

Chapter 12

Phytoplankton of Alchichica: A Unique Community for an Oligotrophic Lake



Gloria Vilaclara, María Guadalupe Oliva-Martínez, Miroslav Macek, Elizabeth Ortega-Mayagoitia, Rocío J. Alcántara-Hernández, and Cecilia López-Vázquez

12.1 The Phytoplankton of Lake Alchichica

Phytoplankton supplies the organic biomass that primarily fuels the trophic web in the pelagic community, especially for deep aquatic systems, and plays an essential role in a myriad of biogeochemical processes (Benoiston et al. 2017). These processes include those associated with nutrient cycling (carbon, silicon, nitrogen, and phosphorus), oxygen generation, and the removal of gaseous carbon through photosynthesis, among others.

The size (Sieburth et al. 1978) and other characteristics of the biological units (e.g., solitary cells or in filaments, aggregates or colonies; with or without mucilage, with or without spines) in which phytoplankton species occur are very important for the role they play in food webs (Peštová et al. 2008; Ortega-Mayagoitia et al. 2011; Bautista-Reyes and Macek 2012; Ciroso-Pérez et al. 2015; Macek et al. 2020). Their study's optimal techniques also vary with size. Identification and quantification methods differ for smaller sizes (picophytoplankton cells below 2–3 μm) and relatively larger ones (nanophytoplankton, 2–3 to 20 μm ; microphytoplankton, above 20 μm).

G. Vilaclara (✉) · M. G. Oliva-Martínez · M. Macek · E. Ortega-Mayagoitia
Grupo de Investigación en Limnología Tropical, FES Iztacala, Universidad Nacional
Autónoma de México, Tlalnepantla, Estado de México, Mexico
e-mail: vilaclara.gloria@iztacala.unam.mx; mirek@unam.mx; eortega@unam.mx

R. J. Alcántara-Hernández
Instituto de Geología, Universidad Nacional Autónoma de México,
Ciudad de México, Mexico
e-mail: ralcantarah@geologia.unam.mx

C. López-Vázquez
Programa de Posgrado en Ciencias del Mar y Limnología, Universidad Nacional Autónoma
de México, Ciudad de México, Mexico

In Lake Alchichica, the smallest sizes (picophytoplankton or autotrophic picoplankton, APP) have been extensively studied (by autofluorescence-based counting, comparing phycobilins and chlorophyll-*a*) as part of the microbial loop. The most common species and the annual dynamics of phytoplankton, emphasizing nano- and microphytoplankton (Utermöhl-based counting), have also been explored.

12.2 Picophytoplankton

Autotrophic picoplankton (APP) and microorganisms included in the microbial loop, which are cycling their primary production, play an essential role in the plankton food web of tropical lakes (Sarmiento 2012). However, the re-evaluated PEG model (Sommer et al. 2012) still underestimated their role, applied to define the plankton dynamics under different climatic conditions (De Senerport Domis et al. 2013). Moreover, exhaustive long-term and complete data are available only from non-tropical monomictic lakes such as Lake Constance (Gaedke and Weisse 1998), Kinneret, Israel (Malinsky-Rushansky et al. 1995; Sukenik et al. 2014), and Lake Biwa, Japan (Maeda et al. 1992; Wakabayashi and Ichise 2004; Sekino et al. 2007).

The APP has been studied in Lake Alchichica by Peřtová et al. (2008), Macek et al. (2009), Hernández-Avilés et al. (2010), Bautista-Reyes (2011), Bautista-Reyes and Macek (2012), and Macek et al. (2020). APP abundances and biomasses were analyzed using their autofluorescence in green excitation and orange/red fluorescence observation and taking photographs for image analysis (ImageJ with specific macros). The images were compared with those taken with the chlorophyll-*a* filter set. Individual cyanobacterial cell volumes used for the organic carbon approximation ($200 \text{ fg}/\mu\text{m}^3$; Weisse 1993) were based on a 2003–2006 evaluation (González-Aguilar, unpublished). The representative carbon content of Alchichica's cyanobacteria used to calculate biomasses was intermediate during mixing ($46 \text{ fg}/\text{cell}$), lowest in the mixing layer during stratification (epilimnion, $32 \text{ fg}/\text{cell}$), and highest in the anoxic hypolimnion ($64 \text{ fg}/\text{cell}$).

Oliva et al. (2001) and Rosiles-Gonzalez (2005) identified the cyanobacteria composition by their morphology, which has been subsequently acknowledged by Peřtová et al. (2008), Macek et al. (2009), and Alcocer et al. (2014a, b). *Synechocystis aquatilis* was reported as the dominant picoplankton in Lake Alchichica (Oliva et al. 2001). Rosiles-González (2005) found *Synechococcus nidulans* and *Synechocystis* sp. in the mixing layer (the whole column in January, the epilimnion during early stratification), and at the metalimnion during the rest of the stratification; colonial cyanobacteria of the genera *Epigloeosphaera*, *Cyanodictyon*, *Lemmermanniella*, and *Eucapsis* appeared mainly during the stratification, either every month or restrained to a few of them.

Callieri et al. (2013) isolated and phylogenetically characterized three clones of phycoerythrin-rich *Synechococcus* from the lake; now *Synechococcus* sp. (PE) 8F6, which is classified as a member of *Cyanobium/Synechococcus* sub-cluster 5.2 (Sánchez-Baracaldo et al. 2019). *Cyanobium/Synechococcus* and *Synechocystis* are

confirmed using molecular methods (see Chap. 11 Bacterioplankton). *Cyanobium* sp. was the most common OTU (Operative Taxonomic Unit), distributed in the epilimnion and below the oxycline layer. The diversity of OTUs is scarce to date, but it is supposed to be greater than that found in the consulted libraries.

Throughout the year, the APP in the whole column averages 1.5×10^5 cells/mL (2.6×10^3 to 9.1×10^5 cells/mL) with annual peaks just during and at the end of circulation, between the end of January and April (Fig. 12.1a). However, the APP distribution is heterogeneous; it follows a very similar annual pattern tightly linked to the lake's warm-monomictic thermal regime, i.e. stratification and circulation periods (Fig. 12.1b). However, the local maxima, which peaked $>1 \times 10^6$ cells/mL, has been observed in the upper zone of the mixed layer during the circulation (typically at 15–20 m).

In contrast, just after the stable stratification of the water column begun, APP numbers used to drop to a minimum in the epilimnion. They concentrated either throughout the thick metalimnion (frequently from July to August) or in the metalimnion upper limit (during the late stratification, from September or October to November), showing lower abundances (about 5×10^5 cells/mL). The abundance peaks do not usually correspond to the deep chlorophyll maxima (DCM) produced by *Cyclotella alchichicana* (Ortega-Mayagoitia et al. 2011).

An apparent relation to photosynthetically active radiation PAR was observed (Fig. 12.1b), with the deepest APP maxima found typically above 1% sPAR. On the other hand, APP were sometimes abundant even in the entirely dark layers that coincided with the oxycline in the years when January mixing was incomplete.

Generally, APP distribution relates to DO concentrations, but picocyanobacteria were also detected below the oxycline. Such behavior is better observed in the plot

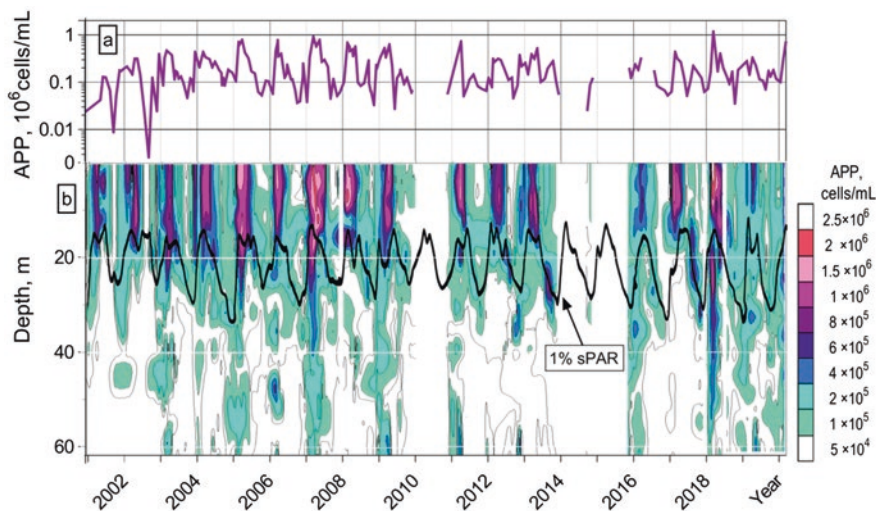


Fig. 12.1 (a) Depth weighted average of autotrophic picoplankton, APP (cells/mL). (b) Isoleths of APP abundances and the depth of the euphotic zone. (The thick black line corresponds to 0.1% of photosynthetically active radiation (PAR) in the surface layer)

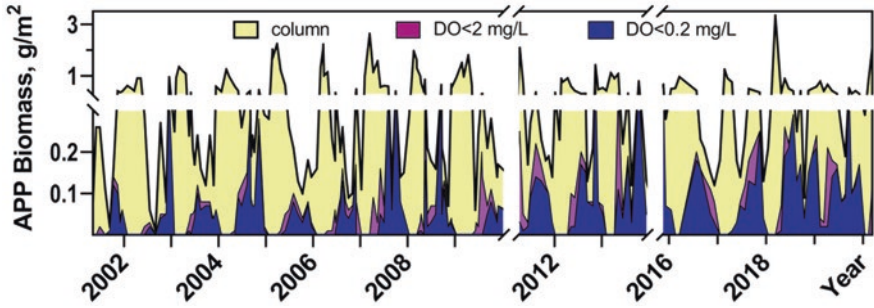


Fig. 12.2 Distribution of the autotrophic picoplankton carbon biomass (g/m^2) within the water column of Lake Alchichica. Total column (column, in yellow), microaerobic layer ($\text{DO} < 2 \text{ mg}/\text{L}$, in violet) and anaerobic ($0.2 \text{ mg}/\text{L}$, in blue) layer

of estimated carbon biomass integrated below a surface area (Fig. 12.2), which considers differences in the specific cell biomass in distinct layers. Usually, the APP biomass observed in the anoxic hypolimnion was important, although smaller than that of the epilimnion and metalimnion biomass.

Typically, APP abundances correlate to other limnological variables. For example, in September 2018 (Fig. 12.3) the APP maximum numbers coincided with the upper metalimnetic limit, where the sPAR dropped to 1%. However, the first DCM peak coincided with oxygen depletion and the biomass maximum of APP colony feeding *Euplotes euryhalinus*. The APP-feeding *Spirostomum teres* biomass also peaked there. The second DCM coincided with a phycocyanin's peak, indicating a local concentration of picocyanobacteria colonies and the second *S. teres* biomass peak. Where the Eh (redox potential) dropped to negative values, the maximum abundance of anoxygenic photosynthetic bacteria, APB (a purple sulfur bacteria, *Thiocapsa* sp.) peaked, which along with APP, supported *S. teres* growth (distribution and dynamics of pelagic bacteria are further explored in Chap. 11, Bacterioplankton, and 13, Protozooplankton).

12.3 Nano- and Microphytoplankton

12.3.1 Particularities on the Composition of the Lake Alchichica's Larger Phytoplankton

A relevant feature in the phytoplankton of Lake Alchichica is their low species richness. The most abundant nano- and microphytoplankton species reported at any time of the year (Table 12.1) are limited to seven (referenced with authorship in Chap. 20, Diversity and Endemisms). All of them have remained dominant numerically and/or in biovolume up to the 2017–2019 timeframe (unpublished data).

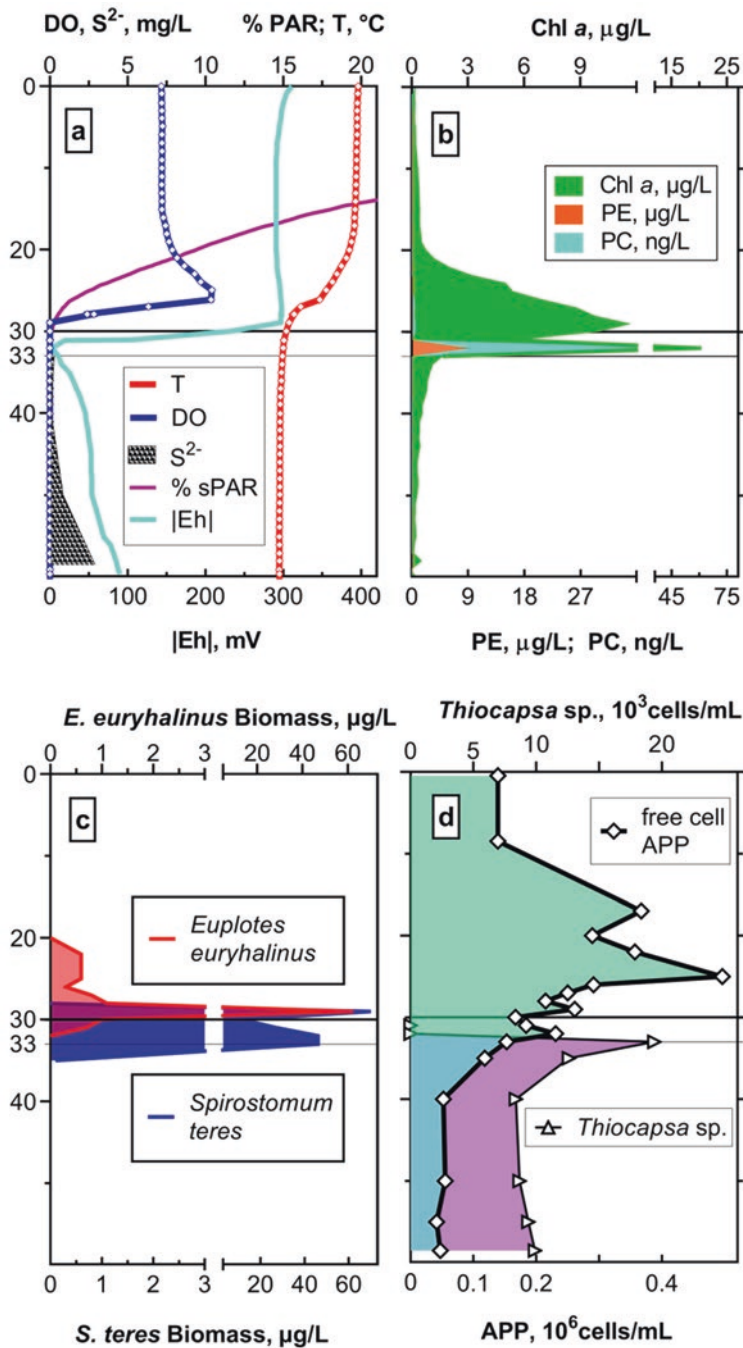


Fig. 12.3 (a) Limnological variables in Alchichica, September 2018: Dissolved oxygen, DO; sulfides, S²⁻; %PAR; temperature, T; and Redox potential (absolute values), |Eh|. (b) Chlorophyll-*a*, Chl-*a*; phycoerythrin, PE; and phycocyanin, PC. (c) Distribution of the most biomass-important ciliates. (d) Distribution of free celled APP and *Thiocapsa sp.* Horizontal lines limit the thermocline and the zone where the redox potential drops to negative values

Table 12.1 Main species of phytoplankton in Alchichica Lake and taxonomic nomenclature as referred to in literature

Species	Size	Rel.	Referred as:
<i>Cyclotella alchichicana</i>	M	bio	<i>Stephanodiscus niagarae</i> 1; <i>C. quillensis</i> 3, 4; <i>Cyclotella</i> sp. 6; <i>C. alchichicana</i> 7, 10, 11.
<i>C. choctawhatcheeana</i>	N	num	<i>Cyclotella</i> sp. 3; <i>C. choctawhatcheeana</i> 4, 6, 8, 10.
<i>Chaetoceros elmorei</i>	M	num	<i>C. similis</i> 1; <i>C. elmorei</i> 3, 4, 6.
<i>Nodularia</i> aff. <i>spumigena</i>	M	bio	<i>N. spumigena</i> 3, 4, 9; <i>N. cf. spumigena</i> 2, 5; <i>N. aff. spumigena</i> 10,12.
<i>Oocystis submarina</i>	M	num	<i>Oocystis</i> sp. 1; <i>O. submarina</i> 3, 4, 6.
<i>O. parva</i>	N	num	3, 4, 6.
<i>Monoraphidium minutum</i>	N	num	

1. Arredondo et al. (1984); 2. Tavera and Komárek (1996); 3. Oliva (2001); 4. Oliva et al. (2001); 5. Komárek and Komárková-Legnerová (2002); 6. Rosiles (2005); 7. Oliva et al. (2006); 8. Oliva et al. (2008); 9. Oliva et al. (2009); 10. Ardiles et al. (2012); 11. Oliva et al. (2019); 12. Vilaclara and Oliva (2019)

Size indicates the greatest dimension of the biological unit (solitary cells, cells plus spines, various cell aggregates -colonies, filaments, chains, including mucilage when present-): *M* microphytoplankton (>20 µm), *N* nanophytoplankton (2–3 up to 20 µm). Relevance (Rel.) numerical (num) or in biomass (bio)

Other species have been seen more rarely and/ or at lower abundances, such as the dinoflagellate *Parvodinium* (*Glenodinium* in Oliva et al. 2001, also detected in 2017–2019, unpublished data); the cryptophyte *Cryptomonas* sp. (Rosiles 2005, practically unobserved at present), and small flagellates that sometimes are hardly identifiable with Lugol fixative (see Chap. 13, Protozooplankton). *Monoraphidium dybowskii* has been recognized since 2003–2004 (Rosiles 2005 up to present). Recently (2017–2019), previously unreported species has been observed in Alchichica's phytoplankton: the nanoplanktonic diatom *Halamphora* sp. (with scarcely silicified frustules and actively dividing in the water column; it should be noted that *Halamphora* is a typical benthic genus but presents a planktonic habit in Alchichica, as has also been found for other genera species in the Gulf of Mexico, Olivares et al. 2017). Finally, the cyanobacterium *Pseudanabaena* sp. shows cell diameters below 2 µm but formed in a row inside a filamentous mucilage that can be of a much longer size (see Chap. 20, Diversity and endemisms).

It is important to note how common it is to report benthic species that can be seen in the phytoplankton samples, in low numbers, with no distinction between the two. These are usually tycho plankton species of the type defined by Hutchinson (1967, in Cahoon 2016) as pseudoplankton, i.e., suspended in the water column by chance, due to mechanical effects as wind-generated turbulence. It should be emphasized that these species have been removed from the Alchichica phytoplankton species list and the others consulted (Table 12.2).

In summary, the specific richness of larger phytoplankton recognized so far for Alchichica does not exceed *ca.* 15 species, a low number compared to the variety of its littoral autotrophic microalgal species (see Chap. 10, The Littoral Benthic

Table 12.2 Comparison of species richness (S) for large-sized phytoplankton in volcanic, alkaline lakes of variable salinity (pseudoplankton diatom species excluded^a)

	Origin and hydrochemical water type	Salinity (g/L)	Trophic state	S	References
Alchichica, Mexico	Volcanic, saline, Na-Mg alkaline (microbialites present)	8.5–9.0	Oligotrophic	15 ^a	This chapter and book
Hayq, Ethiopia	Volcanic, mineralized freshwater, Na-Mg alkaline, low sulfate	0.5	Oligotrophic (1941–1991)	~10 or less	Fetahi et al. (2014)
Hayq, Ethiopia			Eutrophic (1992–2008)	40	
Hazar, Turkey	Tectonic, highly mineralized freshwater, soda-alkaline	1,1	Oligotrophic	15 ^a	Koçer and Sen (2012, 2014)
Metahara, Ethiopia	Lava-dam, saline, soda-alkaline, low Mg	5.3	Mesotrophic	10 ^a	Kebede and Willén (1998); Kebede et al. (1994)
Shalla, Ethiopia	Volcanic, saline, soda-alkaline, low Mg	18.1	Mesotrophic	15 ^a	
Dziani Dzaha, Mayotte Island	Volcanic, hypersaline, soda-alkaline (microbialites present)	ca. 70	Eutrophic	2 ^a	Bernard et al. (2019)

Community). However, other lakes with a chemical signature similar to Alchichica (see Chap. 5, Hydrogeology and Hydrochemistry, and Table 12.2) show comparable specific phytoplankton richness. It is interesting that the species richness decreases with increasing salinity in alkaline environments (Sui et al. 2016, Table 12.2) and rises when there is a shift towards eutrophy (Fetahi et al. 2014) except for hypersaline environments (like the one exemplified by Bernard et al. 2019).

Therefore, the low species richness of large-sized phytoplankton in Alchichica mirrors the hydrochemical characteristics of its saline and soda-alkaline traits (see Chap. 5, Hydrogeology and Hydrochemistry).

The particular aspects of Lake Alchichica's phytoplankton that make it unique are diverse. The ecologically dominant diatom *C. alchichicana* is microendemic to this lake (Oliva et al. 2006, 2019). *C. choctawhatcheeana* has a wide biogeographic distribution, but in Mexico has only been reported from Alchichica and the nearby Lake Atexcac (Oliva et al. 2008). Characteristic morphological arrangements such as the constancy in the linear shape for the filaments of *Nodularia* aff. *spumigena* (Oliva et al. 2009; Vilaclara and Oliva-Martínez 2019) suggest molecular changes that could lead to the definition of a new taxonomic category (based on finding, after a metagenomic study, a *Nodularia* sp. in the pelagic zone of Alchichica, not assimilable to any other *Nodularia* species published in the Silva database libraries; see Chap. 20, Diversity and Endemisms). The presence of a planktonic diatom from the Bacillariophycidae group, *Halamphora* sp., is an unexpected outcome for a mostly benthic genus.

Microendemism also occurs in other groups of organisms in the lake, both pelagic and benthic (see Chap. 20, Diversity and Endemisms). In the case of phytoplankton, probably the composition and concentration of major ions in the water (see Chap. 5, Hydrogeology and Hydrochemistry), which on the one hand imposes restrictions on species richness, to some extent may also serve as a barrier isolating species from other lake environments in the Oriental basin and nearby water bodies. The latter could favor a rapid evolution of some species for such a young lake (late Pleistocene or Holocene origin; see Chap. 2, Geological Evolution), even despite the annual winter stay of migratory waterfowl (Saunders and Saunders 1981), which can act as transportation vectors for microscopic species coming from the intermediate water bodies where they have landed during their journey.

12.3.2 A Yearly Dynamics for Phytoplankton

Cuevas (2017) and Cuevas et al. (2017) summarize “a type year” of chlorophyll-*a* concentration and primary productivity in Lake Alchichica. Primary productivity rates and chlorophyll-*a* concentration show a recurrent annual, seasonal cyclicality. Two peaks stand out, one associated with the mixing period and related to the hemispheric winter diatom bloom. Another evidenced by a Deep Chlorophyll Maximum (DCM), related to *C. alchichicana* during the well-established stratification. The surface bloom of *N. aff. spumigena* during early stratification (sometime between April and June), of variable intensity depending on the year (Oliva et al. 2009), also marks a visible change in the annual lake dynamics, despite its relatively short duration.

Based on the composition and abundances of the larger phytoplankton community and associated physicochemical descriptors published in Oliva et al. (2001), the 1998 data were reanalyzed and presented according to the current knowledge on the phytoplankton composition. The abundance of the seven most common species (cells/mL) was transformed to biovolume ($\mu\text{m}^3/\text{mL}$, Olenina et al. 2006) as a proxy for biomass (from now on, both terms are used interchangeably). The species biovolumes were integrated with the physicochemical descriptors (temperature, T°C; dissolved oxygen, DO mg/L; nutrients mg/L, N-NO₃⁻, N-NO₂⁻, N-NH₃, and Soluble Reactive Phosphorus, SRP; chlorophyll-*a*, Chlor, $\mu\text{g}/\text{mL}$).

A Principal Component Analysis (PCA) was performed with R-Studio (Fig. 12.4). Greater variability in the vertical distribution of species and other limnological descriptors is observed during stratification, compared to a much lesser one during mixing, which tends to homogenize the water column. Components 1, 2, and 3 absorb 33, 14 and 11% of the variability, respectively. Axis 1 is interpreted as compartmentalization of the column in epilimnion on the one hand, with elevated temperatures and DO values, and congregates six of the species, all but *C. alchichicana*; on the other hand, it segregates nutrients into deeper, cooler, anoxic layers. Component 2 is explained as the bloom of the species with higher buoyancy and lower chlorophyll-*a* concentration (the cyanobacterium *N. aff. spumigena*) in the

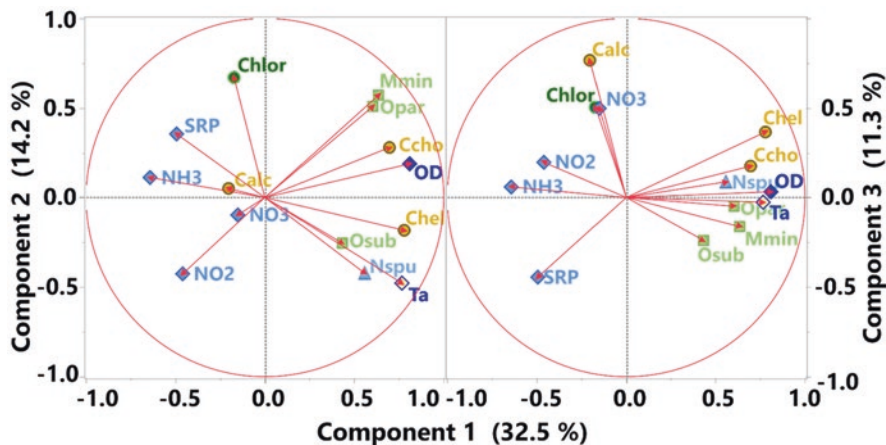


Fig. 12.4 Factorial loading plots of nutrients, chlorophyll-*a*, and the seven main large species: diatoms **Calch** *Cyclotella alchichicana*, **Chel** *Chaetoceros elmorei*, **Ccho** *C. choctawhatcheeana*; cyanobacteria **Nspu** *Nodularia* aff. *spumigena*; chlorophytes **Osob** *Oocystis submarina*, **Opar** *O. parva* and **Mmin** *Monoraphidium minutum*

shallower zone of the epilimnion, with higher temperatures, versus the smaller chlorophyte species (*M. minutum* and *O. parva*) distributed throughout the mixing layer during stratification (epilimnion). Component 3 accounts for the deep maximum of chlorophyll-*a* associated with *C. alchichicana* in and around the metalimnion.

In short, results underscore the higher variability encountered during stratification and segregates species in the epilimnion (all but *C. alchichicana*) from nutrients in colder, deeper, and anoxic layers. It highlights the short but relevant *N. aff. spumigena* bloom in the epilimnion's upper zone, and the deep chlorophyll-*a* maximum, associated with *C. alchichicana*, at the metalimnion. This pattern is consistent with a typical year (Cuevas et al. 2017; see Chap. 7, Physicochemical Characteristics).

A cluster analysis was also applied with R-Studio. Figure 12.5 shows the hierarchical clustering for the biomass of the seven species throughout the year. The dendrogram differentiates between *C. alchichicana* and the other six species mostly distributed at the epilimnion during stratification. The constellation plot arranges the species as endpoints. Each line's length approximates the distance between species; the biovolume centroid lies between the two larger species, *C. alchichicana*, and *N. aff. spumigena*. Due to their contribution to the biomass throughout the year, both species stand out. However, they are differentiated from each other: *C. alchichicana* because it grows in or near the metalimnion during the established stratification and *N. aff. spumigena* because it blooms in the epilimnion during early stratification.

C. alchichicana has a significant impact on the biogeochemical cycles of the lake. As an autotrophic species, it is the leading exporter of nutrients to the bottom sediment, including biogenic C and Si (Ardiles et al. 2012). Despite being so

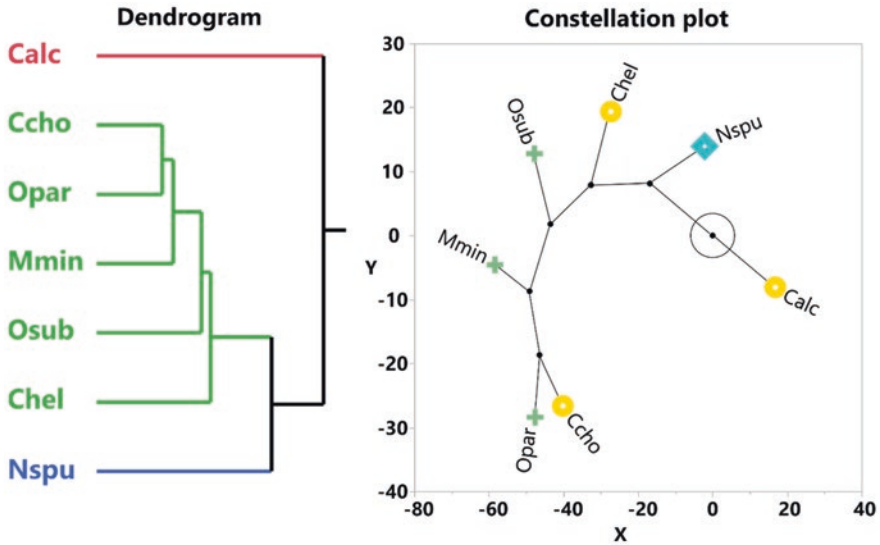


Fig. 12.5 Hierarchical conglomeration (Ward's method). Dendrogram and constellation plot for the biovolumes of the seven most abundant large phytoplankton species of Lake Alchichica. In the constellation plot, yellow circles point to diatoms **Calc** *Cyclotella alchichicana*, **Chel** *Chaetoceros elmorei*, **Ccho** *C. choctawhatcheeana*; the blue square to the cyanobacteria **Nspu** *Nodularia* aff. *spumigena*; and light green x to chlorophytes, **Osub** *Oocystis submarina*, **Opar** *O. parva* and **Mmin** *Monoraphidium minutum*

important in nutrient cycling, it does not enter the grazing food webs because of its large size (35–63 μm in diameter during the sampling lapse): most of the year, adults of the copepod *Leptodiaptomus garciai* cannot feed on it, let alone smaller forms of zooplankton (Ortega-Mayagoitia et al. 2011; Ciroso et al. 2015; Macek et al. 2020). Such characteristics could bestow on it the title of the “Queen of Alchichica” (*sensu* Ortega-Mayagoitia); *C. alchichicana* may be one of the famine story's main culprits in the pelagic realm (see Chap. 14, Metazooplankton). In some way, this species acts as a symbolic exponent of the myth of Tantalus: much food is available, but it is impossible to feed on it, and it ends up being lost, dragging its nutrients to the bottom of the lake, while playing an essential role in the regional carbon balance (Alcocer et al. 2014a, b).

N. aff. spumigena is the second largest species in microphytoplankton (average cell diameter around 9–10 μm , but filaments up to several mm), blooming in the epilimnion's upper layers for a short time during early stratification. Such an extensive growth relatively close to the water surface is attributed to the presence of aerotopes that give it a high buoyancy during an episode of environmental nitrogen limitation (see Chap. 7, Physicochemical Characteristics). Unlike *C. alchichicana*, an important proportion (84%) of the biomass is carried by the wind to the littoral zone, where it decomposes (Alcocer et al. 2012; Oseguera et al. 2013). It does not enter the grazing food web either but directly into the microbial loop's

decomposition route. It can be found in low numbers and shorter filaments (less than 100 μm) during the established and late stratification.

Given the importance of these two species of microphytoplankton for the biogeochemical cycles and linked to the thermal regime and the dissolved oxygen vertical gradients (Time-depth plots, Fig. 12.6a), their distribution throughout the year is depicted in Fig. 12.6b.

Another category of microphytoplankton comprises two species whose individual cell size qualifies them as nanoplankton, *Chaetoceros elmorei* and *Oocystis submarina*. However, organized into biological units, they become microplankton. *C. elmorei* develops as chains of cells with intertwined spines during mixing; nevertheless, they are more frequently found as solitary cells or in pairs during stratification, but their four long spines per cell equally hinder zooplankton feeding. Colonies of *O. submarina* develop some firm layers of mucilage, so they also function as larger biological units; the latter does not facilitate their consumption in grazing herbivores' food webs either.

The nanophytoplankton species *C. choctawhatcheeana*, *Oocystis parva*, and *Monoraphidium minutum* make up the third category. The three species enter the trophic web as food for heterotrophs, such as some ciliates (see Chap. 13 Protozooplankton), the rotifer *Brachionus* sp. 'Mexico' and possibly various life stages of the copepod *Leptodiaptomus garciai* (see Chap. 14, Metazooplankton).

12.4 Conclusions

Large phytoplankton dominate the biomass of Lake Alchichica all year round. Their size prevents them from being consumed by protozooplankton and metazooplankton, resulting in a significant nutrient loss through their primarily transfer to the deep bottom and secondarily into the littoral zone. Thus, large phytoplankton (mostly *C. alchichicana*) drive biogeochemical cycles. For example, a large amount of carbon and nutrients are exported below the thermocline into the sediments, where they accumulate and preserve. The latter impacts the pelagic system's overall functioning in Lake Alchichica, resulting in a key factor regulating zooplankton ecology (e.g., through food limitation) and, most likely, their evolution.

The importance of the small-sized phytoplankton or APP on the microbial loop is relevant by integrating into the food webs of heterotrophic species. However, the relative importance of carbon flux through the microbial loop may appear minor regarding a comparatively lower biomass.

This divergence in phytoplankton functional adaptation (large species as drivers for nutrient loss out of the pelagic zone, small species at the base of the pelagic food webs), together with the low species richness, the presence of a microendemism, and morphotypes that could be new species, confer the peculiar characteristic of uniqueness to Lake Alchichica and its autotrophic producers in the water column.

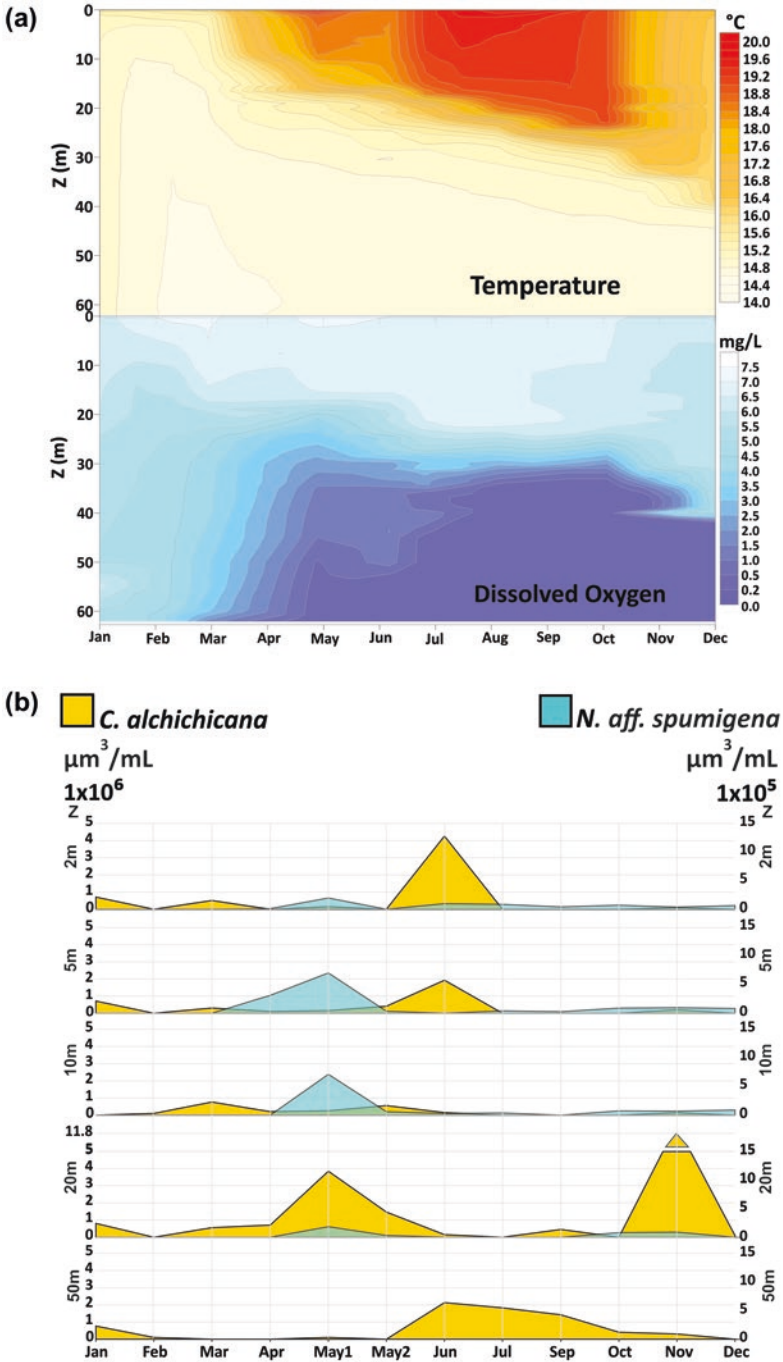


Fig. 12.6 (a) Time-depth plots for temperature and dissolved oxygen. (b) Comparison of the population biovolume for the two larger phytoplanktonic species (note the difference of an order of magnitude between them)

Acknowledgments To Laura Peralta for her technical support in the chlorophyll analysis. Luis A. Oseguera for field sampling (2017–2019). Omar Rivera for helping in statistical analyses and some graphics. Cecilia López-Vázquez thanks CONACYT for her MSc studies' scholarship. G. Vilaclara and M. Macek were supported in the manuscript's preparation through a DGAPA/PAPIIT grant IN231820 and IN219220 (2020–2022). support for the long-term analysis of Lake Alchichica data was granted as UNAM DGPA/PAPIIT IN225517. Previous studies were granted to M. Macek through CONACYT 52387 (2007), SEP-CONACYT 79893 (2009); CONACYT 131689 (2011–2013), CONACYT Mexico - DLR Germany bilateral grant 1203801, DGAPA IN208502 (2003–2005), DGAPA IN207206 (2006–2008), DGAPA IN222709 (2009–2011), and as internal UNAM FES grants PAPCA 2002–2003, PAPCA 2003–2004, PAPCA 2006, and PAPCA 2009.

References

- Alcocer J, Escobar E, Oseguera LA, Ardiles V (2012) El almacén de carbono orgánico particulado en los sedimentos de un lago oligotrófico tropical. In: Paz F, Cuevas RM (eds) Estado Actual del Conocimiento del Ciclo del Carbono y sus Interacciones en México: Síntesis a 2011. Programa Mexicano del Carbono, Universidad Autónoma del Estado de México e Instituto Nacional de Ecología. Texcoco, Estado de México, México, pp 534–540, 869 pp
- Alcocer J, Ruiz-Fernández AC, Escobar E, Pérez-Bernal LH, Oseguera LA, Ardiles-Gloria V (2014a) Deposition, burial and sequestration of carbon in an oligotrophic, tropical lake. *J Limnol* 73(2):223–235, 458 pp
- Alcocer J, Vilaclara G, Ardiles V, Velasco L, Oseguera LA (2014b) Flujos verticales de fitoplancton en un lago oligotrófico tropical: Alchichica, Puebla, México. In: Alcocer J, Merino-Ibarra M, Escobar-Briones E (eds) Tendencias de Investigación en Limnología Tropical: Perspectivas Universitarias en Latinoamérica. Asociación Mexicana de Limnología, A.C., ICMYL, UNAM, y CONACYT, México, pp 177–186
- Ardiles V, Alcocer J, Vilaclara G, Oseguera LA, Velasco L (2012) Diatom fluxes in a tropical, oligotrophic lake dominated by large-sized phytoplankton. *Hydrobiologia* 679:77–90
- Arredondo JL, Vera O, Ortiz AO (1984) Análisis de componentes principales y cúmulos de datos limnológicos en el lago de Alchichica, Puebla. *Biotica* 9:23–39
- Bautista-Reyes F (2011) Selección *in situ* de presas de protistas picoplanctívoros del lago Alchichica. PhD Thesis, UNAM, Mexico
- Bautista-Reyes F, Macek M (2012) Ciliate food vacuole content and bacterial community composition in the warm-monimictic crater lake Alchichica (México). *FEMS Microbiol Ecol* 79:85–97
- Benoiston A-S, Ibarbalz FM, Bittner L, Guidi L, Jahn O, Dutkiewicz S, Bowler C (2017) The evolution of diatoms and their biogeochemical functions. *Philos Trans R Soc B* 372:20160397
- Bernard C, Escalas A, Villeriot N et al (2019) Very low phytoplankton diversity in a tropical saline-alkaline lake, with co-dominance of *Arthrospira fusiformis* (Cyanobacteria) and *Picocystis salinarum* (Chlorophyta). *Microb Ecol* 78:603–617
- Cahoon L (2016) Tychoplankton. In: Kennish MJ (ed) Encyclopedia of estuaries. Encyclopedia of earth sciences series. Springer, Dordrecht, p 721
- Callieri C, Coci M, Corno G, Macek M, Modenutti B, Balseiro E, Bertoni R (2013) Phylogenetic diversity of non-marine picocyanobacteria. *FEMS Microbiol Ecol* 85:293–301
- Ciros-Pérez J, Ortega-Mayagoitia E, Alcocer J (2015) The role of ecophysiological and behavioral traits in structuring the zooplankton assemblage in a deep, oligotrophic, tropical lake. *Limnol Oceanogr* 60:2158–2172
- Cuevas (2017) Variación a largo plazo de la productividad primaria fitoplanctónica en el Lago Alchichica, Puebla. MS Thesis, UNAM, Mexico

- Cuevas-Lara JD, Alcocer J, Osecuera LA, Quiroz-Martínez B (2017) Dinámica a largo plazo (1999–2014) de la productividad primaria fitoplanctónica en el Lago Alchichica, Puebla. In: Paz F, Torres R (eds) Estado Actual del Conocimiento del Ciclo del Carbono y sus Interacciones en México: Síntesis a 2016. Programa Mexicano del Carbono. UAE Hidalgo, pp 280–286
- De Senerpont Domis LN, Elser JJ, Gsell AS, Huszar VL, Ibelings BW, Jeppesen E, Kosten S, Mooij WM, Roland F, Sommer U, van Donk E, Winder M, Lürling M (2013) Plankton dynamics under different climatic conditions in space and time. *Freshw Biol* 58:463–482
- Fetahi T, Schagerl M, Mengistou S (2014) Key drivers for phytoplankton composition and biomass in an Ethiopian highland lake. *Limnologica* 46:77–83
- Gaedke U, Weisse T (1998) Seasonal and interannual variability of picocyanobacteria in Lake Constance (1987–1997). *Arch Hydrobiol Spec Issues Adv Limnol* 53:143–158
- Hernández-Ávilés JS, Macek M, Alcocer J, López-Trejo B, Merino-Ibarra M (2010) Prokaryotic picoplankton dynamics in a warm-monomictic saline lake: temporal and spatial variation in structure and composition. *J Plankton Res* 32(9):1301–1314
- Kebede E, Willén E (1998) Phytoplankton in a salinity-alkalinity series of lakes in the Ethiopian Rift Valley. *Algol Stud* 89:63–96
- Kebede E, G-Mariam Z, Ahlgren I (1994) The Ethiopian Rift Valley lakes: chemical characteristics of a salinity-alkalinity series. *Hydrobiologia* 288:1–12
- Koçer MAT, Sen B (2014) Some factors affecting the abundance of phytoplankton in an unproductive alkaline lake (Lake Hazar, Turkey). *Turk J Bot* 38:790–799
- Koçer MAT, Sen B (2012) The seasonal succession of diatoms in phytoplankton of a soda lake (Lake Hazar, Turkey). *Turk J Bot* 36:738–746
- Komárek J, Komárková-Legnerová J (2002) Contribution to knowledge of planktic cyanoprokaryotes from Central Mexico. *Preslia* 74:207–223
- Macek M, Alcocer J, Lugo-Vázquez A, Martínez-Pérez ME, Peralta-Soriano L, Vilaclara-Fatjó G (2009) Long term picoplankton dynamics in a warm-monomictic, tropical high altitude lake. *J Limnol* 68(2):183–192
- Macek M, Sánchez-Medina X, Peštová D, Bautista-Reyes F, Montiel-Hernández JR, Alcocer J, Merino-Ibarra M, Picazo A, Camacho A (2020) *Spirostomum teres*: a long term study of an anoxic-hypolimnion population feeding upon photosynthesizing microorganisms. *Acta Protozool* 59:13–38
- Maeda H, Kawai A, Tilzer MM (1992) The water bloom of cyanobacterial picoplankton in Lake Biwa, Japan. *Hydrobiologia* 248:93–103
- Malinsky-Rushansky N, Berman T, Dubinsky Z (1995) Seasonal dynamics of picophytoplankton in Lake Kinneret, Israel. *Freshw Biol* 34:241–254
- Olenina I, Hajdu S, Edler L, Andersson A, Wasmund N, Busch S, Göbel J, Gromisz S, Huseby S, Huttunen M, Jaanus A, Kokkonen P, Ledaine I, Niemkiewicz E (2006) Biovolumes and size-classes of phytoplankton in the Baltic Sea. *HELCOM Balt Sea Environment Proceedings* 106
- Oliva Martínez MG (2001) Estudio de la variación vertical y temporal de las comunidades fitoplanctónicas durante el florecimiento de cianofíceas en el lago cráter Alchichica, Puebla. Master Thesis, UNAM, Mexico
- Oliva MG, Lugo A, Alcocer J, Peralta L, Sánchez MR (2001) Phytoplankton dynamics in a deep, tropical, hyposaline lake. *Hydrobiologia* 466:299–306
- Oliva MG, Lugo A, Alcocer J, Cantoral-Uriza EA (2006) *Cyclotella alchichicana* sp. nov. from a saline Mexican lake. *Diatom Res* 21:81–89
- Oliva MG, Lugo A, Alcocer J, Cantoral-Uriza EA (2008) Morphological study of *Cyclotella chocatwathcheeana* Prasad (Stephanodiscaceae) from a saline Mexican lake. *Saline Systems* 4:17
- Oliva MG, Lugo A, Alcocer J, Peralta L, Oseguera LA (2009) Planktonic bloom-forming *Nodularia* in the saline Lake Alchichica, Mexico. *Nat Resour Environ Issues* 15: Art. 22
- Oliva-Martínez MG, Vilaclara G, Ortega-Mayagoitia E (2019) El alga dorada. In: Alcocer J (ed) Lago Alchichica. Una Joya de Biodiversidad. UNAM FES-Iztacala, CONABIO, pp 80–90

- Olivares-Rubio HF, Cabrera LI, Godínez-Ortega JL, Salazar-Coria L, Vega-López A (2017) *Halamphora oceanica* (Catenulaceae, Bacillariophyta), a new species from the epipelagic region of the southwestern Gulf of Mexico. *Phytotaxa* 317(3):188–198
- Ortega-Mayagoitia E, Ciroso-Perez J, Sanchez-Martinez M (2011) A story of famine in the pelagic realm: temporal and spatial patterns of food limitation in rotifers from an oligotrophic tropical lake. *J Plankton Res* 33:1574–1585
- Oseguera-Pérez LA, Alcocer-Durand J, Hernández-Hernández B (2013) 2.7. Variación del flujo de carbono orgánico particulado en un lago oligotrófico con dominancia de fitoplancton de talla grande. In: Paz Pellat F, Wong González J, Bazan M, Saynes V (eds) Estado Actual del Conocimiento del Ciclo del Carbono y sus Interacciones en México: Síntesis a 2013. Programa Mexicano del Carbono, Colegio de Posgraduados, UA Chapingo e ITES de Monterrey, México, pp 328–334, 696 pp
- Peštová D, Macek M, Martínez-Pérez ME (2008) Ciliates and their picophytoplankton-feeding activity in a high altitude warm-monomictic saline lake. *Eur J Protistol* 44:13–25
- Rosiles-González G (2005) Estudio comparativo del picofitoplancton y fitoplancton de talla mayor en el Lago Alchichica. MS Thesis, UNAM, Mexico
- Sánchez-Baracaldo P, Bianchini G, Di Cesare A, Callieri C, Christmas NAM (2019) Insights into the evolution of picocyanobacteria and phycoerythrin genes (mpeBA and cpeBA). *Front Microbiol* 10:45
- Sarmiento H (2012) New paradigms in tropical limnology: the importance of the microbial food web. *Hydrobiologia* 686:1–14
- Saunders GB, Saunders DC (1981) Waterfowl and their wintering grounds in Mexico, 1937–64. United States Department of the Interior, Fish and Wildlife Service, Resource Publication 138
- Sekino T, Genkai-Kato M, Kawabata Z, Melnik NG, Logacheva NP, Belykh O.I, Obolkina LA, Bondarenko NA, Khodzher TV, Gorbunova LA, Taniev AI, Yoshida T, Kagami M, Gurung TB, Urabe J, Higashi M, Nakanishi M (2007) Role of phytoplankton size distribution in lake ecosystems revealed by a comparison of whole plankton community structure between Lake Baikal and Lake Biwa. *Limnology* 8: 227–232
- Sieburth JM, Smetacek V, Jürgen L (1978) Pelagic ecosystem structure: heterotrophic compartments of the plankton and their relationship to plankton size fractions. *Limnol Oceanogr* 23(6):1256–1263
- Sommer U, Adrian R, De Senerpont Domis L, Elser JJ, Gaedke U, Ibelings B, Jeppesen E, Lüring M, Molinero JC, Mooij WM, van Donk E, Winder M (2012) Beyond the plankton ecology group (PEG) model: mechanisms driving plankton succession. *Annu Rev Ecol Evol Syst* 43:429
- Sui F, Zang S, Fan Y, Ye H (2016) Effects of different saline-alkaline conditions on the characteristics of phytoplankton communities in the lakes of Songnen Plain, China. *PLoS One* 11(10):e0164734
- Sukenik A, Zohary T, Markel D (2014) The monitoring program. In: Zohary T, Sukenik A, Berman T, Nishri A (eds) Lake Kinneret. Aquatic Ecology Series, vol 6. Springer, Dordrecht. https://doi.org/10.1007/978-94-017-8944-8_32
- Tavera RL, Komárek J (1996) Cyanoprokaryotes in the volcanic lake of Alchichica, Puebla State, Mexico. *Algol Stud* 83:511–538
- Vilaclara G, Oliva-Martínez MG (2019) La lama. In: Alcocer J (ed) Lago Alchichica. Una Joya de Biodiversidad. UNAM FES-Iztacala, CONABIO, pp 91–102
- Wakabayashi T, Ichise S (2004) Seasonal variation of phototrophic picoplankton in Lake Biwa (1994–1998). *Hydrobiologia* 528:1–16
- Weisse T (1993) Dynamics of autotrophic picoplankton in marine and freshwater ecosystems. In: Jones JG (ed) *Advances in microbial ecology* 13. Plenum Press, New York, pp 327–370