1998; Garg & Bhaskar, 2000; Chellappa et al., 2008). Up to half of annual planktonic production is lost due to sinking in freshwater environments (e.g., Baines & Pace, 1994). Phytoplankton size and structure play a central role in controlling the fate of biogenic carbon and nutrients (Legendre & Rassoulzadegan, 1996). There is a relationship between phytoplankton size and form, and its sinking velocity, as well as its vertical flux, which increases, e.g., as a consequence of the larger size of the phytoplankton and the lower predation pressure (Reynolds, 1984; Round et al., 1990; Legendre, 1999).

There is a large number of investigations dealing with siliceous phytoplankton of different sizes and biogenic silica fluxes; however, they have been carried out mostly in the ocean and in temperate lakes. Few studies have been undertaken to understand this process of diatom flux in tropical lakes (e.g., Kilham & Soltau, 1990; Bootsma et al., 2003; Pilskaln, 2004), and most of them deal with paleolimnology (e.g., Haberyan & Hecky, 1987; Kilham & Soltau, 1990; Bootsma et al., 2003). Despite being the third most abundant element on earth, silica (Si) is one of the limiting nutrients for diatoms in vast regions of the oceans (Dugdale et al., 1995) and lakes (Gibson et al., 2000). This is mainly due to the biological uptake by diatoms themselves, which strips silicic acid out of the surface waters and exports it to depth as particulate biogenic silica. A better knowledge of the control exerted by Si availability on diatom growth is, therefore, a key to understanding the role of diatoms for new production and the export of particulate carbon (Brzezinski & Nelson, 1995; Dugdale et al., 1995; Dugdale & Wilkerson, 1998), as well as its impacts on CO_2 drawdown from the atmosphere (Leblanc & Hutchins, 2005). Diatoms excrete dissolved polysaccharides that abiotically form transparent exopolimer particles (Passow, 2000) and enable the formation of aggregates (Passow et al., 1994; Passow & Alldredge, 1995) that increases the sinking velocity, and removes them from the euphotic zone. In addition, diatoms can form large blooms that sediment in mass also at high sinking rates (Smetacek, 2000), exporting silica and other nutrients below the thermocline and down to the bottom. This process affects the elemental composition of phytoplanktonic cells, which depend on nutrient availability.

Diatoms require nitrogen and silicon in a ratio close to 1:1 (Redfield et al., 1963). Thus, dissolved silicon can be depleted well before available nitrogen and phosphorus are in short supply (Andreassen & Wassmann, 1998). Silica as well as nitrogen and phosphorus are thus of critical importance as macronutrients for diatoms. Besides nutrient concentrations and their fluxes, the stoichiometric proportions between nutrients are key factors for phytoplankton growth (Søndergaard et al., 1999). Variability in relative nutrient concentrations may be judged either by the relative change of a single element or by the stoichiometric ratios between available nutrients (Bray, 1995). Although nitrogen and phosphorus are the key candidates for general nutrient limitation of phytoplankton, different evidence suggests that nitrogen limitation is more important in the tropics than it seems to be in the temperate zone (Lewis, 1996). However, the silica concentrations in Alchichica are low and their availability appears to regulate the abundance of diatoms (Adame et al., 2008).

In this regard, tropical Lake Alchichica, Central Mexico, provides a unique opportunity to investigate the role that nutrient play, especially Si, in controlling diatom blooms, which are a common phenomenon from the beginning of the phytoplankton growing season (i.e., following deep mixing events that renew nutrients and increase turbulence) in temperate and tropical lakes (e.g., Lewis, 1996). This information also represents a baseline to evaluate the fluxes of diatoms, silica and carbon in tropical, oligotrophic lakes.

Lake Alchichica has 16 species of phytoplankton with size larger than 2 μm. Diatoms are represented with the highest number of species (10), followed by chlorophytes (2), cyanoprokaryota (1), dinoflagellates (1), cryptophytes (1), and euglenophytes (1) (Oliva et al., 2001). The most important diatoms are *Cyclotella alchichicana* Oliva, Lugo, Alcocer & Cantoral—a large endemic species (35–63 μm of diameter, Oliva et al., 2006) belonging to the group of *Cyclotella quillensis* Bailey—followed by *C. choctawhatcheeana* Prasad, a small diatom (5–12 μm of diameter, Oliva et al., 2008), with a cosmopolitan brackish water distribution (Prasad et al., 1990), and *Chaetoceros elmorei* Boyer, a colonial species (chain >50 μm, Oliva com. pers. unpublished data) of inland waters from North America (Rushforth & Johansen, 1986). Contrary to findings in other

oligotrophic water bodies, the phytoplankton of Lake Alchichica is dominated by large organisms (Adame et al., 2008), thus implying low predation pressure, as well as higher sinking velocities and nutrient fluxes.

The annual phytoplankton biomass (expressed as chlorophyll *a* concentration) represents the larger fraction (40–48%) of the total accumulated particulate matter (Oseguera et al., unpublished data), and is mainly exported during the diatom bloom that takes place along the winter circulation period. These diatom blooms effectively remove Si from the mixing zone in Lake Alchichica (<280 µg l^{-1} SRSi, unpublished data). In Lake Alchichica, it seems that diatoms are able to exhaust wholly the available Si, thus generating a diatom growth crash and acting as a main control factor for changes in the composition and abundance of the phytoplankton assemblages. Such situations occur along with hypolimnetic oxygen depletion at stratification onset, up to anoxia throughout the stratification (Adame et al., 2008), an unexpected behavior for a temperate unproductive lake, but quite common in tropical oligotrophic lakes (Lewis, 2002). The objective of this paper was to estimate the vertical diatom and silica fluxes in this oligotrophic, tropical lake with saline and alkaline waters, dominated by large-sized, fast sinking diatoms.

Description of the study site

Lake Alchichica is located at 19°24′ N, 97°24′ W at 2,300 m a.s.l., in the endorheic Oriental Basin, Central Mexico. It is one of the deepest lakes in Mexico (max = 62 m, mean = 40.9 m), with a small surface area (2.3 km^2), as expected for a maar lake. Its basin holds 94.2 × 10^6 m^3 of saline (8.5 ± 0.2 g l^{-1}) and alkaline water (pH = 9.0 ± 0.1, total alkalinity of 37 meq l^{-1}), dominated by sodium–magnesium and chloride–bicarbonate ions (Vilaclara et al., 1993; Alcocer & Hammer, 1998; Filonov et al., 2006).

Annual air temperature fluctuates from −5.5 to 30°C, with a mean value of 14.4°C (García, 1988). The daily temperature change averages 13.9°C and ranges from 2.4 to 25°C. The climate is arid with annual precipitation of less than 500 mm, and an annual evaporation of 1,690 mm (Adame et al., 2008). Lake Alchichica is warm-monomictic, with mixing taking place from late December/early January to late March/early April, during the cold-dry season, and remains stratified the rest of the year during the warm-rainy season (Alcocer et al., 2000).

Lake Alchichica is oligotrophic (Ramírez-Olvera et al., 2009). In the mixed-layer, dissolved inorganic nitrogen (DIN) concentration ranges from 9.8 to 53.2 µg l^{-1}, soluble reactive phosphorus (SRP) ranges from 3.1 to 18.6 µg l^{-1} and chlorophyll *a* (Chl*a*) concentrations from 0.2 to 2.2 µg l^{-1}. Two distinctive phytoplankton blooms occur during the year (Alcocer & Lugo, 2003): a winter diatom bloom takes place throughout the mixing period (Adame et al., 2008), and a spring cyanoprokariota bloom appears during the early April–June stratification period (Oliva et al., 2009).

Materials and methods

Sampling was carried out at monthly intervals throughout 1 year from a station situated over the deepest (62 m) and central part of the lake. Temperature (T°) and dissolved oxygen (DO) were obtained by means of a Hydrolab DS4/SVR4 multiparameter water quality logging system. The profiles consisted of records every meter between surface and bottom (0–62 m).

The mixing depth (Z_{MIX}) was estimated through the T° and DO profiles. Z_{MIX} was defined as the upper layer mixed thoroughly by wind to a more or less uniform temperature and delimited by the top of the thermocline. Z_{MIX} corresponds to the entire water column during circulation or to the epilimnion when the lake is stratified. Photosynthetic active radiation (PAR) was obtained by means of a Biospherical PNF-300 vertical profiler. PAR profiles were used for calculating the euphotic zone (Z_{EU}). Z_{EU} was defined as the layer where PAR was ±1% of its surface value.

Samples for nutrients and Chl*a* from the mixed layer were collected using a water sampler bottle at 10 depths during the circulation (2, 5, 10, 15, 20, 25, 30, 40, 50, and 60 m). Due to the progressive thermocline deepening throughout the stratification period, the sampling depths varied in number and depth as follows: 4 in April (2, 5, 10, 17 m), 3 in May and June (2, 5, 10 m), 4 in July and August (2, 5, 10, 15 m), 5 in September and October (5, 10, 15, 20, 25 m), 6 in November (0, 5, 10, 15, 20, 25 m), and 7 in December (0, 5, 10, 15, 20, 30, 35 m).

Dissolved nutrients (dissolved inorganic nitrogen, DIN: NO$_3$-N + NO$_2$-N + NH$_4$-N, soluble reactive

phosphorous, SRP, and soluble reactive silica, SRSi) analysis followed standard methods (Strickland & Parsons, 1972) adapted (Kirkwood, 1994) to a Skalar Sanplus segmented flow autoanalyzer system. Known aliquots of water were also filtered through a Whatman 0.7 μm (GF/F) filter for suspended Chl*a*. The atomic Si:N:P ratio of marine diatoms is about 16:16:1 in a nutrient-replete ecosystem (Redfield, 1958; Brzezinski, 1985). Deviation from the Redfield ratio indicates the potential for N, P, or Si limitation of phytoplankton (specifically diatom) growth. In our assessment of stoichiometric limitations, we applied the Redfield ratio to predict that: (1) N limitation occurs when N:P < 16 and N:Si < 1; (2) P limitation occurs when N:P > 16 and Si:P > 16; and (3) Si limitation occurs when N:Si > 1 and Si:P < 16 (Xu et al., 2008). Since nutrient ratios can be used to assess limitation background only if at least one of them is limiting, we consider the limiting levels according to Sas (1989) as follows: 10 μg l^{-1} for SRP, 100 μg l^{-1} for DIN, and 500 μg l^{-1} for SRSi.

Cylindrical sediment-traps were used to collect the settling phytoplankton in the lake. The aspect ratio of the sediment-traps was 6 (height 45.0 cm; diameter 7.4 cm), suitable for water bodies of low current velocities and turbulence (Blomquist & Kofoed, 1981; Bloesch, 1994). The mooring system consisted of an anchor, cotton rope, three sediment-trap stations (four tubes each), and a surface buoy. During the stratification period, the stations were located: (1) at the base of the epilimnion (Z_{MIX}) (upper traps), (2) just below the metalimnion—thermocline (middle traps), and (3) in the hypolimnion—3 m above the sediment (bottom traps) of the lake. During the mixing period, the bottom trap remained at the same position, while the other two stations were positioned equidistantly.

The material captured in traps was filtered through 100 μm mesh size to remove the large swimmers (Lee et al., 1988). Trap water and settled material were poured into wide-neck 2 l plastic bottles and stored in dark and cold containers until their analysis. Known aliquots of the sedimented particles were filtered through GF/F filters for the analysis of Chl*a*.

Even though chlorophyll undergoes degradation as soon as the cell is senescent or dies, we consider our Chl*a* data are accurate since the chlorophyll degradation process reduces under darkness and anoxic conditions, as well as in colder waters. Wetzel (2001) concluded that photooxidative destruction of chlorophyll occurred in senescent phytoplanktonic cells, although in prolonged darkness, reduced destruction has been observed, which is the case in our traps that were well below the euphotic zone throughout the studied period. On the other hand, comparisons of sediment-trap catch and mean pigment concentration in surface sediments suggest that pigment decay in deep waters is rapid under oxic conditions (>1% day^{-1}) (Furlong & Carpenter, 1988); however, this was not the case most of the time in our study (around 9 months of the year) where the sediment-traps remained under anoxic conditions. Besides, the relatively low hypolimnetic temperatures of Alchichica (ca. 14°C) also diminish the degradation processes.

Both suspended and trap Chl*a* samples were extracted from the filters with 90% acetone at 4°C overnight. Samples were then analyzed with a fluorometer (EPA method 445.0, Arar & Collins, 1997), calibrated annually with a pure Chl*a* primary standard (Sigma Chemical Co.), and during each field trip, with a commercial Chl*a* secondary standard.

Aliquots of the trap samples were fixed in Lugol's solution and adjusted to a known volume in a settling chamber for cell counting. Diatoms >2 μm were identified and further enumerated following the Utermöhl's method (1958). This size was chosen to assure representing even the smallest diatom size reported for this lake (Oliva et al., 2001). The smallest diatom is the nanoplanktonic *Cyclotella choctawhatcheeana*, and the largest the microplanktonic *Cyclotella alchichicana*. The analyses were performed at 400× magnification using a Leika DMIL inverted microscope. Each specimen was identified to the lowest possible taxonomic level.

At least 400 cells were counted per sample. We counted separately: (1) diatoms with cell content corresponding to classes 1 and 2 of Padisák et al. (2003) classification ("mainly living cells with structured cell content and intact chloroplasts, and partly cells that possess some cell content") and (2) empty diatom cells corresponding to classes 3 and 4 of Padisák et al. (2003) classification ("empty diatom cells, either intact or slightly eroded").

Although we are aware the alkaline nature of Lake Alchichica's water favors frustule dissolution, it seems it does not affect frustules in the short term (i.e., 30 days). Microscopic observations of the frustules did not show conspicuous alterations of the valves or their ornamentation pattern. Caballero et al. (2003) found

well-preserved diatoms with valves barely corroded at the bottom of a 44-cm Alchichica's core; with a calculated average sedimentation rate of ca. 0.6 mm/year, it means >700 years old. Based on the later, a 30 days sampling interval seems not to be of concern regarding degradation.

Si fluxes considered diatoms with cellular content, empty frustules, and single valves (two valves equals one frustule). Small fragments (<50%) of valves were not considered. The diatom fluxes (F_{sp}) were calculated according to Reynolds et al. (1982) formula modified to include the time factor, according to the following Eq. 1 and expressed as cells $m^{-2} day^{-1}$:

$$F_{sp} = (C_{sp} * V_{trap})/(t * a_{trap}) \qquad (1)$$

where C_{sp} = diatom concentration in the trap (cells ml^{-1}), V_{trap} = trap volume (ml), t = deployment time (days), a_{trap} = cross-sectional area of the trap aperture (m^2)

At least 25 cells per species per sample were measured to calculate the cell biovolume (μm^3). The average cell size of each diatom species was measured to calculate the average cell biovolume. Silica content was calculated according to Conley et al. (1989) (Eq. 2):

$$\log_{10}(\text{Silica content})(\text{pmol Si})$$
$$= 1.03 \log_{10}(\text{Biovolume})(\mu m^3) - 2.45 \qquad (2)$$

Biogenic carbon (C) content was calculated following Rocha & Duncan (1985) (Eq. 3):

$$C \text{ (pg C)} = 0.1204 * \text{Biovolume}^{1.051}(\mu m^3) \qquad (3)$$

Carbon fluxes were calculated considering just diatoms cells with cellular content and not other biogenic carbon sources (e.g., other phytoplankton species, zooplankton), thus our estimates are conservative and further revisions are likely to increase the total amount of carbon exported to Lake Alchichica sediments.

Results

Physical and chemical conditions in the mixed layer

The mixed layer in Lake Alchichica ranged from 12 m during the early stratification down to the whole water column throughout the circulation (Fig. 1a). Z_{MIX} gradually widened along stratification and progressively deepened from 12 down to 26 m. Temperature in this layer was lowest ($14.8 \pm 0.1°C$) during the circulation period and highest ($19.9 \pm 0.7°C$) during the well-established stratification (Fig. 1b). Dissolved oxygen concentration (Fig. 1c) was low (~ 4 mg l^{-1}, saturation of 60%) at the beginning of the circulation period due to the mixing of the aerobic epilimnetic layer with the anoxic hypolimnetic water. The highest concentration (7.2 mg l^{-1}, saturation of 110%) was measured during the early stratification and remained around saturation for the rest of the stratification period. The euphotic zone ranged between 15 and 24 m (Fig. 1a). Lowest values (15–18 m) were measured in the circulation period (turbid water phase) and highest (24 m) during the well-established stratification (clear water phase).

Dissolved inorganic nitrogen concentration (DIN, Fig. 1d) was higher at the beginning of the year (63 ± 12 μg l^{-1}), dropped during the early stratification and remained low throughout the well-established and late stratification. Soluble reactive phosphorous concentration (SRP, Fig. 1e) was low in January (8 ± 2 μg l^{-1}) and increased during February, reaching its highest concentration in March (16 ± 6 μg l^{-1}); from April on, SRP concentration decreased and remained low for the rest of the stratification. The seasonal pattern of the soluble reactive silica concentration (SRSi, Fig. 1f) was similar to that of SRP. SRSi was low in January (87 ± 26 μg l^{-1}), increased during the circulation up to its highest concentration in April (313 ± 20 μg l^{-1}) and declined during the early stratification down to 50 ± 11 μg l^{-1}, increasing again in June, fluctuating later on around values <140 μg l^{-1}.

Most of the year (February to December), the stoichiometric ratios indicated N to be the limiting nutrient (N:P < 16 and N:Si < 1) for the primary production in Lake Alchichica (Fig. 2). However, SRSi was the most-likely limiting nutrient for diatoms (N:Si > 1 and Si:P < 16) in January.

Chl$a$ concentration and flux

Suspended Chl$a$ concentration in Z_{MIX} (Fig. 3a) was generally low, 3.7 ± 3.4 μg l^{-1} corresponding to oligotrophic conditions. The highest concentrations occurred in January (11.0 ± 1.0 μg l^{-1}) reaching

Fig. 1 Variations of **a** mixed layer (Z_{MIX}, *black circles*) and euphotic zone (Z_{EU}, *white circles*); **b** temperature (°C); **c** dissolved oxygen (mg l⁻¹); **d** dissolved inorganic nitrate (DIN); **e** soluble reactive phosphorus (SRP); **f** soluble reactive silica (SRSi) (all in µg l⁻¹). *Error bars* signify S.D. of the data. *Dotted lines* in **d**, **e**, and **f** are the limiting levels for the phytoplankton growth according to Sas (1989) and Reynolds (1999). See the text for further explanation
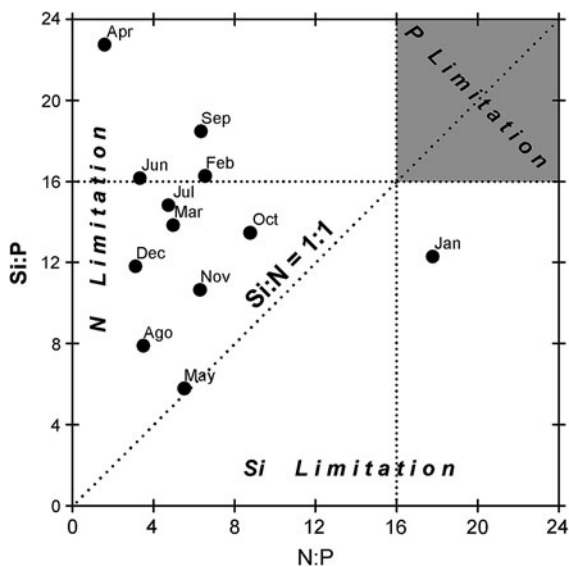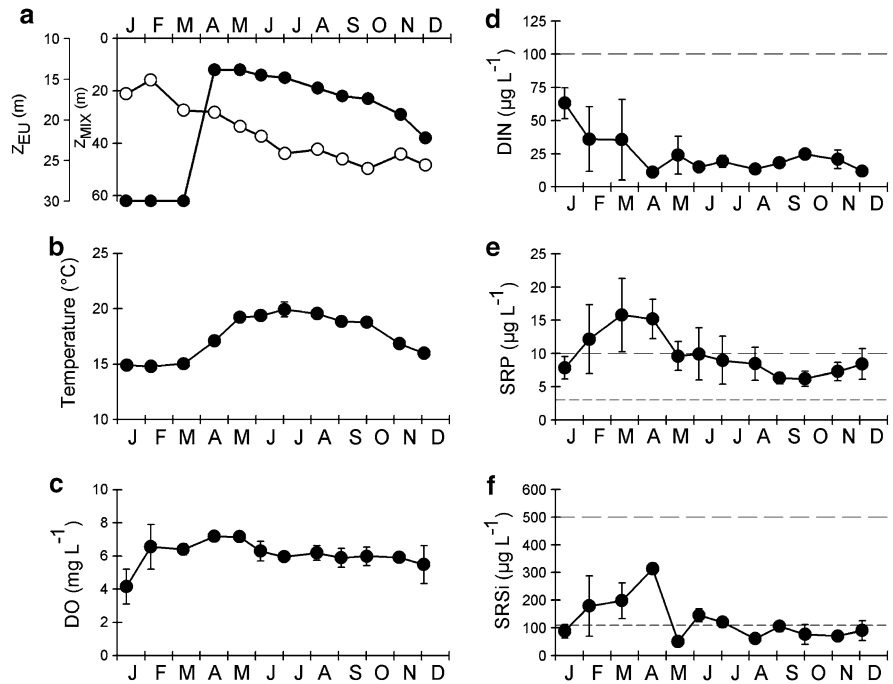
Fig. 2 Variation of stoichiometric ratios from the mixed layer (Si:P; N:P; Si:N). (Soluble reactive Si: soluble reactive P; dissolved inorganic N: soluble reactive P; soluble reactive Si: dissolved inorganic N)

temporary mesotrophic conditions that rapidly decreased at the stratification onset. From then on, concentrations fluctuated around 1.9 ± 1.1 µg l⁻¹; the minimum values were observed in August (0.6 ± 0.0 µg l⁻¹) and October (0.8 ± 0.1 µg l⁻¹).

Ch*l*a fluxes (Fig. 3b) for the entire period averaged 3.1 ± 3.2 mg m⁻² day⁻¹. The maximum Ch*l*a fluxes were observed after the winter diatom bloom (February) with the highest fluxes in the middle (13.1 ± 1.1 mg m⁻² day⁻¹) and bottom (13.3 ± 1.7 mg m⁻² day⁻¹) traps. A second peak of Ch*l*a flux was found in the middle trap in June. The dominant phytoplankton observed in traps was composed of diatoms, while cyanoprokariota and other taxa were hardly present.

Nonparametric correlations (*r* Spearman) were observed between Ch*l*a–SRP and Ch*l*a–SRSi in the circulation period ($r - S = -0.74$ and -0.66, respectively; $P < 0.05$). In contrast, no correlations were found during the stratification period.

Sinking diatoms and associated fluxes

We observed 16 species in traps: 13 diatoms, two chlorophytes (*Oocystis parva* West & G. S. and *Oocystis submarina* Lagerheim) and one cyanoprokariota (*Nodularia spumigena* Mertens). Only two diatoms (*Cyclotella alchichicana* and *C. choctawhatcheeana*) were truly planktonic, while the other 11 were tychoplanktonic (*Cocconeis placentula* Ehrenberg, *Cymbella mexicana* Ehrenberg, *Diploneis pseudovalis* Hustedt, *Ephitemia argus* Kützing,
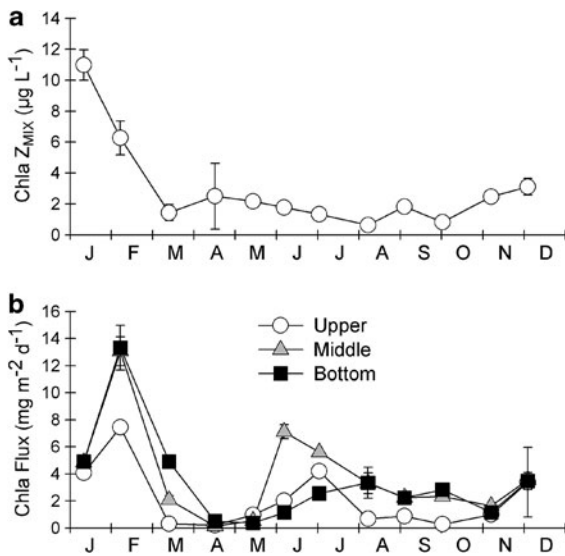
Fig. 3 Variations of chlorophyll *a* concentrations in **a** suspended (μg l^{-1}) and **b** sediment-trap (mg m^{-2} day^{-1}). *Error bars* signify S.D. of the data

Gomphonema olivaceum Dezmazières, *Surirella striatula* Turpin, *Amphora* sp., *Anomoeoneis* sp., *Navicula* sp., *Nitzschia* sp., *Pinnularia* sp.).

Taxonomic richness varied from one (*C. alchichicana* in the upper trap) in February, up to 11 taxa (upper trap) in October. The species diversity (H' as expressed by the Shannon–Weaver Index log base 2, Shannon & Weaver, 1949) fluctuates from 0, during circulation period, up to 2 in the well-established stratification (both in the upper trap).

At blooming conditions along the winter mixing period, phytoplankton was almost entirely composed of *C. alchichicana* (diameter, 57 ± 7 μm, $n = 1,385$), practically a monospecific bloom. The same species reached relatively high numbers again during the stratification, generating a deep chlorophyll maximum (DCM) in the metalimnion. Nevertheless, *C. choctawhatcheeana* (diameter, 10 ± 2 μm, $n = 85$) was also found in relevant numbers during the stratification, particularly in the upper traps, although their biomasses were generally well below those of *C. alchichicana*. At the stratification end, *C. choctawhatcheeana* was once again abundant in the middle trap.

Diatom fluxes

The diatom fluxes varied widely along the year between 3×10^6 and 304×10^6 cells m^{-2} day^{-1} (Fig. 4), with

an average of $40 \pm 55 \times 10^6$ cells m^{-2} day^{-1}. The maximum diatom flux (304×10^6 and 156×10^6 cells m^{-2} day^{-1} in the middle and bottom traps, respectively) took place in February (Fig. 4) and was mainly composed of *C. alchichicana*. A second peak was found in June in the upper and middle traps (93×10^6 and 81×10^6 cells m^{-2} day^{-1}, respectively); however, in this case, the upper trap was mainly composed of *C. choctawhatcheeana* and the middle trap by *C. alchichicana*. Finally, at the end of the year, the fluxes were relatively high, particularly in the middle trap (88×10^6 cells m^{-2} day^{-1}), and were composed of a combination of both *Cyclotella* species. The rest of the year, the fluxes were low ($<35 \times 10^6$ cells m^{-2} day^{-1}). The total annual diatom flux at the bottom trap was $15,000 \times 10^6$ cells m^{-2} year^{-1}.

Diatom and Chl*a* fluxes showed a positive correlation ($r - S = 0.66, 0.87, 0.77$, upper, middle, and bottom trap, respectively; $P < 0.05$).

The relative contribution of the frustules to diatom cells (Fig. 5) changed widely along the year between 3 and 97%, averaging $36 \pm 27\%$ in the upper trap (Fig. 5a), $57 \pm 24\%$ in the middle trap (Fig. 5b) and $59 \pm 19\%$ in the bottom trap (Fig. 5c).

Diatom silica and carbon fluxes

The diatom silica (DSi) fluxes (Fig. 6a) varied from 2 to 2,997 mg m^{-2} day^{-1} with an average of 369 ± 541 mg m^{-2} day^{-1}. The highest DSi fluxes were associated with the winter diatom bloom, particularly in February at the middle and bottom traps (2,997 and 1,545 mg m^{-2} day^{-1}, respectively). During the stratification period, except the middle trap in June when the flux was high (1,093 mg m^{-2} day^{-1}), the DSi fluxes were low (between 2 and 596 mg m^{-2} day^{-1}). *C. alchichicana* contributed with more than 99% to the total DSi flux.

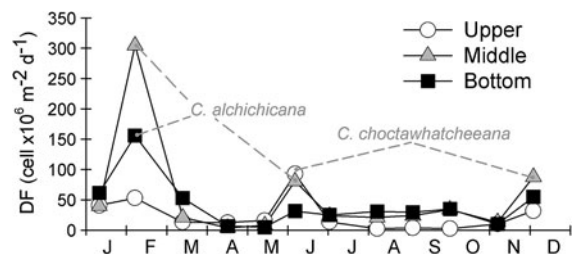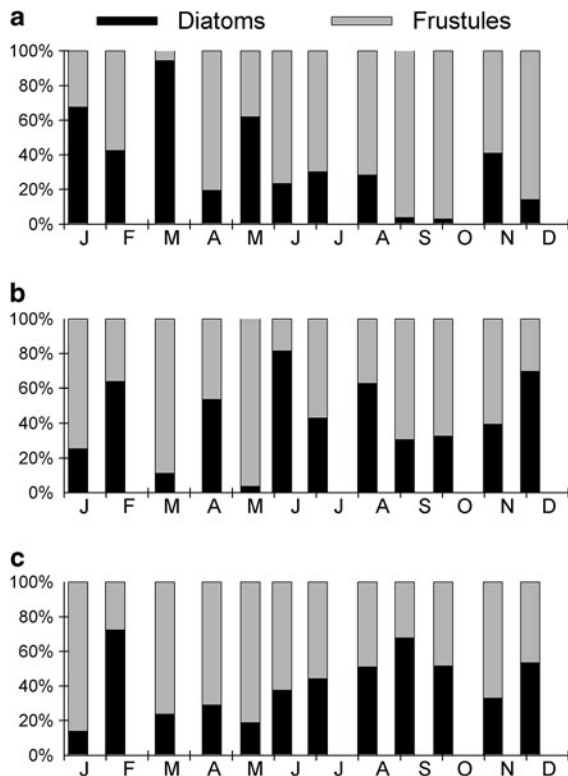**Fig. 4** Total diatom flux (cells x 10^6 m^{-2} day^{-1})

Fig. 5 Percentage contribution of diatoms and frustules to the total diatom flux for the entire study period in the **a** upper, **b** middle, and **c** bottom traps

Fig. 6 Fluxes (mg m^{-2} day^{-1}) of **a** diatom Si (DSi) and **b** diatom C (DC) estimated from monthly sediment-trap samples

Fig. 7 Contribution of *Cyclotella alchichicana*, *C. choctawhatcheeana,* and tychoplankton to the fluxes of diatom carbon in the **a** upper, **b** middle, and **c** bottom traps

The empty diatom frustules contributed to about one half of the total annual DSi flux to the bottom. The total annual DSi flux in the bottom trap was 147 g m^{-2} year^{-1}, which adds up to 337 tons year^{-1} when extrapolated to the total area of the lake.

The diatom carbon (DC) fluxes (Fig. 6b) varied from 1.2 to 2,918 mg m^{-2} day^{-1} with an average of 273 ± 572 mg m^{-2} day^{-1}. *C. alchichicana* contributed with more than 98% (98.5, 99.7, and 99.2% in the upper, middle, and bottom trap, respectively) to the total DC flux (Fig. 7). The DC flux dynamics was similar to the diatom and DSi fluxes. The total annual DC flux in the bottom trap was 92 g m^{-2} year^{-1} which reaches 212 tons year^{-1} when extrapolated to the whole area of the lake.

Discussion

Diatom taxonomic richness and species diversity in Lake Alchichica are extremely low; only two species
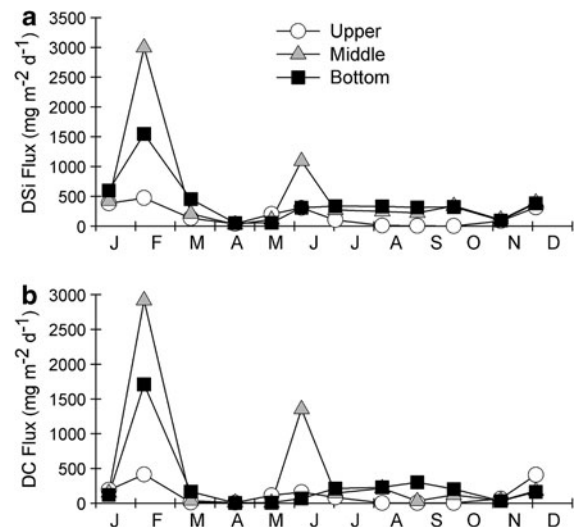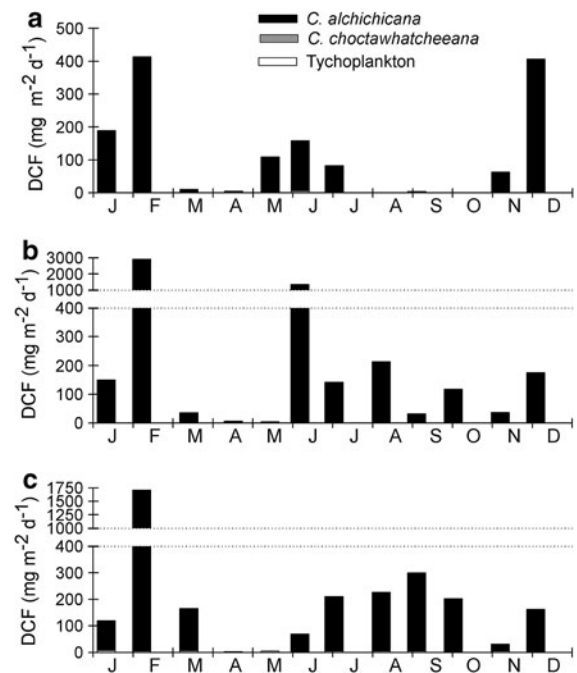
were found consistently along the year, although the contribution of the larger *C. alchichicana* overwhelmed the smaller *C. choctawhatcheeana* in the traps. Such low values of species richness are

common to other soda–alkaline lakes, like East Devils (Leland & Berkas, 1998) and Pyramid (Galat et al., 1981), because both the salinity and the soda–alkaline chemical nature in lakes are factors that overall lead to diminished specific richness (Williams et al., 1990). Similar species richness, taxonomic composition, and biomass dominance by *C. alchichicana* and *C. choctawhatcheeana* in the phytoplankton of Lake Alchichica have been observed along several years (Oliva et al., 2001; Sánchez et al., unpublished data).

The presence of a comparatively large number of tychoplanktonic species in the mixed layer during stratification probably resulted from the random transport of benthic–periphytic diatoms from the littoral zone through wind-generated currents and turbulence, as has been suggested for other lakes by Webster (1990). Although the tychoplankton taxonomic richness was higher than that of the "true" phytoplankton, its biomass was comparatively much lower (not more than 1% of total phytoplankton content in traps), and concomitantly did not represent an important contribution (<1%) to Si and C fluxes. Thus, sinking rates of *C. alchichicana* mainly control nutrient fluxes linked to diatoms in Lake Alchichica.

Related to fluxes and according to the lake dynamics theory of Håkanson & Jansson (2002), resuspension plays a relatively small role in the sediment transportation if the dynamic ratio (a value obtained by dividing the square root of the surface area in km^2 by the mean water depth in m) ranges between 0.1 and 1.1. In our case, the dynamic ratio of Lake Alchichica is 0.04 ($\sqrt{2.3\ km^2}/40.9$ m), far below the limits of "no effect", suggesting that estimations of our fluxes are not biased by resuspension. Supporting this calculation, as mentioned before, we found mostly phytoplankton cells and their remnants in the bottom trap but no sediment.

Diatom sedimentation flux in Lake Alchichica (15×10^9 cells m^{-2} $year^{-1}$) is higher than those reported for other inland water bodies, like oligotrophic Lake Sihailongwan (Chu et al., 2005) or Lake Constance (Sommer, 1984). Lake Sihailongwan is dominated by the small *Cyclotella comta* (7–8 μm), with diatom fluxes of 3×10^9 cells m^{-2} $year^{-1}$. Lake Constance has a lower diatom flux, 7×10^9 cells m^{-2} $year^{-1}$, in spite of its mesotrophic status and the dominance of large-sized colonial diatoms (*Fragilaria crotonensis*, *Stephanodiscus*

binderanus, *Asterionella formosa*, and *Melosira* [*Aulacoseira*] *granulata*). In addition, this lake has a small centric diatom, *Stephanodiscus hantzschii* (average size of 5 μm) that reaches high numbers during the diatom bloom, although its small size results in a minor contribution to the diatom flux, likewise *C. choctawhatcheeana* in Lake Alchichica.

Diatom Si flux in Lake Alchichica (147 g DSi m^{-2} $year^{-1}$) is larger than those reported from other epicontinental oligotrophic and even mesotrophic water bodies. Large and heavily silicified diatoms like *C. alchichicana* have high sinking and low grazing rates, leading to a fast sedimentation of algal biomass and preventing its transference to the higher trophic levels in the herbivorous food web. Pilskaln (2004) reported rather small DSi fluxes for Lake Malawi (values from 5-year study, 1.7–2.9 g $_{bio}SiO_2$ m^{-2} $year^{-1}$). The oligotrophic status of the lake with Chl$a$ $\leq 1.0 \pm 0.3$ μg l^{-1} (Guildford et al., 2007) explains such low values. Lake Sihailongwan (Chu et al., 2005) also displays low DSi fluxes (21 g $_{bio}SiO_2$ m^{-2} $year^{-1}$) associated to a reduced biovolume of the dominant *Cyclotella comta* (1,200 μm^3), when compared to the larger *C. alchichicana* (65,000 μm^3).

A similar situation is described for the oligotrophic Lake Baikal (Kempe & Schaumburg, 1996) and the mesotrophic Trout Lake (Poister & Armstrong, 2003) with DSi fluxes ranging from 12 to 107 mg m^{-2} day^{-1} (6 months study, values calculated from the graph) and 50 to 270 mg m^{-2} day^{-1}, respectively, comparing to 2-2997 mg m^{-2} day^{-1} in Lake Alchichica.

The process of diatom sedimentation contributes as well to the export of carbon. The DC fluxes in Alchichica are also elevated (92 g m^{-2} $year^{-1}$), higher than those reported for other oligotrophic lakes, like Lake Malawi (Pilskaln, 2004) with 0.3–0.9 g m^{-2} $year^{-1}$ (as particulate organic carbon (POC) considering a 5-years span). The organic carbon flux (OC) in oligotrophic Lake Michigan fluctuates from 63 to 259 mg m^{-2} day^{-1} (Eadie et al., 1984), range much lower than the estimated for Alchichica with 1.2–2918 mg m^{-2} day^{-1}. The authors explained the low carbon fluxes through its internal recycling within the mixing zone. Scavia & Fahnenstiel (1987) estimated similar POC fluxes (3–4 months study, 40–340 mg m^{-2} day^{-1}) for Lake Michigan.

These high carbon fluxes are clearly an important factor that explains the anoxic hypolimnion of Lake Alchichica, as suggested by Adame et al. (2008). The role of *C. alchichicana* on carbon fluxes to deep sediments in Lake Alchichica is important and constitutes up to 99% of the total carbon flux annually. Our results reinforce Cole et al. (2007) findings that, in spite of their small area, freshwater aquatic systems are important in processing carbon and can affect regional C balances.

The low nutrient concentration affects phytoplankton by decreasing the available energy for photosynthetic and respiratory processes. Diverse authors consider different nutrient concentrations below that the phytoplankton growth is restrained. According to Sas (1989), DIN (<100 µg l^{-1}) and SRSi (<500 µg l^{-1}) were limiting all over the year, meanwhile SRP reached limiting concentrations (<10 µg l^{-1}) only during the first semester. On the other side, following Reynolds (1999), DIN (<100 µg l^{-1}) was limiting throughout the year and SRSi (<109 µg SRSi l^{-1}) resulted limiting just during the second semester; opposite, SRP with concentrations >3 µg l^{-1}, was at no time limiting in Lake Alchichica.

Observations from mesocosms experiments have demonstrated that the dominance of diatoms in the phytoplankton diminishes rapidly when the concentration of Si is less than 56 µg l^{-1} (Andreassen & Wassmann, 1998) or 84 µg l^{-1} (Interlandi et al., 1999). Lake Alchichica has very low Si concentrations (129 ± 85 µg l^{-1} SRSi) in comparison with most lakes, especially those in volcanic environments (Armienta et al., 2008). Water exchange in Lake Alchichica occurs below the water surface and it seems likely that the hydraulic residence time of the lake is very low, which cuts off the common terrestrial silicate supply (Adame et al., 2008). This could explain the rather low silicate concentration. The latter suggests Si would be the most-likely limiting nutrient for phytoplankton growth in Lake Alchichica, particularly because diatoms dominate the phytoplankton biomass. In addition, based on stoichiometric rates, results showed Si could be limiting solely in January (N:Si > 1 and Si:P < 16), at the beginning of the mixing period when the diatom bloom took place.

It seems Si controls the diatoms at the beginning of the circulation period, but N is used up more rapidly,

and is the nutrient that limits growth and eventually causes a crash in the diatom population. DIN concentration remained <100 µg l^{-1} throughout the year, the minimum concentration proposed by Reynolds (1999), below which the phytoplankton growth is limited by nitrogen availability. Other facts lead to identify N as the most-likely limiting nutrient for the phytoplankton growth in Lake Alchichica. They are: (a) a sharp DIN depletion from January—where DIN concentration was the highest—on, (b) the bloom of *Nodularia spumigena*, and (c) N is stoichiometrically pointed as the most-likely limiting nutrient (N:P < 16 and N:Si < 1) from February on.

Lewis (2002) and Haynes (1988) mentioned the presence of "heterocystous blue-green algae" as a good indicator that they are actually fixing N. Microscopic observations of *Nodularia spumigena* while blooming in Lake Alchichica revealed the presence of numerous heterocytes. Falcón et al. (2002) measured the *N. spumigena* N-fixation rates (4.72–92.91 µM C$_2$H$_4$ m^{-2} h^{-1}), and found that the cyanobacteria associated to the tufa ring diminish their N-fixation rates after the *N. spumigena* bloom, and that it could have been caused by "tissue saturation by reduced nitrogen forms that were generated during the bloom".

Although the magnitude of the June diatom sedimentation peak (Fig. 4) was similar for the upper and the middle traps, the taxonomic composition was different. *C. choctawhatcheeana* dominated in the upper trap representing the Z_{MIX}, meanwhile *C. alchichicana* prevailed in the middle trap (representing the metalimnetic DCM). It should be noted that, in spite of its abundance in June in the Z_{MIX}, the smaller size of *C. choctawhatcheeana* compared to *C. alchichicana*, did not mirror in the Si and C fluxes (Fig. 6) to the deep sediments.

These findings show an interesting differentiation in the ecology of both *Cyclotella* species at the end of the early stratification. The smaller *C. choctawhatcheeana* is more dependent on the turbulence of the Z_{MIX}, and well-illuminated conditions. In addition, this species was benefitted by the N enrichment resulting from the *Nodularia spumigena* bloom (Oliva et al., 2001) degradation. In contrast, the larger *Cyclotella alchichicana* successfully develops to form the DCM at the metalimnion. The following metalimnetic features explain the advantages of developing in the DCM: a large density gradient that

slows down the sedimentation rate of the heavy diatoms, the dimmed light conditions at the bottom of the euphotic zone ($\sim$1% SPAR) and the nutrient source through diffusion from the hypolimnion carried out by internal waves, which reach an amplitude of 1–1.5 m in Lake Alchichica (Filonov & Alcocer, 2002).

New production is commonly exported to the bottom of the lake or consumed by herbivores and eventually exported as fecal pellets, when the phytoplankton of large size dominates (Legendre, 1999). The velocity of sedimentation has been calculated for large species of diatoms, from 11 m day^{-1} for *Stephanodiscus binderanus* (filamentous >40 μm, Sommer, 1984) to >50 m day^{-1} for *Thalassiosira levanderi* (chains of 4–5 cells >50 μm, Passow, 1991). The theoretical sedimentation rate of *Cyclotella alchichicana* has been calculated at about 4 m day^{-1} (Alcocer et al., 2008), considering 15 days to sink from the surface to the bottom of the lake. In the deepest traps, *C. alchichicana* still showed chloroplast content that indicated a fast sinking rate as suggested by other authors (e.g., Sommer, 1984; Lange et al., 1994; Kato et al., 2003).

Taking into account grazing, a low consumption of phytoplankton by the associated zooplankton can be related to, among other factors, the large size of the cells and/or a large amount of biomass production during the blooms. In the case of *C. alchichicana*, it is unlikely that is being consumed by the only species of copepod (*Leptodiaptomus garciai* Osorio–Tafall) present in Lake Alchichica, and certainly not by the small rotifer species (*Brachionus plicatilis* O.F. Müller and *Hexarthra jenkinae* Beauchamp). The abundance of this diatom during the winter bloom (with densities between 10,000 and 25,000 cells ml^{-1}, Oliva et al., 2001) favors lower consumption and, therefore, its exportation out of the photic zone.

The large size of the dominant phytoplankton species (*Cyclotella alchichicana* $\sim$55 μm) in Lake Alchichica, its probable aggregate formation and elevated abundance during blooming conditions that result in low predation pressure by zooplankton explain the high diatom sedimentation rates ($3–304 \times 10^6$ cell m^{-2} day^{-1}). The highest sedimentation rates took place during the circulation and were also probably related to nutrient depletion (SRSi and DIN). The estimated diatom sedimentation rates in Lake Alchichica are higher than those reported for other lakes of similar (oligotrophic) and even higher trophic status. The silica (2–2,997 mg m^{-2} day^{-1}) and carbon (1.2–2918 mg m^{-2} day^{-1}) sedimentation rates mirrored the diatom sedimentation rates reaching higher values than those reported from aquatic systems of similar or even higher trophic levels. Although it is oligotrophic, in relation to the diatom fluxes, Lake Alchichica presents dominance in number and biomass of one species of large size, *C. alchichicana* that contributes almost exclusively to the exportation of biogenic Si and C to the lake sediments.

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