Javier Alcocer *Editor*

Lake Alchichica Limnology

The Uniqueness of a Tropical Maar Lake

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Editor
Javier Alcocer
Facultad de Estudios Superiores Iztacala
National Autonomous University of Mexico
Tlalnepantla, Mexico

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CARO E.

Preface

At the Trans-Mexican Volcanic Belt's eastern sector (Oriental basin), sometime between 13,300 and 6300 years ago, explosive magma-water eruptions gave birth to the small crater (3.83 km^2) that holds Lake Alchichica. This geologically young -Late Pleistocene/Holocene- maar lake at 19°24'49.45" N and 97°24'11.25" W (2,326 m a.s.l.) is almost circular (~1.7 km in diameter), small (~2.4 km^2), and deep (62 m, maximum depth, ~49 m mean depth) for Mexican lake depths standards. It contains saline and alkaline water, sodium chloride dominated, with an uncommonly high proportion of magnesium. A slight trend to increasing salinity coupled with lake level decline seems to be associated with drier climate conditions.

Mostly groundwater-fed, the chemical interchange between meteoric/surface water and groundwater, and foster by microbial activity, formed an almost complete ring of massive mineral rock-like structures, stromatolites (microbialites), running parallel close to the shoreline. The lake is oligotrophic, and the related high water-transparency allows microbialites to grow down to 40 m deep. Temperate by the high altitude (2240 m a.s.l.), water temperature is relatively cold (average 16 °C) for a tropical lake. However, its thermal hydrodynamic behavior fits well with the warm-monomictic pattern, as expected from deep, tropical lakes. An extended stratification period characterized by an early onset and long-lasting hypolimnetic anoxia follows a complete winters' water-column mixing. Besides water column mixing, mountain breeze creates water-level changes and seiches daily, while wind forced internal waves.

A diatom bloom associated with the mixing period, a cyanobacterial bloom at the onset of the stratification, and the development of a deep chlorophyll maximum throughout the well-established and late stratification periods are the main phytoplanktonic events closely associated with the warm monomictic thermal regime. Unlike oligotrophic waters where small phytoplankton cells prevail, a large diatom dominates phytoplankton biomass all year round, the microendemism *Cyclotella alchichicana*, which drives the biogeochemical cycles of carbon and nutrients in the lake, exporting them to the sediments. Only small phytoplankton (pico- plus the smaller nanophytoplankton) enters the herbivorous trophic web; however, the small phytoplankton biomass is relatively scarce, inflicting zooplankton food limitation in the pelagic realm. Lake food web is simplified, particularly in the pelagic (e.g., with only three metazooplankton species) and the deep benthic (e.g., only two benthic macroinvertebrate species) zones, and largely driven by the mixing and stratification hydrodynamic periods. Recent studies show bacterioplankton has a taxonomic- and metabolically complex composition, while protozooplankton seems to play a relevant role in the lake's microbial loop.

However, the very low biodiversity of the pelagic realm and deep bottom contrasts with higher species richness at the littoral zones, which altogether present many endemisms. For such a recent and small lake, the presence of 18 endemic (microendemic) species is both striking and intriguing and includes, among others, the silverside *Poblana alchichica* and the only paedomorphic axolotl known to inhabit saline waters, *Ambystoma taylori*.

From the 1940s on, Lake Alchichica has attracted Mexican and worldwide scientists' interest in uncovering its uniqueness and scientific relevance. Many of them are limnologists, like the Dr. Ramón Margalef (Spain), Dr. Vladimír Sládeček and Dr. Jiří Komárek (Republic Czech), Dr. William M. Lewis, Jr. and Dr. John W. Morse (United States), Dr. Brian V. Timms (Australia), Dr. William D. Williams (the UK and Australia) and others more. Even Dr. Chris McKay and his NASA team of planetary scientists became interested in the microbialites of Lake Alchichica.

The comparatively higher species richness at the littoral zone can be explained by the fact that it is quite heterogeneous in both water and sedimentary characteristics, providing a large variety of habitats displaying a richer species composition. The littoral zone holds six macrophytes and numerous species of benthic macroinvertebrates, protists, and diatoms (benthic/epiphytes). Nonetheless, the continuous water-level descend shrinks the littoral zone, threatening its biodiversity.

Recent findings on stromatolites (microbialites with mineralized structure) of Lake Alchichica have been published in the most prestigious scientific journals. Stromatolites are "living fossils" as they were the first evidence of life on Earth about 3.8 billion years ago. Although common in the fossil record of the Precambrian, they are scarce today, and Alchichica is one of these few sites inhabited by such modern stromatolites. Along with other diverse geological, physicochemical, and microbial characteristics concurring at Alchichica makes this lake an ideal candidate for an analog site for astrobiological studies.

The whole set of peculiarities coinciding in the same water body urge implementing conservation actions at a basin scale. The first steps in this direction have been taken by declaring a Protected National Area (ANP). Still, much more is needed to safeguard and guarantee this aquatic ecosystem's persistence, starting with a Management Program for the ANP.

Finally, Lake Alchichica encompasses precious and ancient cultural, aesthetic, and recreational values for locals, national and international visitors. Archaeological excavations and exploration (e.g., the ancient city of Cantona), historical sources, and cartographic materials revealed the significance of Lake Alchichica from prehispanic times till nowadays. However, a semi-arid zone, drier climate conditions in the Epiclassic (AD 600–1100) are associated with the abandonment of several Mesoamerican cities, including Cantona.

In summary, this book presents a systematization and integration of the knowledge accumulated to date on Lake Alchichica, covering various disciplines (e.g., historical and cultural aspects, geology, past and present climate, surface and underground hydrochemistry, lake hydrodynamics and morphometry, physicochemical and biological characteristics, lake metabolism and food webs, biodiversity and endemisms, environmental conservation, and sustainability). The book is addressed to the specialists of the diverse scientific fields covered but is designed and written to make it accessible to the general public. This book results from the research of many Mexican and foreign scientists dating from the early 1940s till nowadays, much of them from various Institutes and Schools of the Universidad Nacional Autónoma de México (UNAM), but mainly through the more than 20 years of continuous monitoring by the tropical limnology team (Grupo de Investigación en Limnología Tropical, GILT) of the Facultad de Estudios Superiores Iztacala, UNAM.

Birds-eye view of Lake Alchichica. (Photograph: Mariana Vargas Sánchez)

Tlalnepantla, Mexico
Javier Alcocer

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Stromatolites of Lake Alchichica exposed by the lake's water-level descend. (Photograph: Mariana Vargas Sánchez)

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Contributors

Bernardo Águila Programa de Posgrado en Ciencias Biológicas, Universidad Nacional Autónoma de México, Ciudad de México, Mexico

Verónica Aguilar-Sierra Comisión Nacional para el Conocimiento y Uso de la Biodiversidad (CONABIO), Mexico

Rocío J. Alcántara-Hernández Instituto de Geología, Universidad Nacional Autónoma de México, Ciudad de México, Mexico

José Arturo Alcántara-Rodríguez Grupo de Investigación en Limnología Tropical, FES Iztacala, Universidad Nacional Autónoma de México, Tlalnepantla, Estado de México, Mexico

Javier Alcocer Grupo de Investigación en Limnología Tropical, FES Iztacala, Universidad Nacional Autónoma de México, Tlalnepantla, Estado de México, Mexico

Sonia Angeles-García Electronic Microscopy and Microanalysis Laboratory & LANGEM. Instituto de Geología, Universidad Nacional Autónoma de México, Ciudad de México, Mexico

Verónica A. Arellano Peralta Independent Consultant on Environmental Issues, Ciudad de México, Mexico

Juan Arellano-Posadas Posgrado en Ciencias Mar y Limnología, Universidad Nacional Autónoma de México, Ciudad de México, Mexico

María Aurora Armienta Instituto de Geofísica, Universidad Nacional Autónoma de México, Ciudad de México, Mexico

Elizabeth Chacón Baca Facultad de Ciencias de la Tierra, Universidad Autónoma de Nuevo León, San Nicolás de los Garza, Nuevo León, Mexico

Fernando Bautista-Reyes Programa de Posgrado en Ciencias Mar y Limnología, Universidad Nacional Autónoma de México, Ciudad de México, Mexico

Yislem Beltrán DGAPA/UNAM Posdoctoral Stage at the Instituto de Ciencias Del Mar y Limnología, Unidad Académica de Sistemas Arrecifales, Universidad Nacional Autónoma de México, Mexico City, Mexico

Margarita Caballero Laboratorio de Paleolimnología, Instituto de Geofísica, Laboratorio de Paleolimnología, Instituto de Geofísica, Universidad Nacional Autónoma de México, Ciudad de México, Mexico

Rafael Alejandro Calzada-Arciniega Departamento de Zoología, Instituto de Biología, Universidad Nacional Autónoma de México, Ciudad de México, Mexico

Gerardo Carrasco-Núñez Centro de Geociencias, Universidad Nacional Autónoma de México, Querétaro, Mexico

F. Sergio Castillo-Sandoval Unidad Académica de Ecología y Biodiversidad Acuática, Instituto de Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México, Ciudad de México, Mexico

Carla M. Centeno Baden Powell School, Atizapán de Zaragoza, Mexico

Boris Chako-Tchamabé Centro de Investigación Científica y de Educación Superior de Ensenada (CICESE)- División de Ciencias de la Tierra, Ensenada, Baja California, Mexico

Xavier Chiappa-Carrara Escuela Nacional de Estudios Superiores Unidad Mérida, Universidad Nacional Autónoma de México, Yucatán, Mexico

Jorge Ciros-Pérez Grupo de Investigación en Limnología Tropical, FES Iztacala, Universidad Nacional Autónoma de México, Tlalnepantla, Estado de México, Mexico

Daniela Cortés-Guzmán Programa de Posgrado en Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México, Ciudad de México, Mexico

Mónica Cuellar Universidad del Valle de México, Ciudad de México, Mexico

Daniel Cuevas-Lara Programa de Posgrado en Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México, Ciudad de México, Mexico

María del Carmen Hernández Programa de Posgrado en Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México, Ciudad de México, Mexico

Gerardo Pérez Ponce de León Escuela Nacional de Estudios Superiores Unidad Mérida, Universidad Nacional Autónoma de México, Yucatán, Mexico

Maria del Refugio Barba-Lopez Programa de Posgrado en Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México, Ciudad de México, Mexico

María del Rosario Sánchez Grupo de Investigación en Limnología Tropical, FES Iztacala, Universidad Nacional Autónoma de México, Tlalnepantla, Estado de México, Mexico

Elva Escobar Unidad Académica de Ecología y Biodiversidad Acuática, Instituto de Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México, Ciudad de México, Mexico

Laboratorio de Biodiversidad y Macroecología, Instituto de Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México, Ciudad de México, Mexico

Óscar Escolero Instituto de Geología, Universidad Nacional Autónoma de México, Ciudad de México, Mexico

Luisa I. Falcón Laboratorio de Ecología Bacteriana, Instituto de Ecología, Campus Yucatán, Universidad Nacional Autónoma de México, Yucatán, Mexico

Anatoliy Filonov Department of Physics, University of Guadalajara, Guadalajara, Jalisco, Mexico

Sandra Guadarrama-Hernández Programa de Posgrado en Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México, Ciudad de México, Mexico

Andrea P. Guzmán-Arias Programa de Posgrado en Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México, Ciudad de México, Mexico

Omar Hernández-Ordóñez Departamento de Zoología, Instituto de Biología, Universidad Nacional Autónoma de México, Ciudad de México, Mexico

Hoi-Ying N. Holman Molecular Biophysics and Integrated Bioimaging, Lawrence Berkeley National Laboratory, Berkeley, CA, USA

Víctor H. Jiménez-Arcos Laboratorio de Herpetología Vivario de la FES Iztacala, Universidad Nacional Autónoma de México, Tlalnepantla, Estado de México, Mexico

Roberto Esteban Junco-Sánchez Subdirección de Arqueología Subacuática, INAH (Sub-directorate of Underwater Archaeology, INAH), Córdoba, Mexico

Karina Elizabeth Cervantes-de la Cruz Departamento de Física, Facultad de Ciencias, Universidad Nacional Autónoma de México, Ciudad de México, Mexico

Lydia Ladah Department of Biological Oceanography, CICESE, Centro de Investigación Científica y Educación Superior de Ensenada, Ensenada, BC, Mexico

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

Ma. del Socorro Lozano-García Laboratorio de Paleoambientes y Cambio Climático, Instituto de Geología, Universidad Nacional Autónoma de México, Ciudad de México, Mexico

Alfonso Lugo-Vázquez Grupo de Investigación en Limnología Tropical, FES Iztacala, Universidad Nacional Autónoma de México, Tlalnepantla, Estado de México, Mexico

Miroslav Macek Grupo de Investigación en Limnología Tropical, FES Iztacala, Universidad Nacional Autónoma de México, Tlalnepantla, Estado de México, Mexico

Elia Matías-Hernández Departamento de Botánica (Proyecto Flora del Valle de Tehuacán-Cuicatlán), Universidad Nacional Autónoma de México, Ciudad de México, Mexico

Martín Merino-Ibarra Unidad Académica de Ecología y Biodiversidad Acuática, Instituto de Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México, Ciudad de México, Mexico

Ismael Arturo Montero-García Comisión Nacional de Áreas Naturales Protegidas, CONANP (National Commission for Protected Natural Areas), Córdoba, Mexico

Aideé Montiel-Martínez Licenciatura en Gestión de Ciudades Inteligentes y Transiciones Tecnológicas, Facultad de Ciencias de la Electrónica, Benemérita Universidad Autónoma de Puebla, Puebla, México

Lilia Montoya Facultad de Ciencias Biológicas, Universidad Autónoma del Estado de Morelos, Cuernavaca, Morelos, Mexico

María Guadalupe Oliva-Martínez Grupo de Investigación en Limnología Tropical, FES Iztacala, Universidad Nacional Autónoma de México, Tlalnepantla, Estado de México, Mexico

Beatriz Ortega-Guerrero Laboratorio de Paleolimnología, Instituto de Geofísica, Laboratorio de Paleolimnología, Instituto de Geofísica, Universidad Nacional Autónoma de México, Ciudad de México, Mexico

Elizabeth Ortega-Mayagoitia Grupo de Investigación en Limnología Tropical, FES Iztacala, Universidad Nacional Autónoma de México, Tlalnepantla, Estado de México, Mexico

Luis A. Oseguera Grupo de Investigación en Limnología Tropical, FES Iztacala, Universidad Nacional Autónoma de México, Tlalnepantla, Estado de México, Mexico

Gabriela Parra-Olea Departamento de Zoología, Instituto de Biología, Universidad Nacional Autónoma de México, Ciudad de México, Mexico

Ángel Arellano Peralta Newscast Radiophonic Formula Group, Ciudad de México, Mexico

Laura Peralta Grupo de Investigación en Limnología Tropical, FES Iztacala, Universidad Nacional Autónoma de México, Tlalnepantla, Estado de México, Mexico

María Guadalupe Pérez-Ramírez Programa de Posgrado en Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México, Ciudad de México, Mexico

Benjamín Quiróz-Martínez Laboratorio de Ecología Numérica y Análisis de Datos, Unidad Académica Ecología y Biodiversidad Acuática. Instituto de Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México, Ciudad de México, Mexico

Pedro Ramírez-García Departamento de Botánica, Universidad Nacional Autónoma de México, Universidad Nacional Autónoma de México, Ciudad de México, Mexico

Jorge A. Ramírez-Zierold Programa de Posgrado en Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México, Ciudad de México, Mexico

Margarita Reyes-Salas Electronic Microscopy and Microanalysis Laboratory & LANGEM. Instituto de Geología, Universidad Nacional Autónoma de México, Ciudad de México, Mexico

Ximena Sánchez-Medina Programa de Posgrado en Ciencias Mar y Limnología, Universidad Nacional Autónoma de México, Ciudad de México, Mexico

Raúl A. Silva-Aguilera Programa de Posgrado en Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México, Ciudad de México, Mexico

Raúl Alberto Silva-Aguilera Programa de Posgrado en Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México, Ciudad de México, Mexico

Irina Tereshchenko Department of Physics, University of Guadalajara, Guadalajara, Jalisco, Mexico

Jesús Torres-Huesca Programa de Posgrado en Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México, Ciudad de México, Mexico

Elsah Arce Uribe Centro de Investigaciones Biológicas, Universidad Autónoma del Estado de Morelos, Cuernavaca, Morelos, Mexico

Patricia M. Valdespino-Castillo Molecular Biophysics and Integrated Bioimaging Division, Lawrence Berkeley National Laboratory, Berkeley, CA, USA

Gloria Vilaclara Grupo de Investigación en Limnología Tropical, FES Iztacala, Universidad Nacional Autónoma de México, Tlalnepantla, Estado de México, Mexico

Chapter 1
Lake Alchichica: History of Human Settlements

Ismael Arturo Montero-García and Roberto Esteban Junco-Sánchez

1.1 Introduction

Lake Alchichica is geologically defined as a maar, but in ancient Mexico, it was called in Nahuatl *axalapazco*. The word is made up of four words: a (tl), water; xal (li), sand; apaz (tli), bowl; co, in. So *axalapazco* means "in the sand bowl with water." Lake Alchichica is located in a basin, at more than two thousand three hundred meters of altitude and surrounded by the highest mountains in Mexico. Such was its relevance in the ancestral ritual landscape, that it is represented in the indigenous codex Map of Cuauhtinchan II, many are the stories in collective memory of those who live around this lake, gaining importance in historical moments as relevant as the Conquest of Mexico in the century XVI. This chapter presents a historical account of Lake Alchichica from prehispanic times to the nineteenth century drawing from diverse sources such as a linguistic, archaeological and historical documents.

I. A. Montero-García
Comisión Nacional de Áreas Naturales Protegidas, CONANP (National Commission for Protected Natural Areas), Córdoba, Mexico
e-mail: ismael@montero.org.mx

R. E. Junco-Sánchez (✉)
Subdirección de Arqueología Subacuática, INAH (Sub-directorate of Underwater Archaeology, INAH), Córdoba, Mexico

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1.2 Prehispanic Records

The waters in Lake Alchichica have a distinctive taste that gives origin to its name: in Náhuatl, *alchichiccan* translates as *al-chichic-can. Alli* means "water" (it is only used as a component in a word); *chichic* means "bitter;" *can* means "where". So *alchichiccan* means "The place where the water is bitter" (Macazaga 1979:24). Continuing with age-old denominations, the pre-Hispanic worldview gave specific —and accurate— names to this chain of lakes, and as a result, Lake Alchichica is considered an *axalapazco,* which in Nahuatl means "basin of sand and water:" *a(tl)*, water; *xal(li)*, sand; *apaz(tli)*, basin; *co*, in. In contrast, *xalapasco* —without the *a(tl)* or "water"— refers to a crater with no lake.

The crater that nowadays contains the Lake Alchichica was formed 13,300 years ago (see chap. 2, Geological evolution), during the Late Pleistocene; therefore, it is very likely that early humans were already present in the area when the lake was formed, as according to evidence (tools collected in Valsequillo; Pichardo 1997, 2000), humans have been present in the region for the last 16,000 years. The latter suggests that in the early periods, the region was inhabited by hunter-gatherer groups and later by agricultural villages with the emergence of agriculture. However, the occupation of the region we wish to focus on, in archaeological terms, has only been documented in recent years, historically speaking. The studies are based on two excavated sites: "Cerro Jorge", 26 kilometers northeast of Lake Alchichica on the northwestern flank of the Cofre de Perote at 2950 meters above sea level, and the spectacular city of Cantona, 18 kilometers northwest.

Regarding the "Cerro Jorge" site, García (2011) concludes that it was used as a ceremonial center dedicated to the worship of the Cofre de Perote volcano, a place for the veneration of nature in a climate conducive to agriculture, according to the urban layout which points towards the top of the volcano. This site's occupation spans from 400 BC in the Late Preclassic period to AD 900 in the Epiclassic period. As for Cantona, it was an important city inhabited from the year 600 BC to the year AD 1050. This metropolis reached its peak at the end of the Epiclassic period, when it was allegedly occupied by Olmec-Xicalanca groups comprised of Nahuas, Mixtecs, and Chochopopolocas, precisely at the time when Teotihuacan ceased to be the main center of power in the region and when small regional states competed to gain control of the different trading routes, in particular, that of the dark grey obsidian from the Oyameles-Zaragoza site located ten kilometers north of the city.

Cantona was built over a basaltic spillover —malpaís— from the Xalapaxco volcano, and its structures were raised on top of volcanic rock, giving this site its striking appearance. The landscape is overlooked by an endless number of desert plants as well as pines. The buildings were constructed taking advantage of the rugged terrain without creating a symmetrical layout, as is the case in other archaeological sites in Mesoamerica. Cantona is one of pre-Hispanic Mexico's most urbanized cities. Its extensive communication network, with roads up to a thousand meters long inside the city walls, allowed for strict control over its inhabitants. There were walled streets that could easily be closed off in a conflict, making this city a real fortress. The site's 24 identified "Juegos de pelota" (ballgames) courts are, as a whole, a clear demonstration of the importance given to religious ceremonies. To date, many obsidian workshops, over one hundred plazas, five hundred causeways, and around three thousand individual patios have been identified (Montero 2014:124).

Cantona's high population density required a great number of natural resources, many of which were undoubtedly extracted from Lake Alchichica, such as "charal" fishing (an activity that still lives on nowadays as an artisanal fishery). Another species extracted from the lake was the axolotl. It was most probably highly valued for its white meat and delicate taste (Alcocer 2013: 13) and its potential medicinal use. For example, a recent ethnopharmacological study conducted near Lake Pátzcuaro showed that the Purépechas use axolotls to treat respiratory diseases and boost energy levels in breastfeeding both for children and mothers (Velarde 2012).

At the end of the twelfth century, when Cantona was already in decline, a group of Chichimecas was summoned by the Toltecs to subdue the Olmec-Xicalanca groups in Cholula. This is the narrative put forward in the *Mapa de Cuauhtinchan II*, in which the descendants of these Chichimecas, already organized in lordships, formed regional alliances. In this geopolitical discourse, the territorial description englobes our area of the scope by representing two axalapazcos on the map that we identify as Lake Alchichica (Fig. 1.1, num. 1) and Lake Tecuitlapa (Fig. 1.1, num. 2). Lake Alchichica's toponym can be drawn as a circle with seven protuberances that symbolize waves and a spiral at the center; the body of water is represented in blue, characteristic of an oligotrophic lake.[1] On the other hand, Lake Tecuitlapa is a waterbody at the top of a hill, the way it is in the natural landscape. However, researchers specialized in the study of that map disagree on which lake is which: for Tucker (2008 :214) it is not Lake Alchichica but rather Lake Aljojuca; for Yoneda in 1991 (pp. 91 and 184, toponym 157) it is Yayaualulco, nowadays the Ayahualulco municipality,[2] based on its Nahuatl etymology, although it is stated in a subsequent 2005 publication (Table 1, G4), it is no longer the town's eponym. Yoneda changed his mind and identified the glyph as Tecuitlapan.

This controversy stems from the fact that the *Mapa de Cuauhtinchan II* was interpreted from a cartographic point of view rather than a topological one; in cartography, position and distance are decisive; but in topography, what is relevant is the landscape's perceptual signs as seen, in this case, from the roads marked on the map with footsteps. These prints lead us to symbolic and elemental criteria, which derive into an absolute system of privileged representations because if the intention were topographical, we would be addressing the absence of the other existing lakes in the region. We know of an ancient road that would cross between the Pico de Orizaba and Cofre de Perote, originating in the Gulf of Mexico and bound for the central plateau, because that was the route taken by Hernán Cortés in 1519. Contemporary

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[1] Aljojuca, waters of greenish color from its Nahuatl etymology: *alt*, water, *xoxoctic*, greenish-blue.

[2] Ayahualulco, Nahuatl word, *alt*, water, *yahualli*, something round; *co*, place: the place of round water.

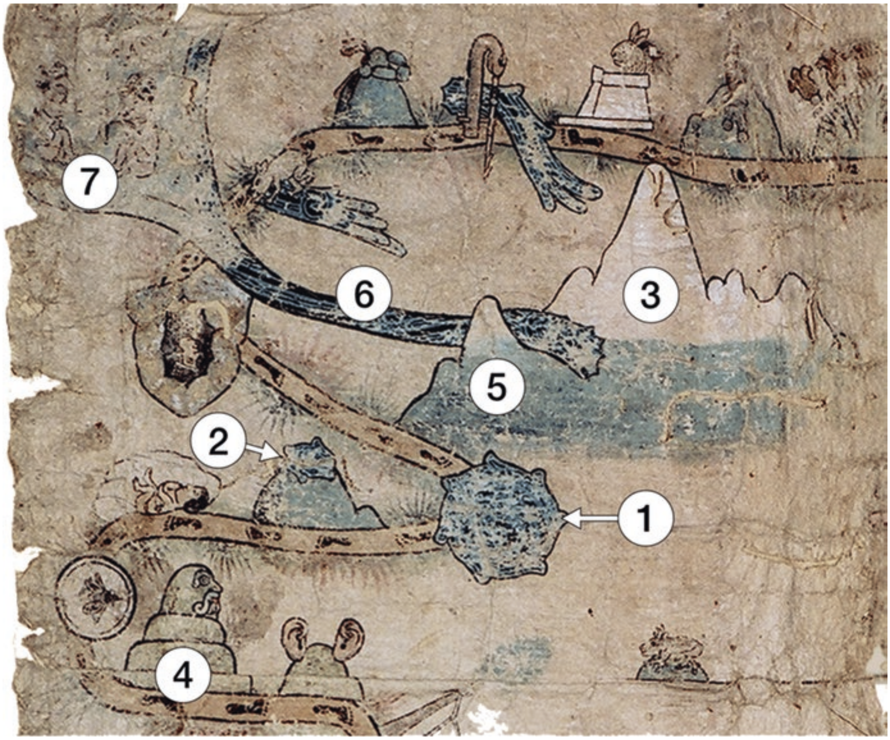

Fig. 1.1 *Mapa de Cuauhtinchan II* fragment 1) Lake Alchichica, 2) Lake Tecuitlapa, 3) Pico de Orizaba, 4) Cofre de Perote, 5) Cerro Sillatepec, 6) Jamapa river, 7) Chocamán

researchers of that route pinpoint Lake Alchichica as being a relevant spot on their maps: Lake Alchichica is a perceptual sign on the road as indicated on the *Mapa de Cuauhtinchan II*, and this is why we do not consider it to be part of the other four axalapazcos.

The *Mapa de Cuauhtinchan II* was drawn up[3] by the region's dominant lineages to declare which of the lands were theirs and to delimitate the extension of their domain before Montezuma I's conquest in 1466. No subsequent event is represented, and the lands within the territory were divided amongst the victorious Mexicas.

1.3 Colonial Period

In 1519, Hernan Cortes' military column ascended the eastern slopes of the Cofre de Perote to reach the Altiplano (Fig. 1.2). They left Xalapa on the 18th of August, traveling across Xicochimalco (Xico Viejo), Ixhuacán (Izhuacán de los Reyes),

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[3] The *Mapa de Cuauhtinchan* ii is a copy, made in 1540, of a document produced by the Cuauhtinchantlacas little after the year 1466 to appeal to the Mexicas regarding their violated rights (Martínez, 2009).

Fig. 1.2 Juan Miralles map fragment (2010) describes the route traveled by Hernán Cortés in 1519; on it, Lake Alchichica is marked as relevant, as is Ramírez de Alba's (2013) version, amongst others

Ayahualulco and Cuauhtotolapan. They arrived at the arid high plateau of the town of Chichicuauhtla, next to Lake Alchichica, where they met up with one of Montezuma's messengers (García 2011: 27). By royal command, Antonio de Solís wrote *Historia de la Conquista de Mexico*, inspired on the accounts of Hernán Cortés, López de Gomora and Bernal Díaz del Castillo. The book was published in 1684 and in chap. XIV he describes this journey "to the summit," that is, the central plateau:

> They next entered upon the rough part of the mountain, the first difficulty they met in their road to Mexico, where they suffered very much, for they were obliged to march over an uninhabitable mountain three days, whose paths were over precipices. They carried the artillery by the strength of arms and some contrivances, and the badness of the weather fatigued them much. The cold was excessive, and the showers of rain very hard and frequent, and the poor soldiers having no convenience to make barracks at night, and no other shelter but their arms, they marched to keep themselves warm and were obliged to seek for ease with weariness. Their provisions also failed them, the last calamity upon these occasions; and their resolution began now to contend with their strength when they gained the top of the mountain.

Once on the high plateau, the situation did not get any better. This is what Andrés de Tapia writes in his *rapport* about the Conquest of Mexico (1866: 567), a work written first-hand and with reasonable temporal proximity to the events, as Tapia is an eyewitness:

> For twenty leagues or more after leaving the territory of these people who had become our allies, we crossed uninhabited badlands where there were salt lakes and where we suffered from hunger, but more from thirst until we reached a town called Cacotlán. The marques asked the lord of this town whether he was a vassal of Moctezuma, to which he replied: "And who can there be who is not a vassal of that lord?"

From Lake Alchichica, they made their way to Tepeyahualco to head north towards Zautla or Xocotlán in the basin of the river Apulco and finally make their way to Tlaxcala or Mexico. Nowadays, Xocotlán has become Santiago Zautla, which differs from the version put forward by Ixtlilxochitl and Cervantes de Salazar, who referred to this town as Zacatlan; Díaz del Castillo talked about both Xocotlán and Castilblanco (it was so renamed because it reminded some Portuguese soldiers of a homonymous town in Portugal), Cortés called it Caltami, López de Gomara referred to it as Zacotlán and Tapia, as previously mentioned, as Cacotlán (Thomas 1995: 694).

During his stay in Tepeyahualco, before arriving in Zautla, local chronicles state that Cortes was given a friendly welcome by the caciques Atonaletzin of Tepeyahualco and Tlamapanatzin of Axapuzco (Achichilacachoca). In the Cortesian documents,[4] These characters gain notoriety as prevailing allies of Cortés on his journey to Mexico. Once baptized, they changed their names to Francisco Moctezuma Atonaletzin and Esteban López Tlamapanatzin, as mentioned in the apocryphal document known as *Merced y mejora de Hernán Cortés a los caciques de Axapusco y Tepeyahualco*, in which their achievements in favor of the conquistadors are detailed (see facsimile document in Martínez 2014). This document was presented in the eighteenth century by an aspiring cacique in Axapusco, who displayed these forged records allegedly signed by Cortés in 1526; the title contains not only the caciques' achievements but also romantic references to ancient prophecies that warned about the arrival of Cortés and Acamapichtli's vision. These forgeries are now clearly identifiable (Gibson 1984: 164).

Once under Spanish rule at the end of the sixteenth century, the region gained notoriety amongst scholars due to the uniqueness of its lakes (Alchichica, Quechulac and Tlachac). Friar Juan de Torquemada started to write about Mexican culture in 1592, and it took him twenty years to complete his magnum opus *Los veinte ivn libros rituales i Monarchia Indiana*, published in 1615.[5] The following extract from his work (book XIV) describes the lakes mentioned above:

> Chapter XLI. Of other mountains and wonderful things about them
>
> From this point viewing toward the west, returning to the center of these aforementioned mountains, there are others running between Mexico and Vera Cruz […].
>
> In the Perote plains lie the lakes that they call Tlachac and Atlchichica and Quicholac, which some say used to be hills and volcanos but were eroded by the passing of time, and sank until what was left of them were these lakes in the numbers of five or six; to this I pay no heed because I know not what the truth is, so I leave it to the judgment of God, since only He knows what used to be; all I can say is that judging by the rim, the middle part seems to have sunk, and in it there are some cauldron-like formations where the waters have caved in underneath; the water of these cauldrons and its waters have sunk; the waters in these lakes

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[4] Except for the *Cartas de relación*, the texts referred to as *Documentos Cortesianos* are those signed by Hernán Cortés and apocryphal documents ascribed to Cortés himself, as well as the reports on the facts that involved him, bonds, provisions, instructions, trials, complaints, allegations, and other documents in favor or against him. They span an extended period, starting in 1518 with the disputes with Diego de Velázquez, governor of Cuba, until 1548, the year after his death.

[5] To complete the work, Torquemada drew on codices, paintings, manuscripts, oral tradition and the work of other sixteenth century chroniclers such as friars Bernardino de Sahagún, Motolinia, Francisco Jiménez and Jerónimo de Mendieta; as well as documents written by Hernán Cortés, Francisco López de Gomara and Antonio de Herrera, amongst others.

> are brackish and very clear, and they resemble breathing holes for the earth itself; in them, a small and fine white fish breeds, that they call pexe-rey. These lakes whose water is sunken and shallow, are apart from each other by one or two leagues and three and more or less distance; the natives of this land know not what they are or how they were formed here, nor where the waters come from because they lie in vast and extended plains, with no currents from any direction. We may say no more, only that God placed them in these high and dry plains to show men His almightiness and His great secrets, removed from the judgment of men.
>
> No bottom has been found in these lakes or water holes, despite various intents to enquire and after having thrown ropes in them; they wax and wane through the day, as does the sea, and for this reason, some of our fellow Spaniards have suggested that they be breathing holes for the sea. In contrast, I consider this opinion not to be a satisfying one because the lakes and the sea are separated by peaks of great heights, which makes it only possible to imagine if it were supreme nature, that is to say, God, who put them in that place and who keeps them the way they are. The truth is that I remember having read in the book *Ecclesiastes* a note written by our Nicolao de Lira [*Eccles*. 1. Et ibi Lira.], stating the words from the first chapter that the rivers stem from the sea and return to their place of birth. This wise man, therefore, says that water from the sea comes out from hidden underground spaces towards remote destinations on land, and through natural movement, they can climb as high as the surface and depth of the sea, and more; and the reason for this, he says, is because as it flows through the veins of the earth, the water becomes fresh as it sifts its way through this colander, leaving behind the blend and mixture of salt that was part of it and it acquires a sweet taste unlike the saltpeter it once had, and as a result, it becomes milder and lighter than before, which enables it to climb to the summit and to rise above the surface of the seawater; and if we accept this explanation, it is also most probable that these waters do indeed come from the sea and that those who first said it was right.

Over time, New Spain became the site of a continuing confrontation; by the sixteenth century, the political scene was characterized by disputes with the Jesuits, interests of the Portuguese crown, the payment of tithes, the Inquisition, amongst others. These are the social differences that don Juan de Palafox y Mendoza had to face as Bishop of Puebla.[6] His followers were humble people pitted against corruption. Amidst all this turmoil, Palafox, the reformer, was threatened and decided to quietly renounce his bishopric and go into hiding on the 17th of June 1647, pending a more favorable political climate; he took shelter in a cave in Alchichica, as told in the *Colección de providencias diocesanas del obispado de Puebla…* by Fabián y Fuero (1719-1801, chap. XXVI):

> […] when he (don Juan Palafox) left this city surreptitiously on the 17th of the aforementioned month of June and fled from the temerity of his opponents, spending 16 or 17 days in the desert Mines of Alchichica, amidst the greatest waves of tribulation and embitterment, which is the Mexican definition of Alchichica or Bitter waters, and writing in defense of Dignity, hidden away in the discomfort of a small cave behind the two mountains called Las Derrumbadas, next to the crevices and flanks on the west side of the famous towering and steep volcano, commonly called Pico de Orizaba.[7]

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[6] Don Juan de Palafox y Mendoza, archbishop and viceroy of New Spain, and bishop of Puebla, founder of the first public library in the American continent —known nowadays as the Biblioteca Palafoxiana— promoter of free access to information, Church reformer, builder of the cathedral of Puebla. He was beatified by the Catholic Church on June 5, 2011 by pope Benedict XVI.

[7] For a reader wishing to learn more about this period of don Juan de Palafox, see Gallego, 2000.

Our findings indicate that during the Novo-Hispanic era, there were two towns by the name of Alchichica, both located in what nowadays is the state of Puebla: San Martín Alchichica, a neighboring town of what nowadays is Izúcar de Matamoros (cf. Alcedo 1784: 48 y 56), not to be confused with San José Alchichica that is next to the lake of the same name, subject of our interest here.[8] It must be said that Alexander von Humboldt (2011: 225) himself when talking about San Martín Alchichica, mentions a mine with the name Alchichica that details the amount of mercury lost during the amalgamation processes used in different silver-mining districts. This can lead to confusion since there were also mines near San José Alchichica, as mentioned in the above Torquemada quote. In fact, Lake La Preciosa, ten kilometers away from Lake Alchichica, is also called Lago Las Minas (The Mines Lake) due to the nearby goldmines (no longer in production nowadays). In Antonio García Cubas' 1877 *Plano orográfico de la zona recorrida por el ferro-carril mexicano*, it is mentioned that near Lake Alchichica there is a body of water-bearing the name La Preciosa Mineral (Fig. 1.3), which confirms the existence of mining activities in the region in former times.

1.4 19th and 20th Centuries

Another noteworthy nineteenth-century map that acknowledges the L-Alchichica (sic) with a parenthetical note that describes it as a "water volcano" is the 1876 *Plano de la Hacienda de Techachalco* (Fig. 1.4).

Fig. 1.3 Fragment of the *Plano orográfico de la zona recorrida por el ferro-carril mexicano,* 1877. Antonio García Cubas, which highlights Lakes Alchichica and La Preciosa Mineral

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[8] According to the *Diccionario geográfico, histórico y biográfico de los Estados Unidos Mexicanos* by Antonio García Cubas (2015), there is a ranch named Alchichica in the Tlaltizapan municipality, in the State of Morelos.

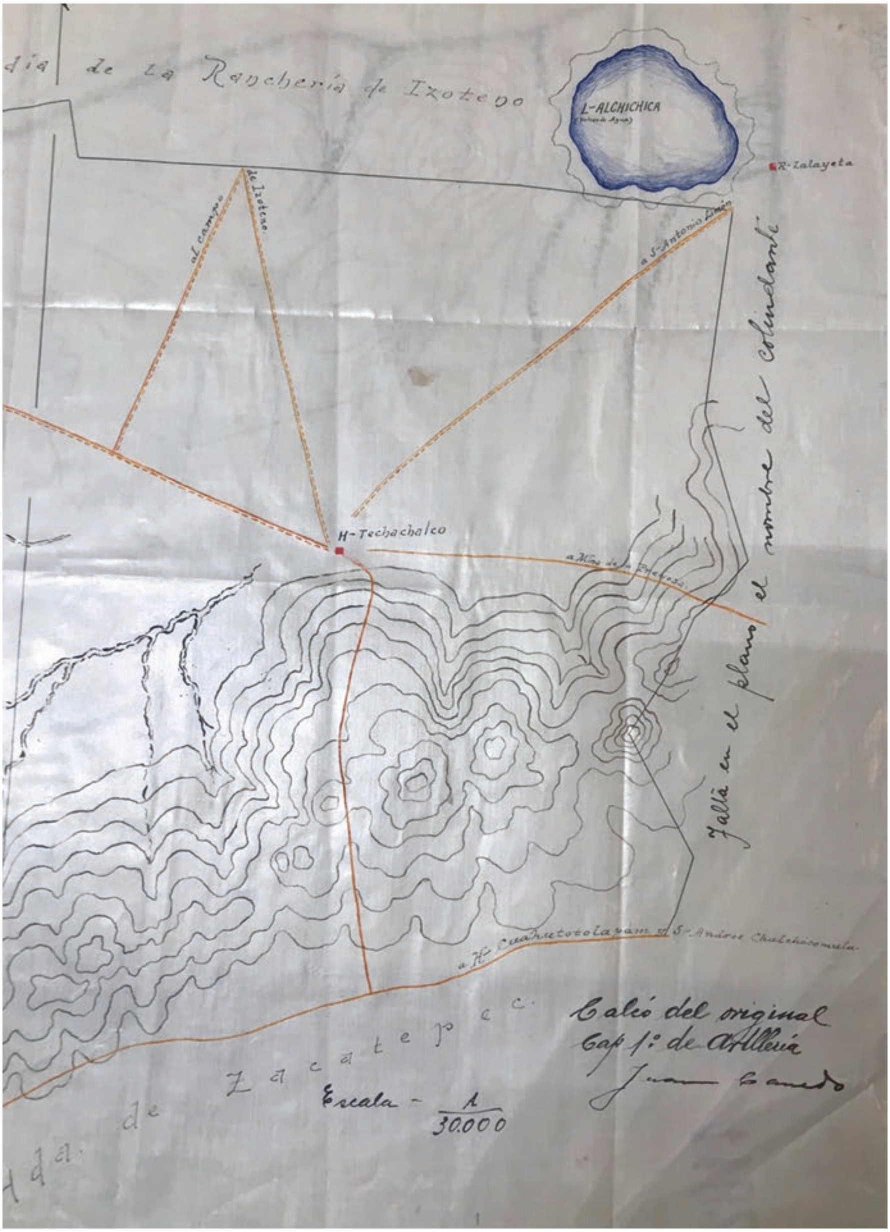

Fig. 1.4 Fragment of the *Plano de la Hacienda de Techachalco,* 1876. Orozco and Berra collection, Mexico, rod cgpue07, classifier number 4182-cge-7247-A, unknown author, a decal on canvas, traced by cavalry Capt. Juan Garrido

Concerning the archaeological evidence in Lake Alchichica, no vestiges have been recorded despite the fact that in 2004 the INAH undertook prospection work on the crater's outline. Several dives were carried out in its waters. It is worth mentioning that due to its proximity to Mexico City, for years, Lake Alchichica was a go-to place for high altitude recreational diving practices in its cold waters, which represent a challenge for those who partake in this activity.

Even though Lake Alchichica has not yet offered any archaeological material, further preliminary research has been conducted in other lakes, in the central part of the eastern lakeside basin, by the Subdirección de Arqueología Subacuática of the INAH. In 2014, three maars were inspected: Atexcac, La Preciosa, and Quechulac, with an immersion in the latter (Junco and Hernández 2014). These three bodies of water resemble Lake Alchichica, and they probably have similar archaeological features worth mentioning. For instance, Lake Atexcac, located in the extreme southwest of the Sierra de Techachalco, is a crater whose peaks vary between 60 and 130 meters above the valley floor. Its walls present an abrupt inclination forming a circular system of cliffs or escarpments that hinder access to the maa lake. Its maximum width is 780 meters and has an estimated maximum depth of 40 meters. During prospection in Atexcac, no archaeological material was found on the banks. However, it is not ruled out that there may be underwater evidence since Valencia (2011) has reported ceramic fragments and stone tools in the vicinity.

Regarding the Lake La Preciosa, 7 kilometers south of the town of Alchichica, its irregular shape resembles a triangle, its maximum width reaches 1300 meters, its highest ridge is 50 meters above the water body, and it is estimated to be 45 meters deep. While inspecting the northern area outside the maar, some "tepalcates" (fragments of a broken piece of pottery) were found, which were related to the ceramic wear extracted from the Cantona archaeological site from the Late Preclassic and the beginnings of the Early Postclassic, as well as obsidian sherds.

Lake Quechulac is located only 2.5 kilometers east of Lake La Preciosa, near the town of Santa Cruz; it has a maximum width of 983 meters and a maximum depth of 40 meters. There is a small islet in the northeastern part of the lake where a wooden cross is erected, giving it ritualistic characteristics. On the day of la Santa Cruz (the Saint Cross), the locals carry offerings to the island at the beginning of the rainy season. Due to the island's ritual nature, the decision was made to explore the lake in waters over 11 meters deep. However, the lake's sedimentation makes it impossible to tell with the naked eye if there are any archaeological materials. After inspecting the area outside the maar around the crater's rim, ceramic wear from the Middle Preclassic to the end of the Classic and beginning of the Postclassic was found. Obsidian from the Pico de Orizaba was also identified.

Nowadays, it is interesting to value how the Lake Alchichica sacred nature transcends its borders: in the town of Xico (remember the route of Cortés) an all-floral arch is manufactured every year on July 22nd to commemorate the Patron saint day of Santa María Magdalena. A group of believers sets off towards Lake Alchichica one week prior to the beginning of the celebration to pick “cucharilla” flowers[9] for the arch. They start off at two o’clock in the morning, after having prayed and asked the Patroness of Xico for help in finding a copious number of flowers. Upon their return, the Virgin receives them in front of the church. The flowers they succeeded in picking are then placed on the arch to adorn it, and once it is ready, it is placed at the temple entrance. It should be mentioned that according to their beliefs, those chosen to pick the flowers must only take with them white food or else the flowers would wither (Torres 2016).

Lake Alchichica continues to provide a sacred space as well as stories that fuel the collective imagination of the faithful. New memories are created in order to emphasize its importance; a captivating sense of mystery attracts the world’s most famous seafaring explorers such as Jacques Cousteau; many stories relate that this body of water is bottomless and that it is connected to the sea; it is also a place of wonder due to the fleeting lights that disappear into its waters —supposedly evidence of another dimension or alien space ships (UFO), a collective explanation product of a psychosocial reductionism, which is attributable to the modern technological and space era, fueled by cinema and T.V. science fiction (see Chap. 24, Lake Alchichica Traditions, Myths, and Legends). In the end, Lake Alchichica is a redoubt of the extraordinary, not only from an imaginary point of view but also a natural one. The latter has made this axalapazco a site that has not gone unnoticed in our nation’s history and that will undoubtedly continue to captivate our emotions and inspire our tales.

Acknowledgments Thanks are due to the Servicio de Información Agroalimentaria y Pesquera, SAGARPA, the digital reproduction of the floor plan of the Hacienda de Techachalco, Puebla, varilla CG- PUE07, control number 4182- CGE-7247-A, anonymous author, from 1876, corresponding to the Acervo de la Mapoteca (Mapoteca Collection) “Manuel Orozco y Berra”. The authors thank the CONANP, especially Dr. Gloria Fermina Tavera Alonso, Regional Director of the Centro y Eje Neovolcánico of the CONANP. As well as Iris Hernández and Mateo Junco.

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[9] The “cucharilla” flower (*Dasylirion acrotrichum)*, great desert spoon, is slow growing since it can take up to twelve years after germination for the first blooming to appear. The “cucharilla” thrives in arid and semi-arid climates. Due to its slow growth and its extraction for food and ritualistic purposes —with over one hundred arches elaborated in the center of Veracruz every year, and with each arch using 240 plants—, this species is threatened according to the Norma Oficial Mexicana NOM-059-SEMARNAT-2010 (Official Mexican Norm).

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Chapter 2
Geological Evolution of the Alchichica Crater

Gerardo Carrasco-Núñez and Boris Chako-Tchamabé

2.1 Introduction

Lakes, especially those found in volcanic areas, are among the most beautiful landscapes worldwide. However, the definition, origin, and even the difference between such structures remain crucial as several studies have revealed their importance to understand specific processes related to magmatic activity, paleoclimate, and paleo-vegetation.

Alchichica is a quasi-circular crater lake with an asymmetric profile characterized by a higher relief towards the western rim (Fig. 2.1). With 1.8 km in diameter and over 60 m in depth, it is the largest and one of Mexico's deepest crater lakes. Alchichica is the northernmost crater lake of the Serdán-Oriental Basin (SOB). It belongs to a group of endorheic lakes (Gasca-Durán 1981), including Atexcac, Quechulac, and La Preciosa, to the north, and others like Tecuitlapa and Aljojuca, which occur to the south of the SOB (Fig. 2.2). Only Alchichica and Atexcac are saline (alkaline), contrasting with the others filled with fresh water.

Alchichica is characterized by a notable exposition of masses of white carbonate microbialites, which emerged several meters along its western and northern shoreline at the lake level due to the progressive lowering of the water table. The Alchichica lake is rich in littoral benthic macroinvertebrate populations due to the presence of aquatic vegetation.

G. Carrasco-Núñez (✉)
Centro de Geociencias, Universidad Nacional Autónoma de México,
Campus UNAM Juriquilla, Querétaro, Querétaro, México
e-mail: gerardoc@geociencias.unam.mx

B. Chako-Tchamabé
Centro de Investigación Científica y de Educación Superior de Ensenada (CICESE)- División
de Ciencias de la Tierra, Ensenada, Baja California, Mexico

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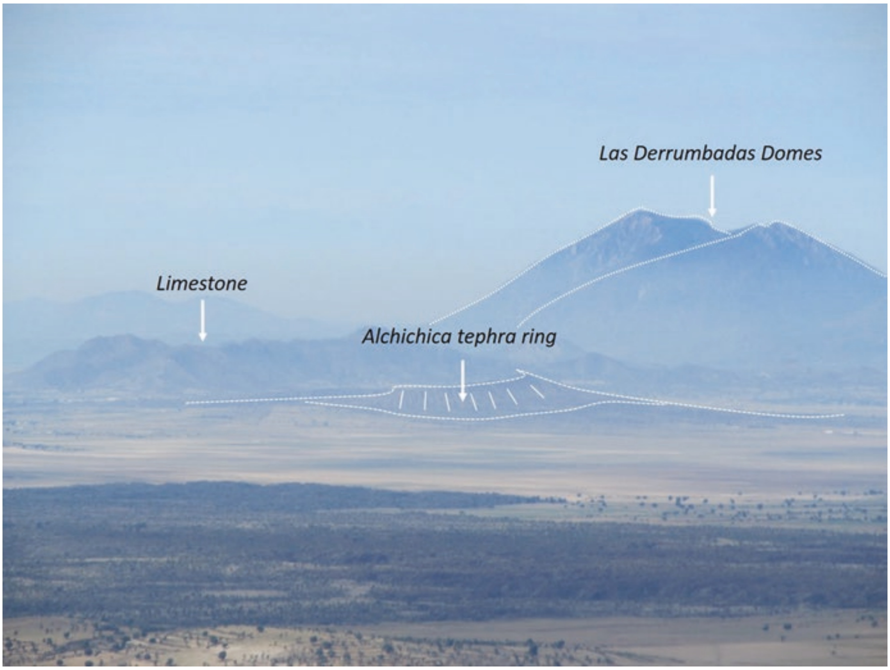


Fig. 2.1 A panoramic view of the Alchichica crater from the NNE to the SSW showing an asymmetric profile to the West of the tephra ring. It was formed over previous paleo topography (pre-maar rocks)

Although Alchichica is one of the largest volcanic crater lakes in Mexico, the processes behind its formation and the environmental conditions that favor its evolution with time are still far from being understood. Nevertheless, recent geologic studies indicate that the Alchichica crater was formed during a change in the eruptive behavior from magmatic to phreatomagmatic eruptions (Chako-Tchamabé et al. 2020a, b).

2.2 Regional Geological Setting

The Alchichica crater is located within the eastern sector of the Trans-Mexican Volcanic Belt (TMVB), a Neogene to Holocene geologic province characterized by an irregular E-W-trending belt (~ 160,000 km^2) that goes from the Pacific coast to the Gulf of Mexico (~ 1000 km, Ferrari et al. 2012), covering most of the central part of Mexico (Fig. 2.2a). The origin of the TMVB is commonly associated with the subduction of the Cocos and Rivera plates under the large North American plate along the Mesoamerican trench. However, its early evolution is related to the Farallon Plate's subduction beneath Mexico's western margin (Ferrari et al. 2012).

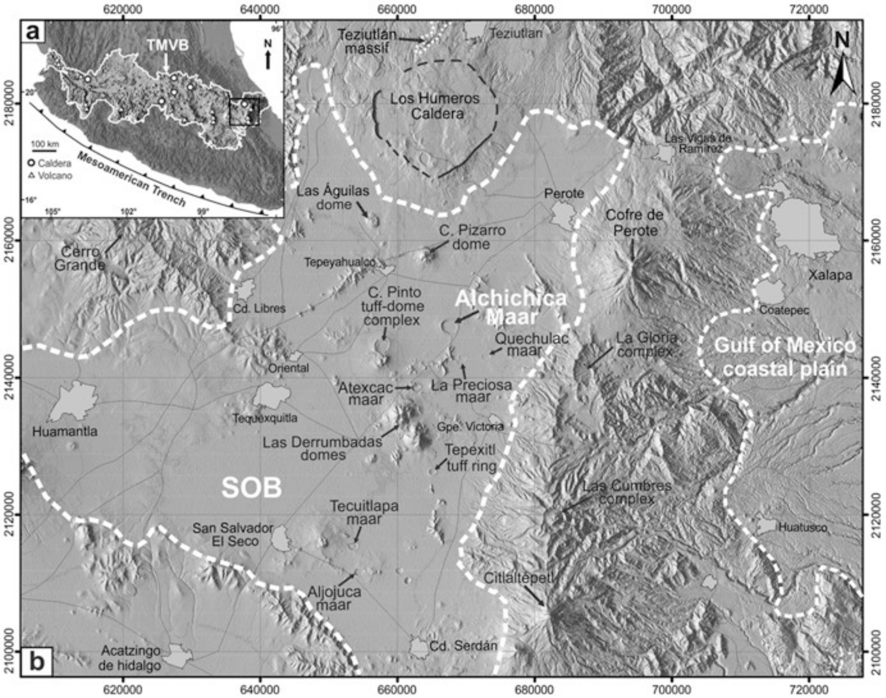


Fig. 2.2 (**a**) Location of the Alchichica crater within the eastern sector of the TMVB; (**b**) Digital Elevation Model (DEM) obtained from the Instituto Nacional de Geografía e Informática (INEGI), Mexico, showing the location of the Alchichica crater in the northern part of the Serdán-Oriental Basin (SOB)

A summary of the geodynamic, geologic, tectonic, and magmatic features of the volcanic belt is presented in Ferrari et al. (2012).

The easternmost sector of the TMVB comprises the SOB, a broad closed basin located in a high plain (average altitude of 2300 m asl without permanent river drainage). The SOB is bounded to the east by the large Citlaltépetl-Cofre de Perote volcanic range formed by large stratovolcanoes, composite volcanoes, and eroded calderas, which serves as a prominent physiographic barrier separating this (SOB) so-called Altiplano from the Gulf of Mexico coastal plain (Fig. 2.2b). Another volcanic range comprising the Miocene andesitic Cerro Grande volcanic complex and La Malinche stratovolcano is observed at its western part. To the north, it is bounded by the large Los Humeros caldera complex.

Volcanoes in the SOB include maars (more than 10), several tuff rings, and dome complexes built on a relatively complex geologic basement (Reyes-Cortés 1979). Regionally, the stratigraphic timeframe includes rocks from the Paleozoic Era represented by a suite of intrusive (granites and granodiorites), metamorphic (greenschists), and meta-sedimentary rocks forming the Teziutlán Massif (Reyes-Cortés 1979). The metamorphosed basement is covered by a thick Mesozoic sedimentary succession, which was highly deformed by the Late-Cretaceous-Eocene compressive orogenic event that formed the Mexican fold, thrust, and belt. The sedimentary basement is composed mainly of marine carbonates, shaly limestone, and minor amounts of red sandstone and shale (Viniegra 1965). Between the Eocene and Oligocene, several spotted granodioritic, gabbroic, and syenitic intrusions occurred in the area. Some of them dated at 15 Ma (Carrasco-Núñez et al. 2018), which locally produced marble, skarn, and hornfels facies (Reyes-Cortés 1979).

A relatively voluminous volcanism occurred during the Miocene-Pliocene period, which is characterized by intermediate to mafic lavas associated with the formation of the Cerro Grande Complex (8.9–10.5 Ma, Gómez-Tuena and Carrasco-Núñez 2000), followed by the Alseseca and Teziutlán andesites dated between 3–5 Ma by K/Ar (Yáñez-García and García-Durán 1982), though some Ar/Ar dates recently provided more precise ages at 1.4 to 2.6 Ma (Carrasco-Núñez et al. 2017). This volcanism is also widely distributed on the SOB, but it is entirely covered by Quaternary lava flows and pyroclastic materials of a peculiar bimodal composition. The later are associated to several isolated cinder cones and lava domes, and explosive craters of mafic to intermediate composition such as Atexcac maar (López-Rojas and Carrasco-Núñez 2015; Carrasco-Núñez et al. 2007), Tecuitlapa maar (Ort and Carrasco-Núñez 2009), Aljojuca maar (De León-Barragán et al. 2020) and Alchichica maar (Chako-Tchamabé et al. 2020a; Chako-Tchamabé et al. 2020b), as well as scattered domes (Las Derrumbadas, Cerro Pizarro, Las Águilas), tuff rings (Tepexitl; Austin-Erickson et al. (2011), and tuff-dome complexes (Cerro Pinto; Zimmer et al. 2010) of rhyolitic composition. Parts of those Quaternary pyroclastic materials are also associated with voluminous caldera-forming eruptions derived from Los Humeros caldera (Cavazos and Carrasco-Núñez 2020) at the northern end of the SOB (Fig. 2.2), which were widely distributed as ignimbrites and fallout deposits. The evidence of the Miocene-Pliocene volcanism is mainly attributed to the good correlation of that volcanism with the rock units described in all the geothermal wells of Los Humeros caldera and geothermal complex identified as an important pre-caldera volcanism by Carrasco-Núñez et al. (2017).

The distribution of the volcanoes in the SOB is generally random. However, some of them are aligned in E-W or ENE-WSW trends, especially in the southern sector of the SOB, a pattern that is well-developed in the Michoacán-Guanajuato monogenetic field within the central Mexican Volcanic Belt.

2.3 Maar Crater Lakes: Origin and Mechanisms of Formation

Volcanic lakes or crater lakes are volcanic structures formed due to either tectonic, geomorphic, and volcanological processes, or a combination of all of those processes, making their genetic backgrounds challenging to unravel. A better pathway to deciphering a lake's origin and formation mechanism starts by classifying it among other types of lakes. Christenson et al. (2015) proposed a genetic classification based on which, Alchichica classifies as a maar-diatreme lake type, i.e., a lake filling a maar crater.

Maars are defined as volcanic craters formed due to explosive interactions between an ascending magma batch with external water, derived either from an aquifer or a nearby lake (Ollier 1967). The explosion produces the recurrent deposition of fallouts and pyroclastic density currents forming tephra layers. These particular explosive events are commonly known as phreatomagmatic eruptions associated with Molten Fuel Coolant Interaction (MFCI) process, where the fuel material is magma, and the coolant is water. The thermal shock produced by the extreme differences in temperature causes a sudden transference from thermal to mechanic energy, responsible for the country-rock fragmentation. In the contact zone between the melt (magma) and water, an ephemeral thin vapor film is formed and suddenly collapses, producing fluid instability and a vapor explosion (Sheridan and Wohletz 1983). MFCI experiments have been performed to describe how these energetic magma-water interactions occur (Zimanowski et al. 1997).

As initially defined in Germany, the term maar refers only to craters where the country-rock is exposed, reflecting a deep excavation of the dominant phreatomagmatic explosions to the diatreme growth process. In contrast, other volcanoes such as tuff rings or tuff cones that only expose the pyroclastic tephra succession (with very shallow – to no crater) are apparently developed under less efficient magma-water interaction conditions or near-surface explosions with a limited contribution of magma, and thus, without diatreme construction.

In Mexico, maar volcanoes are collectively named as *xalapazcos* (Ordóñez 1905), which is originally a Náhuatl term meaning “vessel with sand”; however, when a lake is inside the crater, they are named as *axalapazcos* (“a” meaning water), that is why all the craters in the SOB starting with an “a” means they have an internal lake. Therefore, these terms have genetic implications in association with a crater formed by intense fragmentation producing fine particles due to the energetic interaction between magma and water.

Two main genetic models explain the formation of those particular explosive volcanic eruptions that, instead of progressively constructing a positive landform such as a cone or a dome structure, cause a sudden disruption of fragmented materials, leading to the eventual formation of a crater and a diatreme that grow inwards with time. Lorenz (1986) proposed the first model for maar-diatreme volcanoes’ growth, which corresponds to an incremental widening of the crater resulted from a progressive deepening of the explosive locus (Lorenz et al. 2017). The model also suggests that one part of the fragmented material derived from both the country-rock and the magma injected from bellow is violently ejected outside the crater. In contrast, the other part returns inside the carrot-shaped diatreme to fill the space left by the explosions, forming a brecciated deposit denominated as diatreme infill.

Lorenz’s model was used for a long time as a universal model to explain maar volcanoes’ formation. However, more recent models proposed by Valentine and White (2012) and Chako-Tchamabé et al. (2015) consider that magma ascending through a fracture or dike interacts with a body of water to produce MFCI explosions in different subsurface levels with time, without following a systematic deepening as depicted in the Lorenz's model. In their model, Valentine and White (2012) suggest that the explosions generally occur at shallow depths (lower than 2 km), with the shallower explosions (lower than 1 km) being particularly more effective. They also demonstrated that explosions might occur at a different location, not only vertically but laterally. In that sense, Chako-Tchamabé et al. (2015) also proposed that such shallow explosions contribute to juvenile-rich deposits, while the lateral distribution of the explosion locus is critical in both the progressive growing (enlargement) and the shaping (final morphology) of the crater (Chako-Tchamabé et al. 2016). The latter is because, at each explosion site, a small shallow crater might form, and a further coalescence of multiple shallow craters will lead to a larger and more irregular crater (Valentine et al. 2011; Chako-Tchamabé et al. 2015; López-Rojas and Carrasco-Núñez 2015). In any of those processes, as the explosions continue fragmenting the country-rocks, both the sudden ejection of fragments described as debris jets (Valentine and White 2012) towards the surface and the eventual collapse and deposition of brecciated material will occur to create a maar tephra ring, and a diatreme infill, respectively (Fig. 2.3).

The crater's final size also depends on the substrate type in which the maar is cut (Auer et al. 2007; Martín-Serrano et al. 2009; Ross et al. 2011). In a soft substrate, i.e., composed of unconsolidated volcaniclastic or sedimentary deposits, explosions (even in a limited number) are more susceptible to fragment and excavate the country-rock, leading to relatively large, bowl-shaped, and deep craters (Auer et al.

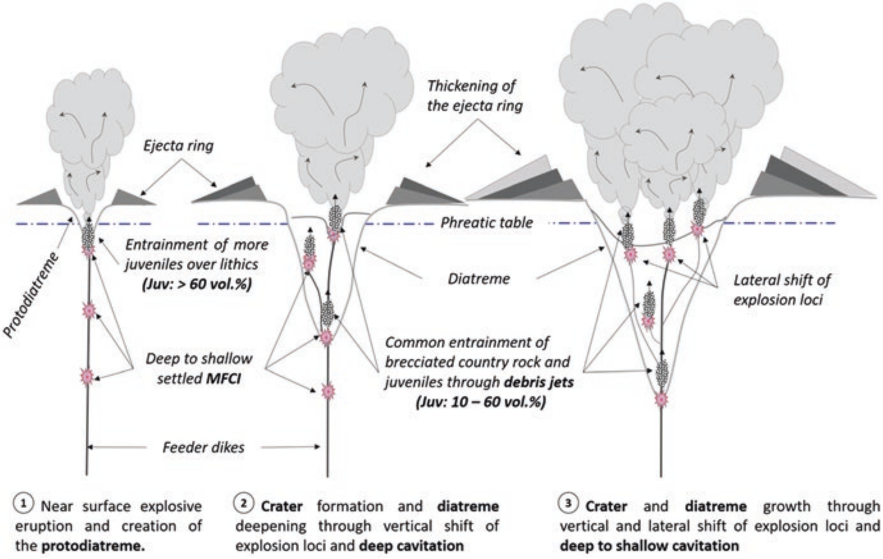


Fig. 2.3 A simplified model for maar-diatreme formation, modified after Valentine and White (2012) and Chako-Tchamabé et al. (2015). In this model, deeper MFCI could occur when magma met wet sediments or a water pond

2007; Chako-Tchamabé et al. 2016). On the other hand, maars formed in the hard-rock substrate (plutonic and metamorphic basements) tend to present relatively irregular craters, smaller in diameter and deep steeply crater walls like Joya Honda, Mexico (Aranda-Gómez and Luhr 1996) or Lake Nyos, Cameroon (McCord and Schladow 1998). In such a hard-rock context, the crater depth will tend to be shallow (< 50 m). However, an extensive collapse or subsidence of the diatreme deposits could lead to a very deep crater (> 100 m), as observed with Lake Nyos, which is about 200 m deep.

With its 1.8 km diameter and 60 m depth and the evidence of a slightly steeper crater slope at the southeast sector, Alchichica fits well as a maar crater cut in a hard substrate. Most of the maar craters in the SOB also fit these characteristics. All are shallower than Alchichica, some filled by a lake, but others not, as they do not reach the regional water table. Most of those dry craters are tuff rings of rhyolitic composition. Like Alchichica, many other maars in the SOB have relatively circular to sub-circular crater shapes, though some like Atexcac and Quechulac are elliptical and irregular, depending on the complexity of their eruptive evolution.

2.4 Volcanic Stratigraphy of the Alchichica Crater

As described above, the size (diameter and depth) and final shape of a maar crater mainly depend on the complexity of its eruptive evolution. However, to depict the eruptive process behind their origin and formation, detailed studies of the tephra deposits must be performed (Brand et al. 2009). Maar deposits usually comprise successions of layered pyroclastic materials, showing important variations in grain size from fine ash to sand and gravel (lapilli size), mixed granulometry, and several other sedimentary features that reveal the extreme changes in fragmentation due to the conditions on how the interaction between magma and water occur (Clarke and Troll 2005), as well as the associated sedimentary/depositional processes (Sohn and Chough 1989).

The Alchichica maar's stratigraphy can be grouped into two main volcanic members: pre-maar and maar members (Fig. 2.4), following the scheme proposed by Chako-Tchamabé et al. (2020b).

The pre-maar member consists of volcanic rock units of different ages, compositions, and origins. It comprises a basal lava flow (Lf), a stratified tuff layer (S), a well-stratified rhyolitic pyroclastic unit (RF), and an eroded scoria cone (SC) (Fig. 2.4). All of them are outcropping inside the western sector of the Alchichica.

The lava flow unit (Lf) is about 10 m thick and exposed at the sequence's base. It is a jagged aa-type basaltic andesite lava flow (Fig. 2.5a), covered by a thin paleosol layer that separates it from a 1 m thick lapilli tuff bedded unit (Fig. 2.5b). The microtextural features of the juvenile particles in this unit and the presence of accretionary lapilli suggest that it is derived from a dilute pyroclastic density current (Surge) of phreatomagmatic origin (Chako-Tchamabé et al. 2020b).

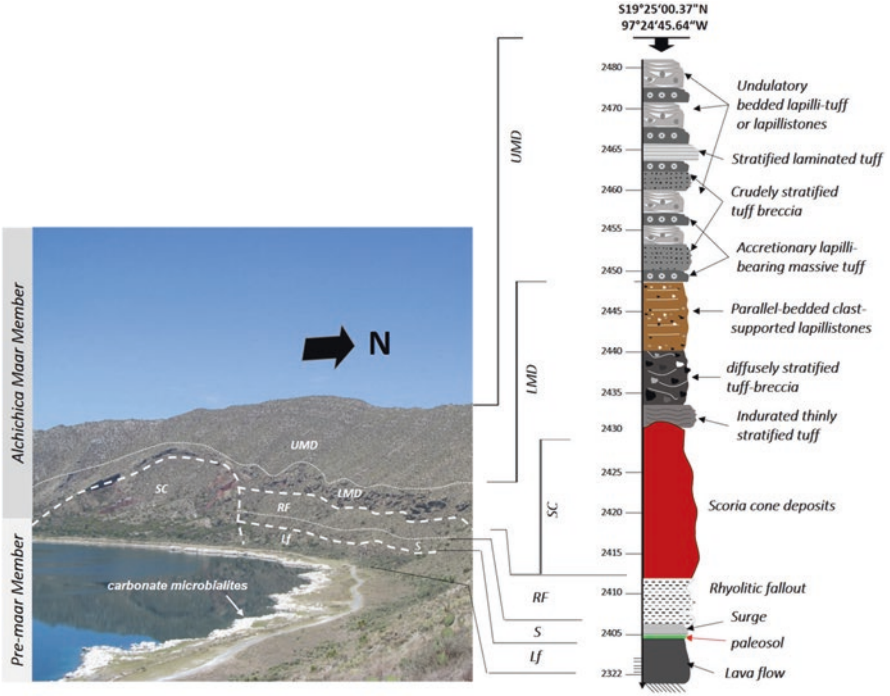


Fig. 2.4 Photograph of the western crater rim of the Alchichica maar exposing the tephra ring formed by the maar deposits (LMD: lower maar and UMD: upper maar deposits) as observed in Fig. 2.1, which are covering the pre-maar sequences (RF: Rhyolitic fallout; S: Surge, Lf: Lava flow and, SC: scoria cone). An interpretative composite stratigraphic column is presented to the right-hand side

Overlaying this, is a bedded rhyolitic pumice-rich deposit (Fig. 2.5d), which is interpreted to be formed by a dominant mechanism of fallout (RF). The deposit is dominated by pink grey to white vesiculated rhyolitic pumice, minor limestone, and agglomerate fragments. This deposit was dated at 114.0 ± 6.0 ka by the Ar/Ar method (Chako-Tchamabé et al. 2020b). Although there are some volcanoes with pyroclastic deposits of rhyolitic composition in the nearby area, the age and geochemical similarities of this unit with the rhyolitic pyroclastic deposits of the Cerro Pizarro volcano (Carrasco-Núñez and Riggs 2008), located about 10 km northeast of Alchichica, allow Chako-Tchamabé et al. (2020b) to make a good correlation between both deposits.

The youngest pre-maar unit is represented by red-color massive scoriaceous block-sized deposits forming part of an eroded scoria cone located in the crater's western sector. The deposits represent low-energy Strombolian explosions driven by magmatic degassing in an open conduit, with rapid deposition of eruptive material in quick succession. The scoria cone (SC) deposits are cut by a few thin (40–50 cm wide) sub-vertical feeder dikes (Fig. 2.5d).

Fig. 2.5 Photographs showing the pre-maar units: (**a**) basal lava flow (Lf in Fig. 2.4), (**b**) stratified lapilli-tuff unit (Surge in Fig. 2.4), (**c**) rhyolitic fallout unit (RF in Fig. 2.4), and (**d**) deposits of the eroded scoria cone (SC in Fig. 2.4), showing thin sub-vertical dikes

On the other hand, the maar member consists of an alternated succession of layers dominated by pyroclastic density currents (flow) layers, intercalated with some fallout layers. The maar sequence was grouped into a lower (LMD) and an upper (UMD) unit based on the deposits' sedimentary features (Fig. 2.4).

The lower unit (LMD, in Fig. 2.4) is about 18 m thick, composed at its base by matrix-supported medium-to-coarse ash indurated tuff subunit in which clasts firmly adhere to one another. In the middle part, deposits consist of a diffusively stratified heterolithic, chaotic, and unsorted tuff-breccia subunit, which is clast-supported by angular to sub-rounded lapilli and metric blocks (Fig. 2.6). In the upper part, some clast-supported lapilli stones are observed.

The upper maar unit (UMD, in Fig. 2.4) includes several horizons of crudely stratified tuff-breccia, thinly parallel lapilli-tuff, and undulatory bedded lapilli tuff and lapilli stone deposits. Some outcrop photographs of this unit (Fig. 2.7) highlight the common presence within the unit of soft-sedimentary deformed structures,

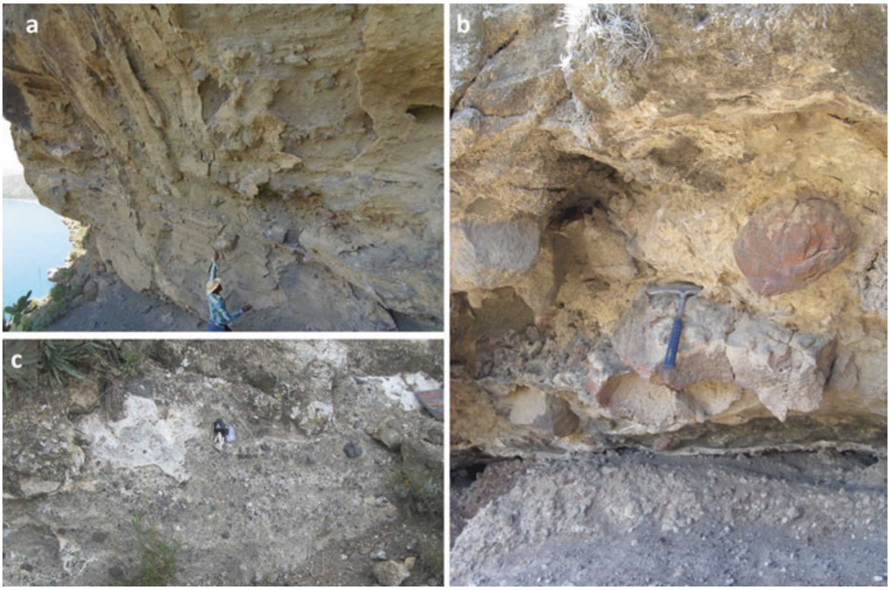


Fig. 2.6 Photographs showing representative outcrops of the lower maar deposits (LMD in Fig. 2.4). (**a**) Diffusively stratified to massive, cohesive pyroclastic sequence; (**b**) Detail of the diffusively stratified cohesive sequence showing some big scoria blocks derived from the lower pre-maar unit and incorporated within the pyroclastic maar deposit; underlying this block is the contact with the pre-maar scoria deposits (**c**) Crudely stratified clast-supported lapilli stones

bomb sags, and poorly indurated fine-grained tuff beds, mainly observed at its uppermost part. One of this upper maar unit's particularities is the repetitive occurrence of some massive matrix-supported and poorly indurated accretionary lapilli-rich (~80 vol.%) deposits (Fig. 2.7). These deposits intercalate repetitively between the other types of deposits mentioned above. These features are clear indicators of wet conditions involved in their emplacement. In the absence of a paleosol between these subunits (Chako-Tchamabé et al. 2020b), these characteristic features of the deposits were used to distinguish between the lower and the upper units, as they represent changes in the eruptive regime but within a relatively continuous eruption with an inferred very short reposed interval between both phases. Two juvenile bombs collected from both units were dated by K-Ar at 13.3 ± 6.4 ka and 6.3 ± 5.1 ka for the lower and upper units, respectively, showing an evident overlapping where it is not possible to discriminate two different ages. Nevertheless, a recent ^{14}C age was reported at 9240 yrs. B.C. by Chédeville et al. (2020) confirming the young age for the Alchichica maar's formation.

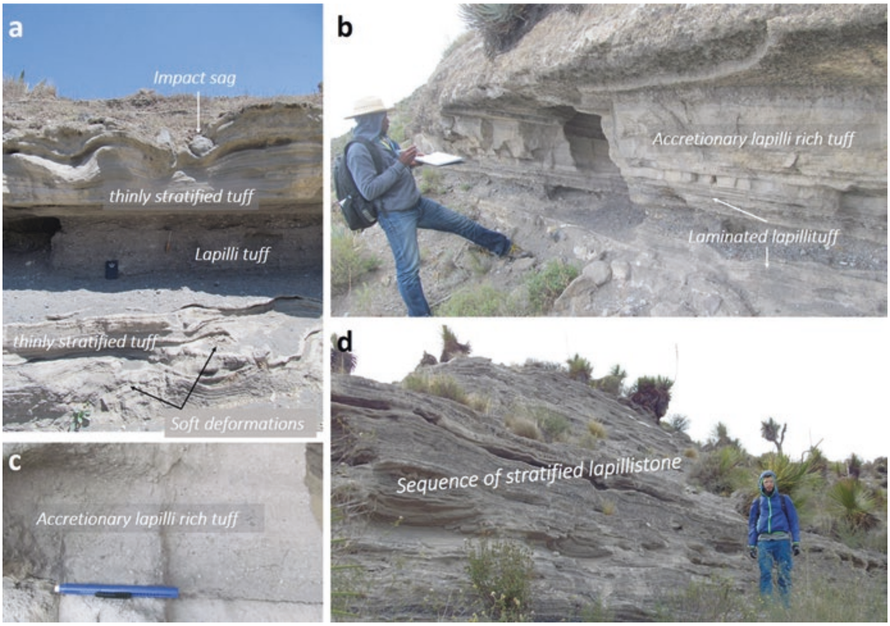


Fig. 2.7 Photographs showing representative features from the upper maar deposits (UMD). (**a**) alternated layers of stratified tuff and massive lapilli tuff horizons showing some soft-sediment plastic deformation structures produced by the impact of a few ballistic blocks coming from the left of the photo, where the crater is located; (**b**-**c**) a massive layer containing abundant accretionary lapilli particles within an ashy matrix; (**d**) stratified sequence of lapillistone layers

2.5 Geological Evolution of the Alchichica Crater

The formation of maar craters generally records a complex eruptive history, primarily when magma interacts differently with shallow groundwater. Three main eruption types are often observed: (1) phreatic eruptions, which occur during sudden heating of an aquifer o water body (Carrasco-Núñez et al. 2007); (2) phreatomagmatic eruptions that reveal the direct interaction between ascending magma and shallow water (White and Ross 2011), generating a rapid ejection of pyroclastic clouds flowing radially from the vent area over the ground at a speed over 200 km/hour. Within this eruption style, repeated instantaneous explosions might produce a rapid accumulation of layers that eventually forms a thick succession of thin layers. Some are derived from ash clouds, while others come from fallout deposition of ephemeral low to moderate eruptive column's heights, often accompanied by ballistic blocks that reach near distances from the source. (3) Sometimes, magmatic eruptions occur without significant interaction with external water, producing a lava lake or strombolian eruptions with short eruptive columns, ejecting vesicular scoriaceous material close to the emission vents (Lorenz 1986).

The stratigraphic distribution of the erupted materials at Alchichica suggests such variations in eruption styles in the area. A detailed description of these changes is presented in Chako-Tchamabé et al. (2020b), where based on the presence of some paleosol and Ar-Ar ages, they proposed four eruptive episodes; three episodes corresponding to the pre-maar activities and the last one to the Alchichica maar formation.

Therefore, the pre-maar is characterized by (1) an aa lava flow emplacement before 114 ka, (2) a phreatomagmatic eruption probably from a nearby aborted maar that deposited the pre-maar pyroclastic density current unit (surge). The deposition of the rhyolitic pumice fallout (not considered an eruptive episode here) occurred around 114 ka (age of the rhyolitic pumice) from an eruption Cerro Pizzaro. (3) The third episode corresponds to a Strombolian eruption that led to constructing a scoria cone just before the formation of the maar crater.

(4) The Alchichica maar formation occurred between 13 ka– 6.4 ka with the injection of new magma batches that interacted with the local aquifer. Chako-Tchamabé et al. (2020b) demonstrated that lateral migration of the explosion sites towards a wetter part of the substratum occurred during that maar formation, implying either the possible opening of fissures or the injection of new magma batches. This hypothesis was confirmed through a geochemical characterization of the different units (Chako-Tchamabé et al. 2020a) and allowed to separate the pre-maar eruptions from those that formed the maar. While the pre-maar eruptions were fed by basaltic andesitic (lava flow and scoria cone) and basaltic (pre-maar surge) magmas, the Alchichica maar was fed by basaltic magma batches. Considering the sedimentary features (Chako-Tchamabé et al. 2020b) and the slight geochemical variation presented by the lower and upper maar units (Chako-Tchamabé et al. 2020a), it was also demonstrated that the maar constructed throughout a minimum of two distinctive eruptive phases. The variation in the behavior of eruptions during both eruptive phases, marked by a less wet condition during the first phase and a wetter condition during the second phase (infer from the abundance of accretionary lapilli and soft sedimentary deformations), and the possible lateral migration of the explosion points, as highlighted by Chako-Tchamabé et al. (2020b), contributed to the growth and shaping the actual Alchichica crater.

To constrain the cratering process at Alchichica, we follow the method used by Chako-Tchamabé et al. (2015), which focuses on the variation in the number of juvenile and recycled juvenile clasts compared to the lithic ones among the different units, backing-up with Valentine's model. Componentry analysis at various maars has shown that the number of fresh juvenile clasts might be varying between 0–60 vol.% among the deposit layers (Brand et al. 2009; Ort and Carrasco-Núñez 2009; Chako-Tchamabé et al. 2015). Such variation has often been interpreted to infer that explosions taking place at a deeper position might entrain through debris jets an extensive number of lithic clasts from the mostly lithic-dominated upper crater infill to deposit juvenile-poor (<10 vol.% juvenile clasts) tephra beds (Chako-Tchamabé et al. 2015).

On the other hand, deposits with the content of juvenile clasts between 10–60 vol.% might have resulted from deep to shallow (approximately 200–50 m)

Table 2.1 Componentry analysis of the Alchichica upper and lower maar units

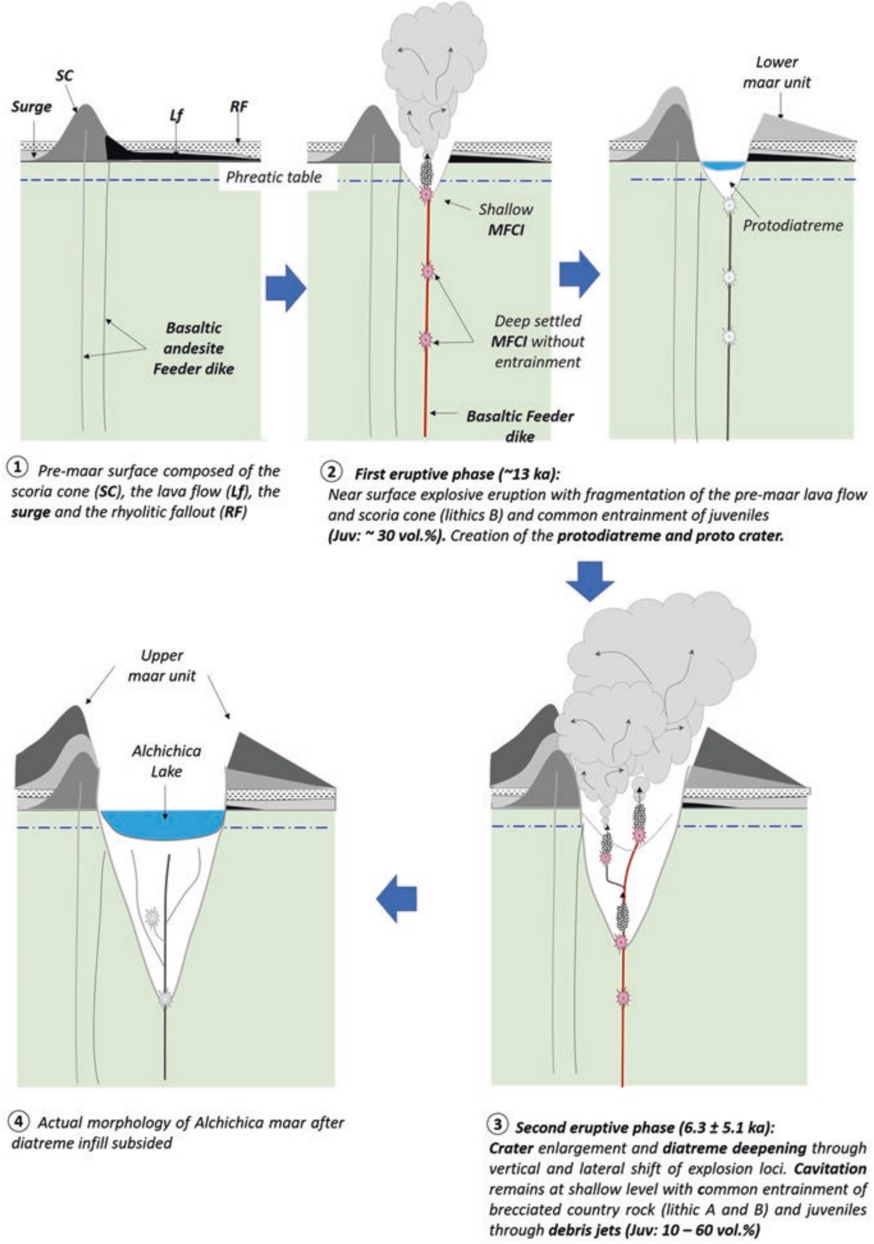
Stratigraphic unit	Sample ID	Number of clasts	Lithics A	Lithics B	Recycled juvenile	Juvenile
Upper maar unit	Al-15-log3-Py5	634	12,5	13,9	68,2	5,4
	Al-15-log3-Py4	666	30,2	8,1	53,6	8,1
	Al-15-log3-Py3	719	24,8	25	40,5	9,7
	Al-15-log3-Py2	563	23,1	19,9	50,1	6,9
	Al-15-log3-Py1	597	18,8	23,1	49,6	8,5
	Al-15-log2-Py7	568	26,1	18	40,1	15,8
	Al-15-log2-Py6	740	28,9	10,3	52,2	8,6
Lower maar unit	Al-15-log2-Py3	1063	17,3	22,8	32,1	27,8

seated explosions (Sottili et al. 2009), with common entrainment of lithics and juveniles from the crater infill region, and with much of the remobilized tephra being transported to the ejecta ring sequence. In contrast, explosions occurring at significantly shallower positions (< 50 m), generally without magma-water interaction, would produce mainly juvenile-rich beds (i.e., juvenile >90 vol.% Chako-Tchamabé et al. 2015).

Component analysis performed for the Alchichica maar and summarized in Table 2.1, reveals a mixture of fresh juveniles (5–28 vol.%), recycled juveniles (16–68 vol.%), and accidental lithics (26–71 vol.%), including fragments of sandstone, agglomerates, limestones, obsidian, and (grouped as Lithics A), and rhyolitic pumice, reddish scoria, and dense andesitic fragments (grouped as Lithics B).

A close look at these data (Table 2.1) shows a tendency of the number of fresh juveniles that decreases from the lower to the upper unit. In contrast, the recycled juvenile clasts increase almost regularly from the bottom to the top. This variation can be interpreted following the crater growth process during the two main eruptive phases (Fig. 2.8) as follow:

1. During the first eruptive phase that occurred at *ca.* 13 ka (Chako-Tchamabé et al. 2020b), the cratering process began with series of phreatomagmatic explosions that occurred at a very shallow level, pulverizing the pre-maar lava flow and scoria cone preferentially. This shallow explosion concords with the lower maar unit's fine-grained bottom layer, in which type B lithic clasts are mainly represented (Fig. 2.8a; Table 2.1). The abundance of type B over type A lithic clasts in this layer as well as in the upper layers of this lower maar unit suggests that explosions occurred at shallow levels, probably near 50 m deep, and preferentially at the western part, near the scoria cone and the lava flows as observed by



① *Pre-maar surface composed of the scoria cone (**SC**), the lava flow (**Lf**), the **surge** and the rhyolitic fallout (**RF**)*

② ***First eruptive phase (~13 ka):***
*Near surface explosive eruption with fragmentation of the pre-maar lava flow and scoria cone (lithics B) and common entrainment of juveniles **(Juv: ~ 30 vol.%)**. Creation of the **protodiatreme and proto crater.***

③ ***Second eruptive phase (6.3 ± 5.1 ka):***
Crater** enlargement and **diatreme deepening** through vertical and lateral shift of explosion loci. **Cavitation** remains at shallow level with common entrainment of brecciated country rock (lithic A and B) and juveniles through **debris jets (Juv: 10 – 60 vol.%)

④ *Actual morphology of Alchichica maar after diatreme infill subsided*

Fig. 2.8 A schematic model describing the geologic evolution of the Alchichica crater

Chako-Tchamabé et al. (2020b). On the other hand, the massive and breccias-rich character of those layers also coincides with the general vent-clearing (protocrater) and protodiatreme creation stages during maar-diatreme formation (Brand et al. 2009). So, as the water supply continued, subsequent explosions occurred relatively downward as supported by the juvenile content (28 vol.%; Chako-Tchamabé et al. 2015), fragmenting and entraining more lithics A and lithics B observed within the deposits of the middle and upper horizons of this lower maar unit.

2. The second eruptive phase, represented by the upper maar units (Fig. 2.8b), started with the formation of a layer that includes a limited number of juvenile clasts (9 vol.% at the base and 16 vol.% at the top). Here, an apparent reduction in the number of type B lithic clasts (10 vol%) and a relative increase of both type A lithic clasts (28 vol.%) and the recycled juvenile clasts (52 vol.%) is observed, suggesting that the subsequent explosions probably occurred at different locations. For example, while a limited amount of type B lithics would suggest a relative migration of the explosion loci towards the East. The abundant number of type A lithics and the small number of juveniles (9 vol.%) would support that further explosions occurred in a slightly deeper position, leading to a deep-seated lithic A and recycled juvenile material enrichment, which were transported upwards by debris jets (Chako-Tchamabé et al. 2015). The other successive horizons of the upper maar unit show a slight increase and decrease in recycled juveniles and fresh juveniles, respectively, and a relatively constant amount in both lithics A and B. This constant number of lithic clasts, together with the finer grain size of the deposits, could indicate that further explosions occurred at focused points, fragmenting both parts of the substrate and leading to the formation of a collapsed breccia present in the protodiatreme (Fig. 2.8). Besides, the limited number of erupted juvenile clasts might coincide with a little supply of magma as the eruption moved to its waning stage.
3. In contrast, the relative increase in recycled juveniles confirms the constant collapse and reworking of previously ejected materials. If so, very deep explosions are not expected to occur. Therefore, the crater quarrying (cavitation) was probably limited to the upper 100 m (Chako-Tchamabé et al. 2015) within the substrate, leading to a shallow (60 m deep) crater after the final subsidence of diatreme infills.

2.6 Conclusions

Alchichica crater is a volcanic lake that originated as a maar volcano with a complex eruptive evolution involving a strong interaction between magma and water. The Alchichica maar volcano was built over an irregular paleo-topography represented by very variable volcanic materials. The maar evolved during two main eruptive phases. The first one occurred at the foot of the actual scoria cone, disrupting both parts of the cone and other pre-maar materials like the lava flow, which are abundantly represented in the lower maar unit. This eruption resulted in the formation of the protocrater and protodiatreme of the Alchichica maar. The second eruptive phase that deposited the upper maar sequence took place at a laterally different position, with an abundant water supply. During this phase, more fragments of the substrate were produced, erupting through a series of wetter phreatomagmatic explosions occurring mainly at a fixed point and probably at shallow levels.

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Chapter 3
Paleoenvironmental Change in Central Mexico During the Last 20,000 Years

Margarita Caballero, Ma. del Socorro Lozano-García, and Beatriz Ortega-Guerrero

3.1 Introduction

In this chapter, we review the records that document the climatic and environmental changes that occurred in central Mexico during the last 20,000 years before the present (yr BP). This interval includes the end of the Pleistocene and all of the Holocene (last 11,700 yr. BP) and represents a period of rapid environmental changes at the end of the last glaciation, that was also characterized by intense volcanic activity, all of which frames the formation of the Alchichica maar by 13,300 yr. BP (Chako-Tchamabé et al. 2020). Given that the focus of this book is on the history and ecology of Lake Alchichica, we will give a particular emphasis on the available information on the climatic evolution of the basin in which this maar-lake is located: Oriental (Fig. 3.1).

3.2 The Nature of Quaternary Climatic Variability

The Quaternary represents the last 2.6 million years in the history of our planet, during which the global climate showed a series of cyclic oscillations between cold, glacial conditions and warmer, interglacial periods. These glacial-interglacial cycles

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M. Caballero (✉) · B. Ortega-Guerrero
Laboratorio de Paleolimnología, Instituto de Geofísica, Universidad Nacional Autónoma de México, Ciudad de México, Mexico
e-mail: maga@igeofisica.unam.mx; bortega@igeofisica.unam.mx

M. d. S. Lozano-García
Laboratorio de Paleoambientes y Cambio Climático, Instituto de Geología. Universidad Nacional Autónoma de México, Ciudad de México, Mexico
e-mail: mslozano@unam.mx

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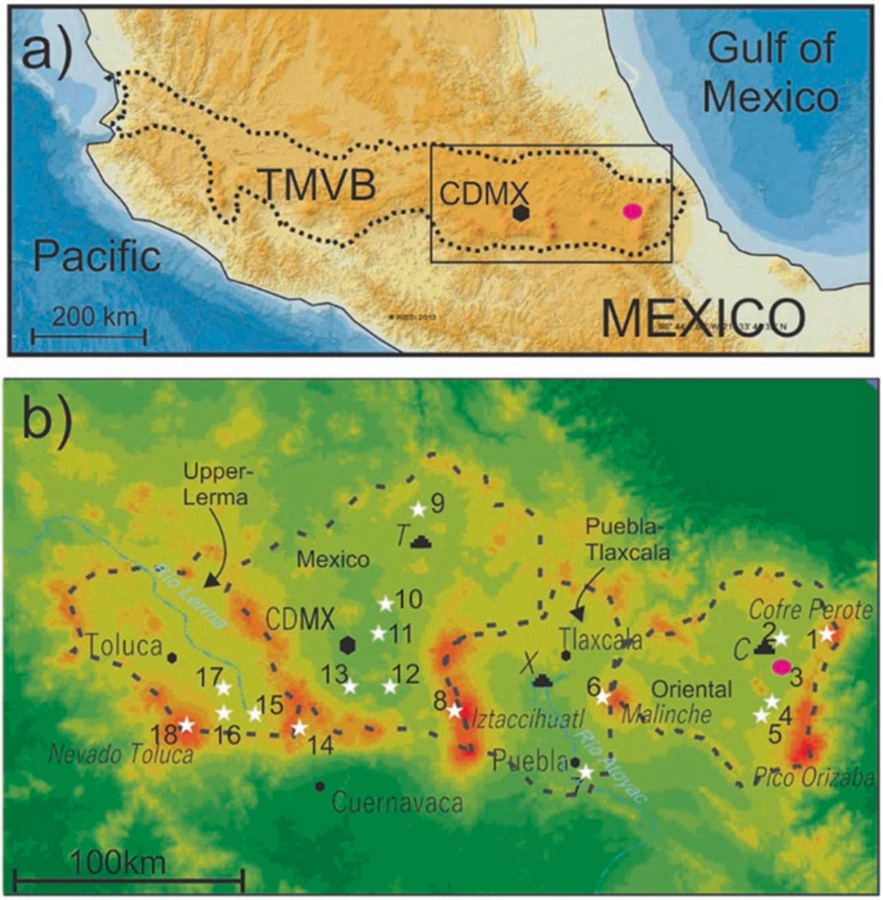

Fig. 3.1 Location maps (**a**) Lake Alchichica (pink circle) at the eastern end of the Trans-Mexican Volcanic Belt (TMVB) (**b**) The four eastern basins along the TMVB, white stars are the sites with paleoenvironmental records listed in Table 3.1. ▲ = Archaeological sites: T = Teotihuacan, X = Cacaxtla, C = Cantona

are considered to be primarily driven by changes in insolation associated with the Earth's orbital parameters (eccentricity, obliquity, and precession), which were amplified by climatic feedback mechanisms such as albedo and ice-oceanic-atmospheric interactions (Paillard 2015). The transitions between glacial to interglacial intervals (known as deglaciations or terminations) were times of intense climatic changes that occurred over only a few hundredth years. During deglaciations global temperatures increased by serval degrees Celsius (~6 to 8 °C), extensive ice sheets melted rapidly, sea level increased by several tens of meters (80 to 120 m) and atmospheric CO_2 concentrations increased in the range of 80 to 100 parts per million by volume (ppmv) (Denton et al. 2010). The last time our planet experienced maximum cooling during a glaciation was approximately between 27,000 to

Table 3.1 List of the sites with pelaeoenvironmental records for the last 20,000 yr. BP in the Oriental, Puebla-Tlaxcala, Mexico and Upper Lerma basins that were reviewed in this chapter. Analyses: A = testate amoeba, CH = charcoal particles, CL = Cladocera, D = diatomas, GC = Geochemistry, I=Stable Isotopes, MS = magnetic susceptibility, MM = magnetic mineralogy, OC=Organic carbon, P = pollen, S=Snails. References: (Aguirre Navarro 2013; Almeida-Leñero et al. 2005; Bhattacharya and Byrne 2016; Bhattacharya et al. 2015; Bradbury 1971, 1989; Caballero et al. 2019; Caballero et al. 1999; Caballero et al. 2001; Caballero and Ortega-Guerrero 1998; Caballero et al. 2002; Caballero et al. 2003; Caballero et al. 2020; Correa-Metrio et al. 2013; Cuna et al. 2014; González-Quintero et al. 1980; Guerra Ramírez 2019; Lamb et al. 2009; Lozano-García et al. 1993; Lozano-García and Sosa-Nájera 2011; Lozano-García and Ortega-Guerrero 1998; Lozano-García et al. 2005; Lozano-García and Vázquez-Selem 2005; Ludlow-Wiechers et al. 2005; Ohngemach and Straka 1983; Ortega-Guerrero et al. 2018a; Ramírez Nava 2002; Roy et al. 2009; Roy et al. 2008; Ruiz-Córdova et al. 2019; Sandoval Montaño 2000; Sedov et al. 2010; Sosa Nájera 2001; Stevens et al. 2012; Straka and Ohngemach 1989)

Basin	Location	Altitude (m asl)	Precip. (mm)	Temp. (°C)	Core/Site	Localtion details	Length (m)	Chronological control	Max Age (cal ka BP)	Min age (cal ka BP)	Analyses	References
Oriental:												
1.Cofre de Perote	97°09'W, 19°30'N	3,717	1700	10	La Teta	morraine	4.5	3(^{14}C)	13	0	P, A	Aguirre-Navarro 2013; Guerra, 2019
2. Tepeyahualco	not clear	2,350	400	14.4	Oriental	litoral E	8	Pollen types correlation	>15?	¿?	P	Ohngemach & Straka 1983; Straka & Ohngemach 1989
3. Alchichica	97°24?N, 19°25'N	2,320	400	14.4	Oriental	litoral E	1.6	2(^{14}C)	>2.5?	<1?	D	Caballero et al. 2003
4. Jalapasquillo	97°25'W, 19°13'N	2,400	400	14.4	Jalapasquillo	dry maar	20	3(^{14}C)	41?	9?	P	Ohngemach & Straka, 1983; Straka & Ohngemach,1989
5. Aljojuca	97°32'W, 19°5'N	2,400	840	15	Aljojuca	maar	12	15(^{14}C)	6.2	0	I,GC, P, CH	Bhattarchaya et al. 2015, Bhattarchaya & Byrne 2016
Puebla-Tlaxcala:												
6. Malinche	98°02'W, 19°13'N	3,100	650	14	Tlaloca	crater	3	1(^{14}C)	11.5?	1?	P	Ohngemach & Straka 1983; Straka & Ohngemach 1989
7. Valsequillo	98°09'W, 18°55'N	2,100	913	18	Caulapan	terrestrial	4.5	3(^{14}C)	40?	8?	S, I	Stevens et al. 2012
Mexico:												
8. Iztaccihuatl	98°39'W, 19°12'N	3,860	-890	-10	Marrano	morraine	4	3(^{14}C), 1(T)	11	1	P	Lozano & Vazquez-Selem 2005
9. Tecocomulco	98°23'W, 19°51'N	2,500	600	15	T-A + T-B	litoral S	6	5(^{14}C)	>50	2?	MS,MM,OC,P,D	Caballero et al. 1999; Roy et al. 2008, Roy et al. 2009
					T-A95		2.6	2(T)	~30	2?	GC	Roy et al. 2009
10. Texcoco	98°56'W, 19°36'N	2,255	550	15.6	Tepexpan	litoral NE	4.5	5(^{14}C)	36	2?	P,I	Sedov et al. 2010
					Tepexpan		4	4(^{14}C)	23	0.5	OC,GC,D, I	Lamb et al. 2009
					Tepexpan		2.6	1(T)	>20?	?	D,P	Bradbury 1989
11. Texcoco	99°00'W, 19°29'N	2,230	550	15.6	TXB	dry lake , near depocenter	10.8	5(^{14}C), 2(T)	40	1	MS,MM,D,P	Lozano & Ortega 1998; Ramírez, 2002
					TXA		6.6	4(^{14}C), 2(T)	40	3?	P	Sandoval-Montaño 2000
	not clear	2,230	550	15.6	Cruz del Lago		7.2	3(^{14}C), 2(T)	30	<5?	D,P	González & Fuentes 1980; Bardbury 1971, 1989
12. Chalco	98°58'W, 19°15'N	2,240	680	15	**CHB**(CHA)	dry lake , near depocenter	26	7(^{14}C), 2(T)	35	4?	MS, MM, OC,D,P	Lozano et al. 1993; Caballero & Ortega 1998; Caballero et al. 2019
					CHD		12	8(^{14}C), 2(T)	30	2?	MS,P	Lozano & Ortega 1993; Correa-Metrio et al. 2013
	98°56'W, 19°14'N	2,240	680	15	CHE		10	15(^{14}C), 2(T)	18.6	2?	P	Sosa Nájera, 2001, Lozano & Sosa 2011
	not clear	2,240	680	15	Chalco	depocenter?	5	3(T)	17	?	D	Bradbury, 1980
13. Xochimilco	99°08'W, 19°13'N	2,240	800	16	XOC16-II	depocenter	2.5	1(^{14}C), 2(T)	18	5?	MS, MM, F, D, OC	Ortega et al. 2018
Upper Lerma:												
14. Zempoala	99°18'W, 19°03'N	2,800	1,700	12	Zempoala	lake	5.2	6(^{14}C)	6.3	0	P	Almeida Leñero et al. 2005
	99°19'W, 19°04'N	3,100			Quila	lake	8.8	4(^{14}C)	11.6	0?	P	Almeida Leñero et al. 2005
15. Chignahuapan	99°32'W, 19°10'N	2,570	1,000	12.2	STCRZ	dry lake, near depocenter	9.54	6(^{14}C), 2(T)	27	2	MS,MM,OC, P,D	Caballero et al. 2002; Lozano et al. 2005
					Santa Cruz		1.35	3(^{14}C)	11	2	P	Ludlow et al. 2005
	99°31'W, 19°9'N	2,570	1,000	12.2	Almoloya		5.1	4(^{14}C), 2(T)	15	2?	D	Caballero et al., 2002
					Cabeza Negro		2.5	5(^{14}C)	7	1	P	Ludlow et al. 2005
16. Chignahuapan	99°33'W, 19°9'N	2,575	1,000	12.2	Isla II	litoral W	5.7	2(^{14}C), 3(T)	17	5?	MS,OC,D	Caballero et al., 2001
17. Metepec	99°35'W, 19°14'N	2,600	850	13	Metepec	fluvial	7	4(^{14}C), 4(T)	42	0.1	MS,P	Caballero et al. 2001
18. Nevado Toluca	99°45'W 19°06'N	4,200	1,213	3.8	Luna03	crater lake	0.7	^{210}Pb,1(^{14}C)	0.1	-0.05	D, P, CL, GC, OC	Cuna et al. 2014
					Luna13	crater lake	1.18	4(^{14}C),2(CD)	6.5	-0.05	D, P, CL, GC, OC, CH	Ruiz Córdova et al. 2019; Caballero et al. 2020

19,000 yr. BP, a time known as the Last Glacial Maximum. The deglaciation that followed between 15,000 to 11,700 yr. BP lead to the present interglacial, the Holocene (Fig. 3.2).

Quaternary climatic variability has been recorded in many paleoenvironmental archives across the globe such as deep-sea sediments (Lisiecki and Raymo 2005), corals (Camoin and Webster 2015) lacustrine sediments (Barker et al. 2003), cave speleothems (Asmerom et al. 2010), and ice cores from mountain glaciers (Thompson et al. 2003) as well as from the polar ice sheets in Greenland (Grootes and Stuiver 1997) and Antarctica (Petit et al. 1999). The study of these records has allowed a relatively good understanding of global climatic variability during glacial cycles, particularly during the last deglaciation and through the Holocene. Some of these records have also shown the existence of shorter-term (millennial) climatic oscillations superimposed over the longer-term (orbital) glacial cycles. This is another level of Quaternary climate variability that is not related to orbital insolation changes, but more likely to variations in solar output (sunspot cycles) or to internal oscillations in the stability of the ice sheets that modulate the intensity of the North Atlantic deep water (NADW) formation (Hemming 2004; Maslin et al. 2001). In this way, the last deglaciation was not a straight forward warming interval but showed at least two warming events interrupted by a short, abrupt cooling (Fig. 3.2). The first warming pulse corresponds to the Bølling interstadial (15,000–12,700 yr. BP) while the second represents the onset of the present interglacial (the Holocene, 11,700 yr. BP). The intermediate cooling between 12,700 and 11,700 yr., BP is the Younger Dryas, which can be considered as the last in a series of rapid cooling events of the Northern Hemisphere during the last glaciation. These cold events, known as Heinrich Stadials (HS), are an important part of the short-term (millennial) Quaternary climatic variability. Many authors have proposed that during HS

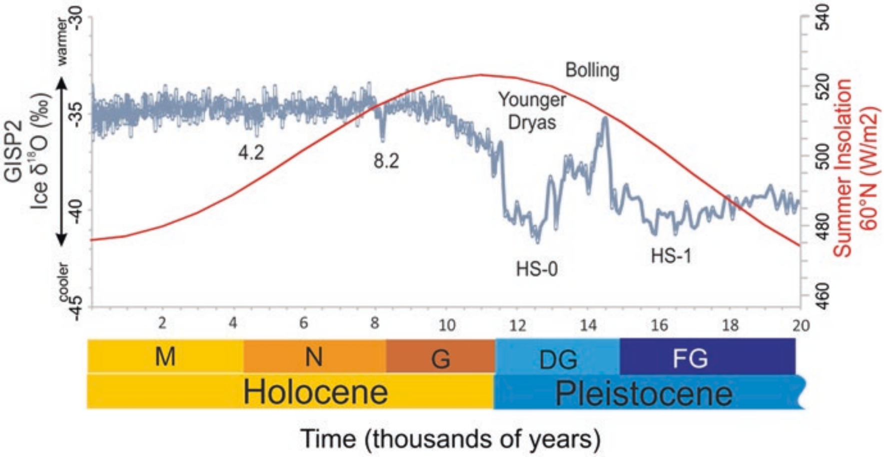

Fig. 3.2 Late Pleistocene to Holocene transition recorded in the oxygen isotopes record from Greenland ice cores (GISP2) and summer insolation changes at 60°N. FG = full glacial, DG = deglaciation, G = Greenlandian, N = Northgrippian, M = Meghalayan, HS = Heinrich Stadial

there was a reduction or near cessation of NADW formation and its associated meridional poleward oceanic heat transport. Numerous paleoenvironmental archives have recorded HS as times of dry conditions in the Northern Hemisphere tropics, related with a southward migration of the latitudinal location of the Intertropical Convergence Zone (ITCZ) and a reduction in the intensity of the Northern Hemisphere monsoons (Wang et al. 2001).

Climatic oscillations during the Holocene were less intense compared to the deglaciation but they also included a series of short-lived cool episodes (Bond cycles) such as the 8200 and 4200 yr. BP cold events or the Little Ice Age (Bond et al. 2001; Wanner et al. 2011). The climatic conditions of the early Holocene (Greenlandian, 11,700 to 8200 yr. BP) were considerably different from the rest of the Holocene as summer insolation was at its highest, therefore summers were warmer than the present, but at the same time winter insolation was lower, and winters were cooler; the annual cycle was, therefore, more extreme. Some tropical regions of the world, particularly Africa, record the early Holocene as a period of increased moisture associated with stronger monsoons and a more northerly location of the ITCZ. The mid-Holocene (Northgrippian 8200 to 4200 yr. BP) showed a trend to dryer conditions in the tropics as summer insolation and monsoon intensity reduced and the ITCZ migrated southward (Haug et al. 2001). During the late Holocene (Meghalayan, 4200 to 0 yr. BP) “El Niño” style climatic variability increased (Conroy et al. 2008), with its associated teleconnections that for central Mexico imply warmer and dryer summers (Magaña et al. 2003). Temperature and moisture oscillations during this period greatly influenced the development of early cultures around the world, the best documented of these oscillations is probably the Little Ice Age (AD 1450–1850). However, another climactic event of importance in the Mesoamerican region (central and southern Mexico) is a series of droughts from AD 800 to 1000, known as the Late Classic Droughts (Evans et al. 2018; Hodell et al. 2005; Rodríguez-Ramírez et al. 2015), which have been associated with the downfall of many ancient cities across Mesoamerica, but particularly those in the Maya region.

3.3 Overview of Paleoenvironmental Changes in Central Mexico Since the Last Glacial Maximum

Lake Alchichica is located in one of several hydrologically closed basins along the Trans- Mexican Volcanic Belt (TMVB, Fig. 3.1), these basins are ideal sites for the development of lakes. The sedimentary sequences from these lakes can preserve good records of environmental change in their mineral and geochemical composition as well as in their microfossils (pollen, diatoms, ostracodes, etc.). Besides, geomorphological studies documenting past glacier advances on the mountains that separate these basins are another good source of paleoclimate information.

The only paleoenvironmental studies for the last 20,000 yr. BP conducted directly in the Oriental Basin, are a series of palynological analyses carried out in the 1980s (Straka and Ohngemach 1989) that, unfortunately, had a poor chronological framework that greatly limits their contribution to the understanding of the environmental evolution of the region. However, paleoenvironmental studies undertaken in the other basins on the eastern end of the TMVB can give relevant information on the climatic and environmental evolution of the region during this time window. In the review that follows we will include paleoenvironmental information regarding the last 20,000 yr. BP from the Upper Lerma, Mexico, Puebla-Tlaxcala (Upper Atoyac), and Oriental basins (Fig. 3.1, Table 3.1). Amongst these, the Upper Lerma and Puebla-Tlaxcala are hydrologically open basins where two important rivers originate (Lerma and Atoyac); the Upper Lerma contained a series of extensive shallow lakes at the headwaters of this river that have a good paleolimnological record of the last 20,000 yr. (Caballero et al. 2002; Lozano-García et al. 2005). On the other hand, the Mexico and Oriental basins are hydrologically closed basins with relatively large lake systems, in the case of the Basin of Mexico, the lake system included several permanent water bodies (Chalco, Xochimilco, Texcoco, Xaltocan, Zumpango, and Tecocomulco) that preserve a long sedimentary record (>400 yr. BP in the case of Chalco, Martínez-Abarca et al. 2021), but that currently have nearly disappeared under the pressure of the modern urbanization in and around Mexico City. In the case of Oriental, there are two intermittent, playa type lakes (Totoltcingo and Tepeyahualco) even though in this basin there are also several deep maar lakes that can have a good sedimentary record of the Holocene (Bhattacharya and Byrne 2016; Bhattacharya et al. 2015). The information will be presented in three-time windows, the full glacial (20,000 to 15,000 yr. BP), the deglaciation (15,000 to 11,700 yr. BP), and the Holocene (last 11,700 yr. BP).

Volcanic activity in these basins has been an important factor of environmental change during the last 20,000 yr. BP, ranging from explosive and effusive activity in large stratovolcanoes and calderas to the formation of small monogenetic volcanoes which can include scoria cones, lava flows, domes, shield volcanoes, tuff-rings, and maars. In the Oriental Basin, there are at least 47 monogenetic vents (Carrasco-Núñez et al. 2012; Negendank et al. 1985; Yáñez García and García Durán 1982), the youngest (< 20 ka) include Cerro el Brujo, Tepexitl, Las Derrumbadas, Piedras Negras and several maar structures like Alchichica, Aljojuca, Atexcac, and Tecuitlapa (Bernal et al. 2014; Bhattacharya et al. 2015; Chako-Tchamabé et al. 2020; Chédeville et al. 2020). Besides, there were two particulalr large Plinnian eruptions that occurred during the last 20,000 yr. BP, the first at 17,000 yr. BP for Popocatépetl volcano, (Sosa-Ceballos et al. 2012) and the second for the Nevado de Toluca at 12,400 yr. BP (Arce et al. 2003).

3.3.1 Full Glacial (20,000 to 15,000 yr. BP)

Even though the time that represents the global last glacial maximum (27,000–19,000 yr. BP) predates this time window, this still represents a period of full glacial conditions, when global climates were close to their coldest. Glacial geomorphological evidence indicates that during this time the volcanoes along the TMVB that were higher than 3800 m asl had their summits glaciated (Caballero et al. 2010; Lachniet and Vazquez-Selem 2005; Vázquez-Selem and Heine 2004; Vázquez-Selem and Lachniet 2017). The best records of past glacial advances in the region come from Iztaccihuatl and Cofre de Perote; these records show that glaciers had their maximum extend between 20,000 to 14,000 yr. BP, with a depression in their equilibrium line altitudes (ELA) of 1000 and 1250 m. This lowering in the ELA can be translated into a temperature descend of 6.2 to 7.6 °C (Caballero et al. 2010; Lachniet and Vazquez-Selem 2005). Glacial moraines in Iztaccihuatl show an intermediate recession stage dated at ~17,500 yr. BP, but this recessive stage is not evident in the Cofre de Perote. The Cofre the Perote is a 4230 m asl volcano at the eastern margin of the Oriental Basin that currently has no glaciers or permanent snow. During this time window, nevertheless, its summit was covered by glaciers which termini reached altitudes of around 3390 m asl (Caballero et al. 2010; Vázquez-Selem and Lachniet 2017), with a similar situation in the other high-altitude volcanoes in Oriental, such as Pico de Orizaba and Malinche.

Some sedimentary records (Table 3.1) give evidence that at lower altitudes there were also important environmental changes during the full glacial. Amongst these probably the best record corresponds to Lake Chalco, where continuous sedimentation, good chronological control, and a multiproxy research approach come together. The pollen and diatom records from Chalco have been used to produce quantitative estimates of temperature changes using transfer functions (Correa-Metrio et al. 2013, Caballero et al. 2019). Diatom-based transfer functions were also developed for the reconstruction of changes in precipitation and lake salinity in Chalco (Caballero et al. 2019). There are two records for this time window from the Oriental basin, from the dry maar Jalapaquillo and from the eastern shores of Tepeyahualco playa lake (Oriental sequences) where pollen analysis were undertaken (Ohngemach and Straka 1983; Straka and Ohngemach 1989). However, as mentioned before, these sequences have poor chronological control and their contribution to the understanding of the vegetation changes in the region is therefore limited. Besides, they are mostly dominated by *Pinus* and *Quercus,* with relatively low values of Poaceae or other elements of the local vegetation (xeric shrubs), showing very small changes in the plant community composition during this period. The location of these sites, at the foot of the Sierra Madre Oriental and with the dominant wind flowing from the east, can explain the high proportion of anemophilous pollen types (*Pine, Quercus*) in these sequences, which were very likely were transported from the nearby mountains.

On the other hand, the pollen diagrams of this period from Chignahuapan (Upper Lerma) (Lozano-García et al. 2005), Chalco, and Texcoco (Basin of Mexico)

(Lozano-García and Ortega-Guerrero 1998) show a high abundance of herbaceous elements that give evidence of an altitudinal expansion of the alpine grasslands of around 1000 m (Caballero et al. 2010). This expansion would have been associated with a concomitant reduction in the forests' altitudinal distribution. These pollen diagrams also suggest that the forests were less densely vegetated, with more open spaces where grasses could grow. A change in species composition is also recorded, with the presence of low numbers of *Picea,* a taxon that today only lives at higher latitudes, in climates with mean annual temperatures that are at least 3 to 5 °C lower than in central Mexico. Temperature decrease estimates based on the pollen and diatom transfer functions from Chalco agree on a reduction of 3 to 4 °C compared to modern conditions (Caballero et al. 2019; Correa-Metrio et al. 2013) (Fig. 3.3). These estimates are somewhat lower than those based on glacier advances (6.2 to 7.6 °C), however, it must be taken into consideration that they come from a lower altitudinal location and it is likely that temperature decreases during the last glaciation were attitude dependent. Besides, each proxy (glaciers, pollen, diatoms) can be sensitive to slightly different environmental controls and thresholds, and their reconstructions could reflect either extreme or average environmental fluctuations.

The generally colder conditions during the full glacial were associated with lower evaporation rates, which explain the low salinities recorded in some of the lakes in the region (Chignahuapan, and Chalco, Caballero et al. 2019; Caballero et al. 2002). The climate, however, was far from stable, as it was punctuated by moments of colder and dryer conditions evidenced by the presence of *Mimosa* and herbaceous taxa in some pollen records (Lozano-García and Ortega-Guerrero 1994; Sedov et al. 2010) and also by increases in salinity or the reduction in lacustrine levels, with the formation of caliche layers (Texcoco and Tecocomulco, Caballero et al. 1999; Sedov et al. 2010). The Chalco record points to at least two of such cold-dry events, the first one by 19,000 yr. BP with a temperature decrease of around 4 °C and a second during Heinrich Stadial 1 (HS1), between 17,000 to 16,000 yr. BP, with temperature reductions of around 3.5 °C (Fig. 3.3). This two-phased maximum cooling in Chalco is in agreement with the glacier advances on Iztaccihualt, with a recessive stage at 17,500 yr. BP, even though there is no evidence of a two-phased pattern in the Cofre de Perote. Moreover, in Chalco, HS1 shows a complex pattern of rapid temperature fluctuations, further complicated by the environmental impact of the large Plinian eruption of Popocatepetl volcano at ~17,000 yr. BP (Pomez Tutti Frutti, Sosa-Ceballos et al. 2012); in the Basin of Mexico the interval from 17,000 to 16,000 yr. BP represents a time of very rapid environmental changes.

These cold and intermittently dry full glacial climates, with more open forests restricted to lower altitudinal bands and with extended alpine grasslands and mountain glaciers was the scenario for the presence of an abundant and diverse Quaternary megafauna which included giant sloths (*Megatherium*), glyptodonts, bears, lions, saber-tooth cats, mammoths, camels, and bison amongst others, and which remains have been found widely in the area (Ferrusquía-Villafranca et al. 2010).

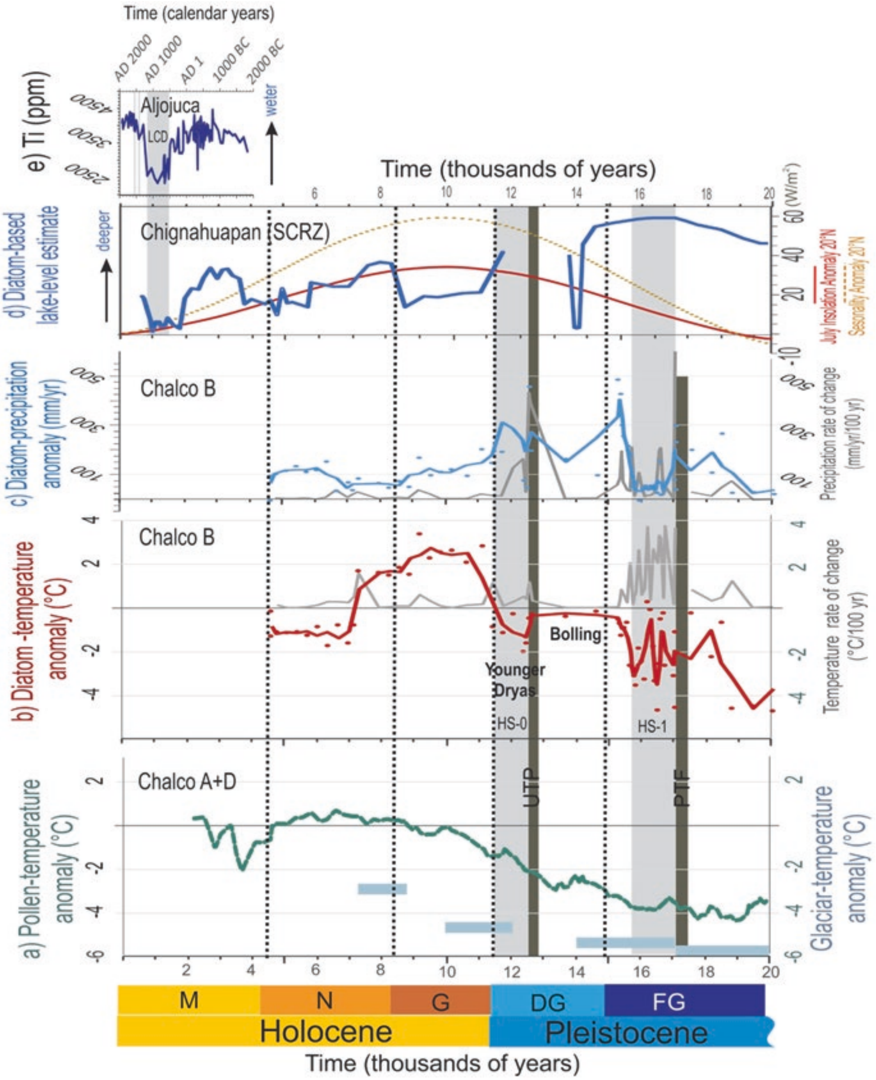

Fig. 3.3 Late Pleistocene to Holocene records from central Mexico: (**a**) Temperature anomaly reconstructions based on pollen with glacier advances, (**b**) diatom based temperature reconstruction (**c**) diatom based precipitation reconstruction (**d**) diatom based relative lake level fluctuations (**e**) Titanium record from Aljojuca. FG = Full glacial, DG = deglaciation, G = Greenlandian, N=Northgrippian, M = Meghalayan, LDC = Late Classic Droughts, UTP=Upper Toluca Pumice, TTF = Tephra Tutti-Frutti, HS = Heinrich Stadial

3.3.2 Deglaciation (15,000–11,700 yr. BP)

The deglaciation represents a time of intense climatic change worldwide and in central Mexico, the glacier advances recorded at Iztacchiuatl and Cofre de Perote are important evidence of its pace and intensity. At both volcanoes glaciers retreated rapidly between 14,000 and 12,500 yr. BP, with ELAs displacing to higher altitudes, 300 to 400 m higher compared to those during the full glacial. The rapid deglaciation at Cofre de Perote could have caused the collapse of its eastern flank (Vázquez-Selem and Lachniet 2017). There is evidence of a glacier re-advance at Iztaccihuatl dating to the Younger Dryas cold event (12,000 to 10,000 cal BP), with ELAs that were 750 m lower than modern. At the lower altitude Cofre de Perote (4230 m asl), however, nearly all the ice had disappeared by 12,000 yr. BP. Temperature estimates based on ELAs shifts are in the range of 4.5 to 5.5 °C colder than the present, this means that during the deglaciation temperature in the region increased by 2 to 2.5 °C (Caballero et al. 2010; Vázquez-Selem and Lachniet 2017).

Pollen records in the region (Table 3.1) give evidence of general vegetation changes occurring during the deglaciation, with high palynological rates of change estimated from Chalco (Lozano-García and Sosa-Nájera 2011). The common pattern in these records (Chignahuapan, Upper Lerma; Chalco and Texcoco, Basin of Mexico; Jalapaquillo, Oriental) is an increase in arboreal pollen (mostly *Pinus*) that gives evidence of reforestation of the higher altitude areas and an increase in the forest density as climates became warmer. However, some of the lacustrine sequences during this time window show sedimentation hiatuses (Texcoco and Tecocomulco, Basin of Mexico) or are disturbed by the impact of an extremely destructive Plininan eruption of the Nevado de Toluca by 12,400 yr. BP (Chignahuapan, Upper Lerma), others have poor chronological control (Texcoco, Basin of Mexico; Jalapasquillo, Oriental), all of which makes it difficult to have a more detailed picture of the climatic variability during this period. The sequences from Chalco and Xochimilco (Basin of Mexico) have the best-preserved records. In Chalco, the pollen and diatom temperature estimates show a warming trend that was underway by 15,000 yr. BP, even though they differ on their pace and numerical estimates (Fig. 3.3). Diatoms show a rapid temperature increase, reaching temperatures that were ~ 0.5 °C cooler than modern during most of the deglaciation (Bølling interstadial), while pollen suggest a gradual temperature increase, reaching temperatures that were about 2.5 °C colder than modern. In any case, both estimates contrast with the 4.5 to 5.5 °C cooling based on ELAs. As mentioned before, each paleoenvironmental indicator might be showing temperature reconstructions from different altitudinal levels, but interestingly all agree on a temperature increase during the early phases of the deglaciation (15,000 to 13,000 yr. BP, Bølling interstadial) on the order of 2 to 2.5 °C.

The Chalco diatom record shows a slight cooling of ~1 °C during the Younger Dryas (12,500 to 11,500 yr. BP), right after the eruption of the Nevado de Toluca, in agreement with the glacier re-advance at Iztaccihuatl from 12,000 to 10,000 yr. BP. The evidence regarding precipitation variability during this interval is somewhat controversial, as mentioned before several locations show sedimentation hiatuses that suggest dry conditions (Texcoco, Tecocomulco, Basin of Mexico). The reconstruction from Chalco, nevertheless, points to higher precipitation during the deglaciation (Caballero et al. 2019; Lozano-García et al. 2015) (Fig. 3.3), with short term reduction in precipitation after the B/A oscillation, by 14,300–13,300 yr. BP, which correlates with a period of higher lake salinity at Xochimilco (Ortega-Guerrero et al. 2018b) and of reduced lake levels at Chignahuapan (Upper Lerma).

These variable climatic conditions with a rapid temperature incerese of around 2 to 2.5 °C and probably wetter conditions, were the scenario for the formation of the Alchichica maar by 13,300 yr. BP (Chako-Tchamabé et al. 2020). The deglaciation was also an important period that witnessed human migrations in the area, with populations that were very likely preying on herds of mammoths and other kinds of megafauna, the remains of which are abundant in late Pleistocene records but that disappear by the beginning of the Holocene (Gonzalez et al. 2001).

3.3.3 Holocene (Last 11,700 yr. BP)

The number of sedimentary records documenting climatic variability increases during the Holocene (Table 3.1), but the glacial record becomes poorer as glaciers retreated from most of the volcanoes in the region. Geomorphological studies in Iztaccihuatl suggest that after 10,000 yr. BP glaciers retreated rapidly and that by 9000 yr. BP all areas below 4000 m asl were ice-free. However, there was a second interval of glacial stability or re-advance from 8500 to 7500 yr. BP during which ELAs were ~ 550 m lower than modern, and temperature estimates are between 2.6 to 3.3 °C cooler (Lozano y Vazquez-Selem 2005). This glacial re-advance occurred during the 8200 dry-cold event that marks the end of the Greenlandian and the beginning of the Northgrippian. By 7000 yr. BP ice had retreated to similar to modern altitudes, even though there was still a last, younger (<1000 yr. BP) glacier re-advance assumed to correspond with the Little Ice Age.

The pollen diagrams of mid and high-altitude sites (Marrano on Iztaccihuatl; Tlaloca on Malinche, and Zempoala, Fig. 3.1) show that forests were between 500 to 700 m below their modern altitudes at the beginning of the Greenlandian (Lozano-García and Vázquez-Selem 2005) but between 7500 and 7000 yr. BP *Pine* forest had recolonized the higher altitudes where alpine grasslands were previously present. The sharp increase in arboreal pollen also suggests an increase in forest density and a change in the forest composition is recorded, although a lower palynological rate of change is documented during the Holocene compared to the deglaciation (Lozano-García and Sosa-Nájera 2011).

Lacustrine records during the Greenlandian (11,700 to 8200 cal BP) are consistent in pointing to relatively dry conditions; some show sedimentation hiatuses (Texcoco, Tecocomulco, Basin of Mexico), others give evidence of lowering lake levels (Chignahuapan, Upper Lerma), and others of shallow conditions associated with high salinities and authigenic carbonate deposition (Chalco, Xochimilco, Basin of Mexico). The paleosol record also shows a change in the kind of soils that were most common in the region, from Luvisols or Andosols that formed under the colder conditions during the late Pleistocene to Vertisols during the warmer and dryer Holocene (Sedov et al. 2009; Solleiro-Rebolledo et al. 2015). The diatom-based temperature reconstruction from Chalco points to rapid warming after the Younger Dryas, with temperatures that were 2 to 3 °C higher than modern. Pollen temperature reconstruction on the other hand shows a slower warming trend during the Greenlandian, and temperatures only 0.5 °C higher than the present. In any case, both reconstructions contrast with the glacial evidence showing a re-advance centered at 8200 yr. BP, with temperature estimates ~3 °C cooler than modern. These reconstructions show a large environmental contrast between the different altitudinal levels during the Greenlandian, which could reflect the larger range in temperature oscillations along the annual cycle during this time of higher seasonality. It seems clear, nevertheless, that higher summer temperatures during the Greenalndian were associated with i) an altitudinal recovery of the forests and an attitudinal retreat of the alpine grasslands, ii) an increase in forests density and a change in its composition losing the cold-weather elements such as *Picea*, iii) higher evaporation rates at lower altitudes that lead to reducing lake levels, increasing lakes salinities and higher carbonate deposition in lakes and soils in the area. This last trend was an important driving force in the evolution of the lakes in the region, and most certainly also for lake Alchichica, and its characteristic high salinity waters.

The diatom-based temperature reconstruction from Chalco shows that after 8200 yr. BP, during the Northrippian, temperatures slowly decreased, with a concomitant reduction in lake salinity at both Chalco and Xochimilco (Basin of Mexico); the pollen-based reconstruction at Chalco agrees in showing lowering temperatures by the end of the Nothgrippian, but the records from Chalco and Xochimilco end by 5000 to 4000 yr. BP. The record from Chignahuapan, Upper Lerma, suggests a recovery in lake levels during the early Northgrippian that mirrors the cooling trends in Chalco and points to a period of higher moisture availability. Nevertheless, by the end of the Nothrgrippian, there is another shallow water episode (ca. 5500 to 3500 yr. BP) centered on the 4200 cold-dry event that marks the end of this age.

In Chignahuapan (Upper Lerma) lake level was variable, but with generally high water stands during the early Meghalayan (4200 to 2000 yr. BP), but after ~2000 yr. BP a lowering lake level trend begins, reaching particularly shallow conditions from 1500 to 1000 yr. BP (AD 300 to 1000), a very similar trend is recorded in lake Aljojuca, and in fact in many other paleoenvironmental records from Mesoamerica (Rodríguez-Ramírez et al. 2015). This shallow water event occurs in a time window that overlaps with the Late Classic Droughts (AD 600 to 900) that have been associated with the demise of many Mesoamerican cities. In central Mexico, this time involves the collapse of Teotihuacan by AD 600 (Beramendi-Orosco et al. 2009) and the later abandonment by AD 900–1000 of many of the cities that developed after the great power of Teotihuacan diminished, during the Epiclassic (AD 600–900), such as Xochicalco, Cacaxtla, or Cantona (Alvarado León 2015; García Cook 2004).

For the more recent times, the glacial record from Iztaccihuatl as well as the record from lake La Luna, in the crater of the Nevado de Toluca (Upper Lerma), give evidence of the impact of the Little Ice Age (LIA) cooling, the most important cooling event during the Meghalayan, with particularly cold-dry conditions identified at La Luna from AD 1570 to 1890 (Caballero et al. 2020; Cuna et al. 2014; Ruiz-Córdova et al. 2019).

3.4 Lake Aljojuca: A Record of Climatic Variability During the Meghalayan in the Cuenca de Oriental

The maar likes in Oriental Basin represent excellent ecosystems for paleoenvironmental research given that many of them are relatively deep lakes (>15 m), with anoxic hipolimnia where sediments and bioindicators can accumulate and be preserved in extremely good conditions. However, the depth of these lakes represents a technical challenge for the recovery of sedimentary sequences and up to now, the only long (>1 m) paleoenvironmental sequence recovered and studied from these maars comes from Aljojuca, a 40 m deep lake. Another challenging situation for paleoenvironmental studies in these lakes is to obtain a reliable chronology as old carbonates circulate in these systems and produce the "old carbon effect" that can produce radiocarbon dates that are older than the real age of the sediment. In 2007 a series of 3 cores were retrieved from Aljojuca, reaching a maximum sediment recovery of 12 m. A reliable chronology based on 15 radiocarbon determinations was produced by dating terrestrial materials without the old carbon effect such as charcoal, wood, and plant fragments as well as pollen concentrates. An integrated master sequence was analyzed for elemental geochemistry (Al, Ti), oxygen isotopes from authigenic calcite, charcoal particles, and pollen. The sediments recovered correspond to the last 6000 yr. BP, however, only the data from the last 4000 yr. BP have been published (Bhattacharya and Byrne 2016; Bhattacharya et al. 2015). The authors interpret the periods with higher oxygen isotope values ($\delta^{18}O$) and lower Al and Ti concentrations as signatures for dry climatic conditions. Based on these indicators they identify a centennial-scale arid interval from AD 500 to 1150, on top of a long-term drying trend since ~2000 yr. BP (50 BC). The authors identify the beginning of agricultural practices in the region by the precense of *Zea mays* pollen at 2400 yr. BP (450 BC). They also correlate the dryest interval with the history of Cantona, a large Mesoamerican city that reached its peak population druing the Epiclasic (AD 600 to 900) and had its final decline and abandonment by AD 900 to 1000. A short sequence recovered at the edge of lake Alchichica also gave evidence of a shallow water phase of uncertaing age in this lake, but probably starting around or after 1600 yr. BP (300 BC) (Caballero et al. 2003), in accordance with the data from Aljojuca.

This pattern of climatic change is very similar to the sequence from Chignahuapan (Upper Lerma) (Fig. 3.3); as mentioned in the previous section, in this site there is also a trend to lowering lake levels after ~2000 yr. BP, reaching particularly low lake levels during the Classic and Epiclassic (AD 300 to 1000). In this case, the climatic signal is also associated with patterns of human occupation, with the first evidence of human impact on the environment recorded as an increase in charcoal particles and a decrease in arboreal pollen by 4000 yr. BP (1500 BC) even though the presence of *Zea mays* in the sequence is only recorded much later, until AD 550. In this lacustrine basin, lower lake levels during the Classic allowed for the development of artificial islands as occupational sites that were abandoned at the end of the Epiclassic as a consequence of increasing lake levels after AD 900 to 1000 (Sugiura et al. 2010).

In Aljojuca, the authors consider that the arrival of European style farming practices is recorded in the sediments younger than 1521 by a decline in *Pinus* and *Quercus* and an increase in high spine Asteraceae that they associate with landscape clearance and the introduction of livestock like sheep. They therfore support the view that pre-hispanic anthropogenic impact was relatively low in the area compared to post-European times.

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Chapter 4
Recent Climate of Serdán-Oriental Basin

Raúl Alberto Silva-Aguilera, Óscar Escolero, and Javier Alcocer

4.1 Introduction

The Mexican territory extends through an extensive and particular latitudinal belt from 14° 32′ 27″ to 32 ° 43′ 06′‘N making it a region susceptible to fluctuations in the global atmospheric circulation (GAC) (Endfield 2011). Mexico is one of the few countries with coasts boarded by two oceans: the Atlantic Ocean to the east (the Gulf of Mexico and the Caribbean Sea) and the Pacific Ocean to the west. Furthermore, it has varied orographic features, including the Sierra Madre Occidental, Sierra Madre del Sur, Sierra de Chiapas, along the Pacific coast, and the Sierra Madre Oriental towards the Gulf of Mexico (Salgado et al. 2014). Due to these two factors, location and orography, several climate types are present in Mexico, from arid in the north, to tropical and humid in the south (Bravo-Cabrera et al. 2017).

The most influential components of the GAC in the country are the trade winds, the Intertropical Convergence Zone (ITCZ) during summer, and the Subtropical High-Pressure Cells (SHPC) during winter (Mosiño et al. 1974). Throughout the

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R. A. Silva-Aguilera (✉)
Programa de Posgrado en Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México, Ciudad de México, Mexico
e-mail: raul.s@ciencias.unam.mx

Ó. Escolero
Instituto de Geología. Universidad Nacional Autónoma de México, Ciudad de México, Mexico
e-mail: escolero@geologia.unam.mx

J. Alcocer
Grupo de Investigación en Limnología Tropical, FES Iztacala, Universidad Nacional Autónoma de México, Tlalnepantla, Estado de México, Mexico
e-mail: jalcocer@unam.mx

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summer, the ITCZ moves towards the north, causing most of the Mexican territory to be under the influence of trade winds, which flow from east to west, transporting moisture from the Caribbean Sea and the Gulf of Mexico into the continent (Caballero et al. 2019; Mosiño et al. 1974). Low atmospheric pressure zones, known as Easterly Waves (EW), flow along with the trade winds. When EW reaches the Caribbean Sea warm waters, they promote tropical cyclones that often progress into hurricanes. In the Pacific Ocean, there are also warm waters which can lead to the formation of cyclones. Hurricanes transport significant amounts of humidity and precipitation to the continent from the end of summer to the start of autumn, reaching its maximum in September (Caballero et al. 2019).

During July and August, the development of high-pressure zones may disrupt the flow of moist air, producing a mid-wet season of drought events called "*canicula*" over southern Mexico and Central America (Peralta et al. 2008; Magaña et al. 2003). High summer insolation produces low-pressure zones over northern Mexico and the southern United States. The latter favors wind flow and humidity transport from the Gulf of Mexico, the Pacific Ocean, and the Gulf of California to this continental region (northern Mexico) in a circulation known as the Mexican Monsoon (Caballero et al. 2019; Douglas et al. 1993).

During winter, the ITCZ displaces south, and the Mexican territory remains under the influence of the SHPC. This condition leads to a dry season in most of the territory, except northern Baja California and some parts of Sonora, influenced by the Western Winds (westerlies), triggering a modest rainy season (Caballero et al. 2019; Magaña et al. 2003). Cold winds flowing from the north collide with warm air masses resulting in cold fronts known as "nortes". Nortes generate winter rains and a significant decrease in temperature across the country (Caballero et al. 2019).

Following the described atmospheric dynamics, seasonality is controlled by precipitation in Mexico similarly to other tropical regions. In summary, there is a rainy season during summer-autumn, a dry and relatively cold season during winter, and a dry and hot season during spring (Caballero et al. 2019). However, there are specific regions where precipitation occurs throughout most of the year, as in the Isthmus of Tehuantepec or the Caribbean seacoast (Magaña et al. 2003). The amount and distribution of the total annual precipitation depend on changes in the mentioned atmospheric circulation systems (Endfield 2011).

Several authors have studied the correlation between El Niño-Southern Oscillation (ENSO) and precipitation in Mexico (Bravo-Cabrera et al. 2010, 2017; Magaña et al. 2003). In general terms, ENSO influences precipitation depending on its phase (El Niño or la Niña), the region of the country (north or center-south), and the season (cold or warm) (Table 4.1). Other global climatic phenomena that may affect local conditions of temperature and humidity are the Atlantic Multidecadal Oscillation (AMO) and the Pacific Decadal Oscillation (PDO) (Bravo-Cabrera et al. 2017; Mantua et al., 1997; Méndez et al., 2010; Stahle et al., 2016) (Fig. 4.1).

Table 4.1 Effect of the ENSO phase on precipitation in Mexico depending on the season of the year (From Bravo-Cabrera et al. 2017)

ENSO phase	Cold season	Warm-season
El Niño	Precipitation increases across most of the territory and diminishes in some southern locations	Precipitation diminishes in the south and increases northwest of the territory
La Niña	Precipitation diminishes in most of the territory but increases in some southern locations	Precipitation increases in the south and diminishes northwest of the territory

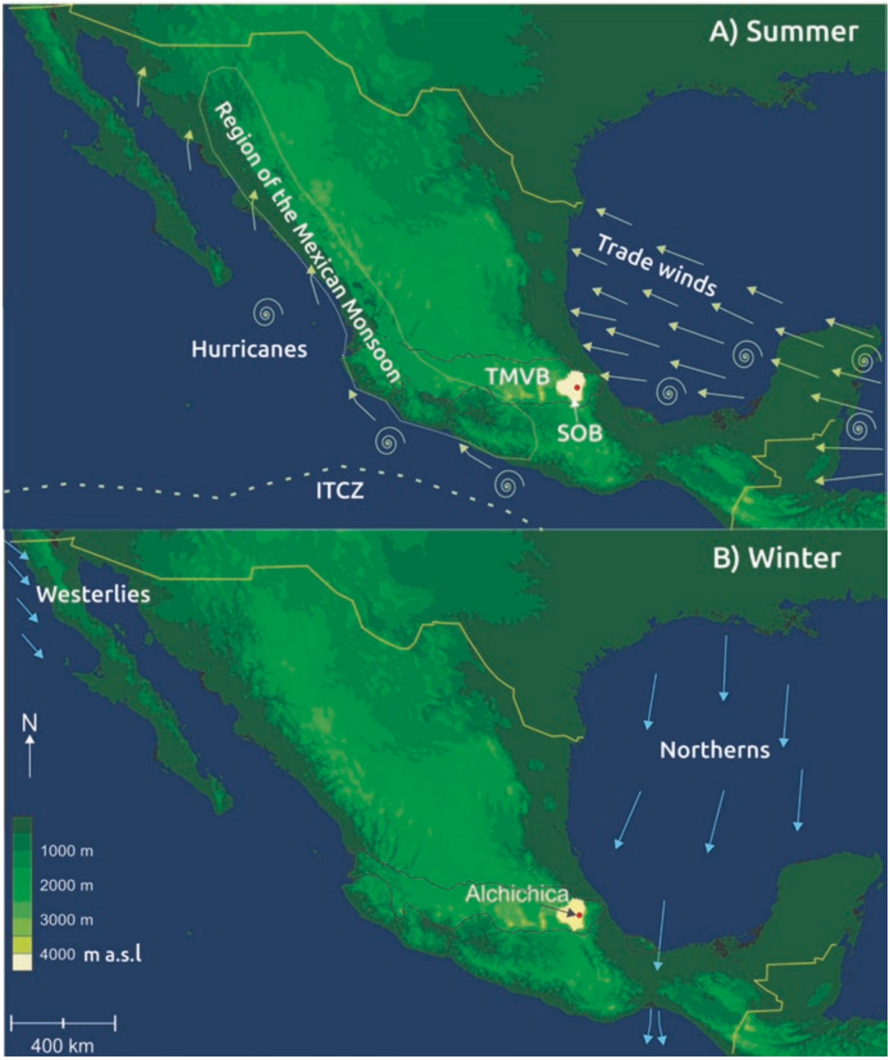

Fig. 4.1 Schematic representation of global atmospheric circulation traits affecting Mexican territory climate during (**a**) summer and winter (**b**). (ITCZ = Intertropical Convergence Zone, TMVB = Trans Mexican Volcanic Belt, SBO = Serdán Oriental Basin). The location of Lake Alchichica within SOB is shown (From Caballero et al. 2019)

4.2 Climate in Serdán-Oriental Basin

The Serdán-Oriental Basin (SOB) is south of the Tropic of Cancer between 18°57' N and 19°44' N, encompassing the country's tropical region. The SOB reaches altitudes ranging from 2300 m a.s.l. in the plateau, to its highest elevations in mountains' summits as La Malinche (4461 m a.s.l.), Cofre de Perote (4282 m a.s.l.), and Pico de Orizaba (5610 m a.s.l.) volcanoes (Alcocer et al. 2004; Gasca 1981).

According to the basin's latitude, the climate type should be subtropical; however, its orography and perpendicular position to the dominant airflow modify it. Additionally, trade winds have a strong influence on its climate, and the Gulf of Mexico represents a temperature and humidity regulator for the basin, given its proximity (Alcocer et al. 2004; Gasca 1981).

The eastern limit of the basin is also the Central Mexican Plateau's limit, comprising the mountainous area between the Pico de Orizaba and Cofre de Perote volcanoes. This barrier separates the Central Highlands to the west, from the Gulf of Mexico Coastal Plain to the east (Alcocer et al. 2004; Gasca 1981). Adiabatic cooling of ascending air over the cordillera leads to the release of moisture, resulting in convective rains to the east in the coastal plain (Endfield 2011). This mountain range prevents the Gulf of Mexico air currents from reaching the western region, where the SOB is. This phenomenon, called orographic rain shadow, produces dry and cold climate areas in the SOB (Alcocer et al. 2004; Gasca 1981).

The SOB has a seasonal climate. Most of the rainfall occurs during summer (from May to October), although winter storms can also represent a small portion of annual rainfall (Douglas et al. 1993; Peralta et al. 2008; Bhattacharya and Byrne 2016). The summertime convective activity is associated with the land surface's seasonal heating, linked to the Mexican Monsoon (Bhattacharya et al. 2015). Frosts are common during the dry season.

According to the Köppen classification of climates modified by García (1988) for the Mexican territory, there are mainly two climates' groups in the SOB: dry (B) and temperate rainy (C); although the cold or polar climate group (E) is present at the highest elevations. These groups further divided into the following types: temperate semi-arid (BS1kw), temperate arid (BSokw), temperate subhumid (Cw), semi-cold humid (Cb'(m)(f)), semi-cold sub-humid (Cb'(w)), cold (E(T)CHw) and very cold (EFHw).

There is a transition of climate subtypes (Fig. 4.2) from the highest areas (both in La Malinche to the west and Citlaltepetl mountain range to the east), with cold and semi-cold climates, to temperate subhumid in the lower areas. There is a transition from west to east in the plateau, from temperate subhumid to temperate semi-arid climate, which finally surrounds the arid temperate zone northeast of the basin. The factors that may explain the climatic variation in these relatively short distances (<10 km) are the attitudinal differences and the proximity to the orographic shadow area to the east (Caballero et al. 2019).

There are six crater (maar) lakes and two playa lakes in the SOB. Lakes Tecuitlapa, Aljojuca, and Atexcac are within the subhumid temperate zone, while

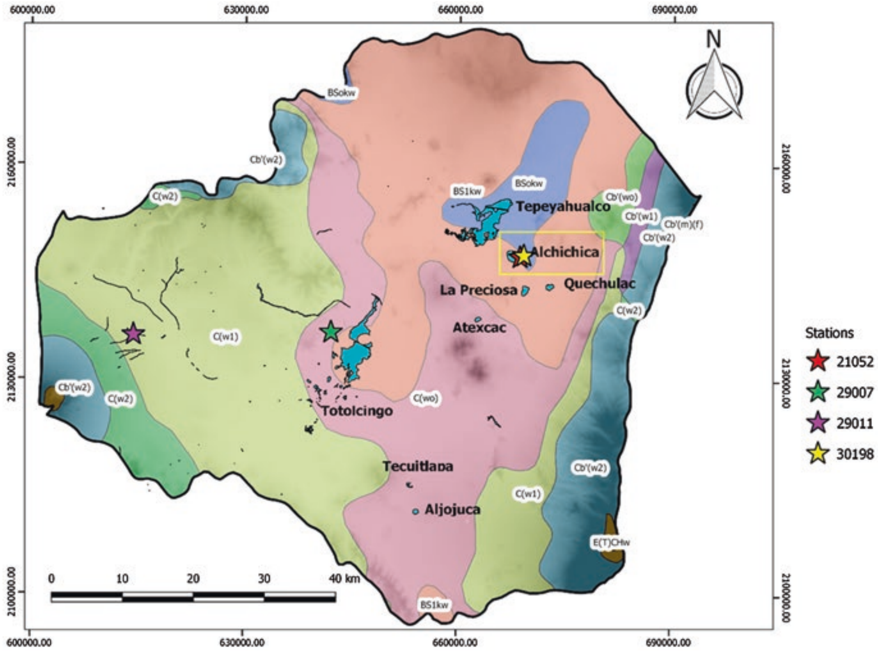

Fig. 4.2 Climate subtypes polygons in the SOB. (Based on CONABIO 1998 data, and according to Köppen classification modified by García 1988). Locations of the Sistema Meteorológico Nacional climatological stations and codes are indicated

Lakes Quechulac, La Preciosa and Alchichica, and playa Lakes Totolcingo and Tepeyahualco are within the temperate semi-arid zone. The temperate arid area of the basin is northeast of Tepeyahualco and Alchichica. Both semi-arid and arid zones are within the Llanos de San Juan sub-basin. Water evaporation directly from these water bodies occurs, and its contribution to local climate must be analyzed, which is relevant considering the water level drop reported in some of the lakes during the last decades, including Alchichica (see Chap. 5, Hydrogeology and hydrogeochemistry of the Serdán-Oriental Basin and the Lake Alchichica). In the Cofre de Perote volcano, a humid semi-cold climate type adjoins the plateau's temperate semi-arid area northeast of the basin. Gasca (1981) noticed that the northern part of the Cofre de Perote has a lower slope and does not represent a barrier for the circulation of air currents. In this sense, he suggests that winds flowing uphill to the west form clouds dispersed when they reach the plateau.

Annual mean temperature and annual precipitation maps (Fig. 4.3), built with Fick and Hijmans (2017) data, show a linear relationship with elevation. Lower temperatures occur in higher elevations, expressing a negative relationship between these two parameters. Conversely, precipitation shows a positive relationship with elevation; the highest precipitation values are associated with the highest elevations, while the lowest is present in the lower parts of the basin. A relatively high annual mean temperatures and low annual rainfall characterize the plateau, particularly in

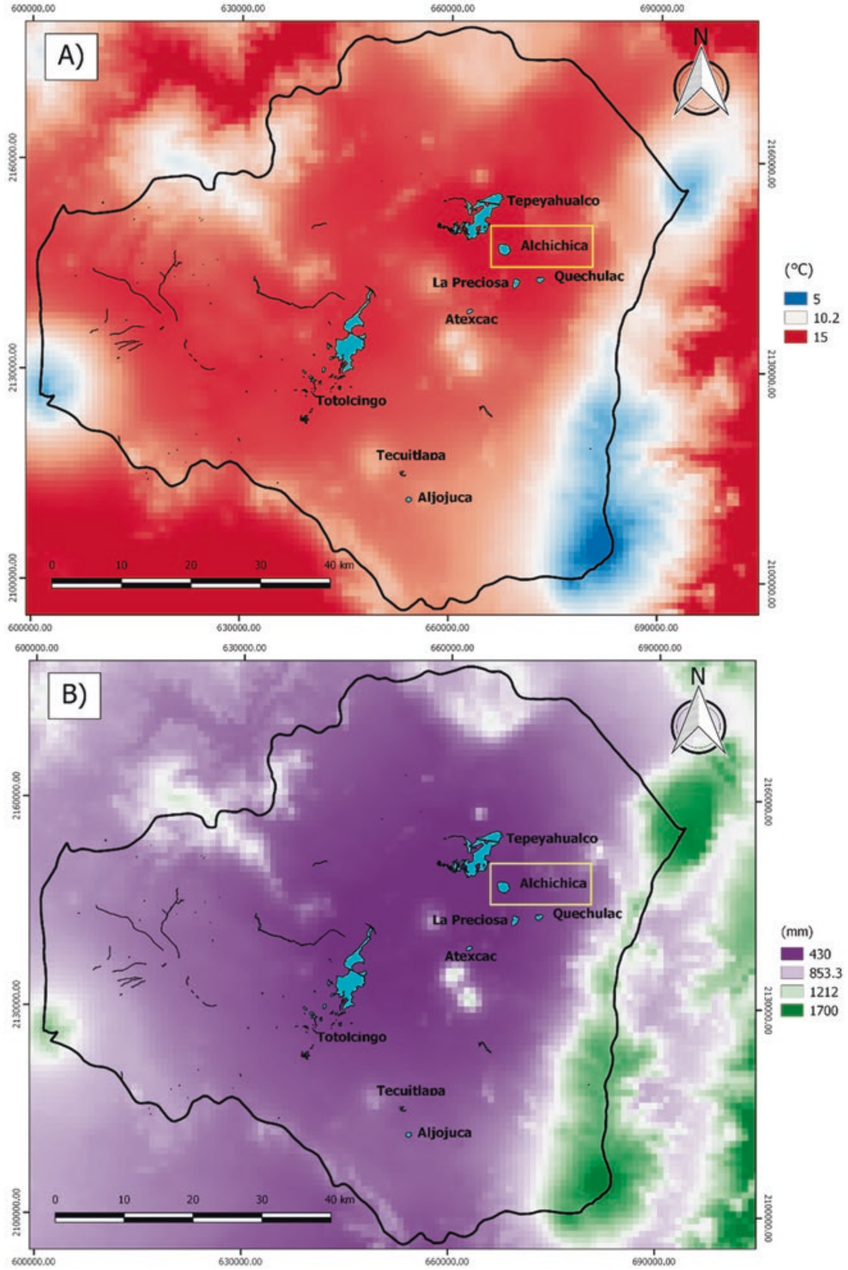

Fig. 4.3 Spatial distributions of the annual mean temperature (**a**) and precipitation (**b**) across the SOB. (Base on Fick and Hijmans 2017 data)

Lakes La Preciosa, Quechulac, Alchichica, and Tepeyahualco. The summit of the various mountains within the plateau presents relatively high precipitation values and low-temperature values, which their higher altitude can explain.

4.3 Vegetation

Climatic variables such as temperature and humidity and pedological and altitudinal variables condition the vegetation distribution within the basin (Gasca 1981). Another critical factor affecting vegetation is land use, particularly agricultural land development (Bhattacharya and Byrne 2016). Vegetation plays a vital role in climate, contributing to mass and moisture exchange (Maxwell and Kollet 2008).

In the mountainous areas, vegetation changes as elevation vary. At the highest parts of the volcanoes (~4000 m a.s.l.), there are *zacatones* (*Muhlenbergia macroura*). Below alpine grasses, there are pine forests, and in the next lower level, oak forests. Arborescent monocots (Yucca filifera and Y. elephantipes), and Juniperus deppeana dwell close to the base of the hills and the central plains, where volcanic materials predominate. Halophyte vegetation grows at the playa lakes edges, while saline grasses, such as *Distichlis spicata* and *Bouteloua hirsuta* grow better in alkaline, clayed soils with high salinity (Bhattacharya and Byrne 2016; Gerez-Fernández 1985; Gasca 1981).

4.4 Temperature and Precipitation Seasonality and Annual Variability

The Servicio Meteorológico Nacional (SMN) provided data from four weather stations (SMN-29011, SMN-29007, SMN-21052, and SMN-30198). The stations' location represents the different climate subtypes from west to east in the plateau (Fig. 4.2). Table 4.2 shows the monthly normal values (1981-2010) of temperature (°C), precipitation (mm), and evaporation (mm). Normals are period averages computed for a uniform and relatively long period comprising at least three consecutive ten-year periods (WMO 2017). Normal temperature and precipitation decrease in W-E direction, with the westernmost station (SMN-29011) having significantly higher values than the rest of the stations, particularly in precipitation. Station SMN-29007, close to playa Lake Totolcingo, exhibits the highest evaporation rate, followed by station SMN-30198, in the easternmost arid zone. Evaporation/Precipitation ratio (E/P) indicates how much water leaves either the soil or water surface of lakes, concerning how much water enters, and its value indicates the water deficit magnitude. E/P values for the various stations show the water deficit increases W-E, with the SMN-21052 station in Lake Alchichica having a value of

Table 4.2 Annual normal values for mean temperature (°C), precipitation (mm), and evaporation (mm) calculated for the 1981 to 2010 period. (Data provided by Servicio Meteorológico Nacional)

Station	Parameter	Annual
29,011	Mean temperature	14.2 °C
	Precipitation	616.9 mm
	Evaporation	1521 mm
	E/P	2.47
29,007	Mean temperature	13.9 °C
	Precipitation	454 mm
	Evaporation	1889.2 mm
	E/P	4.16
21,052	Mean temperature	13.9 °C
	Precipitation	392 mm
	Evaporation	1685.9 mm
	E/P	4.30
30,198	Mean temperature	13 °C
	Precipitation	374.6 mm
	Evaporation	1833.8 mm
	E/P	4.90

4.30 (see Chap. 5 for a more detailed description about the water balance of Lake Alchichica as influenced by climate).

Climograph (Fig. 4.4) shows the rainy season is from May to October with a slight decrease in July and August, reflecting the "*canicula*", while the dry season extends from November to April. The temperature reaches its highest value in June, then slightly decreases until September, and decreases with a higher rate from that moment, being December and January the coldest months. There are also differences in precipitation regarding the maximum values reached before and after the "*canicula*" (June and September, respectively). With respect to June, precipitation in September reduces: 21.6% in station 29,011, 7.1% in station 29,007, 4.7% in station 21,052, and only 0.7% in station 30,198. Precipitation increases gradually during the dry season from January to March in all the stations, except in station 29,007, where the low values remain practically constant until its increase in April. Assuming that these stations are representative, the average values for the plateau are 13.75±0.52 °C of annual temperature, 459.38±110.41 mm of annual precipitation, and 1732±165.05 mm of annual evaporation.

Daily records for mean temperature and precipitation have multiple missing values (Fig. 4.5). The long-term record for station SMN-29011 (1945-2013) shows a decrease in temperature, with a relatively warm period from 1945 to 1975, and has a significant negative trend of −0.02 °C year^{-1} ($p < 0.05$). In the station SMN-21052 (1966-2016), there is an apparent increase in temperature from 1965 to 1995 with a significant positive trend of 0.02 °C year^{-1} ($p < 0.05$). The other stations do not have

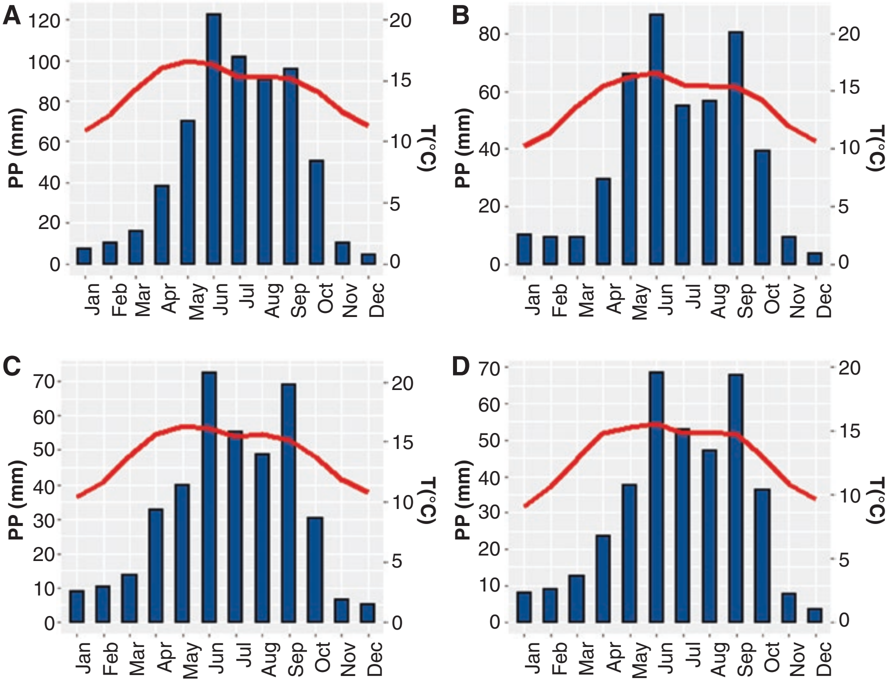

Fig. 4.4 Climographs for monthly normal values of total precipitation -PP- (blue bars) and average mean temperature -T- (red curve) with Servicio Meteorológico Nacional (SMN) data for the selected meteorological stations: 29011 (**a**), 29,007 (**b**), 21,052 (**c**) and 30,198 (C)

significant trends and show inter-annual variability. Station SMN-29007 had an evident low atypical value in 1996; the origin is unknown.

In the case of precipitation, there are no statistically significant trends in any of the records. The inter-annual variability is evident in all the records, with some years showing synchronous increases (e.g., 1981) and decreases (e.g., 1993).

The inter-annual variability in temperature and precipitation strongly correlates with the ENSO and the AMO in central Mexico (Mendez et al. 2010). However, more research is necessary to determine the particular influence of these oscillations in the SOB and the causes of multi-decadal to centennial-scale variability (Bhattacharya and Byrne 2016). As mentioned, there are no generalized trends in precipitation or temperature in the weather stations. Besides, there is some research about paleoclimates in the region revealing fluctuations between wet and dry periods (see Chap. 3, Paleoenvironmental Change in Central Mexico during the last 20,000 years), there are no local studies on recent climate change. Consequently, trend analyses in all the available stations' records lack to determine how recent climate change affects the SOB. The latter is critical considering that the lake's water level and even its hydrogeochemical characteristics are closely related to climate (see Chap. 5).

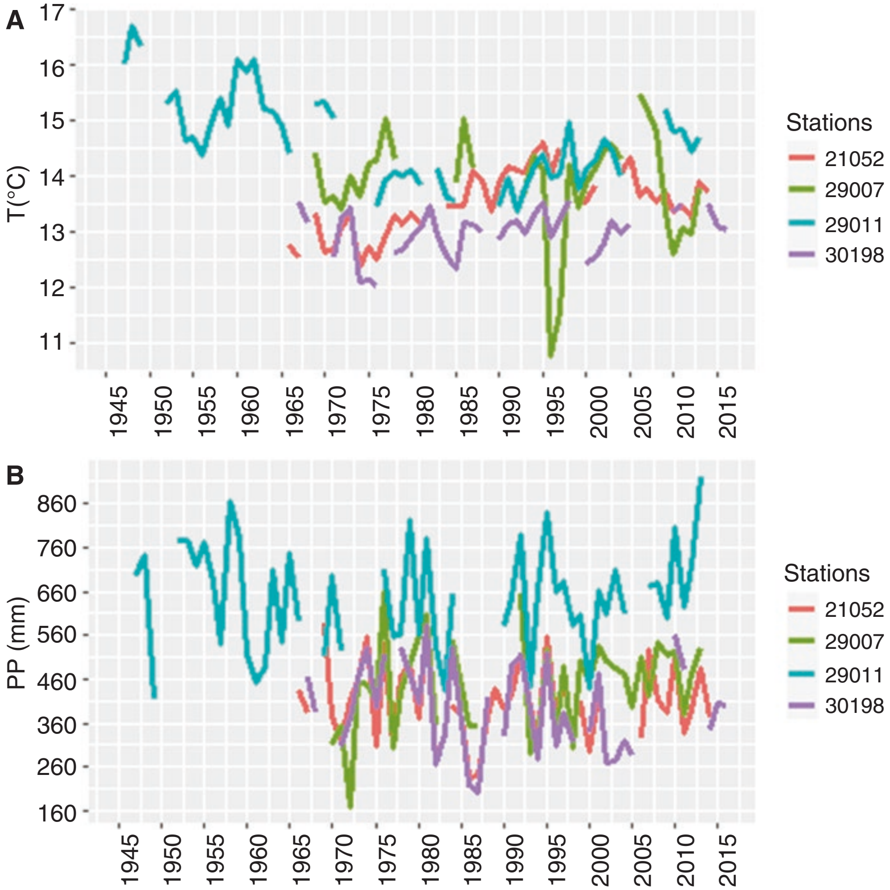

Fig. 4.5 Climographs for annual values of mean temperature (**a**) and total precipitation (**b**). (Each color represents one station). (1966-2016 data from Servicio Meteorológico Nacional)

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Chapter 5
Hydrogeology and Hydrochemistry of the Serdán-Oriental Basin and the Lake Alchichica

Raúl A. Silva-Aguilera, Gloria Vilaclara, María Aurora Armienta, and Óscar Escolero

5.1 The Catchment Area: Surface and Groundwater

Lake Alchichica is in the Serdán-Oriental basin (SOB), the easternmost intermontane basin of the Mexican Plateau, and covers parts of the Puebla, Tlaxcala, and Veracruz states with an approximate area of 5250 km^2. High altitude mountain ranges delimit the central depression plateau (2300 m a.s.l); the most important are La Malinche (4461 m a.s.l.), the Citlaltépetl (5610 m a.s.l.), and the Cofre de Perote (4282 m a.s.l.) volcanoes (Riggs and Carrasco 2004; Gasca 1981).

The SOB is a Quaternary monogenetic volcanic field consisting of a variety of small volume volcanic edifices such as tuff rings, scoria cones, domes complexes such as Cerro Pinto, Cerro Pizarro, and Las Derrumbadas, and six maars (crater lakes) which are locally called *axalapascos* (derived from the náhuatl language, meaning "water in a pot of sand"). Most of them, namely Quechulac, La Preciosa,

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R. A. Silva-Aguilera (✉)
Programa de Posgrado en Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México, Ciudad de México, Mexico
e-mail: raul.s@ciencias.unam.mx

G. Vilaclara
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

M. A. Armienta
Instituto de Geofísica, Universidad Nacional Autónoma de México, Ciudad de México, Mexico
e-mail: victoria@geofisica.unam.mx

Ó. Escolero
Instituto de Geología, Universidad Nacional Autónoma de México, Ciudad de México, Mexico
e-mail: escolero@geologia.unam.mx

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and Alchichica, formed by phreatic explosions, while Atexcac and Tecuitlapa originated from a phreatomagmatic explosion (Chako-Tchamabé et al. 2020; Carrasco et al. 2007; Gasca 1981).

The geological configuration of the SOB encompasses a regional basement of highly folded and faulted Cretaceous limestones and shales, covered by Miocene to Pleistocene andesitic rocks, which are successively overlaid by extensive pyroclastic deposits generated by both local phreatomagmatic volcanoes and large eruptions from neighboring volcanoes, and also by lacustrine deposits (Chako-Tchamabé et al. 2020). Carrasco-Nuñez and Chako-Tchamabé (Chap. 2, Geological evolution of the Alchichica crater) provide a detailed description of the regional geological evolution of the Alchichica crater.

SOB is an endorheic basin with no surface runoff outputs to other basins. The main streams within the basin are “Arroyo Xonecuila” and “Río Barranca La Malinche”, running from the western part, within the state of Tlaxcala, and intermittently discharging into the playa-lake Totolcingo (Conagua 2015). The climatic and geological features in the basin explain the scarcity and intermittent character of surface runoff. Volcanic materials such as pyroclastic deposits and lava spills have relatively high hydraulic conductivities. On the other hand, the prevailing climate in the central part of the basin ranges from temperate arid to temperate semiarid with a mean precipitation value of 459 mm/year and mean evaporation of 1732 mm/year (see Chap. 4, Recent climate of the Serdán-Oriental basin), which entails a negative water balance. Consequently, a significant portion of the rainfall evaporates into the atmosphere, and the other portion infiltrates very rapidly underground (Gasca 1981).

There are two vast playa-lakes locate in the central and lowest parts of the basin: Tepeyahualco or El Salado (2312 m a.s.l.) to the north, and Totolcingo or El Carmen (2334 m a.s.l.) to the south (Alcocer et al. 2007), separated by the Cerro Pinto volcano. Nowadays, saline Tepeyahualco remains dry most of the year and partially fills up during the rainy season as a very shallow wetland, while freshwater Totolcingo, formerly a large single water body, nowadays fills up as two separate lakes during the rainy season, Laguna de Villavicencio to the west and Laguna Santiago de Ovando to the south, reducing their surface largely during the dry season (Alcocer et al., 2007; Silva-Aguilera and Escolero 2019).

Groundwater plays a vital role in the water balance and the lakes’ water chemistry in the basin. The regional aquifer extends mainly in the lowest part of the basin and the mountainous border zones characterized by numerous fractures and dissolution cavities. Its composition is mostly pyroclastic and lava materials, which typically have high hydraulic conductivities. In the lower parts of the basin, medium to coarse grain non-consolidated alluvial deposits constitutes the upper layer. Laterally and inferiorly, the basement composed of Cretaceous limestones bound the aquifer (SOAPAP 1997; Riggs and Carrasco 2004).

In the playa-lakes area, the aquifer is semi-confined by clayey lacustrine deposits with very low hydraulic conductivity. The aquifer is unconfined in the rest of the basin, although it can be locally semi-confined by fine-grain alluvial materials. The aquifer thickness varies between approximately 300 m in the lower parts of the basin to less than 20 m in the higher southern and southeastern areas (SOAPAP 1997). The water level fluctuates between 2 and 80 m (Can et al. 2011).

Aquifer recharge occurs by surface runoff that infiltrates into the subsurface in the lowest parts of the mountain slopes during the rainy season (Cruickshank 1992). Crucial recharge areas are where the pluvial precipitation rate is high, the coarse-grained alluvial materials predominate, and fractured rocks are present. All these characteristics coincide in the La Malinche volcano to the south and the Citlaltepetl – Cofre de Perote mountain range to the east. A minor recharge area is the perennial or seasonal thawing process at the highest peaks (SOAPAP 1997).

Local discharge expressions are the springs at the base of the highest mountains and the plateau. The most important are Vicencio, Ojo de Agua, Lara Grajales, and El Carmen (Reyes 1979). Most of them exhibit yield and drainage depletion or diversion for irrigation purposes (Alcocer et al. 1998). El Carmen, located in the northwest zone of the basin, is the only spring that provided a significant yield in 1997, discharging a mean value of 40 L/s with ample seasonal and annual variations (SOAPAP 1997). Springs suggest local discharges with short residence times in the flow system. Additionally, there were some springs in the southeast zone of Lake Alchichica (García 2010). However, none of them remain nowadays, suggesting an abatement of the phreatic level (Silva-Aguilera and Escolero 2019). The mountain areas' springs discharge minor water volumes, which may imply that most of the infiltrated water percolates deep into the fractured volcanic layers and flows under gravitational control joining the regional aquifer (SOAPAP 1997).

Given the basin's endorheic nature, the main water outputs occur through evaporation from the water bodies' surface (Alcocer et al. 2004). In areas with a shallow phreatic level, direct evaporation from the soil is common, as in the Totolcingo region, where the phreatic level is less than 1 m from the surface. Evapotranspiration occurs where vegetation roots reach shallow phreatic levels, such as in the Huamantla valley; however, it is not significant on a regional scale because the vegetation cover is scarce in the basin (SOAPAP 1997).

Escolero (2018) recently defined this regional groundwater flow system (RGFS) and named it the "Tepeyahualco" RGFS. Groundwater in this system flows from the recharge zones in the basin's borders and converges to the center in the lowest parts (Fig. 5.1). There are local discharges in the six lakes (Alchichica, Atexcac, Quechulac, La Preciosa, Aljojuca, and Tecuitlapa). The global discharge base levels are the playa-lakes Totolcingo and Tepeyahualco (Escolero 2018).

Stratigraphy and geology suggest that the RGFS extends beyond the surface basin. Karstic rocks that underlie or laterally bound the volcanic fill in some basin areas could drag the aquifer to lower levels located in adjacent basins. However, it is unknown whether these formations have the necessary structural continuity (SOAPAP 1997). A numerical model approach suggests a flow component discharging to lower elevation basins through a "port" located between Cofre de Perote and Los Humeros Caldera to the north of the basin (Cruickshank 1992). However, further research is needed in this regard.

Since the early eighties, numerous wells have been drilled for groundwater exploitation purposes in different basin areas, mainly near Lakes Alchichica, La

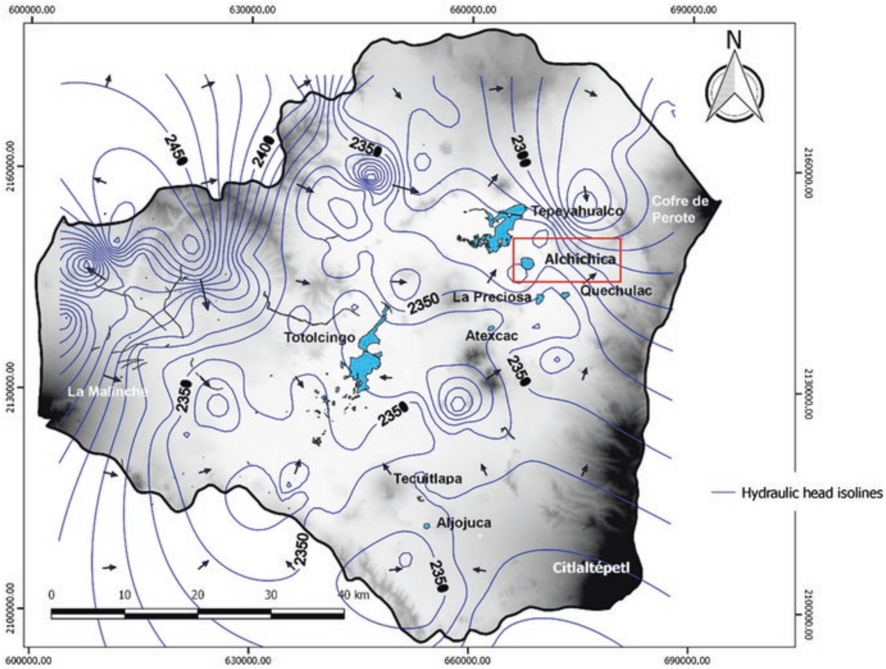

Fig. 5.1 Location of the lakes in the SOB. Hydraulic heads' isolines (m a.s.l) built with SOAPAP (1997) data and the general groundwater flow directions are shown

Preciosa, and Quechulac to the east, and San Salvador El Seco to the north (Alcocer 2004). Eighty percent of the groundwater extracted is for irrigation, increasing as agriculture activities develop (Can et al. 2011).

Along the flow path, groundwater interacts chemically with geological materials. Therefore, groundwater ionic composition and concentrations in the SOB relate to the aquifer's predominant volcanic materials. Regional hydrogeochemical characterizations conducted in the SOB found a sodic-bicarbonate composition and an average, depth-dependent, low ionic concentration (Can et al. 2011; SOAPAP 1997).

The phreatic (shallow) water has a relatively high ionic concentration for freshwater, with a mean value of 865 mg/L. The predominant cations are sodium and magnesium, with a mean concentration of 7.2 meq/L and 6.4 meq/L, respectively, while the predominant anion is bicarbonate with a mean value of 6.9 meq/L. These concentrations result from recharge water interaction with the various filling materials composing the aquifer's upper layers. Shallow wells located in the saline lakes' surroundings (Alchichica, Tepeyahualco, and Totolcingo) exploit phreatic waters with higher ionic concentrations because they are in constant ionic exchange with the materials of the lacustrine stratum, where continuous evapo-concentration occurs (Can et al., 2011; SOAPAP, 1997).

Besides the chemical differences with depth, and according to the main groundwater flow pattern, there is a horizontal trend of increasing salinity and ionic concentrations from the recharge zones to the discharge zones in the playa-lakes at the center of the SOB (SOAPAP 1997; Silva-Aguilera 2019).

5.2 Hydrogeology and Hydrogeochemistry of Groundwater in the Vicinity of Lake Alchichica

There is a topographic gradient of 1 m in Lake Alchichica's surface with a SE-NW orientation. This fact, supported by groundwater flow nets constructed with piezometric data (Alcalá 2004; García 2010; Meneses 2002; Silva-Aguilera 2019), suggests that groundwater inflows and outflows follow the same direction.

The flownets indicate at least two inflow zones: the first to the southeast and the second to the east. Also, there is at least one outflow zone to the north. Silva-Aguilera (2019) measured groundwater samples' physical and chemical characteristics obtained from piezometers representing the shallow aquifer's hydrogeochemical characteristics discharging into Lake Alchichica (Table 5.1). The mean values indicate fresh (Total Dissolved Solids, TDS < 3 g/L) and slightly alkaline water. The relative abundance of anions and cations is as follow $HCO_3^- > SO_4^{2-} > Cl^-$, and $Na^+ > Ca^{2+} = Mg^{2+} > K^+$, respectively.

The chemical characteristics associate with the geological materials of the basin. Lake Alchichica basin comprises a sequence of two stratigraphic units formed predominantly by pyroclastic deposits of basaltic andesitic composition (Chako-Tchamabé et al. 2020). The predominance of bicarbonate suggests the relatively recent water infiltration since this cation is associated with CO_2 coming either from the atmosphere or the soil. However, another source of this anion may be the

Table 5.1 Mean values of major ions and physicochemical parameters of groundwater sampled from piezometers located in the inferred inflow to the lake zone (Silva-Aguilera 2019). (TDS = total dissolved solids)

Parameter	Value
Electrical conductivity (mS/cm)	1.8
TDS (g/L)	0.9
Total alkalinity (mg/L $CaCO_3$)	658
pH	7.2 - 7.7
CO_3^{2-} (mg/L)	0
HCO_3^- (mg/L)	592
SO_4^{2-} (mg/L)	160
Cl^- (mg/L)	153
Na^+ (mg/L)	141
K^+ (mg/L)	10
Mg^{2+} (mg/L)	87
Ca^{2+} (mg/L)	87

Cretaceous carbonate rocks outcropping in some portions of the basin, especially in the central and northeast areas (SOAPAP 1997). The relatively high content of SO_4^{2-} may be explained by the dissolution of evaporites (e.g., gypsum and anhydrite) that could be present within the Cretaceous carbonate's formations. The volcanic rocks' albite minerals confer a sodic character to SOB's groundwaters (Ortega et al. 2002; Can et al. 2011). The lithological magnesium sources are the ferromagnesian minerals from the basic igneous rocks (SOAPAP 1997). Some portions of the aforementioned Cretaceous carbonates may be dolomitized, representing another potential magnesium source (Boggs 1995; Custodio and Llamas 1976). Calcium may come either from the dissolution of calcic feldspar, a constituent of igneous rocks, or the Cretaceous carbonate rocks. However, to know the particular sources and processes taking place in the SOB's groundwaters, a hydrogeochemical modeling approach is needed.

The close relationship between the groundwater flow system and Lake Alchichica has implications in its chemical composition (as discussed in the next section) and its water balance. The latter reminds the relevance of considering the connectivity existing between groundwater and surface water. Water inputs in Lake Alchichica are pluvial precipitation and groundwater inflow, while outputs are evaporation from the lake's surface and groundwater outflows. Consequently, both water level and stored water volume depend on the water balance (Alcalá 2004; García 2010; Silva-Aguilera 2019). Estimations of the lake's mean annual water balance (Fig. 5.2) point out that water that evaporates each year is around 1.2 times higher than the water entering by precipitation and groundwater inflow (Alcalá 2004), highlighting the importance of preserving groundwater inflows.

Since Lake Alchichica formation, sometime in the Late Pleistocene to the Holocene (Chako-Tchamabé et al. 2020), the water balance has changed as a function of climate variability in the region (Silva-Aguilera 2019). Kaźmierczak et al. (2011) found mineralogical and isotopic evidence in the microbialites suggesting

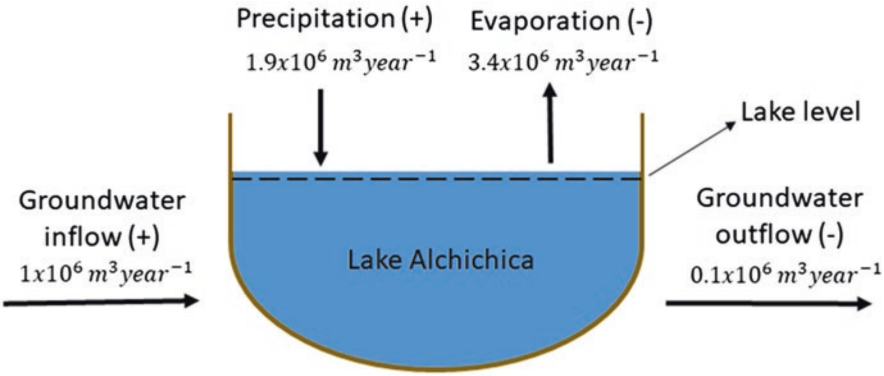

Fig. 5.2 Water balance conceptual model showing Lake Alchichica's water inputs and outputs. (Modified from Silva-Aguilera 2019, based on Alcalá 2004 data)

fluctuations of the lake's water level modulated by dry and wet climatic conditions in the last 3000 years.

During the last decades, the lake's water level reduction has been remarkably evidenced for the region's inhabitants (Alcocer and Escobar 2007). The most apparent indication is that microbialites originally formed underwater (see Chap. 22, Microbialites: diversity hotspots in the Mexican Plateau) are currently exposed approximately 2 m above the water level. The water level records covering the period from 1959 to 1992 reveal a total decrease of 2.57 m, with an estimated rate of 7.6 cm year^{-1} (Silva-Aguilera 2019). Alcalá (2004) estimated that water level decreased 2.35 m from 1992 to 2004, which translates into a higher rate of 20 cm/year. It means a reduction of almost 5 meters in 45 years. From 2004 to the present, there are no records, but there is visual evidence of continued microbialites exposure, suggesting the water level keeps dropping (Silva-Aguilera 2019; Silva-Aguilera and Escolero 2019).

The water level decline is related to climate variability and groundwater exploitation (Alcocer et al. 2004). As mentioned, water output by evaporation from the lake's surface has been significantly higher than water inputs by precipitation and groundwater flows during the last decades, explaining the water level decrease. However, the increase in the water level decline rate from 1992 on could be associated with the intensive groundwater exploitation for irrigation in the region.

5.3 Past and Present Hydrochemical Characteristics

The chemical identity of inland waters comes from the concentration and ratios of major ions (mainly CO_3^{2-}, HCO_3^-, SO_4^{2-}, Cl^-, Ca^{2+}, Mg^{2+}, Na^+, and K^+) and depends on local or regional conditions for each water body. The reference frame for such conditions is the watershed or sub-basin, and they can be divided into (a) the geological substrate type, which contributes with dissolved salts to surface water bodies and connected aquifers; (b) the prevailing climate, mainly related to the precipitation/evapotranspiration balance, which reflects on dilution-concentration phenomena and even on the eventual precipitation of dissolved salts from the water; and (c) the increasing anthropic activities that directly or indirectly alters the inland aquatic resources upon which it so closely depends.

Lake Alchichica is a model example of these local influences on the main chemical identity of its waters. The northern sub-basin, Llanos de San Juan, has the driest climate in the area, with mean annual evaporation rates much higher than the precipitation ones, especially in and around Lake Alchichica (see Chap. 4, Recent climate of the Serdán-Oriental basin). This situation would point to a greater salinity than the current one for the lake, around 8.5-9.0 g/L. The saline condition results from the freshwater aquifer inflow that partially compensates for the precipitation deficit (Silva-Aguilera and Escolero 2019). The lake is also indirectly affected by water abstraction for irrigation, especially in the adjacent area where the groundwater that feeds Alchichica circulates. This situation contributes negatively to the water balance of the lake. It threatens to reduce the water volume in the lake (as clearly shown by the increasing amount of microbialite ring exposed on the shoreline) and the primary chemical identity to which the peculiar biota of Lake Alchichica has adapted.

This section presents data of the major ionic composition for Lake Alchichica water and some variables linked to salinity and alkaline reserve, such as electrical conductivity (at 25 °C), overall ionic concentration and total alkalinity (Tables 5.2 and 5.3). Among a few others, the referred publications have been selected as they present comparable data for the lake's open waters.

The comparative descriptors related to salinity and ionic composition and concentration are shown in Tables 5.3, 5.4, and 5.5, and Figs. 5.2 and 5.3.

Table 5.3 shows a slight trend of increasing electrical conductivity, ionic concentration and total alkalinity over time. For pH, there are no records in the oldest publication (Taylor, 1943), while for most of the subsequent data, the values show homogeneity in the water column. This is so because in saline waters with a high alkaline reserve, such as those of Lake Alchichica, pH shows a conservative behavior, which is also not affected by this oligotrophic lake's low biological activity (see Chap. 7, Physico-chemical characteristics). All pH values ranged around 9.0.

The aquifer's groundwater entering Lake Alchichica (Table 5.1) is highly mineralized but still freshwater with an ionic composition dominated by calcium. Upon contact with the lake's open water, it changes drastically (Tables 5.3 and 5.4). The mixing of both water sources changes the carbonate-bicarbonate equilibrium ($pH < 8.0$ in the surrounding aquifer becomes around 9.0 within the lake). As a consequence, the newly formed carbonates profusely precipitate along with calcium.

At the lake basin's littoral zone, where springs from the aquifer supply water to the lake, the chemical interaction gave rise to a notorious feature of Lake Alchichica: the stromatolite (microbialites) ring. Some autotrophic microorganisms associated with the microbialites contribute actively to such precipitation (see Chap. 22, Microbialites: diversity hotspots in the Mexican Plateau).

A slight change in the composition proportions is observed, mainly towards increasing magnesium and chlorides, which is not evident for the other ions. To further explore this trend, both ions were plotted (Fig. 5.4).

Comparing the six cases -even considering some fluctuation that could relate to different methodologies for data collection, preservation, and/or analysis-, a trend

Table 5.2 Sampling data from information sources. (One sampling date, except for [1]every 3 months, and [2]every month,? unknown month; sampling details in each reference)

Sampling year	Month	Sampling site	References
1941	?	Near shore	Taylor (1943)
1988-89	5 to 5[1]	Water column	Vilaclara et al. (1993)
2001	5	Water column	Armienta et al. (2008)
2007	6	Water column	Kazmierczak et al. (2011)
2011	6	Water column	Sigala et al. (2017)
2019	1 to 12[2]	Water column	Armienta and Vilaclara unpublished

Table 5.3 Electrical conductivity standardized at 25 °C (K_{25}), sum of ionic concentrations as total dissolved solids (TDS), and total alkalinity (T. Alk.) for Lake Alchichica [* inferred data from a 0.66 (TDS/K_{25}) factor; ** TDS data from direct gravimetric analysis.? unknown]. References for years and sampling sites in Table 5.2

Sampling	K_{25}	TDS (ionic sum)	T. Alk.
Year	mS/cm	g/L	mg/L as $CaCO_3$
1941	12.55*	8.19	1915
1988-89	12.88*	8.50**	2087
2001	12.87	8.49*	2114
2007	13.35	8.76**	?
2011	13.52*	9.95	2199
2019	13.53	10.08	2236

Table 5.4 Concentration (mg/L) of main anions and cations in Alchichica through recent times (1941-2019). (*Original data expressed as the sum of both types of anions in meq/L,? unknown). References for years and sampling sites in Table 5.2

Sampling Year	CO_3^{2-}	HCO_3^-	SO_4^{2-}	Cl^-	Mg^{2+}	Ca^{2+}	Na^++K^+
1941	1068	1068	970	2595	349	10	2570
1988-89	462	802	1026	3022	331	12	2222
2001	900	900	996	3115	431	11	2620
2007	?	?	804	3095	433	15	2518
2011	965	720	1065	3860	458	20	2861
2019	876	943	969	3947	485	8	2852

towards a sustained rise in chlorides and magnesium ions stands out. The increase in chlorides is consistent with a light salinity upturn, although such a relationship is less clear for magnesium. The explanation could lie in the type of volcanic rocks at the Alchichica crater and its surroundings (Chako-Tchamabé et al. 2020). Basalt pyroxenes contribute magnesium (Hounslow 1995), calcium feldspars, and possibly dolomitized limestones supply both calcium and magnesium upon contact with the aquifer feeding Alchichica. A similar increase is observed in salinity and alkalinity (Table 5.3). Changes between 1941 and 2019 (in mg/L, computed by the following equation: [(final value–initial value)/initial value]*100) are ≥17% for the ionic sum and total alkalinity and as high as >35% for chlorides and magnesium. These variations suggest a change in the chemical identity set by the composition of the major ions, i.e., an incipient transformation in Lake Alchichica's water's chemical signature.

Given the past fluctuations and recent trends that seemingly point to an increase in some salinity descriptors, could this signify the beginning of a critical change for the biota? Suppose this trend accelerates at human scales (already seen for other maar lakes in Mexico, e.g., Escolero and Alcocer 2004). In that case, an increase in salinization linked to global warming and the local aquifer's exploitation may eventually threaten the unique Alchichica's biota (see Chap. 20, Diversification and Endemisms). Such a scenario would be significantly adverse for the

Table 5.5 Concentration (meq/L) of main anions and cations in Alchichica through recent times. References for years and sampling sites in Table 5.2

Sampling Year	$CO_3^{2-} + HCO_3^-$	SO_4^{2-}	Cl^-	$Cl^- + SO_4^{2-}$	$Na^+ + K^+$	Mg^{2+}	Ca^{2+}	$Ca^{2+} + Mg^{2+}$
1941	38.3	20.2	73.2	93.4	119.0	28.7	0.5	29.2
1988-89	28.5	21.4	85.2	106.6	92.8	27.2	0.6	27.8
2001	44.7	20.7	87.9	108.6	109.8	35.5	0.5	36.0
2007	30.9	16.7	87.3	104.0	105.8	35.6	0.7	36.3
2011	44.0	22.2	108.9	131.0	120.1	37.6	1.0	38.6
2019	44.7	20.2	111.3	131.5	119.9	39.9	0.4	40.3

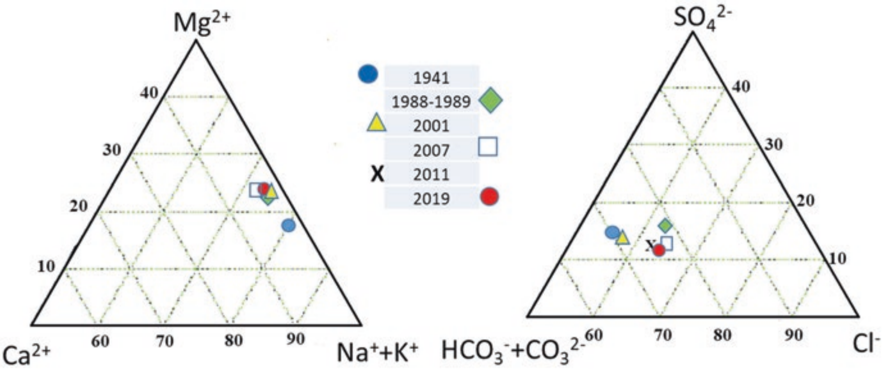

Fig. 5.3 Modified Piper diagrams for cation and anion proportions in % of meq/L. References for years and sampling sites in Table 5.2

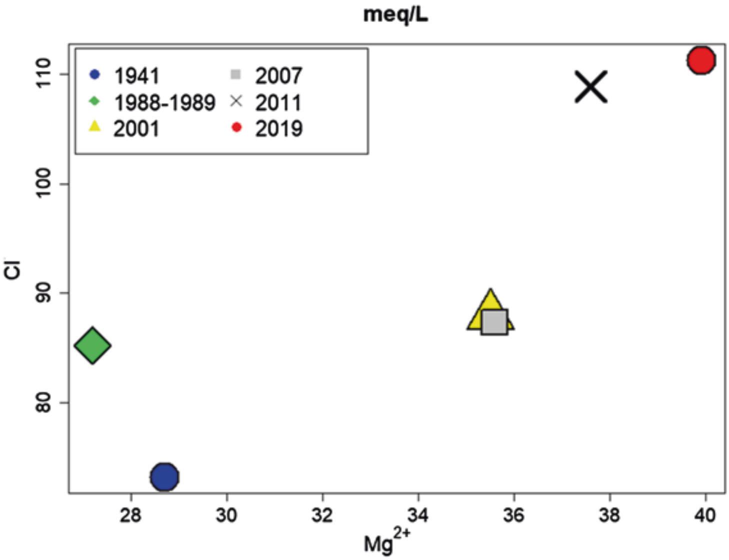

Fig. 5.4 Chloride *versus* magnesium plot (meq/L). References for years and sampling sites in Table 5.2

microendemisms, which exclusively live in the lake. They are very well adapted to the current conditions of Lake Alchichica. However, they could get extinguished if the hydrochemistry were to change substantially in the short term (see Chap. 21, Conservation actions).

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Chapter 6
Meteorological Regime, Local Climate, and Hydrodynamics of Lake Alchichica

Anatoliy Filonov, Irina Tereshchenko, Maria del Refugio Barba-Lopez, Javier Alcocer, and Lydia Ladah

6.1 Introduction

Wind-forced internal motions in temperate stratified lakes have been previously studied and modeled (e.g., Imberger 1985; Monismith 1985). The resultant mixing that occurs when they break has been essential for biological and ecological processes. Unfortunately, there are relatively few studies on wind-forced internal wave mixing for tropical lakes, particularly at high altitudes. Serrano et al. (2002) report on the physical processes associated with the mountain breeze in Santa Maria del Oro, Nayarit, Mexico, a tropical, volcanic lake at 750 m a.s.l. However, there is generally little know about the dynamics of the unique ecosystems of high-altitude tropical lakes.

Lake Alchichica is a volcanic lake on the Mexican plateau, with a circular form, abrupt coastal slopes, a diameter of 1.7 km, and a maximum depth of 62 m (Fig. 6.1).

A. Filonov (✉) · I. Tereshchenko
Department of Physics, University of Guadalajara, Guadalajara, Jalisco, Mexico
e-mail: anatoliy.filonov@cucei.udg.mx; irina.tereshchenko@cucei.udg.mx

M. del Refugio Barba-Lopez
Programa de Posgrado en Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México, Ciudad de México, Mexico
e-mail: marybarba90312@gmail.com

J. Alcocer
Grupo de Investigación en Limnología Tropical, FES Iztacala, Universidad Nacional Autónoma de México, Tlalnepantla, Estado de México, Mexico
e-mail: jalcocer@unam.mx

L. Ladah
Department of Biological Oceanography, CICESE, Centro de Investigación Científica y Educación Superior de Ensenada, Ensenada, BC, Mexico
e-mail: lladah@cicese.mx

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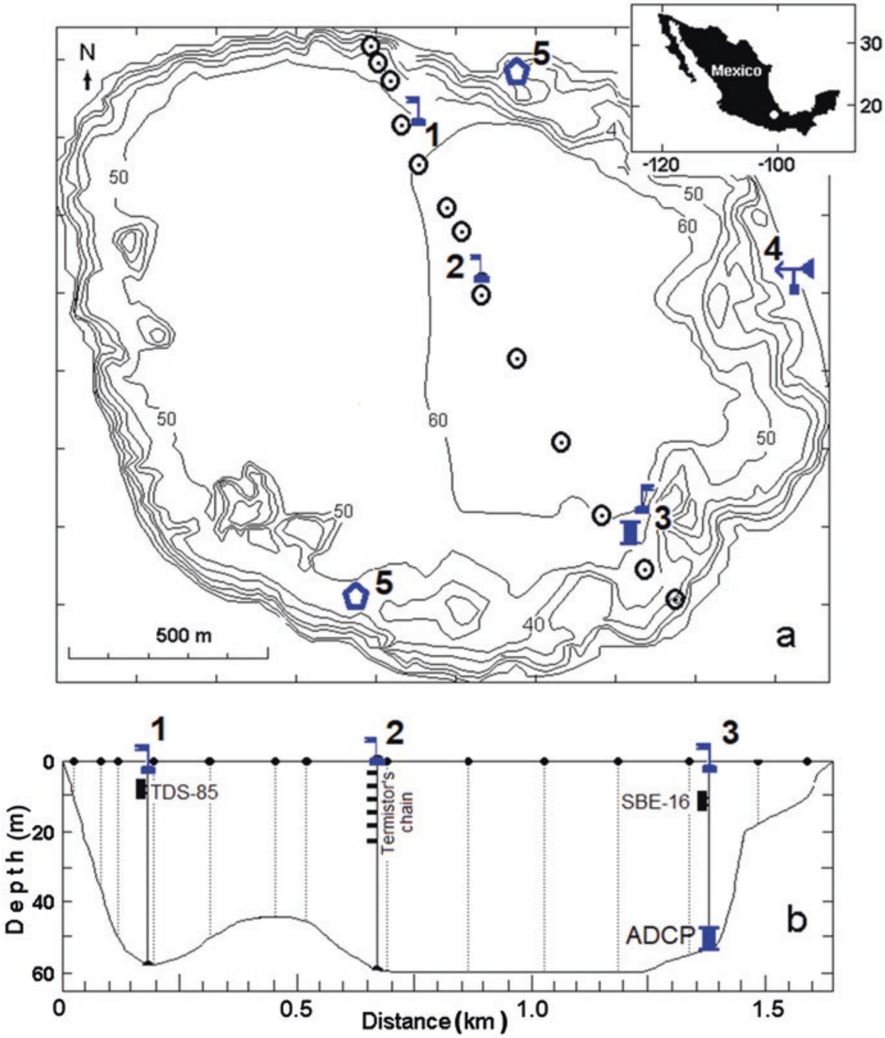

Fig. 6.1 Geographic location and bathymetric chart of Lake Alchichica (a). The numbers show the position of moorings with thermograph TDS-85 (1), the thermograph chain with HOBO-V2 loggers (2), the thermograph Seabird SBE-16 and ADCP (3), the meteorological station (4), and the two water-level meters SBE-26 installed to record seiche oscillations in the lake (5). The circles show the position of the vertical profile casts during the five surveys carried out on May 5, 2002

Water column temperature profiles show the lake is well stratified throughout most of the year. During summer and autumn, there are significant variations in the thickness of the upper homogeneous layer (i.e., mixed layer), the depth of the thermocline, and the vertical gradients in the lake. In August and September, the thermocline's maximum vertical gradients can exceed 1 °C/m in a water layer

20–30 meters deep. However, in the winter, from December to March, the thermocline essentially disappears due to vertical mixing (Filonov and Alcocer 2002).

Alchichica has an arid climate with an average annual rainfall of 398.33 mm/year and evaporation of 1650 mm/year. The climatological records indicate that the average temperature of the area ranges between 13.52 ° C and 5.37 °C (http://clicom-mex.cicese.mx).

The lake's stable density stratification is defined by the temperature decrease with depth from 19.5 °C on the surface to up to 14.7 °C near the bottom. The thermocline and the maximum buoyancy frequency of 20 cycle/h occur between 10 and 18 m depth, whereas the buoyancy frequency in the deeper layers decreases to 1 cycle/h (see Sect. 6.4.2.2 Stratification).

Hourly meteorological measurements taken at the height of 4 m on the lake's Eastern coast show that mountain breeze circulation in Alchichica prevails and plays an important role in the lake's dynamics. The breeze is more intense in the lake area during the dry season than in the wet season (Filonov and Alcocer 2002). As a sharp thermocline enhances the formation of internal waves, lakes with sustained stratification tend to always show internal motions generated by pressure changes and wind on the lake surface (Saggio 1998; Thorpe 1998; Filonov et al. 2015).

6.1.1 Hydrodynamic Modeling in Lake Alchichica

Hydrodynamic modeling and measurements of Lake Alchichica began in 2002. The most comprehensive studies were carried out in 2004 (Filonov et al. 2006, 2015). Available measurements include water-column temperature and salinity using a CTD profiler from five repeating transects (from north to south), three thermograph moorings with currents available from a bottom-mounted ADCP, and meteorological parameters at an automatic weather station installed on the eastern bank.

6.2 Local Climatology

According to the analysis of the CLICOM database of the SMN through its CICESE web platform (http://clicom-mex.cicese.mx), for the 21052-ALCHICHICA, PUE (−97.4 W, 19.4 N, Elev: 2343.0 m) station, the mean temperature in the study area was 13.52 ° C with a minimum average temperature of 5.37 °C and a maximum average temperature of 21.67 °C.

The lowest temperatures occur from November to January, while the highest were recorded from April to June. The average annual precipitation was 398.3 mm/year, while the average annual evaporation was 1650 mm/year. The daily average temperature oscillated between 1 °C and 21.75 °C, with the daily maximum between 4° and 38 °C and the daily minimum between −15 °C and 14 °C. Precipitation throughout the measurement period had a maximum daily value of 130 mm. The

Table 6.1 Dates of the record maximum (Max) and minimum (Min) values of the average (Avg), maximum and minimum environmental temperature (T), as well as precipitation (PP) and evaporation (Evap) in Alchichica (period 1965–2015). (-- = several dates)

Parameter	Max	Max recorded date	Min	Min recorded date
Avg T	21.75 °C	03-04-1980	1 °C	25-01-1988
Max T	38 °C	13-03-1988	4 °C	22-02-1976
Min T	14 °C	15-05-1980	−15 °C	17-11-1970
PP	230 mm	31-08-1969	0 mm	--
Evap	13.89 mm	14-02-2007	0.06	22-02-2009

maximum daily evaporation was 13.89 mm, and the minimum was 0.06 mm (Table 6.1).

Figure 6.2 shows the climatic behavior of (**a**) average temperature, (**b**) power spectrum associated with the time series of average temperature, (**c**) maximum and (**d**) minimum temperature, as well as (**e**) precipitation and (**f**) evaporation 21052 Alchichica station (−97.4 W, 19.4 N, Elev: 2343.0 m) at the Alchichica station during the years 1965–2015. The figures were constructed using monthly averages of the daily averages reported in the CLICOM database (http://clicom-mex.cicese.mx). All the meteorological variables analyzed present a clear annual oscillation.

The average monthly temperature (Fig. 6.2) varied between 7.5 °C and 18 °C, with values almost always greater than 15 °C. The mean temperature spectral analysis showed only one significant peak (above 80% of the confidence level) corresponding to a frequency of 4.2 years (Fig. 6.2). The maximum temperature (Fig. 6.2) ranged between 16.5 °C and 30 °C and the minimum between −3 °C and 11.6 °C (Fig. 6.2). A trend of increasing temperature can be noted (Fig. 6.2) during the years 1970–2000, followed by a decrease from 2000 to 2015. There was no marked trend in the annual average values for precipitation, although lower values can be noted in 1982–1985. The annual average evaporation was similar to the average temperature, with a slight tendency to increase from 1980 to 1997 followed by a decrease from 2005 onwards.

Rainfall occurred between May and October, with the wettest months being June and September with 76.3 mm and 74.24 mm, respectively. The driest months were December (4.18 mm) and January (6.71 mm), with a cumulative total of 404.81 mm/year. Throughout the year, the temperature was above 10 °C, with the lowest value in January (10.03 °C) and the highest in May (16.01 °C) (Table 6.2). Dry months correspond from November to March (Fig. 6.3).

6.2.1 *Variability from One Hour to a Day (2002–2005)*

The scale of variability of hydrometeorological characteristics in the lake area can include fluctuations with periods from ten minutes to one day. The primary energy source driving these changes is the daily variation of temperatures caused by a

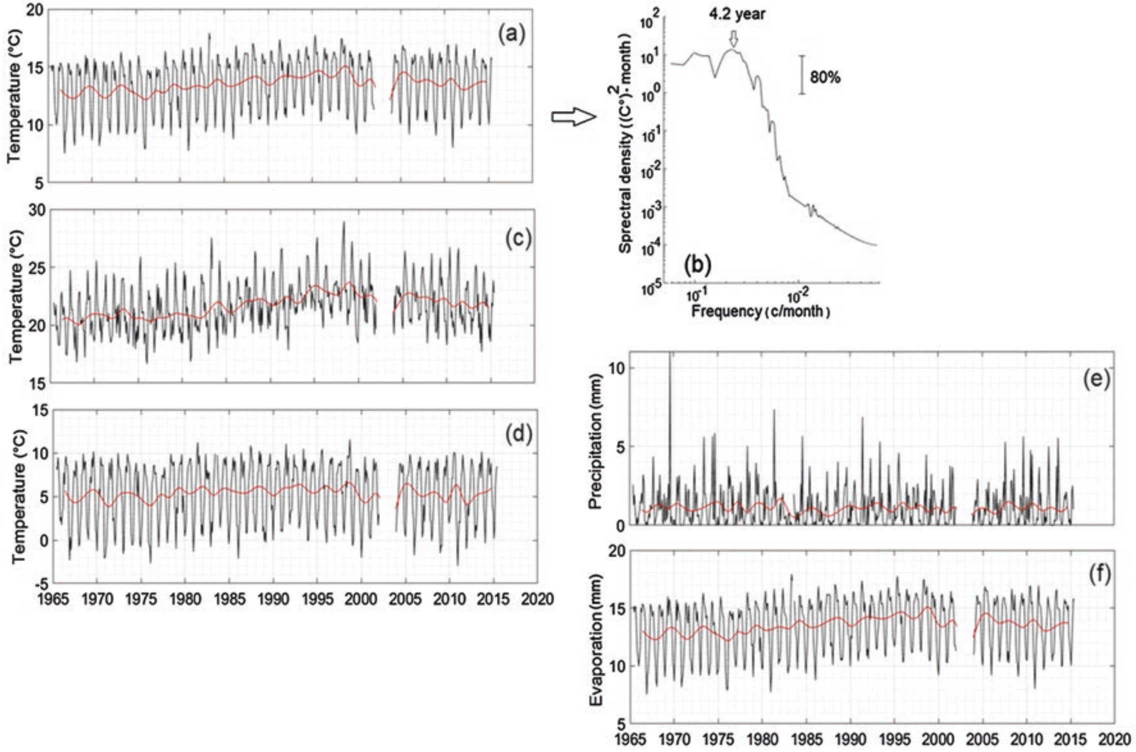

Fig. 6.2 Climatological parameters at 21052- Alchichica weather station (1965–2015). (**a**) Mean temperature, (**b**) mean temperature spectrum, (**c**) maximum temperature, (**d**) minimum temperature, (**e**) precipitation, and (**f**) evaporation. The red lines indicate the annual average values for (a), (c), (d), (e), and (f)

Table 6.2 Monthly average (Avg) values of temperature (T) and precipitation (PP) in Alchichica (1965–2015)

Avg	**Jan**	**Feb**	**Mar**	**Apr**	**May**	**Jun**
T (°C)	10.03	11.27	13.41	15.31	16.01	15.74
PP (mm)	6.71	9.92	12.37	32.18	41.7	76.31
Avg	**Jul**	**Aug**	**Sep**	**Oct**	**Nov**	**Dec**
T (°C)	15.09	15.15	14.85	13.41	11.52	10.47
PP (mm)	53.49	58.32	74.24	28.35	7.04	4.18

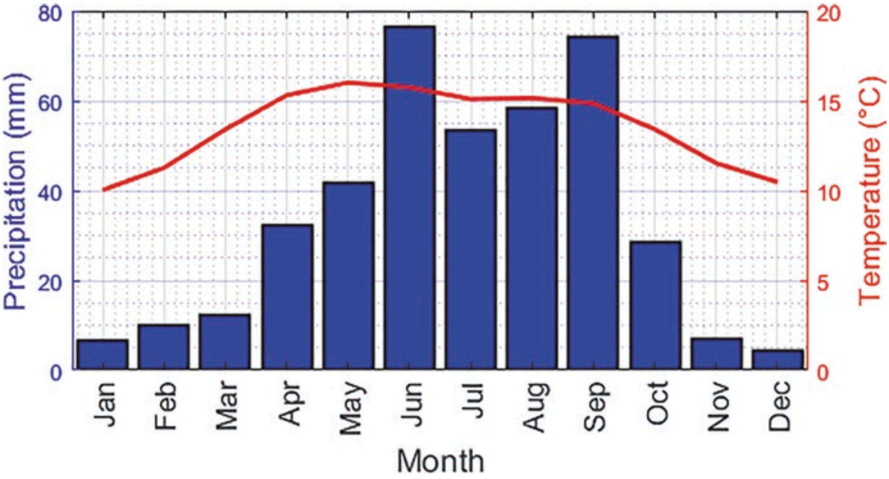

Fig. 6.3 Climogram for 21052- Alchichica station (1965–2015)

change in heat flow to the earth's surface and atmosphere during the day. The energy interaction of the soil-lake-atmosphere system is complex. The area around the lake is mountainous, with valleys of different spatial orientations. Thermal energy patterns were complex and redistributed through oscillations over a wide frequency range (Scorer 1978; Filonov et al. 2015).

On average, the temperature reached its maximum at 15:00 hr., lagging in phase from the maximum solar radiation by almost 2 hours. For over two and a half years of observations "*in situ*," the maximum temperature was recorded at 28.8°C and the minimum −10.0 °C. The maximum inflow of solar radiation was equal to 1188 W/m^2. The distribution of air temperature and solar radiation varied greatly over time and depended on weather conditions in the lake area (Fig. 6.4), particularly on wind and cloud cover.

The climate around the lake is typical for the Mexican mesa. Air humidity in the dry season decreased to 20–-30%, and during the humid season, it fluctuated between 90% and 100%. Precipitation is not very intense and occurred from May to October. The daily maximum is usually no more than 10 mm, although, on some days, it can exceed 20 mm per day (Fig. 6.4). The maximum precipitation is observed in June, about 200 mm, and in early September, more than 220 mm.

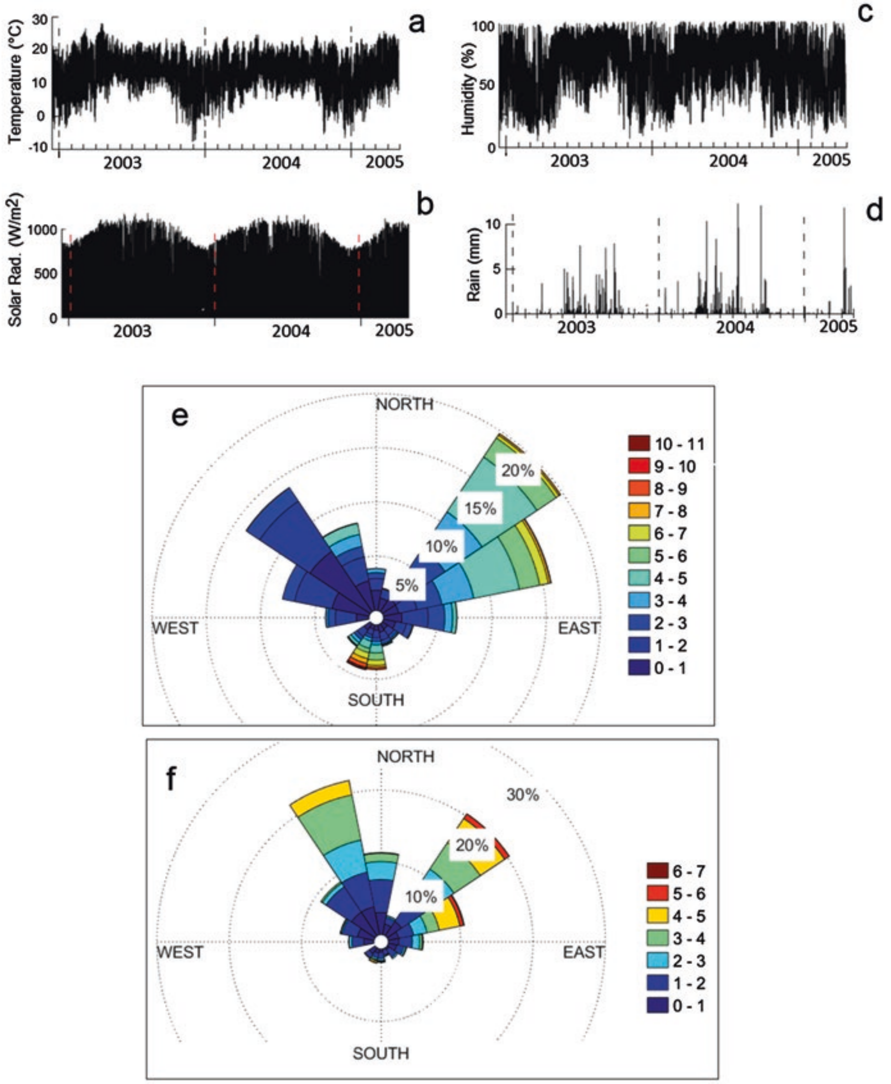

Fig. 6.4 (**a**) Hourly average fluctuation of air temperature, (**b**) solar radiation, (**c**) relative humidity, (**d**) rain, (**e**) wind speed, and (**f**) direction where the wind is blowing (north direction matches the vertical axis of the figure) for the dry (e) and wet (f) seasons in a year

Winds around the lake are weak. Daily fluctuations in wind speed in the lake area are caused by breeze circulation. During the dry season, during the day, the wind usually had a northeast direction, and its speed reached a maximum of 6–7 m/s. On some days, it reached 11 m/s. At night the wind direction changes to the northwest, and its speed is significantly weakened and does not exceed 2–3 m/s (Fig. 6.4). Due to the moisture of the underlying surface in the rainy season and, therefore, the weakened horizontal pressure gradients, the wind is much weaker. However, it rarely changed its daily variation. On average, its speed at night did not exceed 1–2 m/s, and during the day, it is usually 4–5 m/s, with a maximum on some days up to 6–7 m/s (Fig. 6.4).

6.2.2 Synoptic Variability

Spectral analysis of meteorological variables showed that only the peaks of daily fluctuations and their high-frequency overtones predominate in the spectra. For periods from 2 to 21 days, the spectra had a "sawtooth" shape due to the many low peaks with no single dominant peak in spectral density (Fig. 6.5), suggesting that the oscillations in this range do not repeat with the same periods (do not have a certain rhythm). Therefore, the spectral density is "smeared" over the spectrum. All peaks are below the 95% confidence level, are equally likely, and could not be further analyzed.

The variability of meteorological parameters at an altitude of more than 2000 m above sea level in mountainous areas is very complex. The Alchichica lake is located in Mexico, approximately 110 km from the Gulf of Mexico and about 800 km from

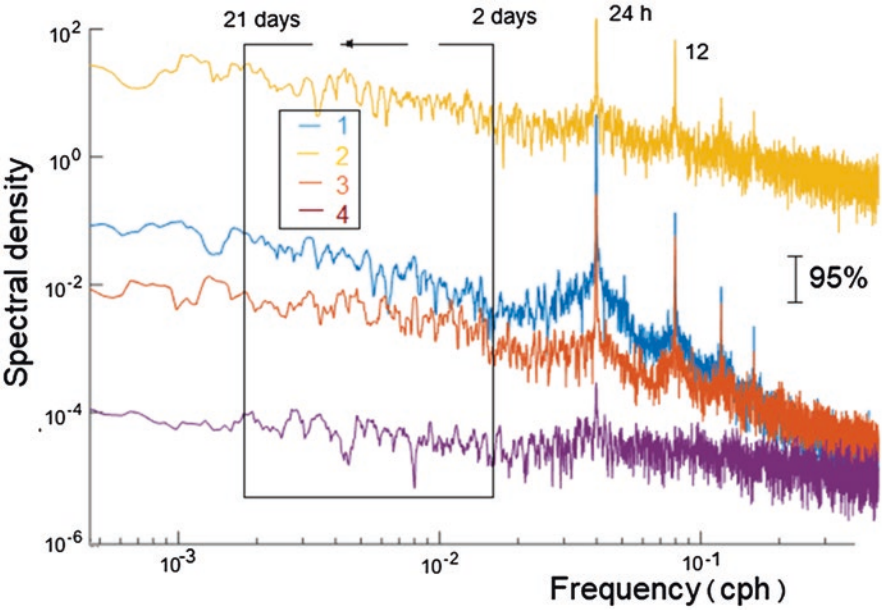

Fig. 6.5 Spectra of meteorological characteristics measured at the meteorological station from UNAM in 2001–2004: 1) air temperature, 2) solar radiation, 3) wind speed, and 4) wind direction (sampling interval 1 h)

the Pacific coast. Synoptic variability is smoothed here and is much weaker in intensity than the local breeze circulation.

6.2.3 Seasonal Variability

Seasonal variability in the lake area is caused by the presence in Mexico of two main tropical seasons of the year: a wet season from June to October and a dry season, or rather a season with low precipitation from November to May (Scorer 1978; Filonov et al. 2015). During this second season, the entrance of cold north winds to the Mexican territory occurs when cold fronts known as "Nortes" are formed, colliding with warmer air masses, generating winter rains and significant temperature drops (Alcocer 2019).

The variability between the wet and dry seasons is well expressed in all meteorological characteristics (Fig. 6.2). In air temperature, the difference between the two main seasons is better expressed in the afternoon and reaches 10 °C. The wind speed reaches, on average, a maximum of 6 m/s at 16:30 hrs. in the dry season, and in the wet season, the maximum wind speed is below 3 m/s at 18:30 hrs. (Fig. 6.4). However, in September–October in the afternoon, wind speed can reach 5–6 and even more than 8 m/s (30 km/h).

6.2.4 Interannual Variability

In 2002–2003, a moderate El Niño was observed in the eastern part of the Pacific Ocean (https://ggweather.com/ensooni.htm), which was noticeable for the following two years. During the El-Niño years, there is an increase in frontal activity in this area of the Mexican territory. Magaña et al. (2003) published a wind circulation map for a level of 500 millibars, which corresponds to an approximate altitude of 5500 meters. It shows a west-east transport up to 12–14 m/s in the winter months during the El Niño year over central Mexico's territory. Figure 6.2 shows the spectrum of the average temperature in Alchichica during 1965–2015 with a high spectral density peak corresponding to the frequency of 4.2 years which might be associated with El Niño frequency and is primarily manifested in the temperature and wind fields, and also causes intense cloudiness and precipitation.

6.2.5 The Effect of Rain on Lake Stratification

Alchichica is located in the central part of Mexico, on the high plateau “Los Llanos de San Juan” at an altitude of 2300 m above sea level. The climate is arid, with an annual rainfall of 398.3 mm and annual evaporation of 1650 mm (http://clicom-mex.cicese.mx).

Alcocer and Filonov (2007) reported disruption of the water column due to heavy rains in Alchichica. In one day, due to heavy rains, 1,810,000 m^3 of water drained into the basin, raising the water level in the lake by about 1 meter. The temperature and salinity profiles showed an atypical temperature inversion up to 1 °C in the upper layer, accompanied by a decrease in salinity to 0.5 g/L. The clarity and pH were slightly changed, but the dissolved oxygen, nutrients, and chlorophyll concentration did not change. Despite heavy rains and associated winds, the event’s consequences were limited to the upper half of the epilimnion. After two days, the water level in the lake returned to its original level. Rapid drainage of wastewater minimizes any long-term effects of heavy rainfall.

6.3 Bathymetry and Morphology

The current bathymetric and morphometric surveys update previous reports (e.g., Arredondo-Figueroa et al. 1983; Kaźmierczak et al. 2011). Detailed bathymetric surveys were carried out using a Lowrance Model LMS-480 M 200 kHz echo sounder. The new bathymetric maps have a spatial resolution of 22.7 × 22.7 m (Fig. 6.6) and allowed for the accurate calculation of the lake’s volume and area and applying numerical hydrodynamic models. The lake is deep 64 m maximum depth, 48.4 m mean depth), bucket-shaped with steep slopes; for example, a 1 m change in the lake’s water level would not change the surface area of the lake significantly, while the volume would change by only 2% (Fig. 6.7).

The shoreline development of the lake, the ratio of the length of the shoreline to the length of the circumference of a circle area equal to that of the lake, is 1.1 (the shoreline development of a perfect circle is 1.0); this means the lake is approximately circular with a surface area of 2.367 km^2. The maximum length is 1902 m, and the maximum width is 1546 m, with a shoreline of 5.84 km and a volume of 114,688,900 m^3 (Table 6.3).

The relative depth of Lake Alchichica is 3.63%; this is the maximum depth expressed as a percentage of the mean diameter. This large percentage, characteristic of relatively deep lakes with small surface areas, promotes great water column stability. The volume development is a measure of the lake basin’s departure from that of a cone calculated using the maximum depth and the average depth. The volume development is usually >0.33 (a conical depression), but in Lake Alchichica, it reaches 0.8 displaying a proportional large and extended flat bottom standard in many calderas, grabens, and fjord lakes.

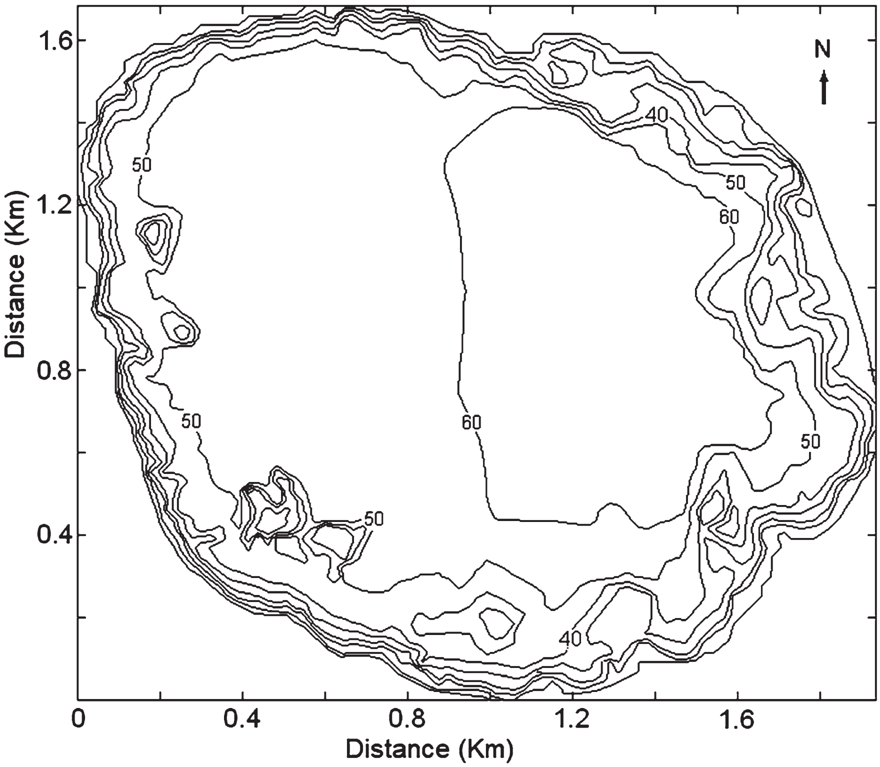

Fig. 6.6 Bathymetric map of Lake Alchichica. (Isobaths in meters)

6.4 Hydrodynamics (Measurements and Modeling)

6.4.1 Lake Level and Current Fluctuations

Analysis of a multiple-year time series of meteorological observations on the lake showed that mountain winds are relatively constant from day to day in the lake area. Lake Alchichica lies in a volcanic crater in the mouth of a wide mountain valley that extends north to south with slopes as high as 300–500 m. To the north, there is an extensive saline plain spanning nearly 200 km^2. These topographic features provide suitable conditions for local atmospheric circulation between the mountain and the saline valley over the lake's entire length.

During the day, temperature differences between the saline valley and the central zone create a reverse pressure gradient. As a result, the wind is directed upwards along the main slopes from the north. The wind's daily course over the lake dictates daily fluctuations in the air temperature and atmospheric pressure (Fig. 6.8).

From 22:00 until 13:00 hours, the weak wind above the lake does not exceed 1 m/s. Its speed grows quickly during the afternoon and reaches an average hourly

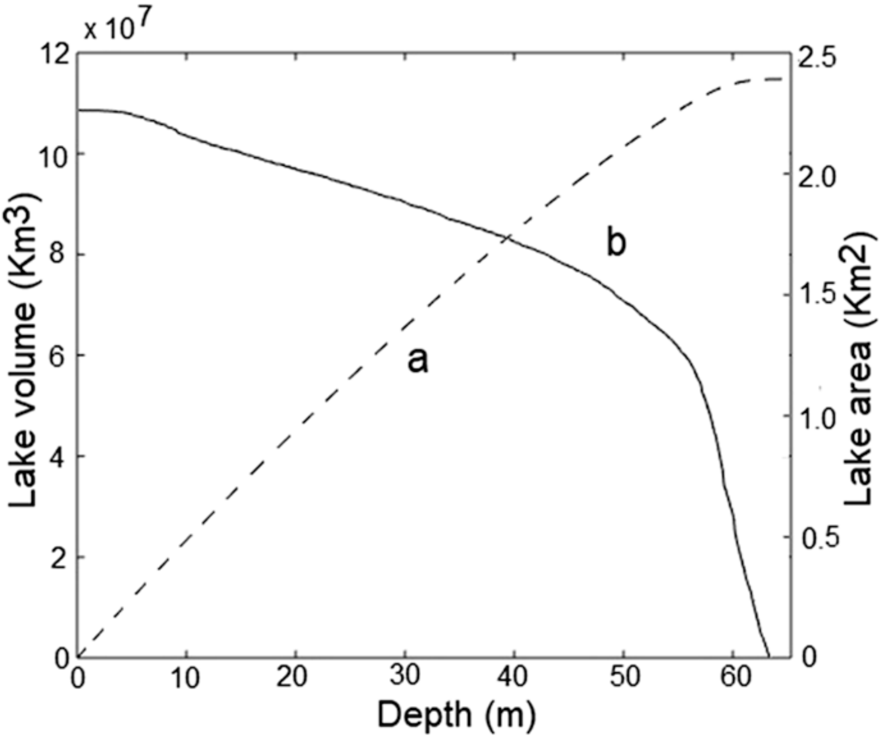

Fig. 6.7 Curves of accumulative volume (**a**) and hypsographic -area versus depth- (**b**) of Lake Alchichica. (The calculations were conducted according to the bathymetric matrix with a step of 22.7 × 22.7 m in the horizontal and 0.1 m in the vertical)

Table 6.3 Main morphometric parameters of Lake Alchichica

Maximum length	1902 m	Relative depth	3.63%
Maximum width	1586 m	Volume	114,688,900 m^3
Area	2.367 km^2	Shoreline	5840 m
Maximum depth	64 m	Shoreline development	1.1
Mean depth	48.4 m	Volume development	0.8

speed of 5–6 m/s with pulses up to 10–12 m/s at approximately 17:00 hours (see in the upper right corner of Fig. 6.8). Near 22:00 hours, the wind begins to return to nocturnal typical low values rapidly. Throughout the day, the wind's direction varies insignificantly and remains within the N-NNW range and presents a non-daily clockwise rotation, typical for a breeze on such large Mexican lakes as Chapala (Filonov 2002).

The analysis of low-frequency time series from the SBE-26 shows that diurnal and weaker semidiurnal harmonics define the water level in the lake's daily course. The measured water level fluctuations coincide with the breeze's strengthening and

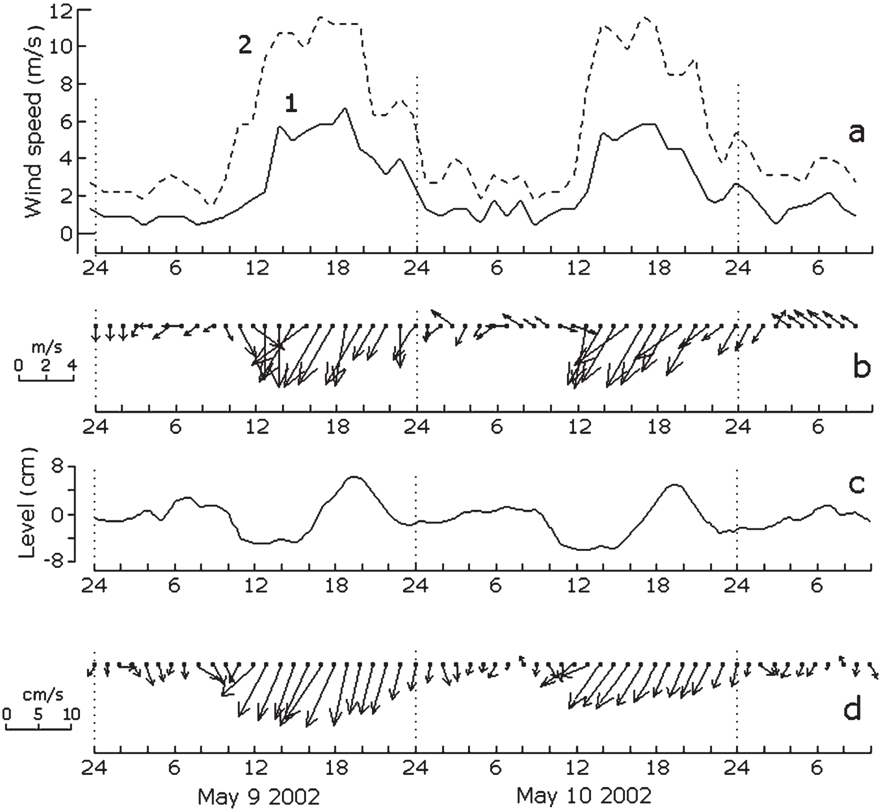

Fig. 6.8 (**a**) Fluctuations of the hourly mean (line 1) and hourly maximum wind velocity (line 2) on May 9–10, 2002. (**b**) Hourly average wind speed vector. (**c**) The low-frequency level fluctuations as measured by an SBE-26 (average value is removed). (**d**) Hourly average current speed vector (in a layer of 0–30 m) in a point of ADCP location

weakening (Fig. 6.8). From 11:00 the water level drops by almost 4 cm and does not change until 16:00, when a slow rise of about 7 cm begins. Water level reaches its daily maximum at 19:00 hours, falls to a zero by 23:00 hours, and gradually rises to 2 cm at 7:00 hours before repeating its daily course. The time shift between the moments of the beginning of wind intensification and the water level change in the lake's northern point takes less than two hours. The rising and lowering of water levels are asymmetrical. The low level is maintained longer than its high position, and this is caused by the dissymmetric time influence of wind on the water surface. Measurements with a high-precision SBE-26 tide guide showed that during the day at the observation point (19°24.44' N, 97°24.34' W), under the influence of a breeze, the lake level fluctuated ±10 cm.

Figure 6.9 shows the average spectrum of time series of high-frequency water level variations (sampling rate of 1 s) with a section shown in Fig. 6.9. The spectrum illustrates that free seiches with periods of 2.7 and 2.1 minutes are present in the

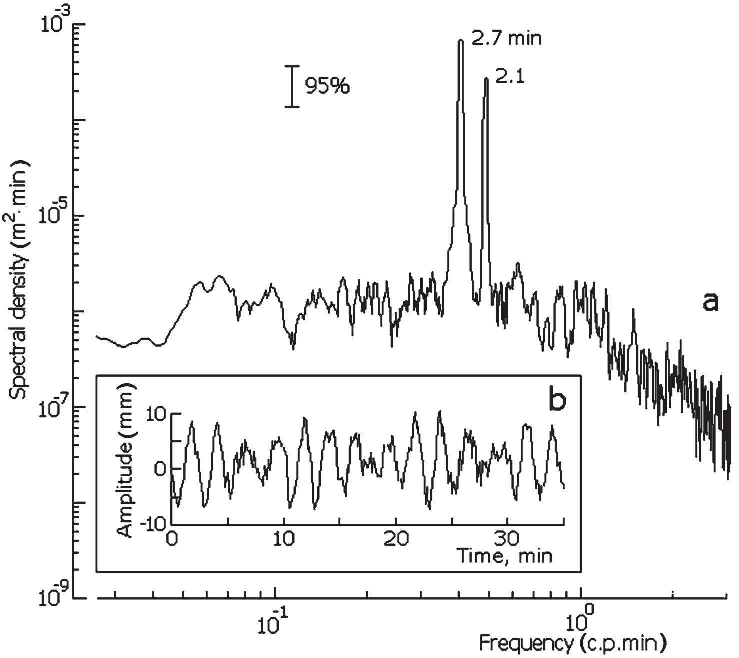

Fig. 6.9 (**a**) Mean spectra of the lake water level fluctuations in the band frequency from 0.01 to 3 cycle/min. (**b**) The height frequency water level fluctuation measured by the SBE-26. The vertical line indicates the 95% confidence interval (Filonov et al. 2006)

lake. Their average mean squared amplitudes equal 7.4 and 4.1 mm, respectively. As the lake is shaped like an ellipse with different axes' sizes, fluctuations with a period of 2.7 minutes likely correspond to seiches extending along the lake's greater axis. The second fluctuation can be related to seiches moving along its shorter axis.

The Merian equation (LeBlond and Mysak 1978) was used to evaluate the two seiches' theoretical periods. The period of water level oscillations for the first mode is given by $\tau = 2L / \sqrt{g \cdot H}$, where H is the depth average and L the length of the lake. Using a length of 1846 m and an average depth of 46.2 m for the first wave along the greater axis and a 1540 m length and an average depth of 51 m for the second wave, we obtained 2.9 and 2.3 minutes periods. These results closely match those obtained by the measurements.

As shown in Fig. 6.10, the wind direction over the lake remains almost unchanged for the dry and wet seasons, yet the average wind speed reduces almost half during the wet season. Due to the constant wind direction, the average vertical currents in the lake in the daytime reach 15 cm/s and do not change their direction during the day. They decrease to 1–3 cm/s and even to zero in some areas of the lake at night. In the eastern part of the lake, the currents form an anticyclonic gyre pressed to the shore with a diameter of about 250 m with maximum currents close to the shoreline in the southern part of the lake, where a weaker elliptical cyclonic gyre is formed with currents of no more than 5 cm/s.

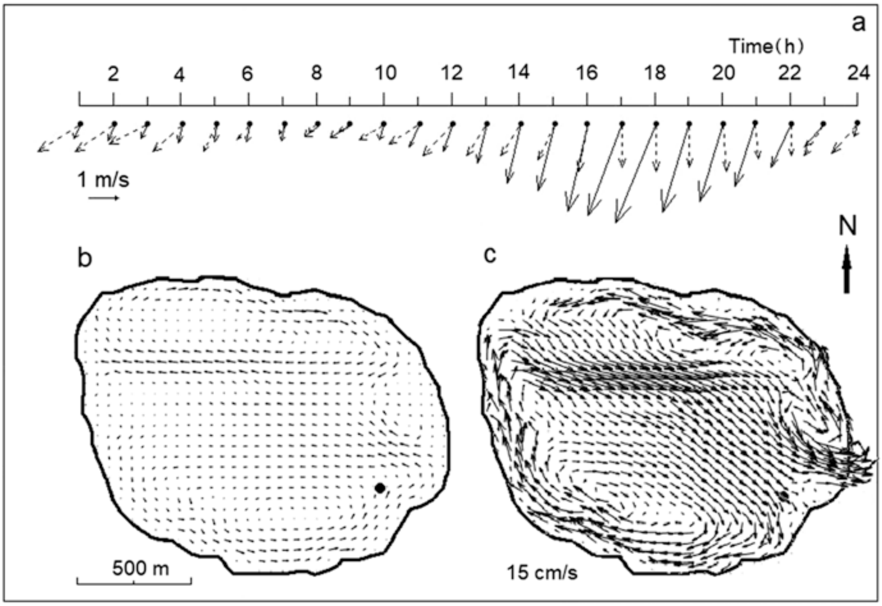

Fig. 6.10 (**a**) Wind speed vectors (north direction matches the vertical axis of the figure) for the dry (line 1) and wet (line 2) seasons in a year. Transport fields in Lake Alchichica, forced by wind circulation (dry season) (**b**) for 9:00 h and (**c**) for 17:00 h. Black circles show the position of the ADCP in the lake

An ordered system of almost constant currents is formed in the lake under the breeze's influence, represented by two circulating ellipses, separated by a flow directed from the west to the southeast. The most significant currents in these circulation structures occur along with the western (clockwise circulation) and the lake's eastern (counterclockwise) shores.

6.4.2 Internal Waves in the Lake

Fluctuations of Water Along the Line of Hydrological Survey

An experiment to measure internal waves was carried out from May 8–11, 2002. The temperature fluctuations were measured by three mooring instruments (Fig. 6.1). Mooring 1 was equipped with a temperature meter TDS-85 at horizon 8 m, with a measuring precision of 0.02 °C. Mooring 2 was equipped with a chain of Waterpro thermistors (Onset Computers Corp., Massachusetts, USA) deployed at depths of 1, 5, 10, 15, 20, and 25 m with a 0.2 °C resolution. On this mooring, the temperature was measured hourly for three months (from March 24 to May 20, 2002). Mooring 3 was equipped with a conductivity-temperature-depth (CTD) meter SBE-16 (made by Sea-Bird Electronics) at horizon 12.5.

Five temperature surveys were done on a transect between moorings, approximately at a 30-degree angle from the average wind direction (Fig. 6.1). Each survey lasted about one hour. During each survey, a CTD profiler SBE-19 was deployed manually from the boat with a speed of about 1 m/s and a 0.5-second sampling rate. A Global Position System (GPS) fixed the coordinates of the sounding points.

An Acoustic Doppler Current Profiler (600 kHz ADCP, RD-Instruments) was placed at the bottom, measuring through the water column. For 2.6 days, it measured the vertical profile of three current speed components with a vertical resolution of 1 m (Fig. 6.1). The sampling rate was 0.5 minutes.

The acquired data were analyzed using unified standard methods and spectral analysis techniques (Jenkins and Watts 1969). To calculate two-dimensional spectra for temperature, wind, and water current fluctuations, we followed the methods described in Konyaev (1990).

The following algorithm was used to calculate the water layers' vertical deviations on data of temperature sections (Filonov and Konyaev 2003). All vertical temperature-pressure profiles $T_j(p_j)$ were interpolated onto a single depth grid $T_j(z)$, and the mean temperature profile was computed as: $T(z) = \frac{1}{J}\sum_j T_j(z)$, where $j = 1{:}J$ is the profile index. The mean profile $T(z)$ describes the unperturbed position of water layers. The inverse functions $z_j(T)$ and $z(T)$ exist if the original profiles $T_j(z)$ and the mean profile T(z) are monotone functions.

Vertical deviations of water layers from the unperturbed position were defined as $\Delta h_j(T) = z(T)\text{-}z_j(T)$. The temperature was then replaced with depth using the mean profile $z(T)$ to give the relationship between deviation and depth $\Delta h_j(z)$. The layer position was then obtained as $h_j(z) = z\text{-}\Delta h_j(z)$.

Each sounding consisted of two temperature profiles $T_{dj}(z)$ and $T_{uj}(z)$, which correspond to the profiler's descending and ascending track. The difference between these profiles $dh_j(T) = z_{uj}(T)\text{-}z_{dj}(T)$ is accounted for by rapid (small-scale) disturbances of water layers. Temperature T was then replaced with depth z with the mean profile $z(T)$ to give the $dh_j(z)$ difference. It was then normalized by $\Delta t_j(z)$, which is the time interval between the observations made on downward and upward sounding profiles: $w_j(z) = dh_j(z)/\Delta t_j(z)$. The normalized difference has the units of velocity. However, this vertical velocity is accounted for not only by the vertical motion of layers but by their horizontal advection as well.

Figure 6.11 shows typical vertical profiles with sharp vertical temperature jumps in the 0–20 m layer and the formation of homogeneous layers, indicating strong mixing caused by overturning internal waves. The largest inversion was recorded on the fourth survey on 05/10/02 when a homogeneous temperature layer with a thickness of almost 10 m (depths 4–14 m) was formed. On the same day, on the fifth survey in the thermocline at a depth of 10 m, a jump in temperature was observed in the form of a step with a gradient of almost 1°C /0.2 m.

It was necessary to perform the following procedure to determine the parameters of the lake's internal waves according to hydrological survey data during their

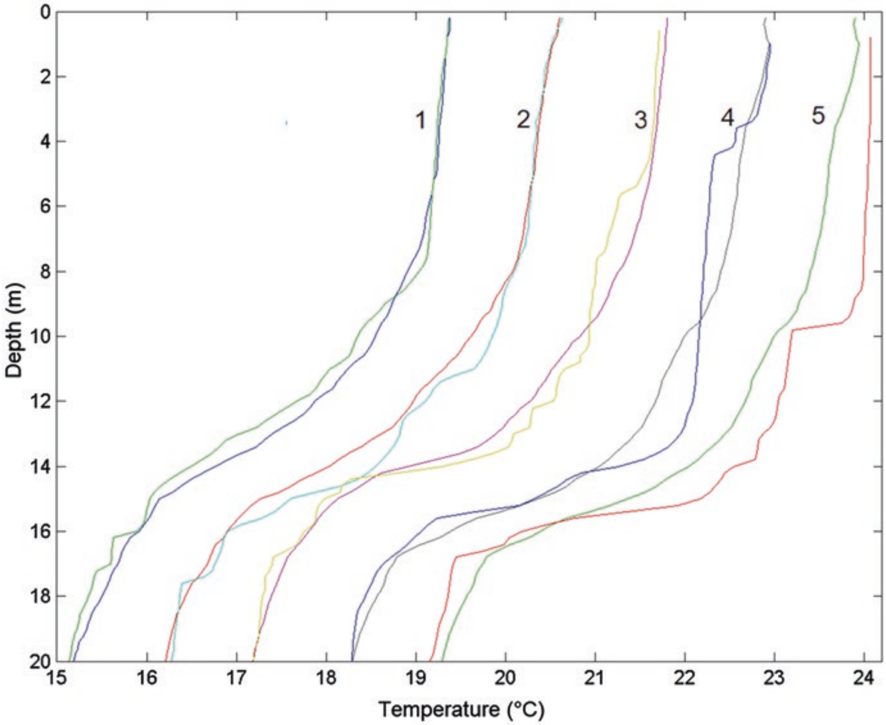

Fig. 6.11 Characteristic vertical temperature profiles with mean profiles (smoother curves) for each survey. The profiles are displaced sequentially by 1 °C relative to profile 1. Arabic numerals indicate the numbers of five surveys conducted on May 10, 2003

processing. A detailed description of these procedures can be found in (Filonov and Konyaev 2003).

- Elimination of inversions of temperature and salinity profiles
- Data interpolation in a single depth scale
- Calculation of average vertical profiles of temperature, salinity, density, and buoyancy frequency
- The transition from temperature profile to pressure profile using an average temperature profile
- Calculation of pressure deviations (vertical deviations of water layers).

Stratification

Long-term measurement of the thermistor chain in the center of the lake (mooring 3) showed that due to the large water transparency (euphotic zone 14–38 m) and the action of wind and internal waves, daily solar warming penetrates to a depth of about 10 m. The total heat influx was small as the rapid increase in the top layer's

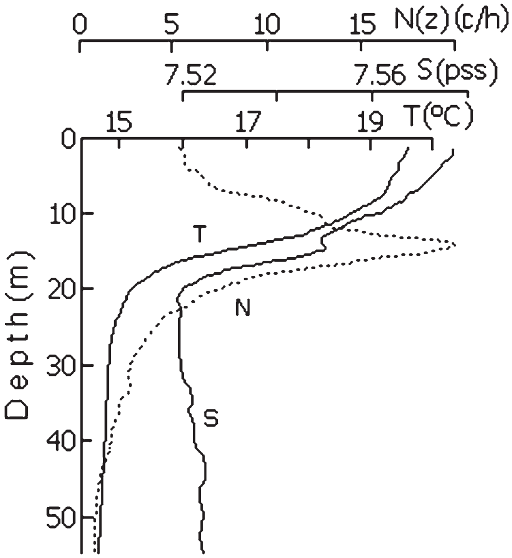

Fig. 6.12 Mean vertical profiles of temperature (T), salinity (S) and buoyancy (N) frequency (data from five repetitive profiles, a total of 48 casts)

temperature in the first half of the day was offset by a similarly swift downturn during the second half of the day. Wide variability in daily air temperature is important for heat absorption and emission in a high-mountain tropical plateau. Wind waves on the lake are small (length 5–7 m and height less than 0.5 m), and they create mixing that does not likely penetrate deeper than a few meters. At midday, the surface temperature decreases slightly with the onset of the breeze.

During the experiment, the lake's density stratification was defined by the temperature decrease with depth from 19.5 °C at the surface to up to 14.7 °C near the bottom. Salinity decreased insignificantly from 7.58 psu at the surface to 7.52 psu at the bottom (Fig. 6.12). Thus, the vertical change in water density is completely determined by temperature. The thermocline with the maximal buoyancy frequency $N(z) = [(g/\rho) \cdot (\partial\rho/\partial z)]^{1/2}$ of 20 cycle/h occurs between 10 and 18 m. The buoyancy frequency in the deep layers decreases to 1 cycle/h.

Temperature Fluctuations in Two Separate Points (Moorings 1 and 2)

Mooring instruments 1 and 3 were located at different depths. On mooring 1, the TDS-85 thermograph was at a depth of 8 m, and the SBE-16 thermograph on mooring 2 was at 12.5 m (Fig. 6.1). Despite the difference in the two devices' depth, the average temperature measured by both was identical and equal to 18.9 °C. Hence, on average, under the action of the wind, the thermocline is sloped. In the northern part of the lake (mooring 1), the thermocline shoaled around 4.5 m concerning the southern part (mooring 3). The towing of the temperature gauge on a line between moorings, during the maximal wind speed (after midday), shows that the water temperature at a depth of 0.2 m increases uniformly from 19.3 °C near mooring 1 to up to 20.2 °C near mooring 3.

The water layers' fluctuations at the moorings have large amplitudes with the predominance of diurnal and semidiurnal oscillations. There are groups of bursts of up to 3 m high (Fig. 6.13). The vertical water layer deviations were determined at the depths where the thermographs were deployed using the temperature fluctuations at each mooring and the average temperature profile. The structure of the deviation spectra was similar at the two moorings (Fig. 6.14). The greatest peak occurs at the semidiurnal frequency. Another peak of almost the same height occurs at the diurnal frequency.

The spectrum is calculated as the module of a Fourier transformation without squares. Thus, the spectrum peaks' spectral density is numerically equal to the amplitude of fluctuations at the appropriate frequencies. It is possible to present the axis of spectral density in the same units in which the time series is measured (Fig. 6.14).

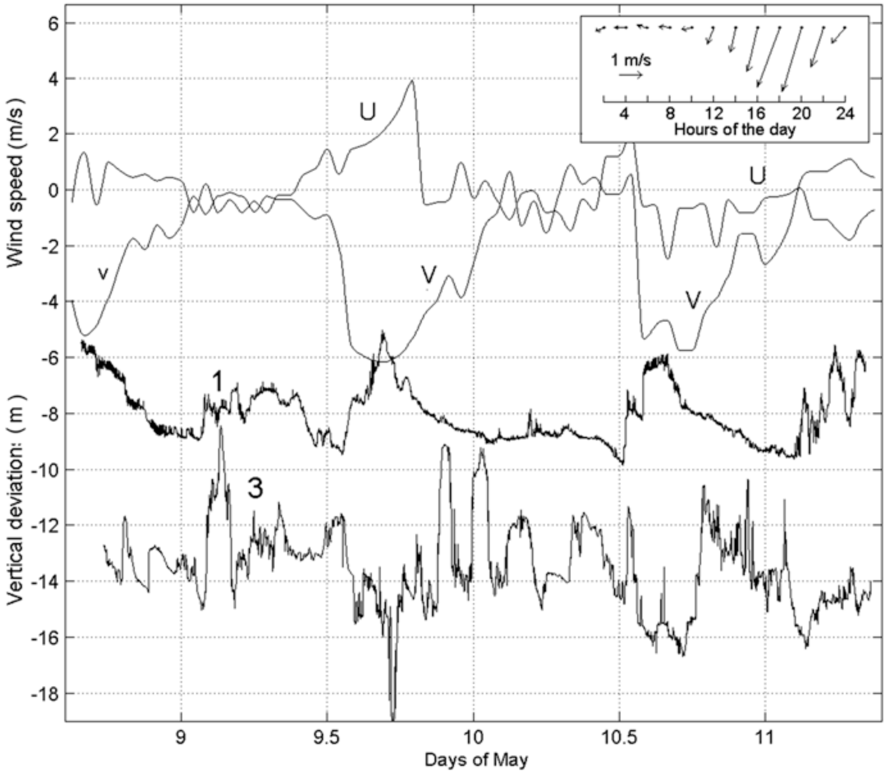

Fig. 6.13 Horizontal wind speed components and vertical deviations of water layers at mooring 1 (8 m depth) and mooring 3 (12.5 m depth). The numbers of the curves correspond to buoys 1 and 2. Daily average wind velocity from January to May 2002 in Lake Alchichica is presented in the upper right corner rectangle

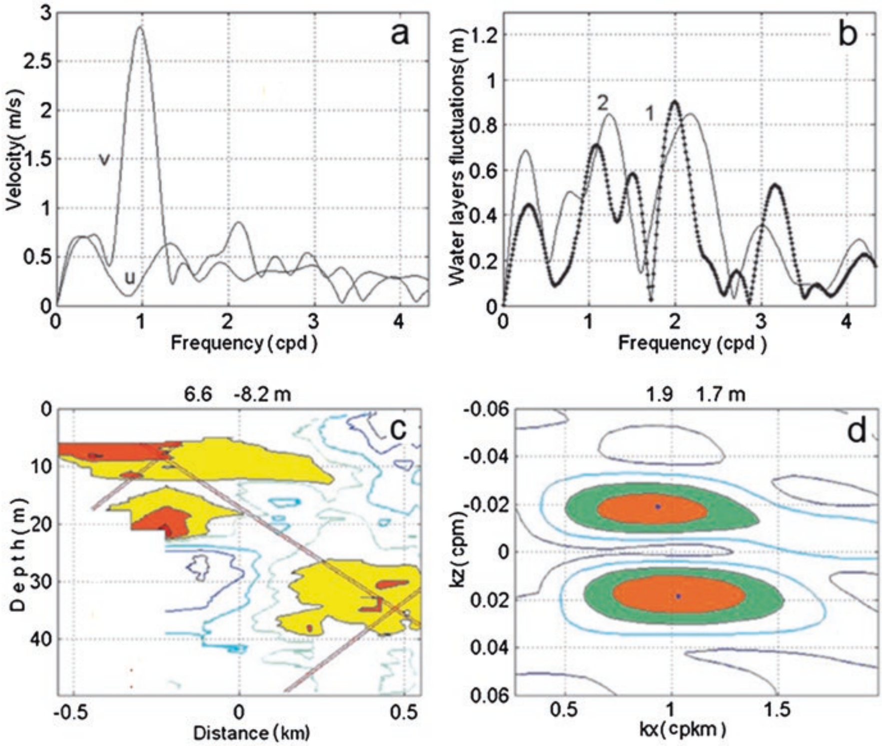

Fig. 6.14 Spectra of the wind speed components (**a**) and water layer fluctuations near buoy 1 and 2 (**b**). The spectral density of the peaks is numerically equal to the oscillation amplitude at the appropriate frequency. Deviations of water layers on the data of the fourth survey (**c**) and two-dimensional spectra of these deviations (**d**). The axis *x* is directed from mooring 1 to 3. The straight lines show crests of two waves corresponding to the spectra's principal peaks (d). Above the figures, the maximum and minimum deviations (c) and the principal fluctuations' amplitude (d) are showed. Isolines on figure (c) are plotted with a 0.3 step from a maximum. Here, the levels above 0.3 are shaded. Isolines on figure (d). Isolines are plotted with a 0.2 step from a maximum; the levels above 0.6 are shaded

The diurnal oscillations alone dominate the correlation function between vertical deviations of water layers under the buoys and the *wind's v*-component (northern component). The correlation between vertical deviations and the *u*-component (eastern component) of the wind is relatively small. Hence, the diurnal internal waves are created by the wind, which direction coincides with the axis *v*.

The correlation analysis shows that the two buoys' oscillations are in opposite phases due to horizontal mode oscillations. The latter suggests that only half of the diurnal wavelength fits (first horizontal mode with antinodes of vertical deviations and nodes of horizontal orbital speed at opposite sides of the lake) between the two moorings.

The spectrum contains two principal peaks with different vertical wavenumber. The horizontal wavelength spectrum's estimations present two peaks at 1.3 and

1.5 km for survey 3 and at 1.1 and 1.8 km on average for all four surveys. The systematic difference in the measured wavelengths might be due to the Doppler effect at the survey. The difference of the measured horizontal wavenumbers, when the diurnal or semidiurnal waves ($f = 1$ or 2 cycle/day) move towards each other, and the boat speed of $V = 1$ km/h, is equal to $\Delta k_x = 2f/V$ =0.08 or 0.16 cycle/km, which is close to the observable shift (Fig. 6.14). Hence, the waves move horizontally towards each other and form a horizontal mode of oscillations.

There is usually a vertical mode of internal waves formed in the ocean due to the reflection of waves from the bottom and the surface. In our case, a horizontal mode can be formed by reflection from the shore slopes, where the angle considerably exceeds the internal waves' inclination.

The Speed of Currents Caused by Internal Waves

The speed field is transformed to depth-constant buoyancy frequency, maintaining the thickness of the observed water layer. After the WKB-normalization, the internal wave beams and crests become rectilinear, and the principal spectrum peaks become more compact (Filonov and Lavin 2003).

Previously, the current speed's average values were removed from each horizon's current time series components. The field of the horizontal u-component of the speed vector on a depth-time plane contains a characteristic interference structure (the u-component is directed towards the east, v – towards the north) (Fig. 6.15). The crest inclination determines the diurnal and semidiurnal waves' vertical phase speed, which is equal to 0.055 and 0.075 cm/s. Tilting diurnal wave crests on the vertical-horizontal plane by the temperature recording is 2.3 degrees so that the horizontal diurnal wave phase velocity is 1.4 cm/s.

In a spectrum of the u-component, there are two peaks with a diurnal frequency and two with semidiurnal frequency (Fig. 6.15). Each pair of peaks corresponds to two inclined waves on a depth-time plane. The waves propagate in opposite directions in depth. More intense waves propagate downwards (group movement) and less intensely upwards. Oscillations of the v-component of the speed are significantly less, so the orbital movements in the waves occur on the strongly extended orbits in a west-east direction.

Trajectories of Beams

Inclined waves can be considered beams. The beam angle of inclination is defined by the buoyancy frequency $N(z)$, the inertial frequency $F = 0.66$ cycle/day, and the wave frequency f: $\alpha(z) = arctg(f^2 - F^2)/(N(z)^2 - f^2)^{1/2}$. A beam's trajectory is calculated by integrating depth $x(z) = x_0 \pm \int_0^z ctg\left(\alpha(z)\right)dz$, where x_0 defines the beam location on the x-axis. The crests and troughs of a wave extend along the beam; the group velocity is directed along the beam.

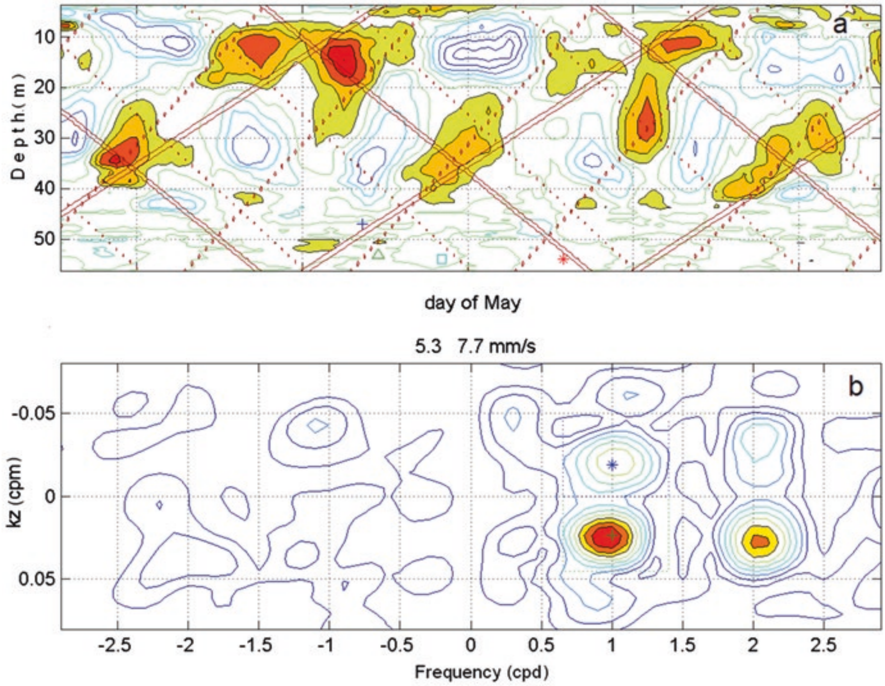

Fig. 6.15 (**a**) A u-component of current speed after WKB-normalization and crests of diurnal and semidiurnal waves propagate in opposite directions on depth (inclined lines). Isolines are plotted with a step 0.2 from a maximum; the positive deviations are shaded. (**b**) The spectra of the u-component (positive semi-axis of frequency) and v-component of the speed (negative semi-axis). Isolines are plotted with a step 0.1 from a maximum; the levels above 0.7 are shaded. The waves moving up are shown as + and those moving down as −

Two characteristics for the diurnal and semidiurnal waves were calculated, taking a vertical section of the lake on a line from west to east (Fig. 6.16). Two and a half vertical lengths of a diurnal wave and one length of a semidiurnal wave fit from the lake's surface to the bottom. Steep side slopes and a practically flat bottom create conditions for resonance for internal waves.

6.5 Discussion and Conclusion

The mountain breeze, which blows with diurnal periodicity, serves as the causing force and energy source for all lake movements. In the afternoon, the wind drives warm water on the surface to one of the lake edges. The movements in the thin top layer of the lake serve as a wave generator, creating an internal wave with a diurnal period.

From the mooring data, vertical fluctuations of temperature at opposite edges of the lake are in opposite phases. Two waves form the horizontal mode with antinodes

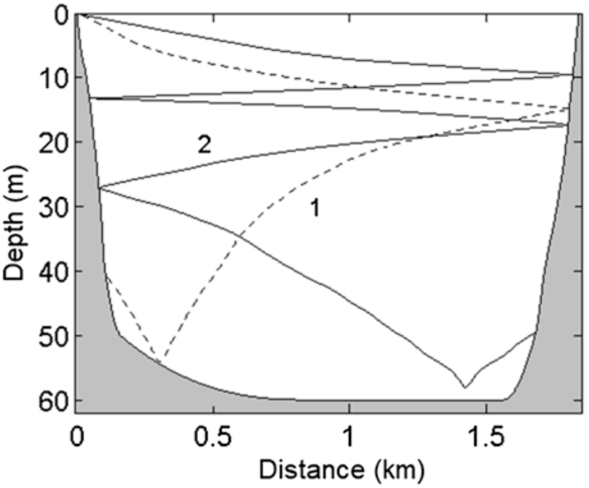

Fig. 6.16 The characteristics beam of diurnal (1) and semidiurnal (2) internal waves

of vertical fluctuations at opposite edges of the lake. The horizontal wavelength is approximately equal to twice the lake diameter.

Based on ADCP data, we found that both diurnal and semidiurnal fluctuations are represented by two oblique waves (four waves in total). Pairs of oblique waves moved towards each other inside the lake. However, according to the temperature survey (taking into account the Doppler effect), only two obliques and internal waves moving towards each other were recorded in the horizontal plane. It is possible that the survey did not detect diurnal and semidiurnal waves because they could have different orientations relative to the survey line. The wind forced diurnal oscillations, and the lake diameter limited their horizontal wavelength. Semidiurnal oscillations arise initially as a result of nonlinear distortions of large diurnal oscillations. However, the amplitude of the semidiurnal oscillations exceeds the amplitude of the diurnal ones. The latter can be a result of the proximity between semidiurnal oscillations and resonance in the lake.

The mountain breeze blows over Lake Alchichica with diurnal periodicity and generates diurnal internal waves with large amplitudes. The second harmonic of the diurnal oscillations arises from the diurnal oscillations' nonlinear distortions and reach large amplitude presumably because the semidiurnal frequency is close to the lake resonance frequency. The internal waves partially break near the coastal slopes in the thermocline area, providing local mixing.

The water volume of the lake Alchichica is similar to a vertical cylinder that allows the occurrence of both horizontal and vertical modes of internal waves and, as a result, provides a cavity resonator for the waves. Semidiurnal internal waves in the lake have a frequency close to the resonance frequency. Their unusual enhancing, despite the diurnal wind forcing, was shown. As far as we know, this cavity resonance of internal waves in a natural basin is one of the first documentations. The generation mechanism of semidiurnal internal waves by forcing the diurnal frequency is new documentation in natural water bodies. It seems likely that the discovered effects are rare for natural basins, as most of them are irregular in shape (rather than cylindrical). This volcanic lake of Mexico may provide an exciting exception worthy of further study.

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Chapter 7
Physicochemical Characteristics

Javier Alcocer, Martín Merino-Ibarra, Jorge A. Ramírez-Zierold, Luis A. Oseguera, Daniela Cortés-Guzmán, F. Sergio Castillo-Sandoval, Andrea P. Guzmán-Arias, María Guadalupe Pérez-Ramírez

7.1 Underwater Light Climate

Javier Alcocer and Luis A. Oseguera

Solar radiation, especially photosynthetic active radiation (PAR = 400–700 nm), is the primary energy source in aquatic ecosystems. Light attenuates and transforms in caloric energy, which influences the thermal structure of the water column. Autotrophic organisms are responsible for transforming light into chemical energy through the process of photosynthesis. Therefore, the quantity, quality, and depth sunlight reach into the water column directly influence primary productivity and phytoplankton distribution.

On the other side, ultraviolet radiation (UVR) ranges from the solar radiation spectrum between 200 and 400 nm. UVR is composed of three fractions: UVR-A (315–400 nm), UVR-B (280–315 nm), and UVR-C (200–280 nm). UVR affects the biogeochemical cycles of the aquatic ecosystem and the energy fluxes. UVR generates a stress factor in phytoplankton and other aquatic biota by affecting the growth

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J. Alcocer (✉) · L. A. Oseguera
Grupo de Investigación en Limnología Tropical, FES Iztacala, Universidad Nacional Autónoma de México, Tlalnepantla, Estado de México, Mexico
e-mail: jalcocer@unam.mx; loseguera@unam.mx

M. Merino-Ibarra · F. S. Castillo-Sandoval
Unidad Académica de Ecología y Biodiversidad Acuática, Instituto de Ciencias del Mar y Limnología. Universidad Nacional Autónoma de México, Ciudad de México, Mexico
e-mail: mmerino@cmarl.unam.mx; castillo@cmarl.unam.mx

J. A. Ramírez-Zierold · D. Cortés-Guzmán · A. P. Guzmán-Arias · M. G. Pérez-Ramírez
Programa de Posgrado en Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México, Ciudad de México, Mexico
e-mail: dacortesgu@unal.edu.co

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and development of organisms, the biomass, the primary productivity and photosynthesis, the buoyancy, and the photosynthetic pigments by interacting and mutating the DNA.

Light climate refers to the factors that determine the nature of the light field in terms of the quantity, quality, and depth sunlight reaches in aquatic ecosystems, focusing on the growth response of autotrophic organisms and the behavior of the organic and inorganic matter (Van Duin et al. 2001). The light climate is the set of light conditions (PAR and UVR) within the water column after considering the different processes' attenuation (absorption and dispersion).

7.1.1 Photosynthetic Active Radiation

Secchi Disk Depth

The Secchi disk depth (Z_{SD}) in Lake Alchichica ranges between 3.6 m and 10.4 m, with an average of 6.3 ± 2.2 m (Fig. 7.1). The lower values of Z_{SD} (4.5 ± 0.7 m) are during the winter circulation period and the early stratification (January to June), while the highest (8.1 ± 1.5 m) along the well-established and late stratification (July to December).

The lowest values of Z_{SD} in April and June associates to the onset of the thermal stratification period, when *Nodularia* aff. *spumigena*, a nitrogen fixing cyanobacteria, blooms. The cyanobacteria's filaments are very large, up to few centimeters

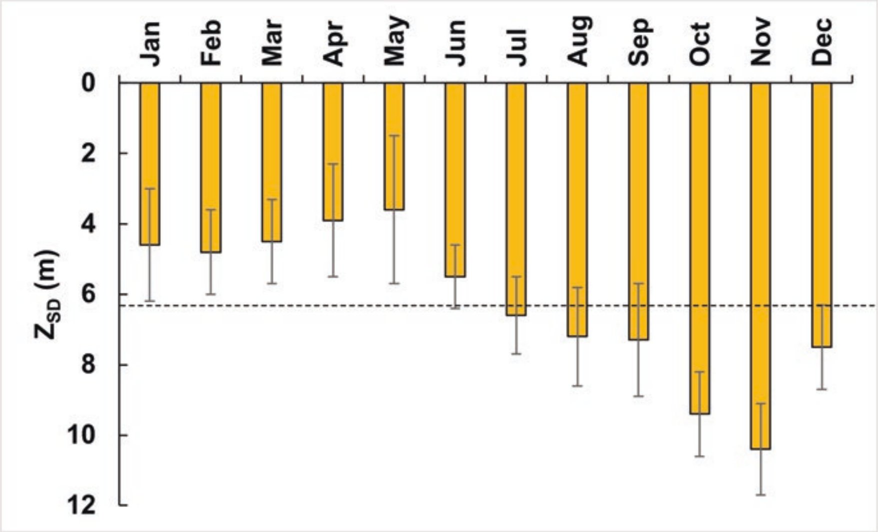


Fig. 7.1 Temporal dynamics of Z_{SD} (average ± s.d.) in Lake Alchichica. (Dotted line = annual average)

long, and own aerotopes, which allows the cyanobacteria to float close or at the water surface. *N.* aff *spumigena* massive development accumulates at the lake's surface as bright green scums preventing light from penetrating the water column below a few meters (biogenic turbidity).

Euphotic Zone

The euphotic zone (Z_{EU}) is the layer of aquatic ecosystems that receives enough sunlight for photosynthesis. This layer comprehends from the water body's surface down to the depth at which PAR reaches 1% of PAR at the surface (SPAR = 100%). Nonetheless, in Lake Alchichica, the lower boundary of Z_{EU} is better defined by 0.1% of SPAR instead of 1% (González Contreras et al. 2015); similar cases have been described elsewhere (e.g., Pinel-Alloul et al. 2008).

Z_{EU} showed the presence of two significantly different periods ($p < 0.5$) according to water transparency (Fig. 7.2) (Adame et al. 2008, Oseguera et al. 2010a, b): a) turbid water phase, from January to March, during the mixing period, when Z_{EU} was lower (25 ± 4 m), and b) clear water phase, from April to December, during the stratification period, when Z_{EU} was more extensive (33 ± 5 m).

There is a general increasing trend in water transparency along with the clear water phase. However, the trend was briefly – one month – interrupted around May when Z_{EU} decrease associated to the spring phytoplankton (cyanobacteria) bloom. Later, the increasing trend in Z_{EU} resumes until December, when Z_{EU} decreases again, indicating the circulation period's proximity accompanying the winter

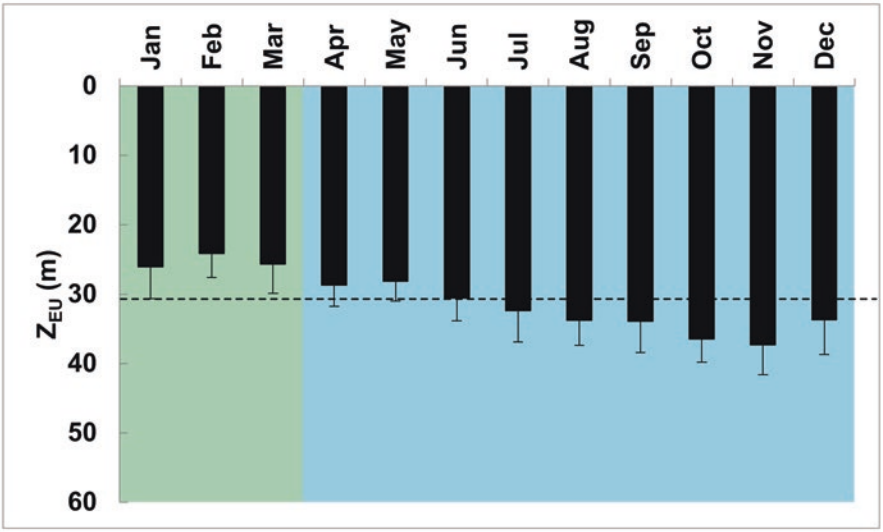


Fig. 7.2 Temporal dynamics of Z_{EU} (average ± s.d.) in Lake Alchichica. (Green square = turbid water phase, Blue square = clear water phase, dotted line = annual average)

phytoplankton (diatom) bloom (González Contreras et al. 2015). Turbidity in Lake Alchichica is biogenic (phytoplankton).

While the overall average is 31 ± 6 m, Z_{EU} reaches its lowest value in February (24 ± 3 m). The highest value in November (37 ± 4 m). When thermally stratified, Z_{EU} is tightly coupled with the metalimnion. The limit of Z_{EU} is at the bottom of the metalimnion or top of the hypolimnion (Macek et al. 2009).

González Contreras et al. (2015) found the Z_{EU} maximum depth reached each year displayed a diminishing long-term (1999–2010) trend suggesting the lake is becoming less transparent. Differently, the Z_{EU} minimum depth remained similar each year.

The Z_{EU} to maximum depth (Z_{MAX}) ratio (Z_{EU}:Z_{MAX}) averages 0.5 ± 0.1, indicating half of the water column at the deepest portion (60 m) of the lake is the productive zone (PAR $\geq$ 0.1%); this is, where the primary productivity could take place. Z_{EU}:Z_{MAX} ratio was 0.4 ± 0.0 in the turbid water phase and 0.5 ± 0.1 in the clear water phase (Fig. 7.3).

The vertical attenuation coefficient (Kd) of PAR (Kd_{PAR}) averages 0.14 ± 0.03 m (0.12–0.20/m); as expected, the Kd_{PAR} maximum (0.18 ± 0.02/m) corresponds to the turbid water phase, while the Kd_{PAR} minimum (0.13 ± 0.01/m) to the clear water phase.

The Z_{SD} to euphotic zone (Z_{EU}) ratio (Fig. 7.4) averages 5.3 ± 1.3 (3.6 to 7.8). This ratio is between 2 and 3 times higher than the ratio reported in most limnology textbooks (Z_{EU} = 2.5–3 x Z_{SD}). Nonetheless, as explained before, we calculated Z_{EU} as 0.1% SPAR instead of the "traditional" 1% SPAR. By reducing the extent of Z_{EU}, the ratio reduces as well.

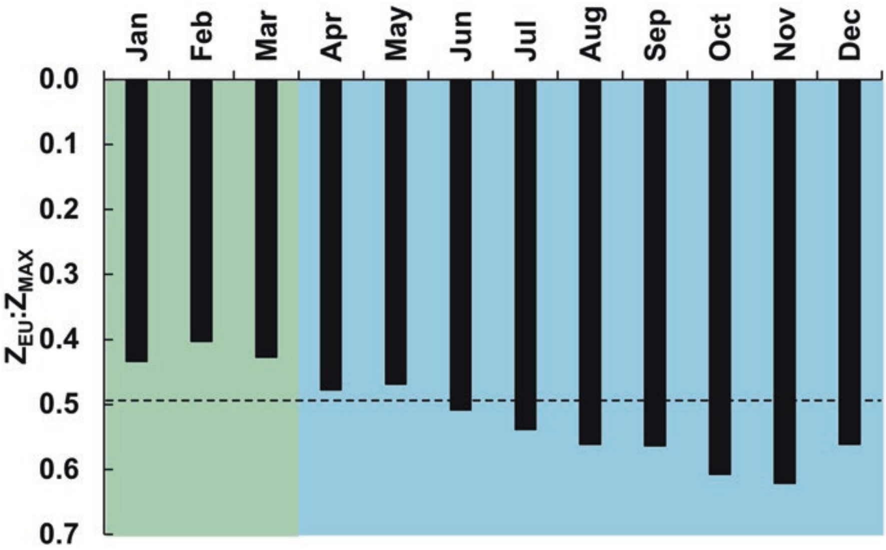


Fig. 7.3 Temporal dynamics of Z_{EU}:Z_{MAX} in Lake Alchichica. (Green square = turbid water phase, Blue square = clear water phase, dotted line = annual average)

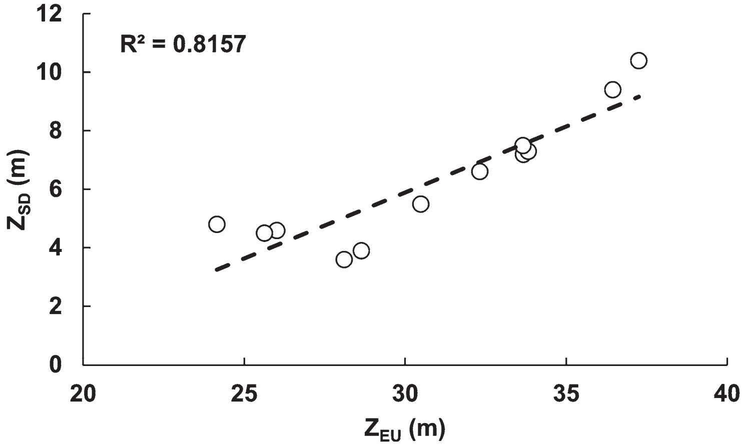


Fig. 7.4 Linear regression between Z_{EU} and Z_{SD} in Lake Alchichica

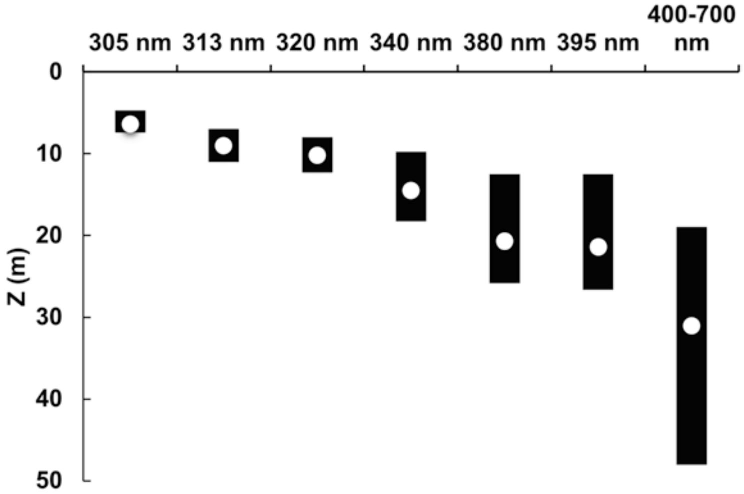


Fig. 7.5 Water depth (max, average, min) at which different UVR wavelengths penetrates Lake Alchichica water column. Z_{EU} (400–700 nm) is provided for comparison

7.1.2 Ultraviolet Radiation

The ultraviolet radiation (UVR) equivalent of the Z_{EU} ($ZUVR_{0.1\%}$) is the layer that encompasses from the surface of the water body down to the depth at which UVR reaches 0.1% of UVR at the surface (SUVR = 100%). The most energetic UVR wavelengths (305 nm – 320 nm) reach only the top ~10 m of the water column. The less energetic UVR wavelengths (380 nm – 395 nm) reach greater depths of ~20 m, compared to Z_{EU} that reaches 30 m (Fig. 7.5).

As expected, UVR penetration on the turbid water phase was lower for all the wavelengths (<15 m) compared to the penetration during the clear water phase (< 30 m). The percentage of change in the penetration range between phases (turbid to clear water) differs from the more energetic (<155%) to the less energetic (>185%), indicating higher attenuation in the more energetic UVR wavelengths.

The $ZUVR_{0.1\%}$:Z_{MAX} ratio ranges according to the UVR wavelength from 0.1 (more energetic UVR) up to 0.4 (less energetic UVR) compared to 0.5 on average for Z_{EU} (Fig. 7.6). Although the upper 40% of the water column is exposed to the UVR, only the top 20 m receive the more energetic and dangerous wavelengths UVR (305–320 nm).

The vertical attenuation coefficient (Kd) of UVR (Kd_{UVR}) averages 0.74 ± 0.13/m (305 nm), 0.52 ± 0.08/m (313 nm), 0.46 ± 0.06/m (320 nm), 0.33 ± 0.07/m (340 nm), 0.23 ± 0.06/m 380 nm), and 0.23 ± 0.06/m (395 nm). As anticipated, the Kd_{UVR} maximum corresponds to the turbid water phase, while the Kd_{UVR} minimum to the clear water phase.

The light climate of Lake Alchichica shows the most energetic wavelengths (UVR) attenuate in the top first meters of the water column, practically at the same depth during the year. The less energetic UVR wavelengths attenuate more during the mixing period while reaching deeper waters along the stratification period, particularly in late stratification. Finally, PAR has a greater penetration range than the UVR, following a similar higher attenuation pattern during the mixing period and lower attenuation during stratification, particularly at the late stratification.

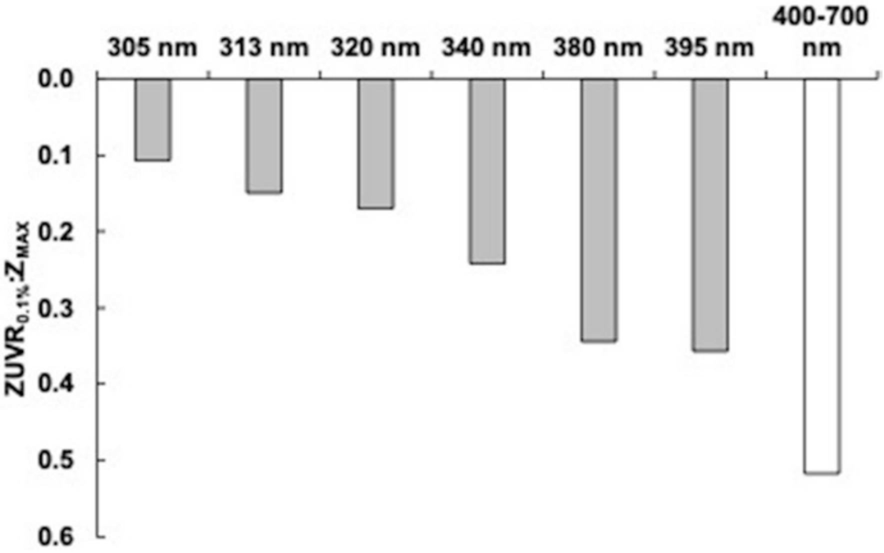


Fig. 7.6 $ZUVR_{0.1\%}$:Z_{MAX} of different UVR wavelengths in Lake Alchichica. PAR (400–700 nm) is provided for comparison

7.2 Temperature and the Thermal Regime

Javier Alcocer and Luis A. Oseguera

Solar radiation defines climate gradients associated with the Earth's curvature. Water attenuates light energy inducing gradients in water temperature and then define the density-layering and mixing of lakes (Lewis 1996). The thermal stratification, which couples to density stratification of the water masses, produces a differential vertical distribution of particulate and dissolved matter throughout the water column. Vertical mixing or overturn distributes particulate and dissolved matter through the water column by transporting nutrients, gases, and biota, from the deep to the shallow areas and vice versa. Also, water temperature influences the speed of chemical reactions (Q_{10}) and then modify the metabolism of the biota and the entire ecosystem. According to the dominant tropical latitude, there are two main lake mixing categories of thermal regimes in Mexico (Alcocer et al. 2000): warm monomixis in deep lakes with relatively small surface area, and warm polimixis in extended, shallow lakes.

7.2.1 Temperature

Although tropical in latitude (19°N), the high-altitude setting of Lake Alchichica (2300 m a.s.l.) tempers water temperature to an average of 15.8 ± 1.4 °C. The type (characteristic) year of average water column temperature dynamics (Fig. 7.7) shows the minimum temperature reaches in February (14.7 ± 0.4 °C), while the maximum in September (16.5 ± 2.0 °C). The "cold" period (below the average,

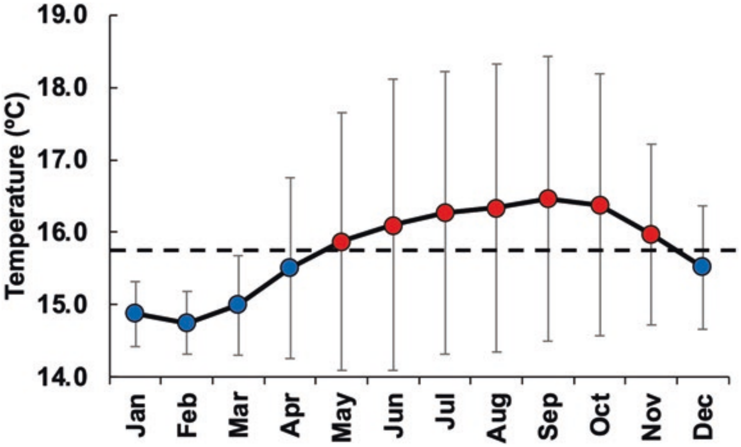


Fig. 7.7 Water temperature (average ± s.d.) in Lake Alchichica. (Below the average in blue, above the average in red; dotted line = annual average)

15.1 ± 0.7 °C) is from December to April. The "warm" period (above the average, 16.2 ± 1.8 °C) takes place from May until November.

The average temperature of the surface layer (0–5 m) is 17.5 ± 1.3 °C; however, the fluctuations ranged from 14.2 to 20.7 °C. Differently, the bottom water (40–60 m) temperature averages 14.7 ± 0.3 °C, with a range that fluctuates between 14.1 to 15.4 °C. A long-term (1999–2014) data set suggests that both water surface and water bottom-layer average temperatures are increasing, 0.030 °C/y and 0.023 °C/y, respectively.

The bottom water temperature is a good indicator of the regional climate; cold air lowers water temperature, increases its density, and sinks to the bottom. Bottom temperatures mirror then the coldest air temperatures. The bottom water temperature of Lake Alchichica increases along the year (Fig. 7.8) from the coldest February (14.58 ± 0.31 °C) to the warmest January (14.71 ± 0.36 °C). There is a sharp drop in temperature from January to February, indicating the full water column mixing occurs in February. The colder period (below the average, 14.62 ± 0.30 °C) is from February to July, while the period of warmer (above the average, 14.69 ± 0.29 °C) bottom water temperatures are from August to January.

The difference between mixing layer (Z_{MIX}) and bottom water temperatures averages 2.8 ± 1.8 °C with a range between 0.1 °C and 4.7 °C (Fig. 7.9). The largest temperature differences (above the average) are from April to October with 4.1 ± 0.6 °C, while the lowest temperature differences (below the average) are from November to March with 0.9 ± 0.9 °C.

The thermocline evolves from superficial (10–20 m), thin (≈ 4 m) and barely defined in April to mid-depth (10–20 m), thick (4–6.5 m), and well defined in May through October, and then gets deeper (>30 m) and thinner (≈ 2 m) in November and December (Fig. 7.10). The thermocline's average width is 4.6 ± 1.6 m, and it ranges between 2.2 and 6.5 m.

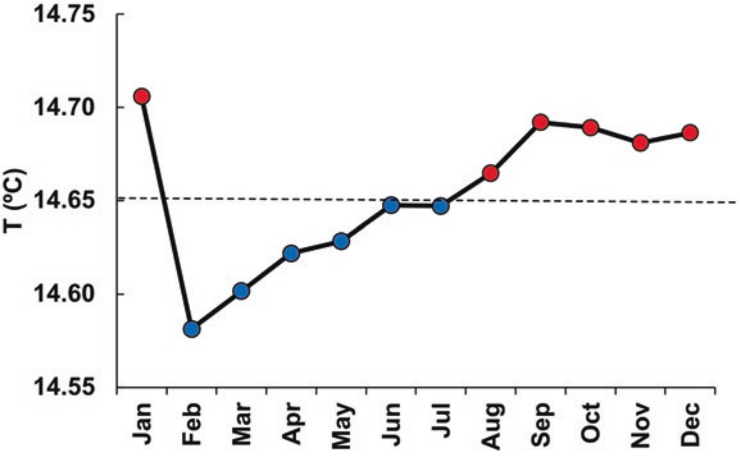


Fig. 7.8 Bottom water temperature in Lake Alchichica. (Below the average in blue, above the average in red; dotted line = annual average)

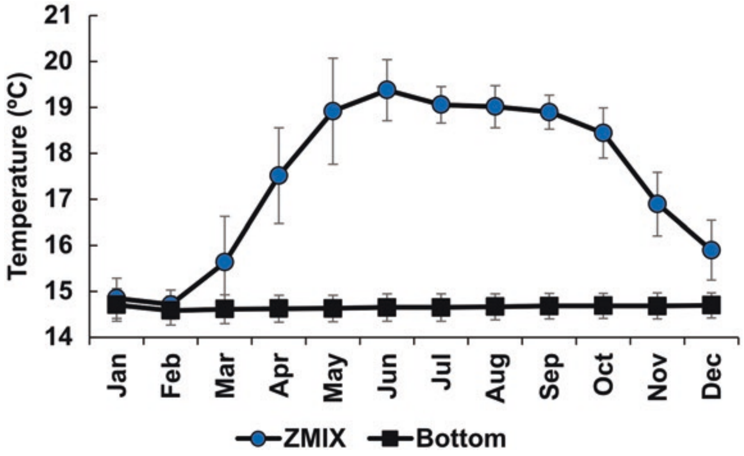


Fig. 7.9 Temporal dynamics of the mixing zone's temperature – Z_{MIX}- and temperature at the bottom (average ± s.d.)

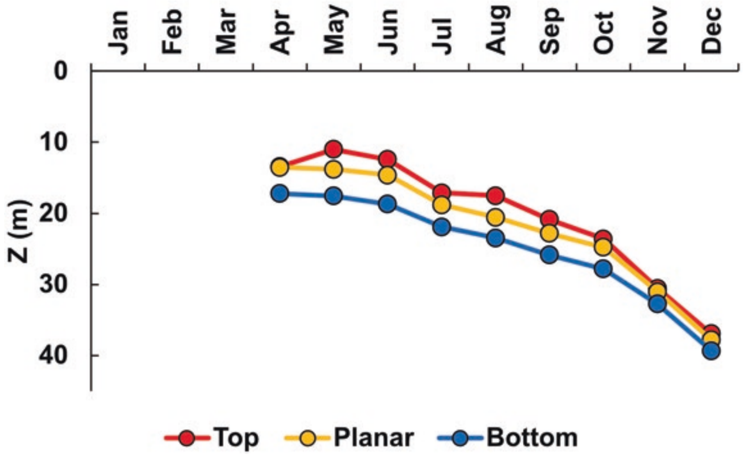


Fig. 7.10 Temporal dynamics of the thermocline in Lake Alchichica

The ENSO (El Niño Southern Oscillation) affects the thermal behavior of Lake Alchichica by producing a shallower thermocline with a stronger thermal gradient and a thinner and warmer epilimnion (Alcocer and Lugo 2001, 2003).

7.2.2 *The Thermal Regime*

Tropical deep Lake Alchichica is warm monomictic (Alcocer et al. 2000). It mixes once a year while stratifies the rest of the time (Fig. 7.11). The mixing period associates with the hemispheric winter (Lewis 1996) and occurred, in most cases, from

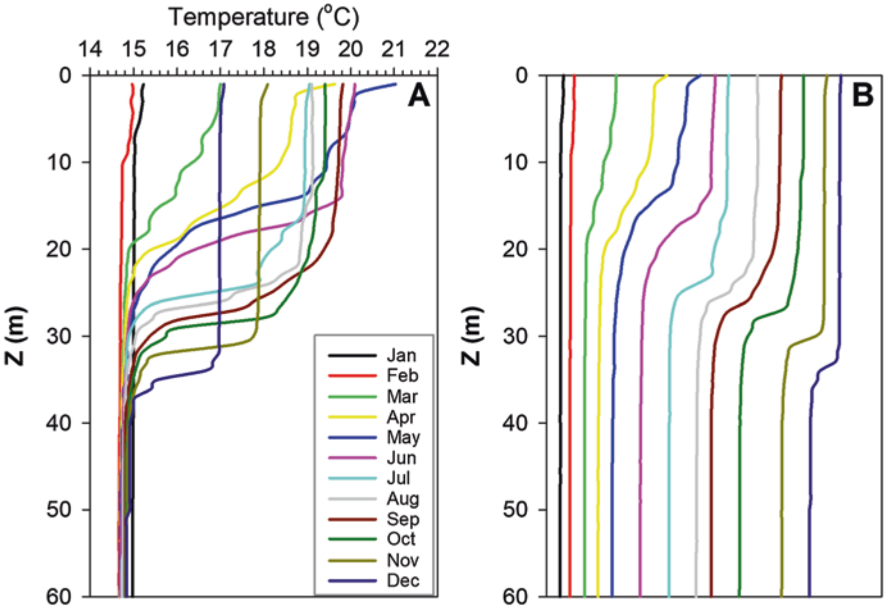


Fig. 7.11 A. Monthly temperature profiles in Lake Alchichica. B. Onset and evolution of the thermocline in Lake Alchichica (from January at the extreme left to December at the extreme right)

January to March. However, sometimes it starts in late December or later in January and seldom until February. The onset of the stratification takes place in April or March (González Contreras et al. 2015). During this transitional period between mixing and stratification, the temperature profile displays an incipient stratification (early stratification), with the highest temperatures at the surface and decreasing progressively with increasing depth (Adame et al. 2008). From June to December, the lake is well-stratified and exhibits the three characteristic layers: epilimnion, metalimnion, and hypolimnion.

The length of the circulation period in Lake Alchichica varies between 2 and 4 months, with an average of 3.1 ± 0.7 months (González Contreras et al. 2015); most of the time, mixing last three months (58.3%), and sometimes four months (25%) or even only two months (16.7%). Correspondingly, stratification lasts on average 8.9 ± 0.7 months; most of the time (58.3%), it stratifies nine months, and occasionally eight months (25%) or even ten months (16.7%).

The Z_{MIX} in Lake Alchichica averages 28.6 ± 18.5 m, ranging between 4 m and a maximum of 60 m (Fig. 7.12). The highest Z_{MIX} (above the average) are found in November to March, while the lowest Z_{MIX} (below the average) is from April to October. Deepest Z_{MIX} is in February, while the shallowest in April. At the transition between mixing and stratification, March shows ample standard deviation (41.2 ± 24.6 m), and a minimum of 7 m and maximum 60 m. From April to December, Z_{MIX} increases from 11.9 ± 4.3 m to 39.1 ± 7.2 m.

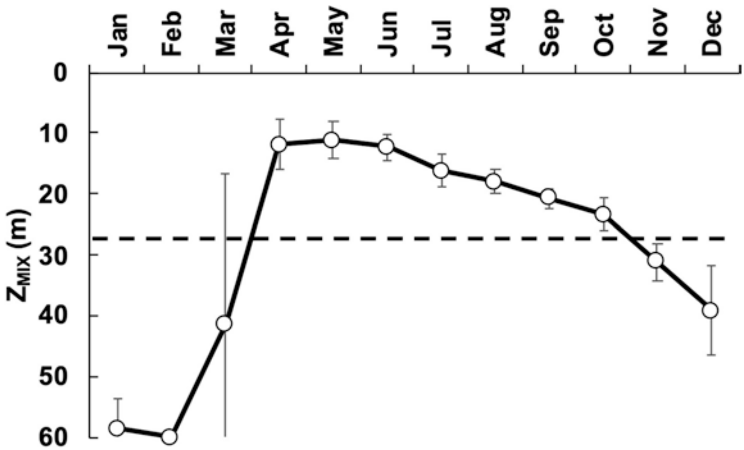


Fig. 7.12 Temporal dynamics of the mixing layer – Z_{MIX}- (average ± s.d.). (Dotted line = annual average)

The traditional criteria for defining the thermocline in temperate lakes is 1 °C/m; nonetheless, in tropical lakes, a gradient of 0.5 °C/m or even 0.3 °C/m is more often accepted (Roldán Pérez and Ramírez Restrepo 2008). The temperature gradient at the thermocline of Lake Alchichica averages 0.57 ± 0.35 °C/m with a range between 0.04 and 1.96 °C/m (Fig. 7.13).

The maximum temperature gradient (°C/m) along the water column (i.e., the planar thermocline when stratified) of Lake Alchichica averages 0.76 ± 0.50 °C/m, with a range between 0.13 ± 0.08 °C/m in February and 1.26 ± 0.25 °C/m in July (Fig. 7.14). An average gradient of 0.3 °C/m applies well to define the top/ceiling and the thermocline's bottom/floor in Lake Alchichica. Nonetheless, to establish a functional thermocline in Lake Alchichica, it requires a higher gradient (0.5 °C/m) when closer to the surface (e.g., 10 m, early stratification), while smaller gradients (0.25 °C) when deeper (e.g., 40 m, late stratification).

The winter water-column circulation starts most of the time in January, while complete water column mixing (i.e., lowest temperature maximum gradient) occurs until February. From then on, the thermal gradient increases until reaching a maximum in July (i.e., highest temperature maximum gradient) at the beginning of the summer. It remains similar until November (mid-autumn). The maximum temperature gradient drastically descends in December by the end of the stratification period mirroring the winter circulation period's onset.

The maximum thermal gradient (below the average, 0.35 ± 0.7 °C) during the"cold" period is from late autumn (December) and winter (January–March) to early spring (April). The maximum thermal gradient (above the average, 1.11 ± 0.36 °C) along the "warm" period takes place from mid-spring to mid-autumn (May–November). Mixing seldom starts in late December. At the onset of the stratification in April, the temperature profile looks most likely a transitional stage between circulation and stratification than showing a typical thermocline profile.

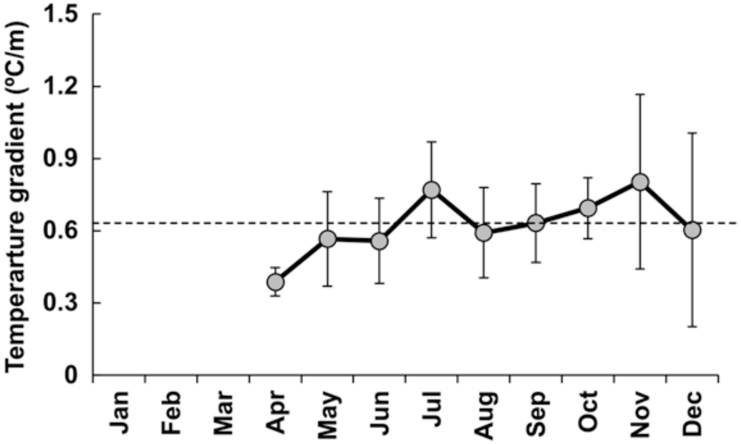


Fig. 7.13 Temporal dynamics of the average temperature gradient (± s.d.) at the thermocline of Lake Alchichica. (Dotted line = annual average)

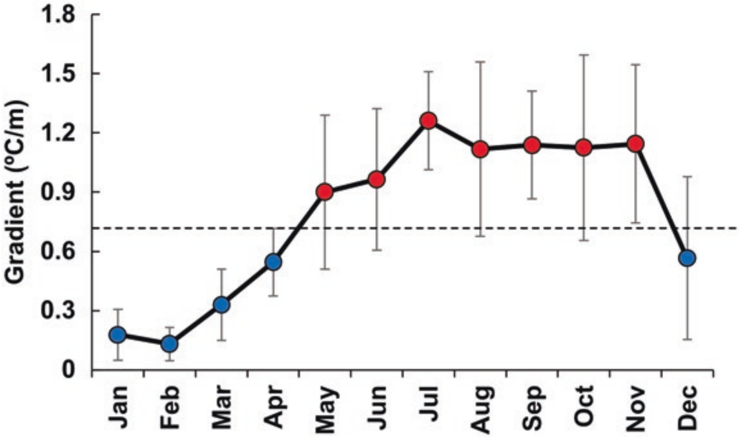


Fig. 7.14 Temporal dynamics of the maximum temperature gradient (average ± s. d.) along the water column. (Dotted line = annual average)

During the onset of and mixing period (December to March), Z_{EU}:Z_{MIX} ratio remains >1; differently, along most of the stratification period (April to November), Z_{EU}:Z_{MIX} ratio <1 (Fig. 7.15).

Z_{EU} extends over the entire Z_{MIX} most of the stratification period (April to November), identifying the well-lilted, productive zone (Fig. 7.16). As Z_{MIX} increases towards the end of the year, Z_{EU} also increases.

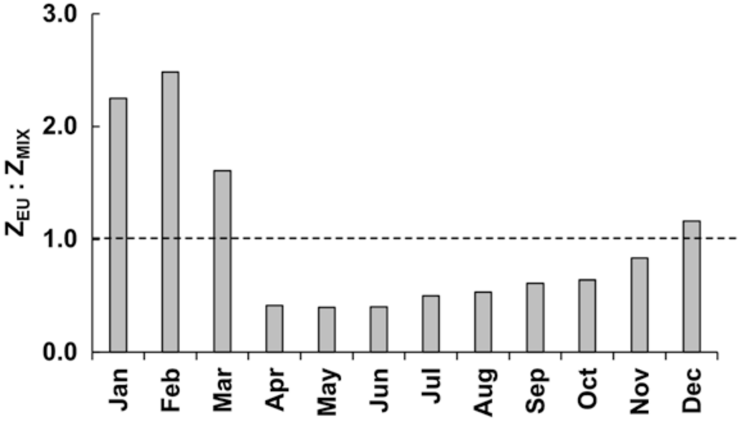


Fig. 7.15 Temporal dynamics of the Z_{EU}:Z_{MIX} ratio in Lake Alchichica. (Dotted line = annual average)

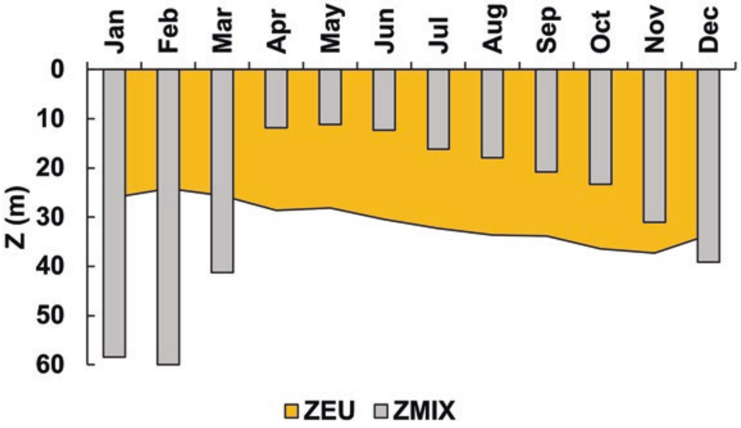


Fig. 7.16 Comparative coverage of the Z_{EU} and the Z_{MIX} in Lake Alchichica along the annual cycle

7.2.3 Temperature Diel Cycle

A two-days monitoring of temperature profiles in Lake Alchichica (Fig. 7.17) reveals the presence of short-term variation in the upper layer (0–8 m) and at the metalimnion; the rest of the epilimnion (8–27 m) was quite homogeneous with 17.86 ± 0.07 °C (17.52–17.86 °C), and also the hypolimnion (36–60 m) with 14.88 ± 0.07 °C. Differently, along the metalimnion the largest diel changes were at the top (28–31 m, 0.50–1.09 °C) while smallest at the bottom (35 m, 0.12 °C).

Filonov and Alcocer (2002) and Filonov et al. (2006, 2015) recorded wind-induced internal seiches in Lake Alchichica of up to 3 m. Internal waves were surely responsible for the short-term temperature variation at the metalimnion.

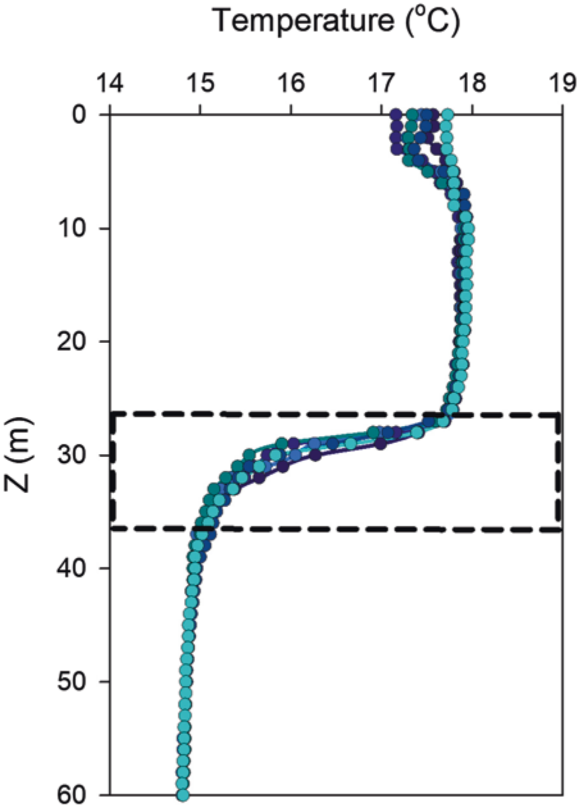


Fig. 7.17 Temperature diel cycle in Lake Alchichica (October 10–11, 1999). (Dashed line = metalimnion)

7.3 Dissolved Oxygen

Javier Alcocer and Luis A. Oseguera

The higher temperature in tropical lakes reduces the oxygen uptake capacity of water. Also, the higher temperature accelerates microbial metabolism frequently resulting in rapid dissolved oxygen (DO) depletion, particularly in the hypolimnion, leading to anoxia (Lewis 1996). Differing from temperate lakes where eutrophic lakes develop anoxic hypolimnia, the hypolimnia of tropical lakes become anoxic independently of their trophic status. Hypolimnia of tropical, deep lakes remain anoxic during the long-lasting stratification in the warm, rainy season (6–9 months) (Lewis 1987).

7.3.1 Dissolved Oxygen Concentration

DO concentration in Lake Alchichica ranges widely (Fig. 7.3.1). At or close to the surface (0–1 m), it remains between saturation (6.5 mg/L, DO_{SAT} = 100%) and oversaturation (7.5 mg/L, DO_{SAT} = 130%). The average in the top shallow meters remains from saturation to slightly undersaturated (>6 mg/L, DO_{SAT} = 92%). Quite differently, deep waters, particularly at and below the metalimnion, DO concentrations reach microaerobic (<1 mg/L) or anoxic conditions (< 0.2 mg/L, a membrane electrode accuracy limit) at the bottom (Macek et al. 2009).

During mixing, the whole water column remains well-oxygenated ($DO_{SAT} > 60\%$), while during stratification, DO displays a clinograde profile (Adame et al. 2008). Even during the mixing period, the DO along the water column is not homogeneous, the DO concentration in upper layer is higher than in the mid and lower portions. The DO concentration difference between surface and bottom layers increases from a minimum of 1.5 mg/L in January to 8.5 mg/L in May, and from there on it diminishes from 7.4 mg/L (June) down to 6.2 mg/L in December. The profile becomes sharper along the stratification (Fig. 7.18). On rare occasions (3–4 times in 20 years), a metalimnetic DO maximum developed in September during the well-established thermal stratification. DO concentration reached up to 10.41 mg/L (160% oversaturation). The metalimnetic DO maximum couples with the deep chlorophyll maximum, both at the metalimnion (see Chap. 12, phytoplankton, Fig. 12.3).

DO concentration in the Z_{MIX} averages 6.29 ± 1.01 mg/L (DO_{SAT} = 97 ± 16%) within a range of 3.42 (DO_{SAT} = 53%) and 8.88 (DO_{SAT} = 137%) mg/L (Fig. 7.3.2). The period of the lowest DO concentration (5.57 0.95 mg/L, DO_{SAT} = 86 ± 15%) in the Z_{MIX} is from mid-autumn to winter (November to March), while the period with the highest DO concentration (6.81 ± 0.68 mg/L, DO_{SAT} = 105 ± 10%). In January, at the beginning of the mixing period, the anoxic water of the previous hypolimnion mixes with the oxic waters of the previous epilimnion, resulting in a DO concentration reduction along the entire water column (4.7 ± 0.9 DO_{SAT} = 72 ± 14%). As mixing of the water column continues, the DO concentration of the entire water column (Z_{MIX}) increases until reaching saturation. As the lake stratifies -early stratification- DO reach the highest concentrations (7.1 ± 0.9 DO_{SAT} = 109 ± 14%). From then on, until October, DO concentrations remain high, around saturation. In November and December, as the thermocline deepens and erodes, DO concentrations start to reduce (Fig. 7.19).

7.3.2 Anoxic Layer

As mentioned, anoxia is a recurrent – every year – and long lasting – from seven up to eleven months – phenomenon in Lake Alchichica. A deep, over the sediments, and thin (1 to 2 m) anoxic layer is often detected in March or April (Figs. 7.18 and 7.20).

Some years, the water column in December is completely oxic, sometimes January display an anoxic layer, and seldom February and March display a thin anoxic layer at the bottom (Fig. 7.21). Soon after (a month) the anoxia started at the bottom of the lake as early as May or June, the entire hypolimnion becomes anoxic and remains so until December. The anoxic layer in July is the widest (36 m) and

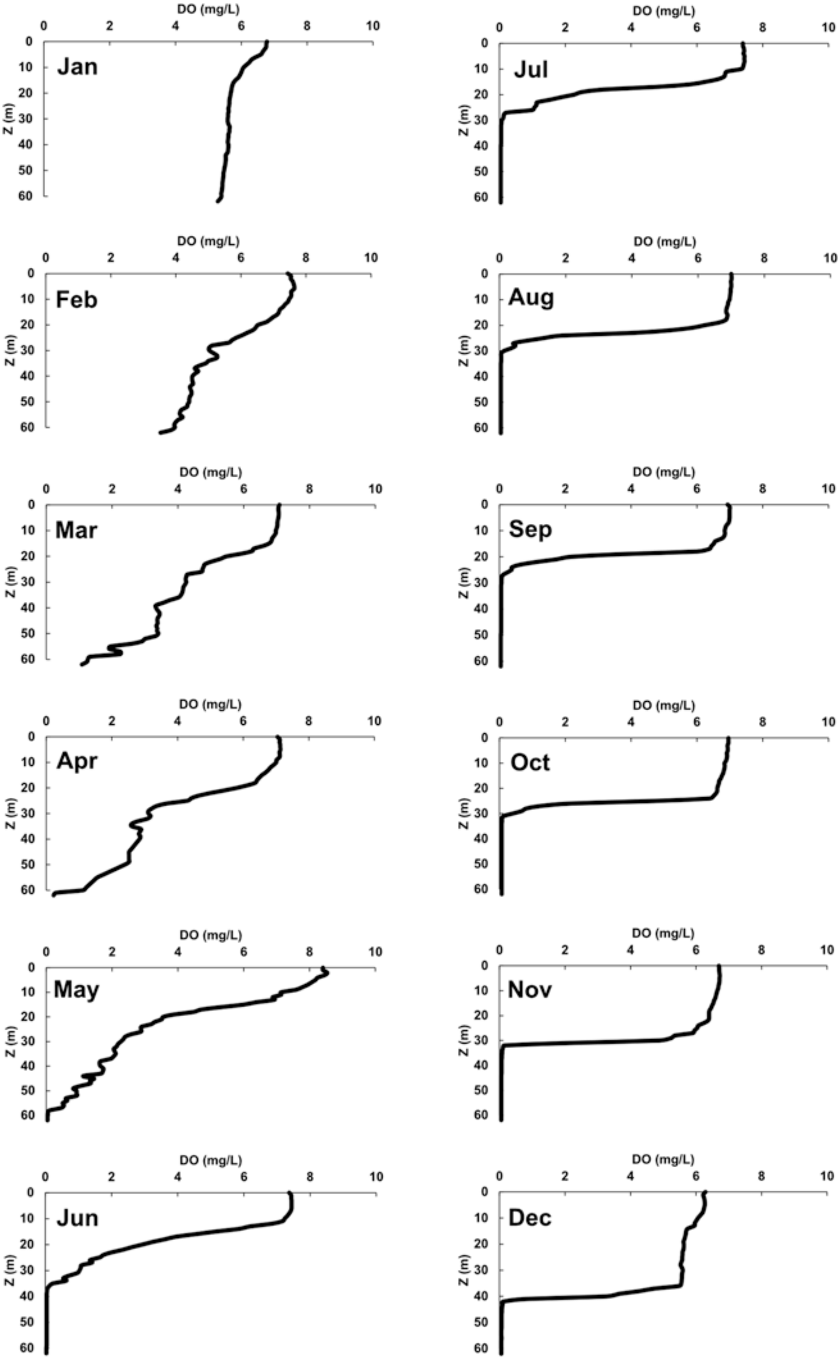


Fig. 7.18 Temporal dynamics of DO profiles in Lake Alchichica

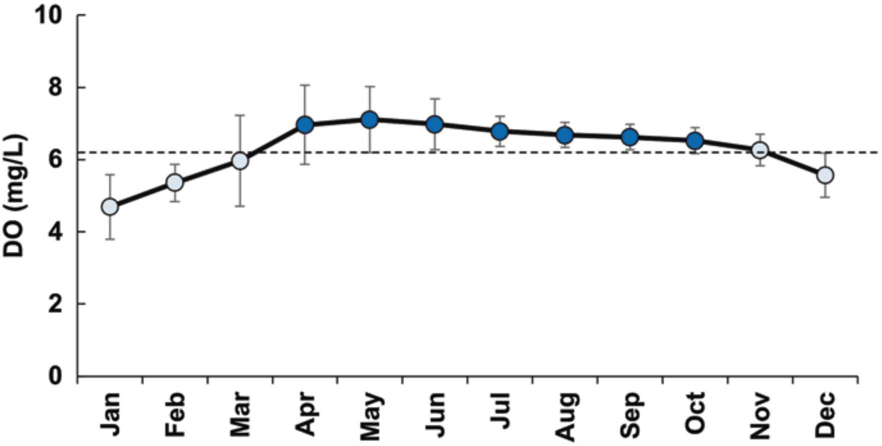


Fig. 7.19 Temporal dynamics of DO concentration (average ± s. d.) on Lake Alchichica Z_{MIX}. (Below the average in light blue, above the average in dark blue; dotted line = annual average)

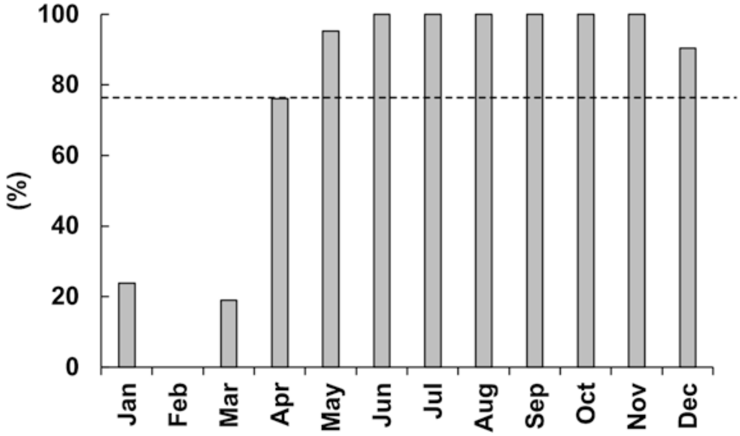


Fig. 7.20 Temporal frequency of anoxia in Lake Alchichica. (dotted line = annual average)

closest to the lake's surface (24 ± 1.9 m). Adame et al. (2008) mention the winter diatom bloom accounts for the hypolimnetic anoxia in Lake Alchichica.

Along the well-established and late stratification, the thermocline is tightly coupled with the oxycline, both located at the metalimnion (Fig. 7.22). The lake is divided in three layers: epilimnion (Z_{MIX}), metalimnion, and hypolimnion.

A homothermal water column is not always a synonym of a well-mixed (circulating) water column. A homothermal water column profile means there is no density related impediment for mixing to take place. However, the actual mixing process requires the wind driving force. In tropical lakes, the mixing process is better reveal by considering both temperature and dissolved oxygen concentration profiles. A

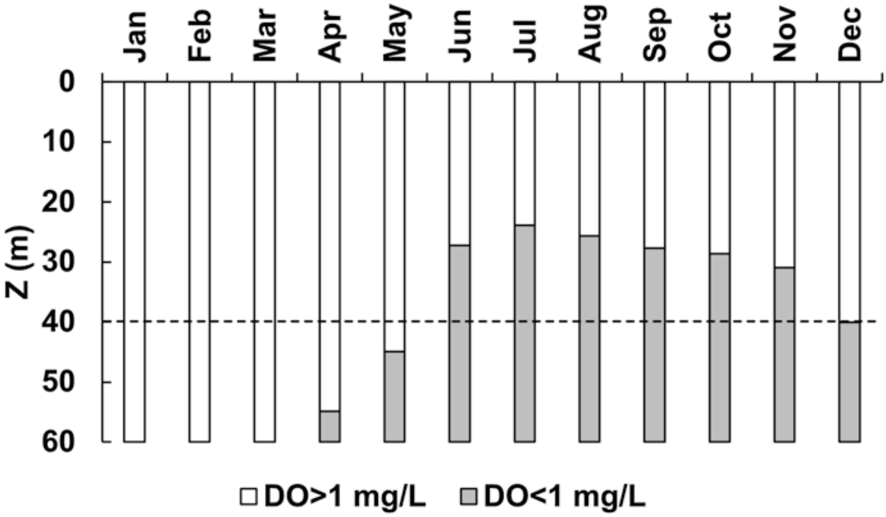
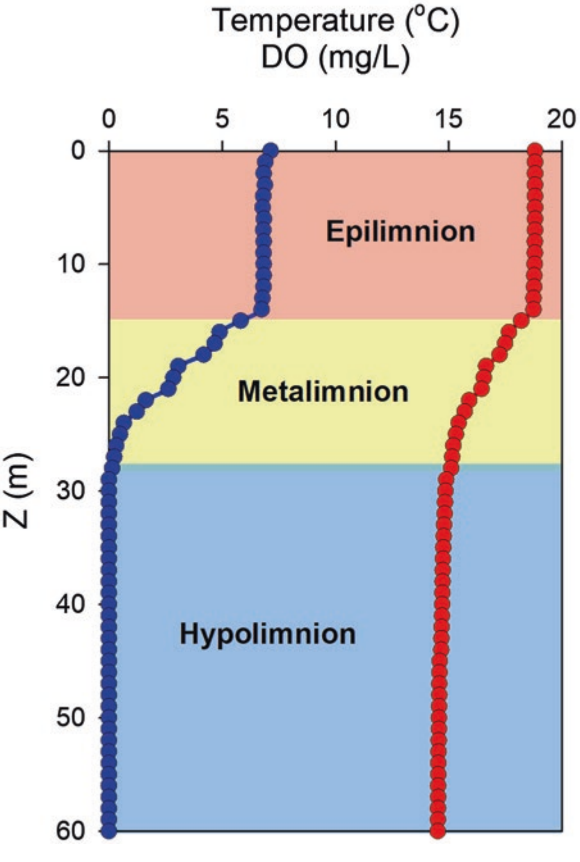


Fig. 7.21 Temporal dynamics of the oxic (DO>1 mg/L) and anoxic (DO<1 mg/L) layers of Lake Alchichica. (dotted line = annual average)

Fig. 7.22 Temperature (red) and DO (blue) profiles in Lake Alchichica (August)



homothermal water column and a homogenous or nearly homogenous DO profile, lacking a deep anoxic layer, indicate the lake is already circulating, and the water column well mixed and re-oxygenated (Fig. 7.23). While a homothermal water column with a clinograde DO profile, and a deep anoxic layer, indicate the water column is not well mixed nor the lake is circulating (Fig. 7.23).

By analyzing a period of 21 years (1998–2018), in January 20 profiles (95.2%) were homothermal (<0.3 °C/m), while just one (4.8%) showed stratification (thermocline), suggesting that in 20 out of 21 years, Alchichica was circulating in January. Differently, 16 (76.2%) out of 21 dissolved oxygen profiles in January indicate aerobic conditions, while 5 (23.8) displayed oxyclines with deep anoxic conditions. This data means, four homothermal profiles in January erroneously indicated the lake was already circulating. Otherwise, 11 (52.4%) out of 21 temperature profiles in December showed thermoclines, while 10 (47.6%) were homothermal. However, 19 (90.5%) out of 21 dissolved oxygen profiles were clinograde with anoxic hypolimnion.

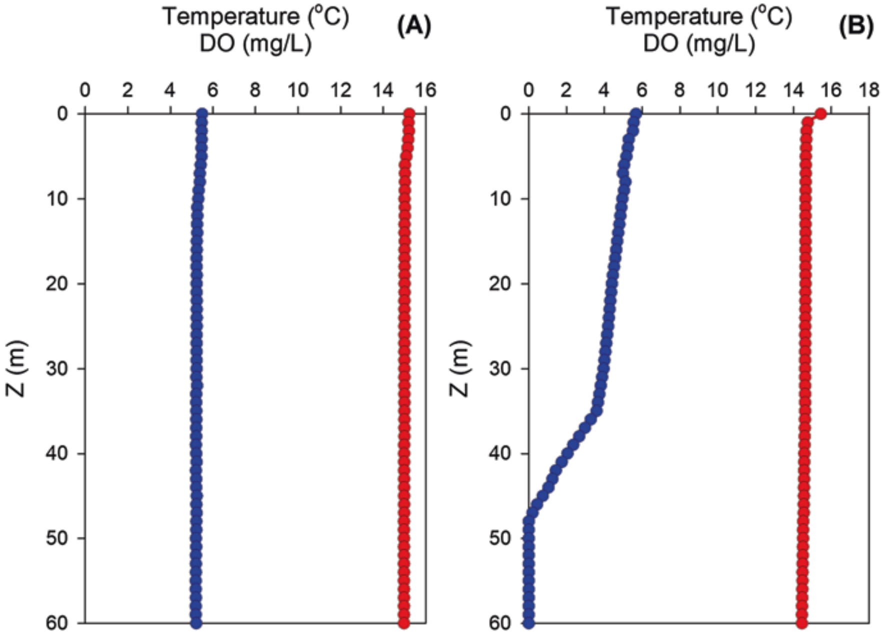


Fig. 7.23 Temperature (red) DO (blue) profiles of Lake Alchichica. A: the water column is circulating and completely mixed (January 2018). B: the lake is not yet in full circulation (note the deep anoxic layer) in spite of the nearly homogeneous temperature profile (January 2001)

7.3.3 DO Diel Cycle

Two-days follow up of DO concentration profiles in Lake Alchichica (Fig. 7.24) reveals the presence of small variations restricted to the metalimnion; the epilimnion (0–27 m) was quite homogeneous with 6.57 ± 0.13 mg/L (6.27–6.87 mg/L), but also the hypolimnion (36–60 m) which remained anoxic. Differently, along the metalimnion the largest diel changes were at the middle portion (30–33 m, 2.03–3.12 mg/L) while smallest at the top (28 m, 0.71 mg/L) and the bottom (35 m, 0.50 mg/L).

It seems quite possible that internal waves (seiches) were responsible for the short-term variations of the DO concentration profiles at the metalimnion. Internal seiches raised the thermocline up to 3 m (Filonov and Alcocer 2002, Filonov et al. 2006, 2015).

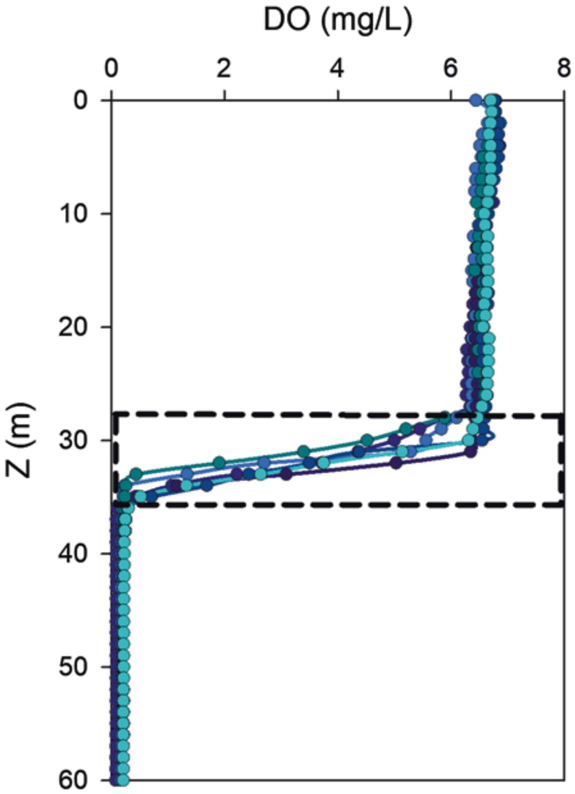


Fig. 7.24 DO concentration diel cycle in Lake Alchichica (October 10–11, 1999). (Dashed line = metalimnion)

7.4 Nutrients

Jorge A. Ramirez-Zierold, Martín Merino-Ibarra, Andrea P. Guzman-Arias,
F. Sergio Castillo-Sandoval, and María Guadalupe Perez-Ramirez

In recent years Central Mexico has undergone rapid human development as repeatedly reported by government environmental agencies (e.g., INEGI, SEMARNAT). Extensive logging and ground water over-exploitation, a growing agricultural and livestock industry too often unrestrained in the use of fertilizers, along with other land use changes, have the potential to affect the biogeochemical cycles of N and P, and therefore the regional in-lake water quality (SNIARN 2009). The prospect of increased nutrient supply to lakes of this region highlights the importance of evaluating their current nutrient status and its effects on primary production.

Lake Alchichica is an oligo-to mesotrophic hyposaline crater Lake, with annual mean Chlorophyll a concentration < 5 µg/L (Alcocer et al. 2000), where nitrogen and phosphorus alternately limit productivity (Ramirez-Olvera et al. 2009). Reported overall concentrations of total N (4.2 ± 0.7 µmol/L) and total P (0.2 ± 0.1 µmol/L) are typically low in the mixed layer (Oliva et al. 2001; Ramos et al. 2008) and have shown spatial-temporal dynamics related to the lake's thermal regime: a marked epilimnetic depletion and hypolimnetic accumulation during the stratification period, and a comparatively high concentration of nutrients homogeneously distributed throughout the water column as circulation takes place.

7.4.1 Phosphorus

Phosphorus is an essential element for cellular structure and function. Its low availability in natural systems (Wu et al. 2000) and its high turnover rates (Benitez-Nelson and Buesseler 1999; Benitez-Nelson 2000; Ammerman et al. 2003) explain its demand by living organisms. Phosphorus is widely distributed in different forms: soluble reactive phosphorus (SRP), dissolved organic phosphorus (DOP), and particulate phosphorus (PP) (e.g., Teubner et al. 2003). After lysis and death of phytoplankton, some of the incorporated phosphorus will be released as inorganic P (e.g., SRP), while some will not be mineralized and be incorporated into the sediment as organic phosphorus. The dissolved phosphorus is again incorporated by the phytoplankton, and again a small part goes to the sediment; process that occurs several times, which makes the amount of phosphorus stored in the sediment considerable (Golterman 2004).

Phosphorus has been widely proposed as the key element for primary production (e.g., Brzakova et al. 2003; Hessen et al. 2003), but such a conclusion has mainly arisen from studies developed in temperate lakes. Conversely, Lewis (2002) suggested that tropical lakes are more likely to be nitrogen limited due to extended stratification periods and rapid progression toward anoxia that led to denitrification.

Even more, some authors have noted the existence of seasonal variations on which nutrient limits phytoplankton growth in lakes (e.g., Steinhart et al. 2002; Morris and Lewis 1988).

Recent (2011–2019) Total Phosphorus (TP) concentrations found in Lake Alchichica has a mean value of 1.7 ± 1.8 μmol/L in Z_{MIX}, and mean hypolimnetic values of 2.6 ± 2.3 μmol/L, which are consistent with an oligo- to mesotrophic status (Nurnberg 1996). The lowest concentrations are observed: 1) during the winter due to a full water-column diatom (*Cyclotella alchichicana* and *C. choctawacheeana*) bloom, and 2) in Z_{MIX} during the well-established and late stratification periods. In April–May, an increase of TP and a decrease of soluble reactive phosphorus (SRP) concentrations are likely a consequence of the spring bloom of the nitrogen-fixing cyanobacterium *Nodularia* aff. *spumigena* that occurs regularly at the onset of the early stratification period (Fig. 7.25).

As stratification progresses, an accumulation of SRP occurs in the hypolimnetic layer, mostly due to the remineralization of organic matter, and reaches a maximum of ~3.5 μmol/L in the near bottom water at the end of this period.

In oligotrophic waters, DOP typically constitutes the major fraction of total dissolved P. Thus, regeneration of P from DOP has been shown to play a significant role in supplying the P required for biological production (e.g., Karl and Björkman 2002), particularly when the availability of dissolved inorganic phosphorus (e.g., SRP) is low in Z_{EU} (Fig. 7.2).

DOP utilization as a phosphorus source by primary producers and microbial communities has been intricately linked to microbial alkaline phosphatases whose affiliation and diversity is largely unknown (e.g., Cunha et al. 2010). A larger potential community for DOP utilization in Lake Alchichica microbialites was consistent with the TN:TP ratio found in surrounding water (49.5 ± 27.0), suggesting P limitation within these assemblages (see also Chap. 22, Microbialites: Diversity Hotspots in the Mexican Plateau). There is a high potential for DOP utilization through microbial Alkaline phosphatases in both the microbialites and the bacterioplankton of Lake Alchichica (Valdespino-Castillo et al. 2014). Organic phosphorus seems to be strongly utilized in Lake Alchichica (Valdespino-Castillo et al. 2017), which would be consistent with the presumably low P inputs from groundwater (Kazmierczak et al. 2011) and atmospheric deposition (Oseguera et al. 2010a, b). The utilization of DOP would be important to regenerate the inorganic phosphorus required to sustain the relatively high primary production during the mesotrophic stages of the lake (Ramirez-Olvera et al. 2009; Macek et al. 2009).

Recorded mean values of Particulate Organic Phosphorus (POP) in the Z_{MIX} in 2005–2008 were 0.8 ± 0.5 μmol/L. Peak POP concentrations of up to 1.9 μmol/L, occurred during the early stratification (May–July), presumably related to the cyanobacterial bloom typical of this period (Alcocer et al. unpublished data). It is important to highlight that 2007 and 2008 were characterized by POP concentrations three times higher than those registered in the two previous years. However, such high concentrations had no echo on the other measured variables (e.g., SRP, particulate organic carbon, chlorophyll a), suggesting the probable presence of a – still to be identified – allochthonous, not bio-available, particulate phosphorus compound.

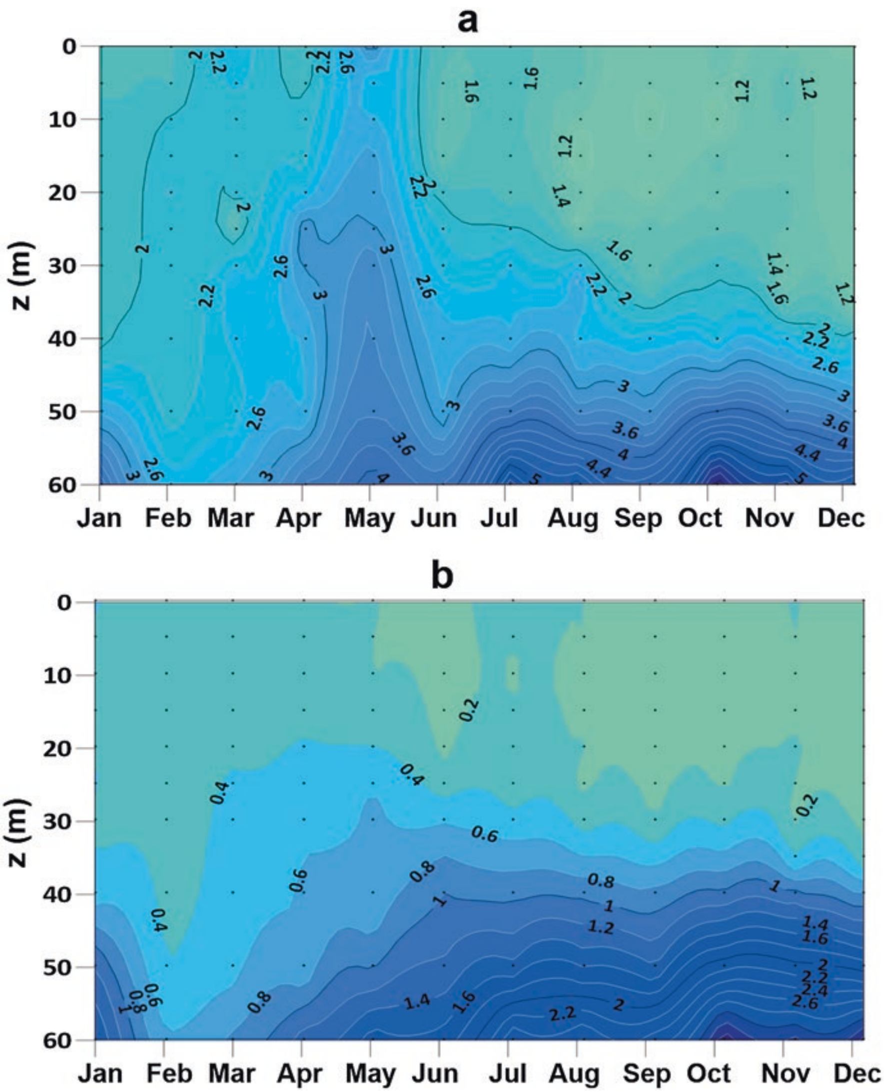


Fig. 7.25 Time-depth distributions of mean (a) TP and (b) SRP (μmol/L) in Lake Alchichica (2011–2019)

7.4.2 *Nitrogen*

The aquatic N cycle entails multiple transformations performed primarily by microbes. While N is lost via heterotrophic denitrification and/or anaerobic ammonium oxidation (anammox) in suboxic or anoxic environments, nitrification links the sources (N fixation) and sinks (denitrification and anammox) of fixed reactive N by transforming ammonium (NH_4^+) to nitrite (NO_2^-) and subsequently nitrate (NO_3^-) in oxic or dysoxic environments (Thamdrup 2012).

In contrast, dissimilatory nitrate reduction to ammonium (DNRA) is an alternative pathway that retains N by recycling NO_3^- to NH_4^+ in suboxic or anoxic environments. Nitrification and denitrification are functionally coupled and are widely used as models for ecology studies, because they are intrinsically linked to emissions of nitrous oxide (N_2O), a potent greenhouse gas (Kowalchuk and Stephen 2001; Philippot and Hallin 2005). Denitrification is an important microbial dissimilatory process that removes N from aquatic ecosystems. The denitrification pathway includes four enzymatically catalyzed reductive steps: nitrate reduction, nitrite reduction, nitric oxide reduction and N_2O reduction (Zumft 1997).

In Lake Alchichica, mean (2011–2019) Total Nitrogen (TN) concentrations in the Z_{MIX} (49.8 ± 17.1 μmol/L), and mean hypolimnetic values (z = 20–60 m) of 55.8 ± 20.5 μmol/L reflect its oligo-to mesotrophic status (Nurnberg 1996). Minimum Z_{MIX} concentrations are observed from July to December, during the well-established stratification period and the beginning of the winter mixing period. The TN concentrations raise and spread over the entire water column in January–February, due to the winter diatom bloom and again in April–May due to the *N.* aff. *spumigena* spring bloom (Fig. 7.26).

N_2 fixation has been recognized as a major nitrogen source in lakes, contributing with 60 to up to 81% of the total N inputs (Horne and Galat 1985; Levine and Schindler 1992). In Lake Alchichica, an heterocystous cyanobacterial species, *N.* aff. *spumigena*, occurs as a free-living form in the water column, and large densities of this species coincide with the end of the wind-driven winter upwelling (Alcocer et al. 2000; Filonov and Alcocer 2002).

Falcón et al. (2002) reported that nitrogen fixation rates by *N.* aff. *spumigena* are of 12.47–92.91 μmol $C_2H_4/m^2/hr$. The intensity of growth and extent of the *N.* aff. *spumigena* bloom in Lake Alchichica has been reported to differ among years; the intensity of growth has been correlated to the annual concentration of nitrates, indicating the role of the cyanobacteria as a source of new nitrogen to the lake (Oliva et al. 2009). Additionally, a vast genetic diversity for N cycling has been described for the microbialites from Alchichica, where microbialites are known to actively fix nitrogen (Alcantara et al. 2017, see also Chap. 22).

Dissolved inorganic species of nitrogen showed different distributions: ammonium nitrogen (NH_4^+) is depleted year-round in Z_{MIX} (1.0 ± 1.0 μmol/L), but it builds up progressively in the hypolimnion reaching a maximum concentration (~30 μmol/L) at the bottom of the lake in the late stratification (Fig. 7.27).

The progressive accumulation of NH_4^+ in bottom waters could be derived from the decaying diatoms after the winter bloom; on the other hand, Pajares et al. (2017) reported that anoxic conditions at the end of stratification were characterized by a relative increase in the abundance of the nrfA gene (dissimilatory nitrate reduction to ammonium) with depth, which was positively correlated with increasing NH_4^+ concentration.

The oxidized nitrogen species, nitrite (NO_2^-) and nitrate (NO_3^-), are also in low concentrations in Z_{MIX} throughout the year. Nevertheless, starting at the early stratification period, it has been observed an increase in both concentrations that built up from the metalimnetic layer towards the hypolimnion (Fig. 7.28). This is mostly due

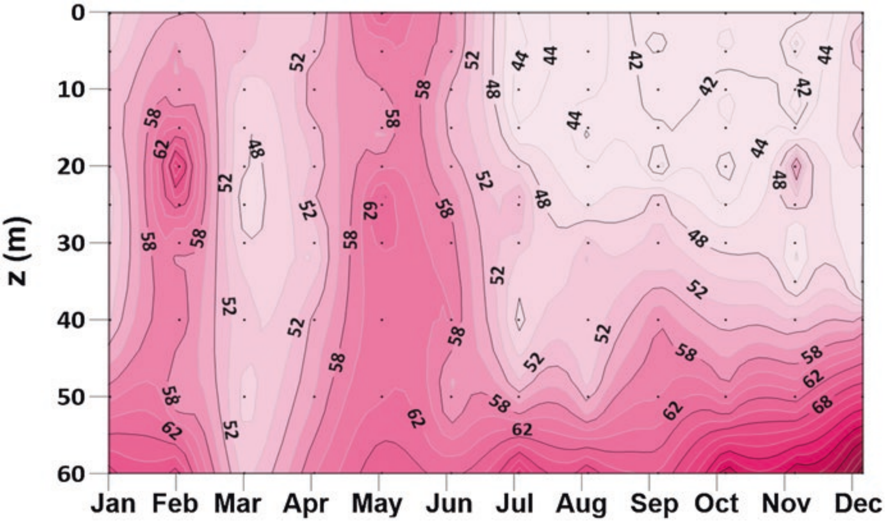


Fig. 7.26 Time-depth distributions of mean TN (μmol/L) in Lake Alchichica (2011–2019)

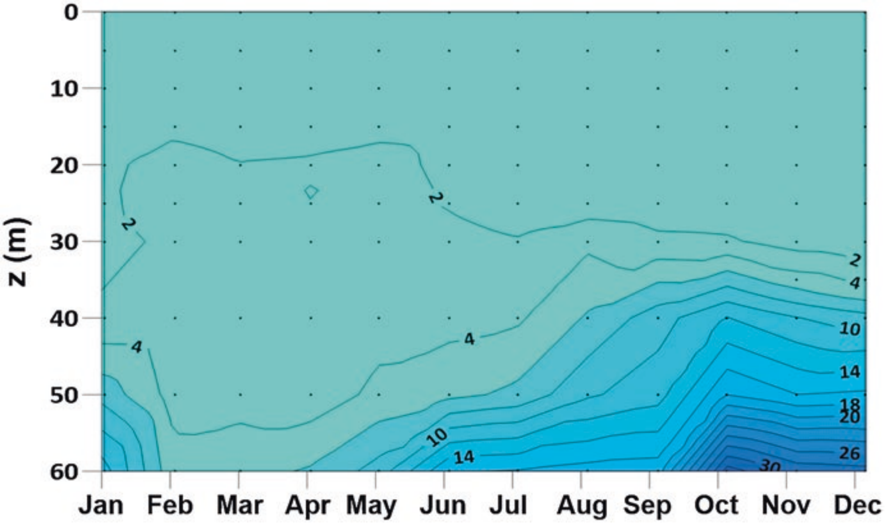


Fig. 7.27 Time-depth distributions of mean NH_4^+ (μmol/L) in Lake Alchichica (2011–2019)

to the remineralization of organic matter originated from the previous *N.* aff. *spumigena* spring bloom. These observations suggest that nitrogen fixed from the atmosphere constitutes an important input of this element into the lake.

Subsequently, it also appears that most of this fixed nitrogen in Lake Alchichica is exported below the thermocline instead of recycled in the Z_{MIX}, where under anoxic conditions it could lead to denitrification, hence sustaining an apparent nitrogen deficiency at surface waters while increasing the trophic status of the lake over time.

Pajares et al. (2017) discussed the effect of temperature and dissolved oxygen stratification on the shaping of the distribution of picoplankton and functional N genes in this lake, highlighting the importance of thermal stratification as one of the main factors influencing the genetic potential for N transformations within the water column in warm-monomictic tropical lakes. These communities also varied in relation to nutrient availability and underwent temporal changes throughout the water column. The amoA genes (ammonium oxidation), along with autotrophic picoplankton, were more abundant during the stratification, indicating that nitrification could be potentially more important during this period, mainly at the oxycline layer. On the other hand, denitrifying genes showed strong variations with highest gene copy numbers at the oxycline and hypolimnion layers.

Mean values of particulate organic nitrogen (PON) in the mixed layer in 2005–2008 were 6.6 ± 4.6 μmol/L. Maximum PON concentrations of up to 16.1 μmol/L, occurred during the early stratification (May–July), presumably related to the cyanobacterial bloom typical of this period (Alcocer et al. unpublished data). Additionally, Filonov and Alcocer (2002) and Filonov et al. (2006) found that breeze circulation in Lake Alchichica, occurring over the entire lake throughout the year, exerts a strong effect on water temperature and therefore induces variations in the thermocline depth. They also found that intense dynamic processes related to baroclinic seiches induce vertical fluctuation of the thermocline (1–1.5 m). Both processes can be expected to play an important role in the exchange of nutrients and particles between the Z_{MIX} and the metalimnion and could help explaining the great variability registered for particulate elemental ratios (Alcocer et al., unpublished data).

7.4.3 Silica

Lake Alchichica is particularly limited in silicates (Si) concentration (5.1 ± 4.8 μmol/L); however, large (>50 μm) diatoms dominate the phytoplankton biomass. Major epilimnetic concentrations (June–July) precedes the first deep chlorophyll maximum (DCM) due to *Cyclotella alchichicana* in August (Fig. 7.29).

Silicates have shown to be limiting primary production particularly during the late stratification and circulation periods when a diatom bloom takes place, although it could be considered that N and Si co-limited the phytoplankton growth (Del Pino-Bastida 2013). Suspended particulate silica in the water column of Lake Alchichica is dominated by the biogenic fraction, which doubles (mean 41.5 μmol/L) the lithogenic silica fraction (mean 21.1 μmol/L; Perez-Ramirez 2015). Most of this biogenic silica is exported below the thermocline instead of recycled in the Z_{MIX}.

The decline of the winter diatom bloom is most likely related to the low silica concentrations (SRSi <17 μmol/L) and the high diatom exportation rates. The dominant settling species, the diatom *Cyclotella alchichicana*, which is composed >90%

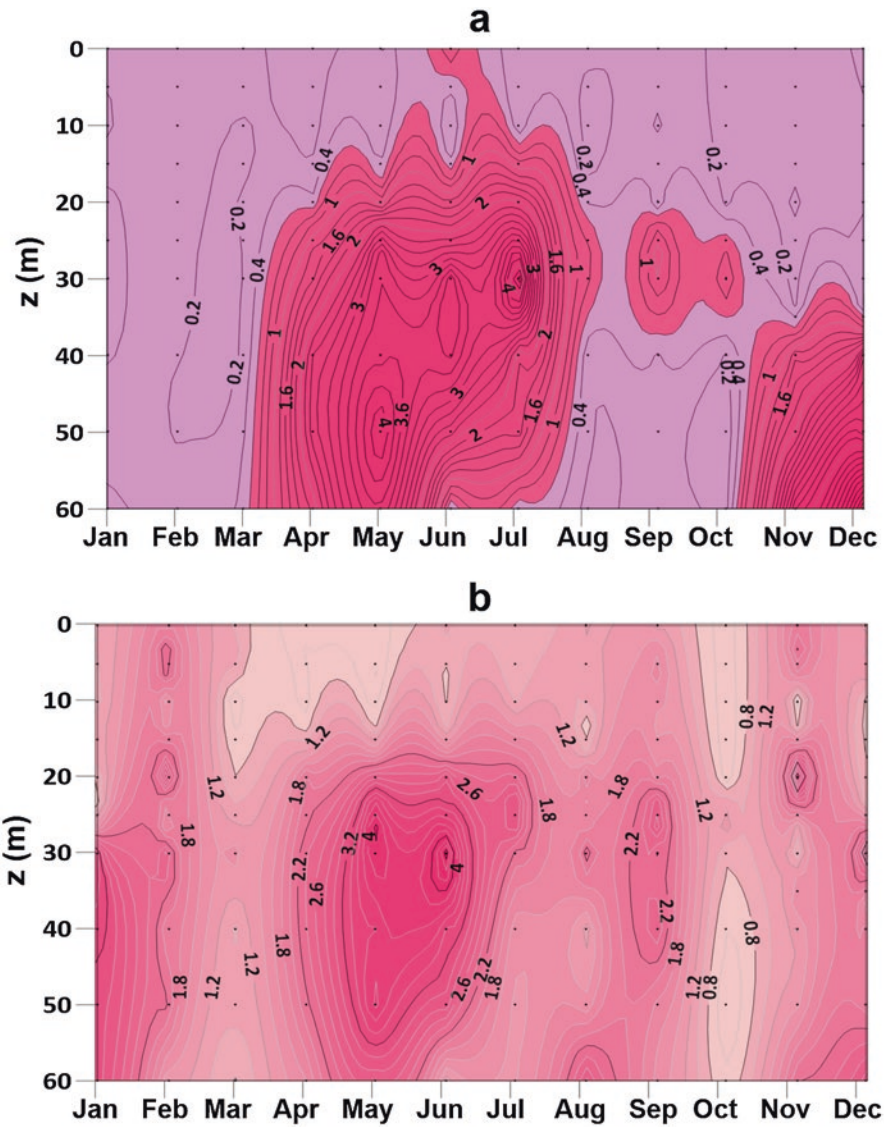


Fig. 7.28 Time-depth distributions of mean (a) NO_2^- and (b) NO_3^- (μmol/L) Lake Alchichica (2011–2019)

of silica, contributes with almost half (147 g/m^2 year, Ardiles et al. 2012) of the high total vertical biogenic silica flux (307 g/m^2 year) towards the bottom of this deep lake (Pérez-Ramírez 2015), a process that is likely perpetuating the silicate limitation there.

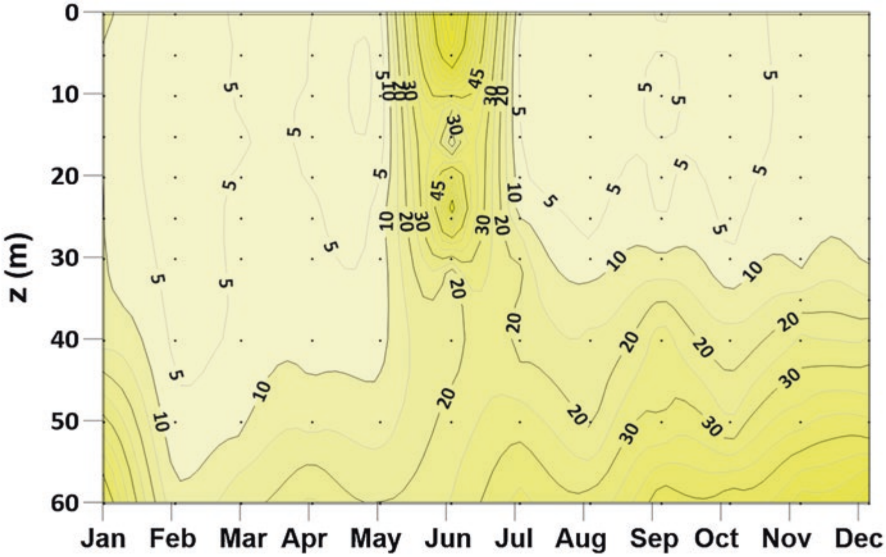


Fig. 7.29 Time-depth distribution of mean soluble reactive silica (SRSi; µmol/L) in Lake Alchichica (2011–2019)

7.4.4 Nutrient Stoichiometry

Nutrient ratios (e.g., N:P) have been related to nutrient limitation of algal growth in lakes. Retention of nutrients by sedimentation and loss by denitrification, reduces the nutrient concentrations in the water column, thereby enhancing nutrient limitation. Differential retention of nitrogen and phosphorus alters their ratios in lakes and thereby contributes to determine whether nitrogen or phosphorus limits algal growth. Only in deep lakes with relatively short residence times is the N:P ratio enhanced by greater retention of phosphorus compared to nitrogen (Verburg et al. 2013).

Mainly four different approaches or experimental designs have been used to detect and identify nutrient limitation of phytoplankton (Talling and Lemoalle 1998): (a) ambient nutrient concentrations, (b) elemental composition of algal biomass, (c) growth response to nutrient additions, and (d) short-period physiological assays.

Very few studies on nutrient limitation have been carried out in tropical and temperate saline lakes (e.g., Lakes Chilwa, Sonachi, and Elmenteita in Africa); most have been on freshwater lakes (e.g., Naivasha and Baringo in Africa, Valencia in Venezuela, Dom Helvécio in Brazil), reservoirs (e.g., Pansoon in Malaysia), and rivers (e.g., Blue and White Niles, Amazons).

Talling and Talling (1965), based on the information from East and Central African inland waters, suggested that N-limitation rather than P-limitation might be regionally prevalent. Nevertheless, there is increasing evidence as reviewed by

Lewis (1996) and Talling and Lemoalle (1998) that N-limitation is of widespread occurrence in tropical lakes and rivers, e.g., Africa, Asia, South America. However, Lewis (2002) stated that this evidence was "mostly circumstantial rather than experimental but involved several kinds of indicators that were known to correlate well with experimental evidence".

The reduced number of studies carried out in some Mexican water bodies so far (e.g., Bernal-Brooks 2002; Bernal-Brooks 2003; Lopez and Davalos-Lind 1998) have pointed out the prevalence of a nitrogen and phosphorus co-limitation attributed to the scarce availability of both nutrients. Nevertheless, this conclusion has arisen from nutrient enrichment bioassays carried out in few samples representing "snap shots" in the yearly cycle of the lakes.

In Lake Alchichica both N and P have been found to limit biological productivity in the water column (Ramirez-Olvera et al. 2009), although N seems to be the limiting element most frequently found, due to low dissolved inorganic nitrogen (DIN) concentrations found in the Z_{MIX} (0.7–3.8 µmol/L) during the year (Ramirez-Olvera et al. 2009; Ardiles et al. 2012).

Additionally, some of the indicators of N-deficiency in tropical lakes mentioned by Lewis (2002) are recognized in Lake Alchichica such as the occurrence of a *Nodularia* aff. *spumigena*, a heterocystous nitrogen-fixing cyanobacterial bloom (Oliva et al. 2009), and prolonged periods of low DIN:SRP ratios (13.9 ± 14.5). Previous studies of nutrient enrichment experiments (Ramos et al. 2008, Ramírez-Olvera 2009) concluded that phytoplankton in Lake Alchichica is primarily N limited, followed by silica (Del Pino-Bastida 2013).

Recent available data from Lake Alchichica (2011–2019) revealed that TN and TP concentrations at the Z_{MIX} were relatively low (49.4 ± 17.0 and 1.7 ± 1.8 µmol/L, respectively) with a TN:TP ratio of 48.9 ± 27.7 (Alcocer et al., unpublish data), which point out to a phosphorus limitation in the lake.

Nevertheless, DIN:SRP ratio, from the same data set, fluctuated from 6 to 48 (Fig. 7.30). These data suggest that there is a wide variation in the nutrient responsible of algal growth limitation throughout the year. Ramirez-Olvera et al. (2009) determined that during 2004–2005 phosphorus limited phytoplankton growth most of the time (41.7%), followed by nitrogen (33.3%), and both nutrients (25.0%). The authors discussed that this apparent alternation in nitrogen and phosphorus limitation in Lake Alchichica could be attributed to the combination of both natural conditions that would favor nitrogen limitation (e.g., young volcanic terrain rich in phosphorus), and of anthropogenic impacts (e.g., agricultural nitrogen fertilization) which would cause phosphorus limitation.

On the other hand, when considering only DIN as the available nitrogen source and TP concentration as the potentially available P-pool in the lake, N:P ratio (e.g., DIN:TP = 1–8) pointed out more clearly towards a prevalent and intense N-deficiency in the Z_{MIX} over time (Fig. 7.31).

During the circulation period of Lake Alchichica neither N nor P seems to limit the phytoplankton growth suggesting Si, and the Si/N ratio, could be playing key roles (Ramos et al. 2008) in controlling the extent of the regularly observed diatom winter bloom. Thus, it is quite possible that if N inputs are high and P is not limiting,

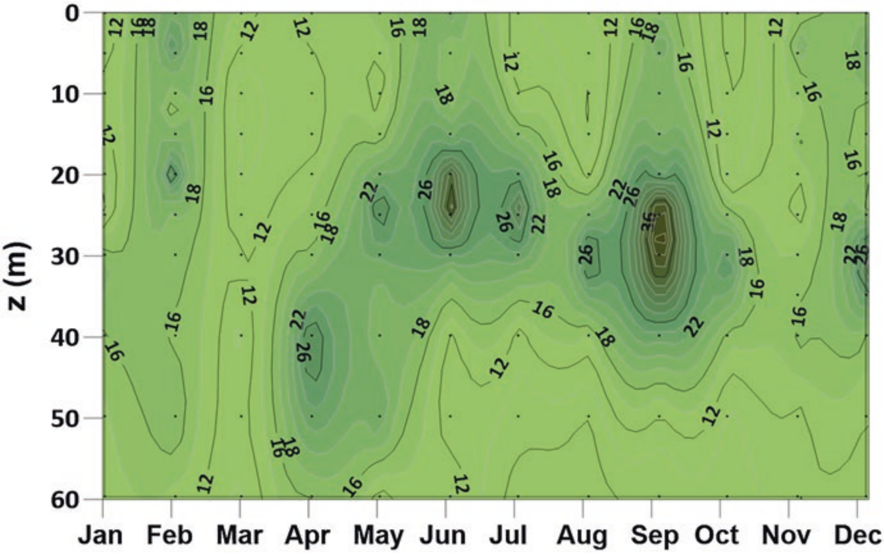


Fig. 7.30 Time-depth distribution of mean DIN:SRP in Lake Alchichica (2001–2019)

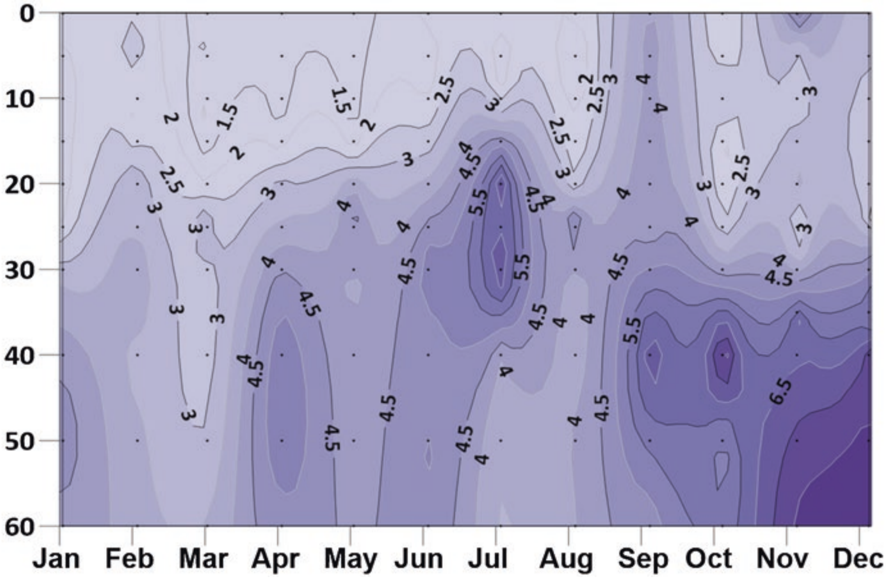


Fig. 7.31 Time-depth distribution of mean DIN:TP in Lake Alchichica (2001–2019)

the late stratification Si limitation (i.e., Si/N ≤ 1) may reduce the magnitude or duration of the following diatom bloom (e.g., 1999 and 2001 winter bloom in Lake Alchichica). Adame et al. (2008) had similar findings regarding the role of Si/N ratios controlling the magnitude and extent of the diatom bloom. The authors observed that Si/N ratios >1 were present for most of the year, thus favoring the large size-fraction phytoplankton (i.e., large, and heavily silicified diatoms).

7.5 Dissolved and Particulate Carbon

Daniela Cortés Guzmán, Javier Alcocer, and Luis A. Oseguera

The role of freshwater ecosystems as active sites of processing and storage in the carbon cycle has been recently recognized (Cole et al. 2007). Worldwide, lakes cover only 2% of the continental surface yet have a disproportionately important role in the carbon cycle, either as sinks of organic matter (OM) or greenhouse gases sources to the atmosphere (Cole et al. 2007, Tranvik et al. 2018). Inland waters transform and transport the materials from their drainage basin, integrating biogeochemical processes and materials from large areas. Transformations include primary production from dissolved inorganic carbon (DIC) and degradation and mineralization of the OM. Fluxes of carbon out of lakes include downstream transport, outgassing to the atmosphere, and burial in the sediments (Wetzel 2001). Carbon inputs into the lakes are stored or mineralized and release back to the atmosphere as CO_2 and CH_4 (Song et al. 2018).

Lake Alchichica characteristics likely influence the carbon dynamics within the lake. Lake Alchichica is alkaline and saline (Vilaclara et al. 1993), which relates directly to DIC processing. It is oligotrophic and groundwater-fed with no surface influents (Oseguera et al. 2011), which defines the organic carbon dynamics. The algal blooms in Lake Alchichica (Oliva et al. 2001) are closely related to the particulate organic carbon (POC) dynamics. Finally, the extended stratification season with the development of an anoxic hypolimnion, characteristic of tropical warm monomictic lakes (Alcocer et al. 2000), influences the OM processing.

7.5.1 Dissolved Carbon

Dissolved carbon is the base for autotrophic and heterotrophic production. Organic and inorganic dissolved carbon regulate light conditions, nutrient availability, and productivity in aquatic ecosystems (Song et al. 2018).

Total Dissolved Carbon

Total dissolved carbon (TDC) in Lake Alchichica varies between 326.2 and 460.4 mg/L (average 429.6 ± 25.5 mg/L). The highest values are found in June (453.8 ± 3.3 mg/L) and the lowest values in September (361.6 ± 25.5 mg/L) (Table 7.1).

TDC distribution varies temporarily (F = 38.32, $p < 0.001$). The highest values are found between June and July (453.8 ± 3.3 to 453.6 ± 5.5 mg/L) and lowest values in September (361.6 ± 25.5 mg/L) (Table 7.1). TDC concentrations do not vary significantly between layers (F = 0.594, $p > 0.05$). DIC contributes to 98.6–99.1% of the TDC in Lake Alchichica; therefore, TDC dynamics are driven by DIC.

Dissolved Inorganic Carbon

Dissolved CO_2, carbonates (CO_3^{2-}), and bicarbonates (HCO_3^-) constitute the dissolved inorganic carbon (DIC) stock in a water body. DIC concentration in lakes results from the drainage basin's geology, the water column stratification, photosynthetic processes, organic matter degradation, respiration rates, and the influx of CO_2 and HCO_3^- from weathering, atmospheric inputs, and groundwaters (Wetzel 2001). DIC is a significant determinant of the photosynthetic processes and the lakes' productivity patterns (Rinta et al. 2015). In Lake Alchichica, particularly, DIC is a major source for the microbialites. Microbialites are built through chemical and biological carbonates precipitation (see Chap. 22). The microbiological activity taking place in the microbialites ring removes DIC from the water column through aragonite ($CaCO_3$) and hydromagnesite ($Mg_5(CO_3)_4(OH)_2{\cdot}4H_2O$) precipitation (Gérard et al. 2013).

DIC concentration in Lake Alchichica varies between 326.2 and 456.5 mg/L (average 422.3 ± 38.4 mg/L) (Fig. 7.32). DIC distribution varies temporarily (F = 39.49, $p < 0.001$) (Fig. 7.33). The highest values are found between June and July (449.2 ± 5.5 to 449.6 ± 3.3 mg/L) and the lowest values in September (357.0 ± 25.5 mg/L) (Table 7.1).

Table 7.1 Dissolved carbon concentrations (mg/L) (mean ± s.d., minimum and maximum) in Lake Alchichica. (DOC: dissolved organic carbon, DIC: dissolved inorganic carbon, TDC: total dissolved carbon)

		Jan	**Feb**	**Mar**	**Apr**	**May**	**Jun**	**Jul**	**Aug**	**Sep**	**Oct**	**Nov**	**Dec**
DOC	*Mean*	4.6	4.6	4.7	4	4	4.2	4.4	4.6	4.6	4.6	4.6	4.6
	s.d.	0.2	0.2	0.3	0.2	0.2	0.4	0.4	0.2	0.3	0.5	0.3	0.2
	Min	4.3	4.3	4.4	3.7	3.7	3.7	3.8	4.3	4.1	4.2	4.3	4.3
	Max	*5.0*	*4.9*	*5.4*	*4.2*	*4.5*	*4.9*	*4.8*	*5.0*	*5.1*	*5.9*	*5.3*	*5.0*
DIC	*Mean*	427.5	414.7	431.0	433.4	438.5	449.6	449.2	404.2	357.0	397.2	433.5	422
	s.d.	6.1	7.9	5.0	7.7	5.0	3.3	5.5	12.5	25.5	14.4	7.1	2.9
	Min	418.8	*407*	*423.5*	*423.5*	*429.5*	*444.2*	*442.5*	*388.1*	*326.2*	*379.7*	*427.4*	*419*
	Max	435.2	*427.8*	*437.4*	*445.2*	*443.6*	*453.9*	*456.5*	*423.2*	*394.6*	*411.5*	*445.3*	*426.2*
TDC	*Mean*	432.0	419.3	435.0	437.5	442.6	453.8	453.6	408.8	361.6	400.6	438.1	426.6
	s.d.	6.0	7.8	4.7	8.1	4.0	3.3	5.5	12.6	25.5	16.3	6.8	2.8
	Min	423.6	411.6	428.9	427.5	433.6	448.6	446.8	392.8	331	379.7	432	423.7
	Max	*439.7*	*432.2*	*442.1*	*449.3*	*447.9*	*457.6*	*460.8*	*428*	*399.5*	*416.2*	*449.6*	*430.6*

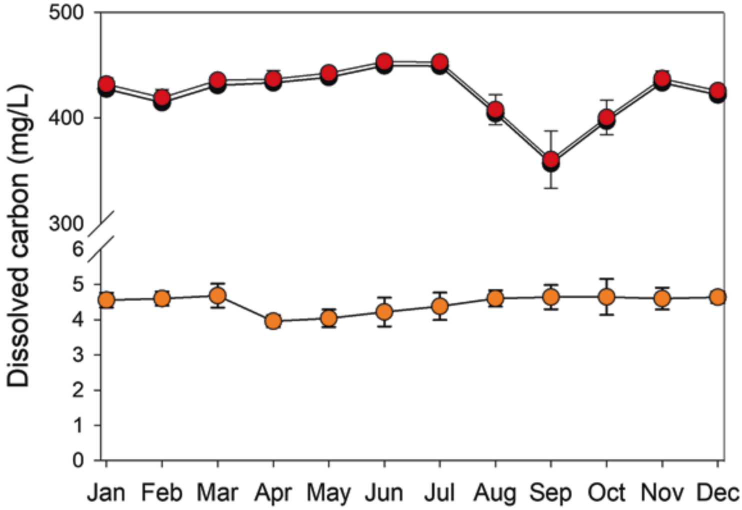


Fig. 7.32 Temporal variation (mean ± s.d.) of TDC (red circles), DIC (black circles), and DOC (orange circles) concentrations along the year in Lake Alchichica

DIC concentrations do not vary significantly between layers ($F = 0.955, p > 0.05$). Slightly higher DIC values are found in the metalimnion (430.7 ± 16.7 mg/L) and hypolimnion (430.2 ± 26.3 mg/L), while the lowest values are found in the mixed layer (422.1 ± 25.5 mg/L). Weathering and groundwater likely provide a relatively constant input to the lake; therefore, DIC variation is low (3–6%).

Carbonate is among the dominant ions in Lake Alchichica (Sigala et al. 2017) and then represents a constant DIC supply to the water column. DIC concentrations in Lake Alchichica are correlated with pH ($\rho = 0.35$, $p < 0.01$), which is expected given that the carbonates equilibrium is a main driver of pH. Although DIC concentrations in saline, oligotrophic lakes can be 6 to 20 times higher than DOC concentrations (Song et al. 2018), DIC in Lake Alchichica was 100 times higher than DOC (Table 7.1).

Dissolved Organic Carbon

Dissolved organic carbon (DOC) originates from the degradation and dissolution of particulate organic matter (Wetzel 2001). Most DOC in lakes is allochthonous, but the trophic state also has a strong effect on DOC's availability in the water column being higher in eutrophic lakes (Song et al. 2018). DOC is an essential component in the functioning of lakes because it is the basis of heterotrophic and biogeochemical processes (Steinberg et al. 2006). Furthermore, DOC mineralization through degradation is a significant source of CO_2 to the atmosphere (Tranvik et al. 2018).

DOC in Lake Alchichica varies between 3.7 and 5.9 mg/L (average 4.5 ± 0.4 mg/L). DOC distribution varies temporarily ($F = 11.25$, $p < 0.001$) and

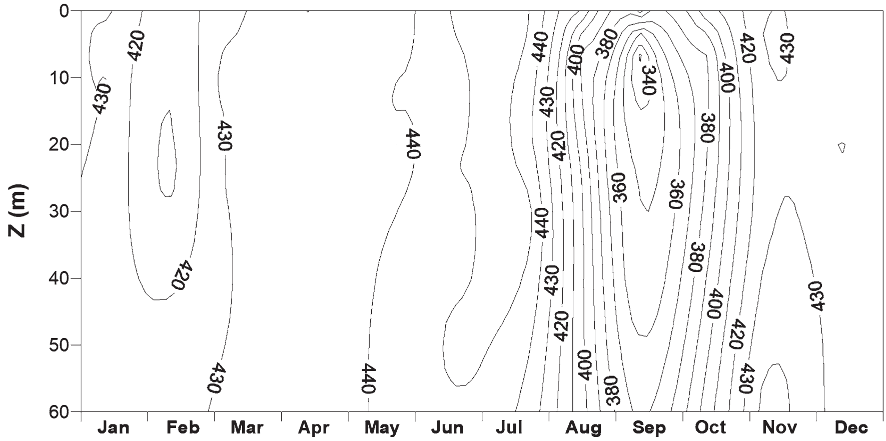


Fig. 7.33 Depth-time diagram of DIC concentration (mg/L) in Lake Alchichica

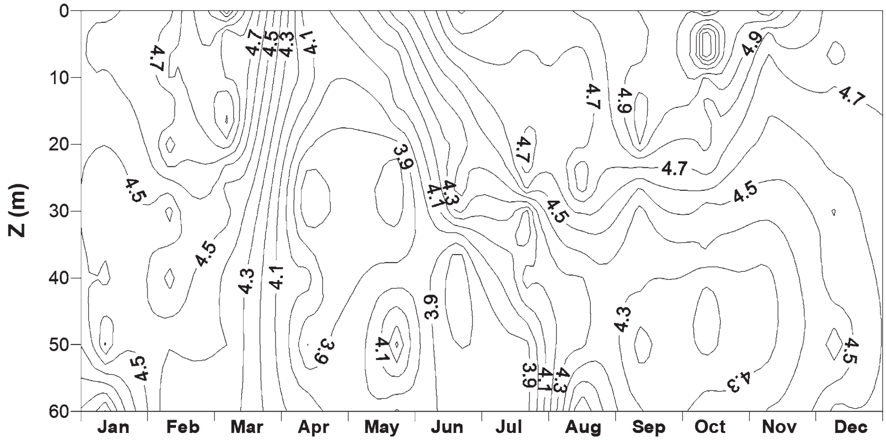


Fig. 7.34 Depth-time diagram of the DOC concentration (mg/L) in Lake Alchichica

along the water column (F = 11.03, $p < 0.001$) (Fig. 7.34). The highest values are found between April and June (4.0 ± 0.2 to 4.2 ± 0.4 mg/L), after the diatom bloom, and the lowest values between July and March (4.4 ± 0.4 to 4.7 ± 0.3 mg/L) (Table 7.1). DOC values are higher in the mixed layer (4.7 ± 0.3 mg/L) and the metalimnion (4.5 ± 0.3 mg/L), while lower in the hypolimnion (4.1 ± 0.3 mg/L).

DOC sources in lakes are usually inputs from the terrestrial ecosystems (Cole et al. 2007); however, Lake Alchichica does not have superficial influents (Alcocer et al. 2014b), and its catchment is reduced. DOC source to the lake is mainly autochthonous through primary production, which is limited due to its oligotrophic status (Alcocer et al. 2014a).

DOC concentrations in Lake Alchichica correlate with temperature ($\rho = 0.51$, $p < 0.001$), dissolved oxygen concentration ($\rho = 0.52$, $p < 0.001$), pH ($\rho = -0.41$, $p < 0.001$), and the mixed layer depth -Z_{MIX}- ($\rho = 0.35$, $p < 0.001$). DOC concentration reaches maximum values in the stratification period along with warmer water temperatures and higher DO concentrations, particularly in the Z_{MIX} where DOC concentrations are higher (Fig. 7.32).

Overall, the temporal variation of DOC concentration is low, most likely related to refractory DOC stock (Rinta et al. 2015). The development of a prompt anoxic hypolimnion in Lake Alchichica and the slow degradation of the organic matter's refractory compounds could explain the low temporal variation in DOC concentrations in Lake Alchichica (Alcocer et al. 2014b). Otherwise, there are spatial differences along the water column. The vertical distribution of DOC is related to the thermal pattern and the development of algal blooms. When particulate organic matter increases, such as in phytoplankton blooms (e.g., diatoms, cyanobacteria), DOC is released to the water column, an essential source for the microbial loop, particularly in oligotrophic lakes (Alcocer et al. 2014a, Song et al. 2018).

Autochthonous phytoplankton is the primary source of DOC in Lake Alchichica. After the *Nodularia* aff. *spumigena* bloom between April and July, DOC concentrations increase. Between September and October, in the well-established stratification, Z_{MIX} and Z_{EU} are deep and broad; both conditions favor developing a deep chlorophyll maximum (DCM) that increases the DOC values (Fig. 7.32).

7.5.2 Particulate Carbon

Particulate carbon in lakes is the fraction of carbon, mainly organic, formed by *in situ* photosynthesis (autochthonous) or imported (allochthonous) from the watershed; it is consumed by the organisms or ultimately exported to the sediments (Wetzel 1984). Although particulate is the minor fraction of total carbon in lake ecosystems, it plays a vital role in sequestering carbon through its exportation to the sediments (Duan et al. 2014).

Total Particulate Carbon

Total particulate carbon (TPC) in Lake Alchichica varies between 0.007 and 1.81 mg/L (average 0.50 ± 0.24 mg/L). TPC distribution varies temporarily ($F = 10.30$, $p < 0.001$) and spatially ($F = 13.89$, $p < 0.001$). Highest values are found in January (0.69 ± 0.27 mg/L) and lowest in September (0.39 ± 0.12 mg/L) (Table 7.2).

TPC shows an increase in December–January, likely related to inorganic particles' resuspension from the sediments during the circulation period, perhaps from the stromatolites and ostracods (*Candona alchichica*) shells (Fig. 7.35).

Table 7.2 Particulate carbon concentrations (mg/L) (mean ± s.d., minimum and maximum) in Lake Alchichica. (POC: particulate organic carbon, PIC: particulate inorganic carbon, TPC: total particulate carbon)

		Jan	**Feb**	**Mar**	**Apr**	**May**	**Jun**	**Jul**	**Aug**	**Sep**	**Oct**	**Nov**	**Dec**
POC	Mean	0.36	0.41	0.42	0.42	0.35	0.34	0.32	0.36	0.33	0.47	0.42	0.33
	s.d.	0.16	0.22	0.27	0.20	0.18	0.10	0.09	0.12	0.08	0.16	0.33	0.09
	Min	0.09	0.09	*0.08*	*0.17*	*0.11*	*0.20*	*0.14*	*0.16*	*0.13*	*0.28*	*0.14*	*0.16*
	Max	*0.72*	*0.85*	0.98	1.02	1.04	0.57	0.46	0.63	0.49	0.85	2.18	0.55
PIC	Mean	0.36	0.26	0.15	0.24	0.34	0.22	0.21	0.14	0.10	0.13	0.24	0.35
	s.d.	0.29	0.25	0.14	0.18	0.30	0.16	0.26	0.10	0.09	0.08	0.14	0.24
	Min	0.03	0.01	0.01	0.01	0.00	0.01	0.00	0.01	0.00	0.01	0.01	0.02
	Max	1.44	1.11	0.54	0.57	1.15	0.68	1.33	0.38	0.39	0.30	0.58	0.81
TPC	Mean	0.69	0.39	0.45	0.47	0.55	0.54	0.45	0.44	0.39	0.45	0.54	0.65
	s.d.	0.27	0.31	0.16	0.24	0.33	0.24	0.25	0.11	0.12	0.10	0.14	0.21
	Min	0.38	0.01	0.17	0.16	0.14	0.21	0.18	0.21	0.17	0.23	0.26	0.31
	Max	*1.81*	*1.51*	*0.72*	*0.96*	*1.43*	*1.25*	*1.55*	*0.67*	*0.68*	*0.64*	*0.80*	*1.06*

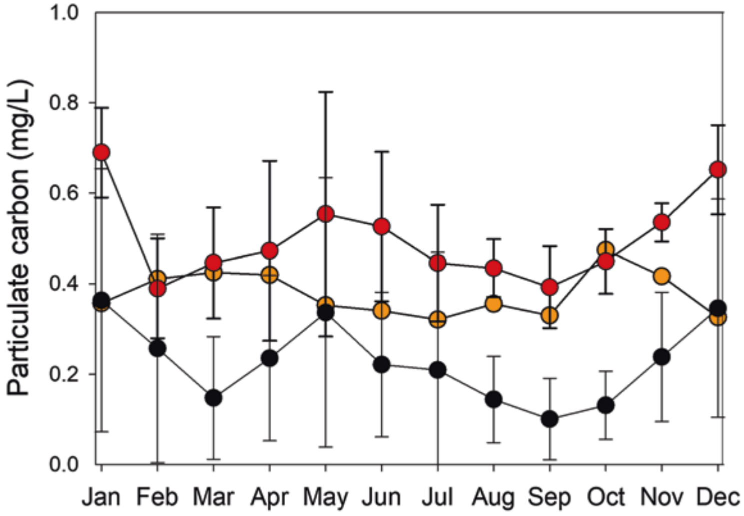


Fig. 7.35 Temporal variation (mean ± s.d.) of the TPC (red circles), PIC (black circles), and POC (orange circles) concentration along the year in Lake Alchichica

Particulate Organic Carbon

Particulate organic carbon (POC) originates from the allochthonous particles that enter the lake from the watershed and the autochthonous primary production (de Castro Bueno et al. 2020). The aggregation and disaggregation of organic compounds within the lakes and the microbial and planktonic processing activities define POC's pathway by its deposition to the sediments or by mineralization in the

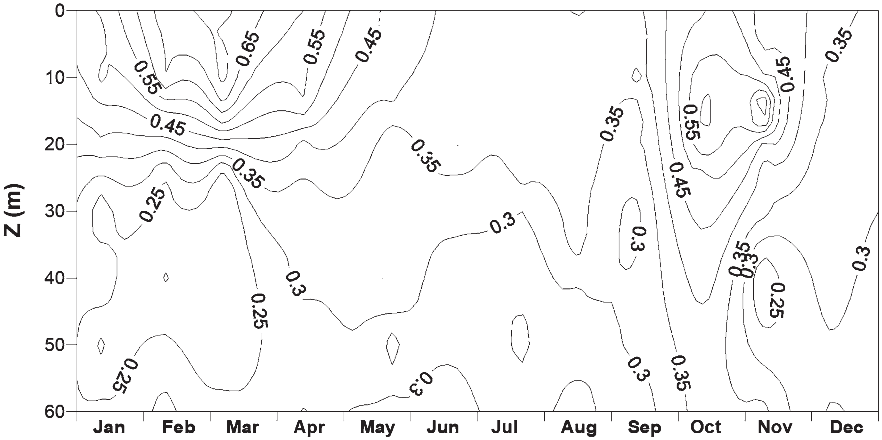


Fig. 7.36 Depth-time diagram of POC concentration (mg/L) in Lake Alchichica

productive zone (de la Rocha and Passow 2007). POC plays an essential role in the metazoan food web as the basal resource for primary consumers (Wetzel 2001).

POC in Lake Alchichica constitutes 50–95% of the TPC. It ranges between 0.08 and 2.18 mg/L (average 0.38 ± 0.19 mg/L). POC distribution in Lake Alchichica varies temporarily ($F = 3.26$, $p < 0.001$) and along the water column ($F = 12.51$, $p < 0.001$) (Fig. 7.36). Highest values are found in October (0.47 ± 0.16 mg/L), and from February to April (0.41 ± 0.22 to 0.42 ± 0.27 mg/L). Lowest values are found in July (0.32 ± 0.08 mg/L) (Table 7.2). POC values in the Z_{MIX} (0.42 ± 0.15 mg/L) were higher than in the metalimnion (0.38 ± 0.07 mg/L), and the hypolimnion (0.31 ± 0.05 mg/L) ($F = 10.82$, $p < 0.001$).

POC shows higher values in the upper layer (0–25 m), where phytoplankton resides. Temporally, there are two peaks: the first in January–April associated with the winter diatom bloom, and the second in October–November, at the metalimnion, related to the deep chlorophyll maximum (Fig. 7.36). POC water column distribution and timing in Lake Alchichica follow the phytoplankton productivity and biomass distribution as indicated by the correlation between POC and chlorophyll-*a* concentration (Oseguera et al. 2010a ,b).

Particulate Inorganic Carbon

Particulate inorganic carbon (PIC) represents 5–50% of the TPC. It varies between 0.001 and 1.44 mg/L (average 0.24 ± 0.22 mg/L). The PIC distribution in Lake Alchichica varies temporarily ($F = 5.61$, $p < 0.001$) but remains similar in the water column ($F = 1.90$, $p > 0.05$) (Fig. 7.37). Highest values are found in January (0.36 ± 0.29 mg/L), and lowest values are found in September (0.10 ± 0.09 mg/L) (Table 7.2). The mixed layer average 0.25 ± 0.13 mg/L, the metalimnion average 0.22 ± 0.10 mg/L, and the hypolimnion average 0.18 ± 0.14 mg/L.

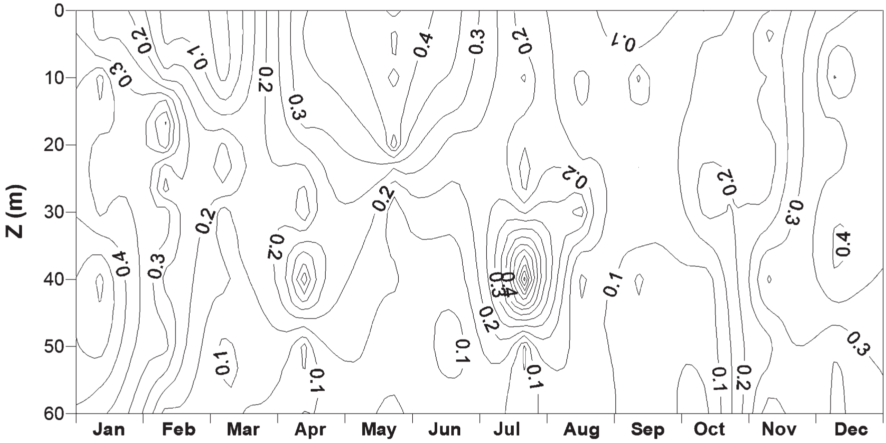


Fig. 7.37 Depth-time diagram of PIC concentration (mg/L) in Lake Alchichica

Table 7.3 DOC:POC values in the water column of Lake Alchichica

DOC: POC	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Mean	14.2	12.8	13.4	10.1	12.3	12.3	13.6	13.4	14.2	9.9	12.5	14.1
s.d.	5.5	5.8	7.2	2.6	3.4	1.4	1.6	1.4	1.5	1.7	4.9	1.2
Min	9.0	6.9	6.6	7.2	9.9	10.6	11.4	11.7	11.8	7.9	5.7	12.6
Max	22.9	23.9	23.6	13.4	20.4	14.9	16.6	15.7	16.6	12.2	22.3	15.6

DOC:POC Relationship

DOC:POC ratio in Lake Alchichica varies between 6:1 and 24:1, with an average of 13:1 (13 ± 4). This value is above the ratio proposed for unproductive lakes (10:1); moreover, the range was ample, which is also unexpected in unproductive lakes (Wetzel 2001).

Maximum values are found in January (14.2 ± 5.5) and minimum values in October (9.9 ± 1.7) (Table 7.3). DOC:POC mean ratios are similar in the Z_{MIX} and the metalimnion (12:1), while higher values in the hypolimnion (14:1). DOC is evenly distributed in the water column, but POC concentrations are higher in Z_{MIX} and metalimnion, where primary production occurs, and phytoplankton biomass higher. Consequently, DOC:POC ratios are lower in the productive layers and higher in the deep, unproductive layer.

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Chapter 8
The Littoral Environment

Javier Alcocer, Elva Escobar, and Luis A. Oseguera

8.1 Introduction

The littoral zone forms a critical interface between the land and the water bodies' pelagic zones; diverse microbial, plant, and animal communities coexist (Sharma et al. 2010). The littoral zone is an ecotone between the terrestrial and aquatic environments (Roldán Pérez and Ramírez Restrepo 2008). It is an autonomous compartment comprising all trophic levels, with many ecological niches and both herbivory and detritus food chains displaying the highest diversity in the water body. The land-water interface is a dynamic habitat that controls or influences the movement of organisms, nutrients, matter, and energy within and through ecosystems (Larmola et al. 2006).

The littoral zone usually displays high temporal variability due to fluctuations in water level, wave energy, biological activity, and climatic conditions. All these forms of temporal variation contribute to shaping the littoral zone's ecology (Strayer and Findlay 2010). The different daily and seasonal rhythms (temporal heterogeneity) tend to increase the number of species and reduce the fluctuations in the use of energy, providing a certain degree of stability or constancy (Lampert and Sommer 2007).

J. Alcocer (✉) · L. A. Oseguera
Grupo de Investigación en Limnología Tropical, FES Iztacala, Universidad Nacional Autónoma de México, Tlalnepantla, Estado de México, Mexico
e-mail: jalcocer@unam.mx; loseguera@unam.mx

E. Escobar
Unidad Académica de Ecología y Biodiversidad Acuática, Instituto de Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México, Ciudad de México, Mexico
e-mail: escobri@cmarl.unam.mx

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8.2 Water Physical and Chemical Properties

The first reports on the water and sediment characteristics of the littoral zone of Lake Alchichica (Alcocer et al. 1993a, b, 1998) showed significant environmental heterogeneity. Pérez-Rodríguez et al. (2013) mentioned the littoral zone of Lake Alchichica presents a high environmental heterogeneity, from areas with fine sediments and extensive vegetation cover with little influence from the waves, to areas devoid of vegetation cover with a strong waves and coarse sediments. The littoral sediments had different degree of vegetation coverage (*Ruppia maritima*, *Cyperus laevigatus*), organic matter and carbonates content, texture, and elemental (C and N) composition (Alcocer et al. 2015; Acosta et al. 2017; Ramos-Hernández et al. 2015, 2016).

Alcocer et al. (2016) implemented a detailed environmental characterization of the littoral zone. The littoral zone is shallow (<1 m) and warm. Water throughout the littoral zone is well oxygenated (above saturation, ~120%) and with an alkaline pH (9.00 ± 0.11). Differently, there are significant differences along the littoral zone in electric conductivity (K_{25}) and nutrient concentrations, particularly in soluble reactive phosphorous (SRP), soluble reactive silica (SRSi), and nitrates ($N\text{-}NO_3^-$). Chlorophyll-a concentration (Chl-a) is also different from site to site (Table 8.1).

Differences in the littoral water's physical and chemical characteristics are mostly explained by the level of communication with the pelagic zone. The decline of the lakes' water level combined with the physical barrier represented by the stromatolite ring has reduced the connection between the littoral and the pelagic zones. Isolation leads to higher evaporation rates and then concentration (K_{25} = 31

Table 8.1 Environmental characteristics of Lake Alchichica littoral water. (Temp = temperature, DO = dissolved oxygen, ORP = oxidation-reduction potential, K_{25} = electric conductivity at 25 °C, Chl-a = chlorophyll-a, SRP = soluble reactive phosphorous, SRSi = soluble reactive silica, $N\text{-}NH_4^+$ = nitrogen as ammonium, $N\text{-}NO_2^-$ = nitrogen as nitrites, $N\text{-}NO_3^-$ = nitrogen as nitrates)

	Temp	**DO**	**DO**		**ORP**	**K_{25}**
	(°C)	**(mg/L)**	**(%sat)**	**pH**	**(mV)**	**(mS/cm)**
X	18.20	8.13	119.9	9.00	327	12
s.d.	1.32	1.60	27.6	0.11	10	7
Min	16.30	6.72	96.2	8.69	311	3
Max	20.36	11.38	174.9	9.11	341	31
	Chl-a	**SRP**	**SRSi**	**$N\text{-}NH_4^+$**	**$N\text{-}NO_2^-$**	**$N\text{-}NO_3^-$**
	(µg/L)	**(µM)**	**(µM)**	**(µM)**	**(µM)**	**(µM)**
X	2.23	0.67	61.97	2.18	0.28	0.72
s.d.	1.13	0.58	67.76	0.63	0.19	0.95
Min	0.97	0.13	13.14	1.19	0.06	0.11
Max	4.44	2.28	252.90	3.29	0.73	3.43

mS/cm). Simultaneously, on the other side, some small freshwater springs that locally dilute (e.g., K_{25} = 3 mS/cm) at localized littoral extents (Alcocer and Oseguera 2019).

8.3 Sediment Characteristics

Littoral sediments are coarse (silty sands) and carbon enriched. Littoral sites range from totally naked sediments to fully covered with macrophytes (*Ruppia maritima*) and/or benthic filamentous algae (Table 8.2).

Macrophyte coverage is the critical characteristic in differentiating the littoral sedimentary areas. Vegetation coverage is closely related to exposure to the pelagic zone (i.e., wave and water current actions)—the higher the kinetic energy, the lower the vegetation coverage. Extreme kinetic energy conditions lead to littoral zones where the rocky basement cannot retain sediments remaining bare-rock (site AL-8 in Fig. 8.1).

8.4 Environmental Heterogeneity and Habitats

Together with the decline of the lakes' water level, the stromatolite ring's presence provides a structural complexity to the littoral zone by imposing different degrees of physical interaction/interchange between the littoral and the pelagic zones. In this way, the littoral zone could be assigned to four different categories (Fig. 8.1): a) fully interconnected (no physical barriers) with the pelagic zone (46%), b) partially blocked from the pelagic zone with stromatolites (18%), c) semi-isolated (mostly obstructed with stromatolites) from the pelagic zone (27%), and d) completely isolated from the pelagic zone (9%).

Table 8.2 Environmental characteristics of Lake Alchichica littoral sediments. (G = gravel, S = sand, s = silt, c = clay, C = carbon, N = nitrogen, Chl-a = chlorophyll-a, Mac = macrophytes)

	G	**S**	**s**	**c**	**C**	**N**		**Chl-a**	**Mac**
	(%)	**(%)**	**(%)**	**(%)**	**(%)**	**(%)**	**C/N**	**(µg/cm^2)**	**(g DW/m^2)**
X	6.8	79.9	12.4	0.9	6.0	0.1	86	18.2	102.8
s.d.	6.0	16.1	11.7	0.9	2.6	0.1	48	10.7	172.2
Min	0.1	45.7	1.1	0.1	2.4	0.0	17	6.5	0
Max	19.0	94.8	32.8	2.6	10.0	0.5	161	40.4	568.9

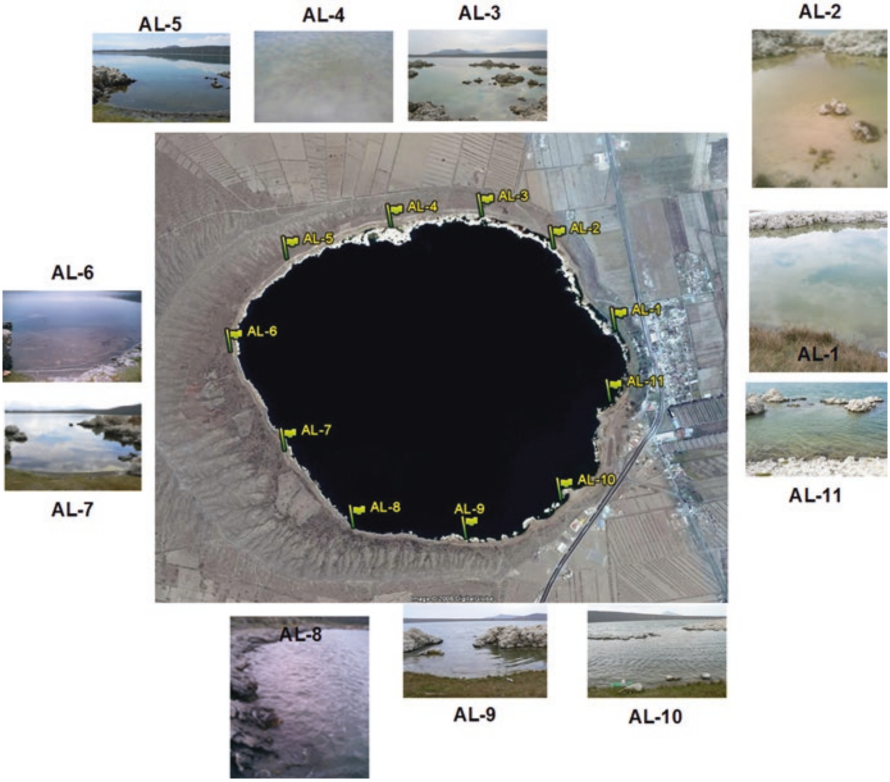

Fig. 8.1 Graphical illustration of the heterogeneity along the littoral zone of Lake Alchichica

There is no clear distinction in temperature, dissolved oxygen, and pH among the four different categories. However, semi-isolated zones display lower K_{25} values associated with freshwater springs, while isolated zones show higher K_{25} values related to intense evaporation. Chl-a and nutrients concentration increase in semi-isolated and isolated zones (Table 8.3).

Regarding the littoral categories' sediment characteristics, the isolated zones show coarser sediments (more gravel, less sand), higher C content, and Chl-a concentration, and the absence of macrophytes. Semi-isolated sites hold the highest amounts of macrophytes. Interconnected and partially blocked sites show no sedimentary differences (Table 8.4).

The lake's desiccation process has the most critical impact on the lake's littoral zone permanence. Historical aerial photographs testified a descend in the lake's water level, and also, three old water-level rulers (physical evidence) are now far away from today's shoreline. Being deposited underwater, a large portion of the tufa deposits are currently above the water surface.

Table 8.3 Water characteristics (X/s.d.) of the Lake Alchichica littoral categories. (Temp = temperature, DO = dissolved oxygen, ORP = oxidation-reduction potential, K_{25} = electric conductivity at 25 °C, Chl-a = chlorophyll-a, SRP = soluble reactive phosphorous, SRSi = soluble reactive silica, N-NH_4 = nitrogen as ammonium, N-NO_2 = nitrogen as nitrites, N-NO_3 = nitrogen as nitrates)

	Temp	**DO**	**DO**	**pH**	**ORP**	**K_{25}**
	(°C)	**(mg/L)**	**(%sat)**		**(mV)**	**(mS/cm)**
Interconnected	17.03	7.08	101	9.0	326	11
	0.56	0.40	5	0.0	8	0
Partially blocked	19.05	9.65	145	9.1	333	13
	1.40	2.45	42	0.1	1	3
Semi-isolated	19.40	8.34	123	8.9	318	8
	0.84	1.72	26	0.2	12	4
Isolated	18.73	9.76	156	9.1	341	31
	1.36	1.92	36	0.1	11	17
	Chl-a	**SRP**	**SRSi**	**N-NH_4^+**	**N-NO_2^-**	**N-NO_3^-**
	(µg/L)	**(µM)**	**(µM)**	**(µM)**	**(µM)**	**(µM)**
Interconnected	2.13	0.41	36.75	2.17	0.25	0.91
	0.74	0.21	23.09	0.41	0.18	1.41
Partially blocked	1.20	0.36	21.06	1.87	0.22	0.63
	0.34	0.04	5.44	0.96	0.03	0.38
Semi-isolated	2.34	0.78	127.95	2.22	0.24	0.32
	1.31	0.19	109.69	0.98	0.06	0.19
Isolated	4.44	2.28	71.90	2.69	0.73	1.08
	2.25	1.99	78.63	0.78	0.48	1.44

Table 8.4 Sediment characteristics (X/s.d.) of the Lake Alchichica littoral categories. (G = gravel, S = sand, s = silt, c = clay, C = carbon, N = nitrogen, Chl-a = chlorophyll-a, Mac = macrophytes)

	G	**S**	**s**	**c**	**C**	**N**	**C/N**	**Chl-a**	**Mac**
	(%)	**(%)**	**(%)**	**(%)**	**(%)**	**(%)**		**(µg/cm²)**	**(g DW/m²)**
Interconnected	8.0	85.5	6.0	0.5	4.8	0.1	107	17.1	57.1
	5.4	8.4	5.9	0.4	1.7	0.0	53	7.5	74.9
Partially blocked	5.0	80.2	13.7	1.1	6.5	0.1	75	9.5	94.7
	0.8	15.7	14.3	0.7	4.9	0.2	51	4.3	10.1
Semi-isolated	2.3	83.5	13.2	0.9	6.1	0.2	78	18.1	202.8
	2.7	16.5	13.1	1.0	2.1	0.2	53	9.7	317.1
Isolated	19.0	45.7	32.8	2.6	9.8	0.2	48	40.4	0.0
	16.7	9.2	31.0	2.4	4.3	0.2	27	23.7	0.1

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Chapter 9
Aquatic Vegetation

Elia Matías-Hernández and Pedro Ramírez-García

9.1 Hydrophytes. Definition and Delimitation of the Group

Lake Alchichica has been scarcely researched from a floristic point of view. Only two research have recorded some of its aquatic flora (Ramírez-García and Novelo 1984; Ramírez-García and Vázquez-Gutiérrez 1989). Other studies focused on benthic fauna (Alcocer et al. 1998), and macrophytes carbon dynamics (Pérez-Rodríguez et al. 2012) refer to plants' importance Alchichica lacustrine coast. This chapter describes lakeside flora and aquatic vegetation.

Hydrophytes or macrophytes are plants adapted to the aquatic environment to a lesser or greater degree, which grow and reproduce submerged or partially submerged. It is a plant group that includes, in a broad sense, charophytes (Charophyta), mosses and livers (Bryophyta), ferns, and related groups (Pteridophyta) monocotyledons and eudicotyledons (Angiospermae). This work only includes herbaceous angiosperms and follows the concept of hydrophyte that groups three categories based on the degree of dependence and adaptation of the plant to the aquatic environment, according to Lot (2013), Lot et al. (1998, 1999), and Ramos and Novelo (1993) in:

1. Strict aquatic: those that develop their entire life cycle in the water.
2. Subaquatic: those that grow up much of their life cycle in the water and cannot survive for long periods in completely dry spells soils.

E. Matías-Hernández (✉)
Departamento de Botánica (Proyecto Flora del Valle de Tehuacán-Cuicatlán), Instituto de Biología, Universidad Nacional Autónoma de México, Av. Universidad, Alcaldía Coyoacán, Ciudad de México, Mexico
e-mail: elia_matias@ciencias.unam.mx

P. Ramírez-García
Departamento de Botánica, Instituto de Biología, Universidad Nacional Autónoma de México, Av. Universidad, Alcaldía Coyoacán, Ciudad de México, Mexico

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3. Tolerant: those that spend much of their life cycle in dry soils but tolerate flooded soils for some time.

In some cases, during the life cycle of hydrophytes, there may be months during the drought, in which the water level is nil, but the soil remains moistured and allows them to complete their life cycle.

Hydrophytes are besides classified by their life forms, according to Lot et al. (1999), Ramos and Novelo (1993), and Ramos et al. (2004) in:

1. Emerging rooted hydrophytes. Plants that are rooted in the substrate with a part of the stem submerged and emerging leaves and reproductive organs.
2. Submerged rooted hydrophytes. Plants rooted in the substrate and maintain fully submerged stem and leaves, and either submerged, emerging, or floating reproductive organs.
3. Rooted hydrophytes of floating leaves. Plants attached to the substrate, with the leaves floating on the water surface and emerging reproductive structures.
4. Free emerging floating hydrophytes. Plants that are not fixed to the substrate with their vegetative and reproductive organs floating on the water surface.
5. Free submerged floating hydrophytes. Plants that are not fixed to the substrate, with their vegetative organs submerged, and only the reproductive organs emerging.

Strict aquatic plants are typical of swamps, streams, lakes, lagoons, reef lagoons, dams, and artificial canals. Most species grow in freshwater and brackish water, but seagrasses are also hydrophytes that grow in reef lagoons. Hydrophytes from freshwater and brackish aquatic environments made up diverse communities and may be associated with bryophytes, ferns, and charophytes.

9.2 Aquatic Flora and Vegetation of Mexico

The aquatic angiosperms in Mexico include 28 monocotyledons families and 38 eudicotyledons families. The three most notable families for their richness are Asteraceae, Poaceae, and Cyperaceae (Lot 2013; Lot et al. 1998). The aquatic vegetation in Mexico develops in all climates, from sea level to inland waters of more than 4000 m of altitude (between 1000 and 2500 m is where it, perhaps, presents its most remarkable richness). The aquatic vegetation concentrates in areas near the sea and where relatively high precipitation matches large areas of poor drainage. According to Rzedowski (2006), aquatic vegetation distributes into several subtypes based on its floristic composition, structure, and distribution as follow:

1. Floating vegetation that grows in slow-moving waters that are either freshwater or moderately brackish where *Lemna* spp. or *Potamogeton* spp. genera inhabit.
2. Submerged vegetation that grows in essentially transparent, freshwater, or slightly brackish waters, where *Potamogeton* spp. and *Ruppia* spp. inhabit. This last genus prefers continental and coastal marine environments.

3. Subaquatic vegetation with the presence of many herbaceous rooted in shallow water, for example, *Agrostis* sp., *Berula* sp., *Bidens* sp., *Cyperus* sp., *Eleocharis* sp., *Juncus* sp., *Polygonum* sp., and *Ranunculus* sp., Some of which, such as *Cyperus* sp. and *Juncus* sp., have a tolerance to water's high salt content.

9.3 Hydrophyte Flora of Lake Alchichica. Composition and Distribution

For the recognition of the aquatic and subaquatic vegetation of Lake Alchichica, an observation route and botanical collection was carried out on the periphery of the lake, systematically in 12 visits per month (1980–1981) (Ramírez-García and Novelo 1984) and *ad libitum* in three visits in dry and rainy seasons (2015, 2018 and 2020). The specimens are in the Herbario Nacional de México (MEXU), Instituto de Biología, Universidad Nacional Autónoma de México (Figs. 9.1 and 9.2).

The floristic composition of Lake Alchichica comprises six species grouped into five genera and three families, belonging to the Poales and Alismatales orders of the Monocotyledoneae class. The predominant family is Cyperaceae, with three species. In Mexico, more than 25% of the Cyperaceae are hydrophytes, and within the aquatic monocotyledons, they rank the first place in species richness (Diego-Pérez and González-Elizondo 2013; Lot 2013). Followed Juncaceae with two species; its moderate species richness associates to a family represented by fewer species than Cyperaceae; among the aquatic monocotyledons, they occupy the third species richness place in the country (Galván-Villanueva 2001; Galván-Villanueva and

Fig. 9.1 Method of botanical collection. Collecting *Juncus* sp. to the W of Lake Alchichica

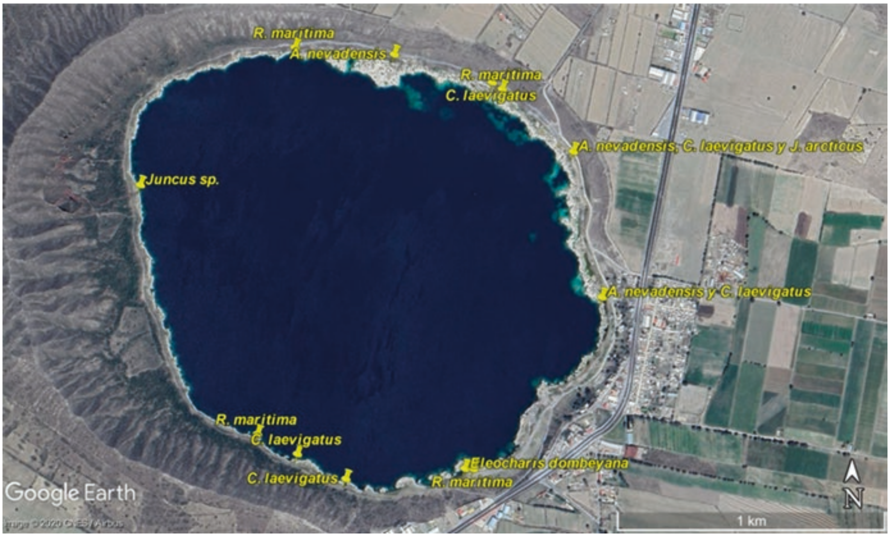

Fig. 9.2 Location of the collection points of the hydrophytes of Lake Alchichica

Table 9.1 Floristic list and life form of the hydrophytes of Lake Alchichica

Type of hydrophyte and life-form	Order / Family / Species	Distribution on the Alchichica littoral	Depth
	Poales		
	Cyperaceae		
	Amphiscirpus nevadensis (S. Wats.) Oteng-Yeb. *	NE. Open and flat areas. Waterlogged sites	0 cm
	Cyperus laevigatus L. *	NE and S. Open and flat areas. Waterlogged sites	0 cm
Subaquatic. Emerging rooted	*Eleocharis dombeyana* Kunth	S. in water cavities	30 cm
	Juncaceae		
	Juncus arcticus Willd *	E. Open and flat areas. Waterlogged sites	0 cm
	Juncus sp.	W. Less open areas. Wet soils	0 cm
	Alismatales		
Strict aquatic.	Ruppiaceae		
Submerged rooted	*Ruppia maritima* L. *	N and SW. In the water body of the lake	300 cm

An asterisk* indicates halophile species

Martínez-Domínguez 2013; Lot 2013). Finally, there is only one species of Ruppiaceae in the lake. There are only two Ruppiaceae species in Mexico, both restricted to saline waters; also, it locates among the aquatic monocotyledons with lower species richness (Lot 2013; Ramírez-García 2013) (Table 9.1).

Environmental features (e.g., altitude, climate, winds, and sediments), and physicochemical variables (salinity, alkalinity, ion composition of water) (Ramírez-García and Novelo 1984), and the morphology of Lake Alchichica influence the hydrophytes development in the lake. The low floristic richness in Lake Alchichica relates to its oligotrophic status (low nutrient and low organic matter production, Alcocer and Oseguera 2019), limiting the growth of species.

The number of species of Lake Alchichica (6) is low compared to that of Lake Texcoco (24), both lakes with similar environmental characteristics and with only four species in common: *E. dombeyana*, *Juncus* sp., *R. maritima*, and *S. pectinata* (Rzedowski 1957; https://datosabiertos.unam.mx/biodiversidad/). Lake Texcoco was considerably larger (100 km^2) (Rzedowski 1957), which allowed many hydrophytes with a complete inventory. Differently, there are fewer species in the smaller Lake Alchichica (2.3 km^2), (Alcocer and Oseguera 2019), and an inventory yet to be completed.

In contrast, the species richness of Lake Alchichica (6) is high compared to that of the other five crater lakes located in the same area to the E of Puebla: Tecuitlapa (7), Aljojuca (6), Quechulac (5), La Preciosa (4), and Atexcac (4) with similar environmental features, of which Lake Alchichica only shares with Lake Atexcac two species in common: *C. laevigatus* and *R. maritima* (Ramírez-García and Novelo 1984). Lake Alchichica is the largest of all, which allows a greater presence of species. The collections made in this study increased its floristic inventory by adding four species to the previous reports by Ramírez-García and Novelo (1984) of two species. A new record of *A. nevadensis* unknown for Puebla state, and the first collections of *E. dombeyana*, *J. arcticus*, and *Juncus* sp.

9.3.1 Cyperaceae

Amphiscirpus nevadensis (S. Wats.) Oteng-Yeb. Subaquatic plant. Emerging rooted. Herbs, perennial, rhizomatous, stems 5–45 cm tall, trigonous, circular or flattened, leaf blades stiff and pointed, sheaths closed, inflorescences terminal, capitate, spikelets 1–8 sessile, scales and flowers spirally arranged in 3 rows or more in the rachilla. Distribution. SW from Canada, the United States of America, Chile, and Argentina. In Mexico has been registered only in the State of Mexico, to the N of Lake Texcoco. Alt. 2250 m. Habitat. Lakes with saline or alkaline soil. Remarks. It is a scarce plant, which due to the drastic modifications suffered by the habitat from where it has been collected in Mexico, should be considered endangered (Diego-Pérez and González-Elizondo 2013; González-Elizondo 2001; González-Elizondo et al. 2008, 2018; Smith 2002).

Fig. 9.3 *Amphiscirpus nevadensis*, to the E of the coastline of Lake Alchichica. (**a**) Emerging rooted plant, (**b**) grows in flooded sandy soils. (Photographs by Elia Matías-Hernández)

In Lake Alchichica, *A. nevadensis* grows in relatively conspicuous populations to the NE of the coast (Fig. 9.2), 3–6 m from the water body, in open and flat areas, near the outcrops of microbialites, in permanent or temporary flooded sandy soils, with other plants such as *C. laevigatus*, with the largest population in the N. Phenology. Flowering and fruiting in spring and summer (Fig. 9.3a, b). Its presence in the site may be explained because it is a hydrophyte adapted to exclusive conditions of saline and alkaline lakes, such as those of Lake Alchichica with salinity 8.5–9 g/L, alkalinity pH 8.8–8.9, and ionic composition of sodium chloride, magnesium salts, carbonates, bicarbonates and borates (Alcocer and Oseguera 2019).

The environmental heterogeneity of the coast explains the discontinuous spatial distribution of this species, which allows their growth in the NE, on the side of the crater where a gentle slope is found, an extensive coast, fine sand waterflooded sites, and the absence of waves due to the distance of the water body and the barrier of microbialites. In contrast to SW, where it does not grow due to the absence of coastline and because there are thick sediments, waves, and less presence of microbialites. This species perhaps inhabited a wider area of the lake in the past, as Alcocer and Oseguera (2019) and Silva-Aguilera and Escolero (2019) indicate that the lake had a large coastal area that was disappearing as the level of its waters descended, by natural and human factors. *A. nevadensis* today faces adverse scenarios caused by water decrease, loss of the coast, and pollution since in the place where it grows has been found garbage in the soil and water.

Importance. The collection of *A. nevadensis* at Lake Alchichica represents a new record of Mexico's flora. Due to its intrinsic importance, its exclusive presence in two saline and alkaline lakes in the country, and the continuous desiccation and contamination of Lake Alchichica, it is urgent to decide and guarantee the conservation status of the species and the lake as its natural habitat. *A. nevadensis* is a species not yet registered in any protection category in Mexico. Therefore, this information is the basis for its future evaluation and inclusion in the Norma Oficial Mexicana NOM-059-SEMARNAT-2010 in the endangered category and to protect the lake as an aquatic ecosystem *sui generis* at risk.

Cyperus laevigatus L. Subaquatic plant. Emerging rooted. Herbs, perennial, rhizomatous, stems 3–30(70) cm tall, compressed, trigonous to circular, leaf blades short or absent, sheaths closed, inflorescences lateral, capitate, spikelets 1–16 sessile, scales and flowers parallel arranged in 2 rows in the rachilla. Distribution. Pantropical. In America, E of the United States to South America. In Mexico, it grows in almost all the states. Alt. 0–2500 m. Habitat. Saline or alkaline water bodies, flooded halophilic grasslands, ditches, streams, and urban wastewater channels. Remarks. An introduced plant (Diego-Pérez and González-Elizondo 2013; González-Elizondo 2001; González-Elizondo et al. 2018; Tucker et al. 2002).

At Lake Alchichica, *C. laevigatus* inhabits relatively abundant populations on the coast, mainly to the NE and S (Fig. 9.2), 0.5–6 m from the water body, in open and flat areas, around and above the microbialites. In sandy soils that are either flooded or not, where cattle constantly graze it. Phenology. Flowering and fruiting in spring and summer (Ramírez-García and Novelo 1984; obs. pers.) (Fig. 9.4). This plant has the most considerable presence and spatial distribution of the recorded hydrophytes because it is a very common sedge adapted to saline and alkaline soils. The fact that it is an introduced plant indicates that it colonized this lake at some point in the past, perhaps carried by birds. Locally may be important as fodder.

Eleocharis dombeyana Kunth. Herbs, perennial, rhizomatous sometimes subcespitose, stems 4–60 cm tall and up to 1 mm wide, leaf blades absent, sheaths closed, inflorescences terminal in a spikelet single. Distribution. South America, Central America. In Mexico, it is present in Mexico City and 15 states. Alt. 1200–3500 m. Habitat. The shore of streams and water deposits, moist grasslands,

Fig. 9.4 *Cyperus laevigatus*, to the E of the coastline of Lake Alchichica, in waterlogged sites

Fig. 9.5 *Eleocharis dombeyana*, to the S of the coastline of Lake Alchichica, in a cavity with water

disturbed areas, *Abies* forests, pine forests, and oak woods (Diego-Pérez 2012; González-Elizondo 1994, 2001; González-Elizondo et al. 2018).

In Alchichica, *E. dombeyana* scarcely grows in a site to the S of the coast (Fig. 9.2), 1–4 m from the water body, in a cavity with water, of irregular shape, size approximately 80 cm by 100 cm, and depth 30 cm, perhaps fed by groundwater and rain, since this plant has not yet been recorded in saline sites. Phenology. Flowering and fruiting in summer. Although the literature does not refer to it as hydrophyte, in this study, it is considered subaquatic, emerging rooted, as it is found with these characteristics (Fig. 9.5). Its habitat is the lake's southern portion, the least alkaline (Silva-Aguilera and Escolero 2019). The existence of more springs to the SE of the lake in the past (Silva-Aguilera and Escolero 2019) suggests that it had a greater presence and southern distribution in less alkaline water deposits of Alchichica. Since it is present in a single place, it could disappear due to the constant loss of springs.

9.3.2 *Juncaceae*

Juncus arcticus Willd. Subaquatic plant. Emerging rooted. Herbs, perennial, cespitose, stems 3–125 cm tall, circular or compressed, leaf blades absent or present according to variety, sheaths open, inflorescences pseudolateral in panicle lax or dense. Distribution. Circumboreal, W from Alaska to South America. In Mexico, it is found in Mexico City and 16 states. Habitat. Edge of canals, lakes, lagoons, streams, flood soils, and generally brackish plains in xerophytic scrub and grassland communities. Alt. 675–3900 m. Remarks. In Mexico, there are three varieties (Galván-Villanueva 2001; Galván-Villanueva and Martínez-Domínguez 2013).

At Alchichica, *J. arcticus* scarcely inhabits the E of the coast (Fig. 9.2), 3–6 m from the water body, in open and flat areas, close to the microbialites and a small population of *A. nevadensis*, in saturated sandy soils, with other grasses. Phenology. Flowering and fruiting in summer. This plant's limited spatial distribution indicates a wide coastline habitat and near waterlogged sandy sites. Also, as Galvan-Villanueva (2001) indicates, these juncaceous usually occupy small areas. Perhaps, in the past, it inhabited a broader coastline than the existing one today.

Juncus sp. The genus consists of herbs, perennial, cespitose, stems slender, leaf blades basal, sheaths open, inflorescences terminal or pseudolateral in panicles, cymes or heads. Distribution. Cosmopolite, mainly in the N hemisphere, in Mexico, there are 35 species, 18 of which are aquatic (Galván-Villanueva and Martínez-Domínguez 2013).

In Lake Alchichica, *Juncus* sp. grows in a single site at the W of the coast (Fig. 9.2), 0.5–2 m from the water body, behind the microbialites, in damp, moderately uneven soils, with other grasses. Its distribution towards the western portion of the lake indicates an ecological preference towards an almost absent littoral zone, with higher energy, surrounded by terrestrial vegetation, and a more temperate microhabitat than in the east, which favors the limited and reduced presence of this juncaceous (Fig. 9.6).

Fig. 9.6 *Juncus* sp., to the W of the coastline of Lake Alchichica, in wet soils, behind the microbialites

9.3.3 Ruppiaceae

Ruppia maritima L. Strict aquatic. Submerged rooted. Herbs, perennial, stems simple or highly branched towards the top, 0.3–0.8 mm in diameter, whitish, leaves generally alternated, inflorescences with two flowers, rarely 1, peduncles up to 12 cm long. Distribution. Cosmopolite. In Mexico, it is registered in Mexico City and 13 states. Habitat. Crater lakes, bays, estuaries, and coastal lagoons of brackish or alkaline water. Alt. 0–2400 m. Remarks. Its common name in Puebla is *lama* (Novelo and Lot 2001; Ramírez-García 2013).

In Alchichica, *R. maritima* appeared to the N and SW (Fig. 9.2), forming a discontinuous strip up to 20 m wide, occupying small inlets and *microbialites*, and is more abundant between 1 and 3 m deep. The sediments where it grows are abundant in sand 80.5% (average), low in organic matter 4.7%, have nutrients with 0.25% nitrogen and assimilable phosphorus with 0.23 ppm, and neutral pH 7.3. It is a dominant euryhaline hydrophyte on the shallow littoral, adapted to high salinity, alkalinity, and water transparency of Lake Alchichica (Ramírez-García and Novelo 1984).

R. maritima inhabited a larger portion of the littoral zone as testified by previous collection sites (Ramírez-García and Novelo 1984), which nowadays are already dry. This constitutes additional evidence of the decline in the water level of the lake and the loss of the littoral zone.

Importance. *R. maritima* has great ecological importance in Lake Alchichica because it constitutes the habitat of diverse aquatic fauna, such as the copepod *Cletocamptus gomezi*, the aquatic insect *Krizousacorixa tolteca*, and the atherinopsid fish *Poblana alchichica*. The last two species are microendemic. Also, *P. alchichica* is a threatened species and critically endangered (Alcocer et al. 2015; Arce-Uribe et al. 2019; Barrera-Moreno et al. 2019; Kato et al. 2019). The local conservation of *R. maritima* acquires relevance since affecting its presence will impact this ecosystem's shelter habitat and the littoral food webs.

Another species recorded in Lake Alchichica, based on the literature, is *Stuckenia pectinata* (L.) Börner (formerly *Potamogeton pectinatus* L.) (www.tropicos.org). According to Ramírez-García and Novelo (1984), there are two specimens deposited in the Herbarium of the Missouri Botanical Garden (MO) and the Herbarium of the Escuela Nacional de Ciencias Biológicas, Instituto Politécnico Nacional (ENCB) respectively. It is a strict aquatic hydrophyte of the family Potamogetonaceae; in Mexico, this species inhabits lakes, irrigation channels, rivers, ponds, and swamps of fresh or saline water, clean or contaminated. Alt. 0–2700 m (Martínez 2013; Novelo and Lot 2001). Perhaps this plant inhabited the lake in the past but disappeared by sparse populations and affected habitat.

9.4 Subaquatic and Submerged Vegetation of Lake Alchichica

The composition and life forms of the species indicate two types of plant communities:

1. Subaquatic vegetation stands out for bringing together five emerging rooted hydrophytes: *A. nevadensis*, *C. laevigatus*, *E. dombeyana*, *J. articus*, and *Juncus* sp. These are perennial herbs with heights of approximately 45–60 cm. They are grass and tufts in flood or wet areas near the *microbialites* and water cavities. *C. laevigatus* is the most abundant and widespread species. *C. laevigatus* and *E. dombeyana* suggest Alchichica is a disturbed lake since these plants are found in affected sites.
2. Submerged vegetation, represented by submerged rooted hydrophyte *R. maritima*, perennial grass that inhabits the water body, in medium extension.

Subaquatic and submerged vegetation is concentrated towards the NE portion of the lake, where the wider littoral zone allows the growth of emerging rooted hydrophyte communities over a larger area than in the W, where the littoral zone is absent with no vegetation. Alcocer et al. (1998) mention that the main factor controlling the species richness, density, and biomass of the benthic macrofauna in Lake Alchichica is aquatic vegetation by increasing the habitat heterogeneity providing food and protection against predators. The annual production of hydrophyte biomass in Lake Alchichica averaged 303 gDW/m^2/y. It includes *R. maritima* and *C. laevigatus* (Ramírez-García and Vázquez-Gutiérrez 1989). On the other hand, Pérez-Rodríguez et al. (2012) reported an annual average of macrophyte total carbon (LOI) of 2.54 ± 3.64 g C m^{-2} ranging from 0.29 ± 0.5 g C m^{-2} y 1.26 ± 2.21 g C m^{-2}. in July and 3.84 ± 4.12 g C m^{-2} in November.

9.5 Importance and Conservation

Aquatic and subaquatic plants are essential because they are the primary producers in the foodweb, oxygenate the aquatic and terrestrial environment, nourish and stabilize sediments, and provide habitat, shelter, and food to aquatic fauna. More than half of the species recorded in this study *(A. nevadensis*, *E. dombeyana*, *Juncus* sp. and *R. maritima*) could disappear locally in the immediate future due to its scarcity and habitat loss caused by the water level declining of the lake. This water reduction seems to be caused by natural (climates that significantly favor evaporation above precipitation and the scarce groundwater inlet) and human factors (groundwater exploitation and pollution), as mentioned by Alcocer y Oseguera (2019).

This study describes some of the aquatic flora of the site. However, there is still the necessity to explore the place to have a complete floristic inventory. Families like Poaceae and Asteraceae are very likely to be present but have not yet been collected and studied. Therefore, it is imminent to document, evaluate, and protect the biota of the site. We consider that it is a priority to study aquatic plant communities' growth dynamics to estimate the vegetation's current state.

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Chapter 10
The Littoral Community

Javier Alcocer, Elva Escobar, Luis A. Oseguera, Alfonso Lugo-Vázquez, María del Rosario Sánchez, Laura Peralta, Mónica Cuellar, and María Guadalupe Oliva-Martínez

10.1 The Littoral Zoobenthos

Javier Alcocer, Elva Escobar, and Luis A. Oseguera

The littoral zone of the lakes is an ecotone that forms an independent compartment comprising all trophic levels (primary producers, consumers, decomposers), a large diversity of ecological niches and food webs (herbivory and detrital), and a great diversity (Roldán and Ramírez 2008). The lake's littoral area presents a high environmental heterogeneity, which leads to a diversity of habitats susceptible to being occupied by a rich and diverse benthic fauna Esteves (1988).

Lake Alchichica embraces a discontinuous stromatolites ring that runs parallel and close to the littoral. This carbonated structure jointly with the gradual decrease of the lake's water level has resulted in different isolation degrees of separation between the littoral and pelagic zones; in this way, there are littoral regions that are in direct contact and interchange with the pelagic zone, while others, in the opposite end, are isolated (see Chap. 8).

J. Alcocer (✉) · L. A. Oseguera · A. Lugo-Vázquez · M. d. R. Sánchez · L. Peralta
M. G. Oliva-Martínez
Grupo de Investigación en Limnología Tropical, FES Iztacala, Universidad Nacional Autónoma de México, Tlalnepantla, Estado de México, Mexico
e-mail: jalcocer@unam.mx; loseguera@unam.mx; lugov@unam.mx; rosarios@unam.mx; sorial@unam.mx

E. Escobar
Laboratorio de Biodiversidad y Macroecología, Instituto de Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México, Ciudad de México, Mexico
e-mail: escobri@cmarl.unam.mx

M. Cuellar
Universidad del Valle de México, Ciudad de México, Mexico

J. Alcocer (ed.), *Lake Alchichica Limnology*,
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The littoral area of Lake Alchichica characterizes an ample range of environmental and biological characteristics resulting in a wide variety of habitats exposed to high temporal variability associated to fluctuations in the weather conditions, water level, wave energy, and biological activity.

10.1.1 Background Studies

The first study of the littoral benthos of Lake Alchichica revealed 10 chironomid species ranging between four and seven in different littoral areas (Alcocer et al. 1993a). The most important chironomid numerically and in biomass contribution was *Tanypus* (*Apelopia*) sp. Alcocer et al. (1993b) reported 15 taxonomic groups of benthic macroinvertebrates (BMI) in the littoral of Lake Alchichica. Tubificids, hirudinean, amphipods, and chironomids were the most frequent and abundant groups. Macrophytes coverage and salinity played an essential role in explaining the taxonomic richness of BMI in Lake Alchichica.

Subsequently, Alcocer et al. (1998) reported 44 taxa of littoral BMI in Lake Alchichica. Four taxa composed up to 99% of the organisms present: oligochaetes, amphipods, midges, and leeches; the most important species were *Limnodrilus hoffmeisteri*, *Hyalella azteca*, *Tanypus (Apelopia)*, and *Stictochironomus* sp. Once again, aquatic vegetation is the critical variable explaining taxonomic richness. Some studies provide additional information on the biology/ecology of specific taxa.

Hyalella azteca displayed a high density (13,496 ± 20,740 ind/m^2) that remained constant throughout the annual cycle with no significant difference among the littoral zones (Alcocer et al. 2002). The vegetation type and coverage play a significant role in the amphipod dynamics. The population structure of *H. azteca* showed juveniles were numerically dominant (55–64%), followed by females (13–20%), males (10–17%), and ovigerous females (8–14%). The male to female ratio was 1:1.75. Fecundity was positively correlated to female size; the number of eggs carried by the ovigerous females was 4.5 ± 2.8 eggs/female.

Oligochaete species richness of Lake Alchichica (i.e., *Limnodrilus hoffmeisteri* and *Tubifex tubifex*) is among the lowest worldwide. High oligochaete densities and biomasses values (>45,000 ind/m^2 and >2700 mg AFDW/m^2) in the littoral zone of Lake Alchichica associated with surface sediments with high organic matter content. Density and biomass values of oligochaetes did not show significant seasonal differences (Peralta et al. 2002). *Limnocytherina axalapasco* and *Candona alchichica* in the littoral zone reached densities up to 3612 ± 4148 ind/m^2 and 22,812 ± 16,045 ind/m^2, respectively, and biomasses of 9.83 ± 11.6 mg C/m^2 and 366.2 ± 281 mg C/m^2, respectively (Hernández et al. 2010). Finally, *Cletocamptus gomezi* in the littoral zone reached a density of 4106 ± 10,962 ind/m^2 with biomass of 3.66 ± 9.75 mg C/m^2, with no statistical temporal differences in density or biomass (Alcocer et al. 2015).

10.1.2 Structure: Composition and Richness

A total of 53 taxa of benthic organisms (Table 10.1) has been mentioned to inhabit the littoral zone of Lake Alchichica (Acosta et al. 2017; Alcocer et al. 1993a, b, 1998, 2002; Cohuo-Durán et al. 2014; Escobar-Briones and Alcocer 2002; Peralta et al. 2002; Suárez-Morales et al. 2013).

However, a more recent study by Alcocer et al. (2016), considering 11 sampling stations equally distributed along the littoral zone of Lake Alchichica found only 21 macroinvertebrates. The taxonomic richness ranges from 2 to 13 with an average of 9 ± 3 taxa (Fig. 10.1).

The only species present in all localities (100%) is the tubificid worm *Limnodrilus hoffmeisteri*, followed by the amphipod *Hyalella azteca* (90%), the leeches

Table 10.1 Taxonomic list of the benthic invertebrates that inhabit the littoral zone of Lake Alchichica

Crustacea	*Hyalella azteca*	Chironomidae	*Cricotopus (Isocladius) triannulatus*
	Limnocytherina axalapasco		*Psectrocladius*
	Candona alchichica		*Limnophyes*
	Cletocamptus gomezi		*Micropsectra sp. 1*
Oligochaeta	*Limnodrilus hoffmeisteri*		*Micropsectra sp. 2*
	Tubifex tubifex		*Chironomus alchichica*
Hirudinea	*Helobdella stagnalis*		*Tanypus (Apelopia)*
	Glossiphoniidae		*Procladius*
Nematoda	*Neotobrilus*		*Dicrotendipes neomodestus*
	Semitobrilus		*Psectrotanypus*
	Tobrilus		*Apedilum elachistus*
	Hoplolaimus sp. 1		*Chironomus (s. str.)*
	Hoplolaimus sp. 2		*Cryptochironomus sp. fulvus gr.*
	Paracyatholaimus		*Stictochironomus*
	Daptonema		*Paratanytarsus*
	Monhystera		*Labrudinea pilosella*
Mollusca	*Physa*	Trichoptera	*Grensia*
Odonata	*Enallagma praevarum*		*Oecetis*
	Aesxhna dugesi		*Oxyethira*
Hemiptera	*Ambrysus*		*Polycentropus*
	Buenoa	Coleoptera	*Berosus*
	Krizousacorixa tolteca		*Stenus*
Ephemeroptera	*Callibaetis montanus*		*Tropisternus*
Diptera	*Culicoides occidentalis sonorensis*		*Donacia*
	Culex		*Hydroporus*
	Stratiomys		*Lacodytes*
	Ephydra hians		

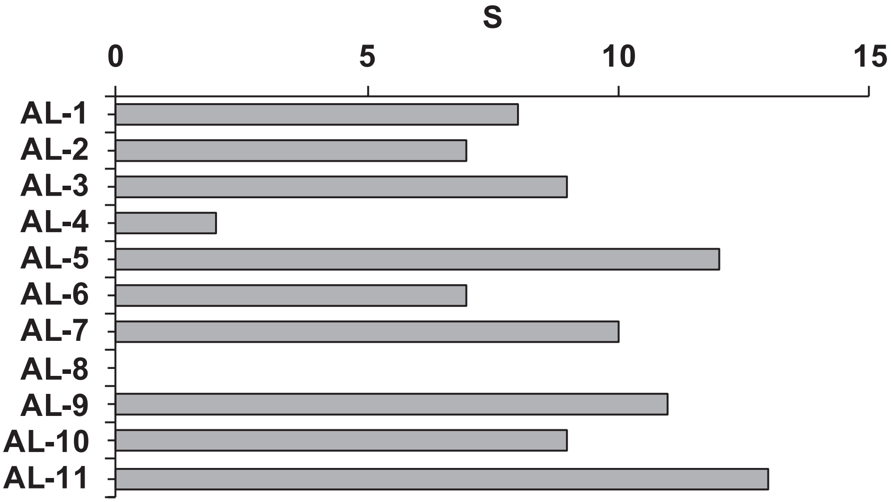

Fig. 10.1 BMI taxonomic richness (S) in the littoral zone of Lake Alchichica. (AL-1 to AL-11 = littoral sampling stations; see Chap. 8, Fig. 8.1)

Helobdella stagnalis, Glossiphoniidae, and the midge *Micropsectra* (80%), and the water boatmen *Krizousacorixa tolteca,* and the midges *Cricotopus (Isocladius) tri-annulatus* and *Chironomus stigmaterus* (now *Chironomus alchichica*) (60%).

10.1.3 Distribution and Seasonal Variations

The BMI distribution along the littoral zone was heterogeneous, which was not surprising considering the littoral area is environmentally diverse (see Chap. 8). Regarding abundance, the oligochaete *Limnodrilus hoffmeisteri* (43%) and the amphipod *Hyalella azteca* (39%) contributed with the largest percentage (82%) well above the other taxa (Fig. 10.2). *Limnodrilus hoffmeisteri* (0–80%) dominated in 60% of the sampling stations, while *Hyalella azteca* (18–100%) dominated in the other 40%. At located littoral areas, *Micropsectra* and *Tanypus (Apelopia)* (≈5%) reached higher abundances (≈10% and 5%, respectively).

The average density of the MIBs ranged from 7437 ± 5724 ind/m^2 to 70,252 ± 14,407 ind/m^2, with a global mean of 33,536 ± 20,463 ind/m^2. The BMI abundance peak was associated with the diatom and cyanobacteria blooms, most likely providing abundant and fresh food (Pérez-Rodríguez et al. 2013). Sediment texture played a key role in explaining BMI distribution. The diversity of Shannon ranged from 0.002 to 1.69 with an average of 1.26 ± 0.54. Shannon's maximum diversity fluctuated in a range of 0.33 to 3.06 with an average of 2.49 ± 0.84. Finally, Shannon's evenness ranged from 0.002 to 0.73 with an average of 0.46 ± 0.20 (Alcocer et al. 2016).

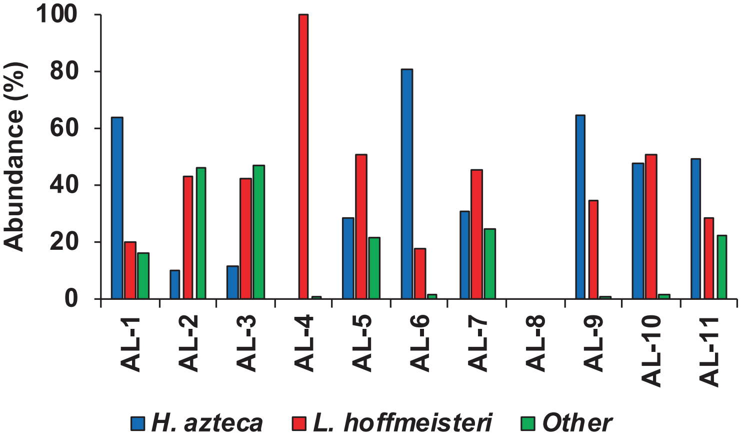

Fig. 10.2 Relative abundance of the dominant BMI in the littoral zone of Lake Alchichica. (AL-1 to AL-11 = littoral sampling stations; see Chap. 8, Fig. 8.1)

Total BMI biomass was 88.5 ± 309.5 mg C/m^2. Temporarily, July displayed the lowest average biomass (37.52 ± 138.71 mg C/m^2), while May the highest average biomass (129.75 ± 450.06 mg C/m^2). Spatially, the biomass among sampling stations ranged from 25.72 ± 104.86 mg C/m^2 to 151.48 ± 484.52 mg C/m^2 (Alcocer et al. 2016; Pérez-Rodríguez et al. 2013).

10.1.4 Function and Trophic Complexity

The community structure of the littoral ecosystem simplifies as littoral-pelagic isolation increases. Although simplification is graphically evident in a decrease in taxonomic richness, diversity, maximum diversity, and equity (but not in density), it is not supported statistically (Alcocer et al. 2016).

Detritivores (43.3 ± 23.1%) and herbivorous (40.1 ± 25.7%) BMI dominated numerically over carnivorous (16.6 ± 16.0%) in the littoral zone of Lake Alchichica (Fig. 10.3). Detritivores and herbivores were dominant in 40% of each of the littoral stations, in 10% were co-dominant, while 10% dominated the carnivorous.

According to Pérez-Rodríguez et al. (2013), there are four trophic guilds in the littoral BMI of Lake Alchichica. Herbivorous composed the highest percentage (50%, 155 ± 471.9 mg C/m^2) of the total biomass, while filter feeders constituted the lowest percentage (3%, 39.4 ± 72.1 mg C/m^2); detritivores accounted for 28% of the total biomass (85.8 ± 274.6 mg C/m^2), while predators contributed 19% of the total biomass (47.1 ± 152.9 mg C/m^2). Throughout the year, the biomass of detritivores and predators BMI remained similar, while herbivorous peaked in May, followed by a minimum in July. Filter feeders peak in January and diminished in July. Spatially, all littoral stations were different in their percentual composition of trophic guilds.

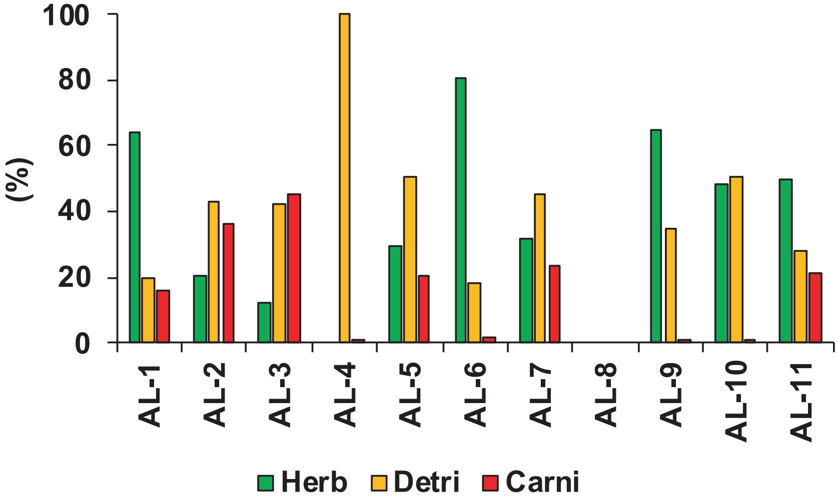

Fig. 10.3 Trophic groups of BMI in the littoral zone of Lake Alchichica. (*Herb* herbivores, *Detri* detritivores, *Carni* carnivores; AL-1 to AL-11 = littoral sampling stations; see Chap. 8, Fig. 8.1)

In general, the stations with the highest vegetation cover presented the highest BMI biomass composed mainly of herbivores. Plant coverage and sedimentary organic matter content were the most critical factors in explaining the MIB biomass and distribution.

There are six Functional Feeding Groups -FFG- in the littoral BMI assemblages of Lake Alchichica (Fig. 10.4). Most of the BMI are collector-gatherers (40.5 ± 25.9%), shredders (35.2 ± 28.0%), and predators-engulfer (14.2 ± 15.7%), while piercers-predators, piercers-herbivorous and scrapers were scarce (<1%).

10.1.5 Cryptic Fauna

The shape of the lake's basin approximates that of a cylinder (see Chap. 6). Nowadays, the lake has a reduced littoral area and a very abrupt slope with calcareous deposits called "tufa" (stromatolites). Tufa forms when carbonate-rich groundwater emerges in an alkaline-sodium lake, precipitating the carbonates in the form of calcite and, to a lesser extent, aragonite; microbial activity promotes carbonate precipitation (see Chap. 22). Tufa deposits that come in the form of a ring on the lake's periphery resemble, by their appearance, coral reefs. More critical, tufa deposits constitute an available habitat for cryptic species.

Stromatolites are solid mounds or cylinders of carbonate deposition that hardly retain sediments preventing benthic organisms from settling. Nonetheless, Escobar-Briones and Alcocer (2002) found and described a new asellid isopod species, *Caecidotea williamsi*, cryptically inhabiting in tufa crevices. *C. williamsi*

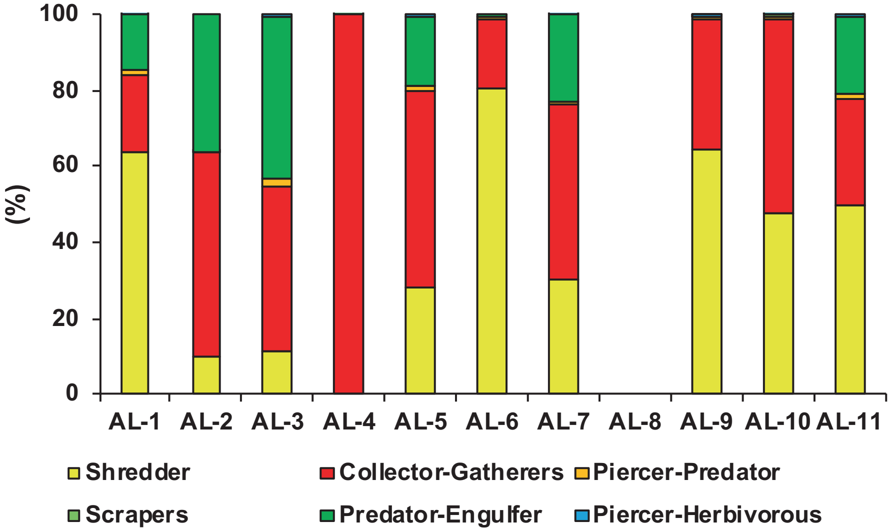

Fig. 10.4 FFG of BMI in the littoral zone of Lake Alchichica. (AL-1 to AL-11 = littoral sampling stations; see Chap. 8, Fig. 8.1)

constitutes the first report of an epigean asellid isopod inhabiting inland saline waters in America. Hernández et al. (2010) found *C. williamsi* shares this habitat with the amphipod *Hyalella azteca*, and two ostracods, *Limnocythere inopinata* (now *Limnocytherina axalapasco*) and *Candona* sp. (now *Candona alchichica*).

C. williamsi is a small isopod (1–8 mm) with pigmented eyes. The body is mottled pale and light brown or gray. Many individuals inhabit empty trichopteran cases cemented within the tufa crevices. Its crevicular habitat explains its absence from other benthic habitats in the lake (Alcocer and Escobar-Briones 2007).

10.2 Littoral Heterotrophic Protists

Alfonso Lugo-Vázquez, María del Rosario Sánchez, Javier Alcocer, and Elva Escobar

10.2.1 Introduction

As previously mentioned, the presence of stromatolites in the littoral zone of Lake Alchichica favors the formation of numerous microenvironments, with a wide range of biological and environmental conditions and a great diversity of habitats. In this work, heterotrophic protists diversity associated with the littoral zone was studied in a lake site where the stromatolites' littoral conditions combine with an area more related to open waters. To carry out the study, we use the colonization method of artificial polyurethane foam units (PFU) substrates proposed by Cairns et al. (1969). Cairns et al. (1979) found that the equilibrium in the number of protist species colonizing the PFU is reached around 21 days. In the present study, the substrates stayed in place until 38 days. During this period, the presence of 39 species of heterotrophic protists was observed in Alchichicica.

Protists perform numerous important functions in water bodies: autotrophic flagellates contribute to primary production through their ability to photosynthesize. Heterotrophic nanoflagellates (HNFs) are the primary consumers of bacteria, as are ciliates and small amoebae. Larger ciliates can consume, in addition to bacteria, flagellates, phytoplankton, diatoms, and other ciliates; large amoebae also consume algae, flagellates, ciliates, diatoms, etc. (Fenchel 1987). Protists are usually abundant in the littoral zone of water bodies since there are abundant and different types of food; in addition to diverse ecological niches, such as parts of aquatic plants, biofilms on surfaces (on the rocks and sediment), and filamentous algae. In turn, they are part of the food of larger organisms as rotifers, microcrustaceans (copepods, cladocerans), and macrocrustaceans such as ostracods or *Hyalella* (Monakov 2003).

In 1990, the study of protists from the littoral zone was carried out in Lake Alchichica using the method of polyurethane foam units (PFU) colonization (Cairns et al. 1969). It is a simple method that allows obtaining comparable samples at various sampling sites and at different times, reducing the difficulty in studying the various taxonomic groups and simplifying information on the community's structure (Bamforth 1982; Pratt et al. 1986). Polyurethane foam constitutes a habitat used in different ways by protists: as a refuge, as a fixation site, and as a place for feeding.

The PFUs (three replicates for each sampling date) were placed in the littoral zone, in the outer part of the barrier formed by the stromatolites. The environmental conditions of the littoral are fully described in the Chap. 8. According to Plafkin et al. (1980) the PFU colonization process behaves like a colonization of islands and follows the McArthur-Wilson model.

Since the study was carried out with the water extracted from the PFU, it was not possible to quantify the species' absolute density. The densities are in ind/mL referred to as one milliliter of water volume squeezed from the PFUs. In the present study, the substrates were in place until 38 days.

All the species observed are considered free-living (Table 10.2). In Fig. 10.5, it is evident that Alveolata (Ciliata) and Discoba groups had the highest number of species throughout the colonization process. After them, Stramenopiles and Amebozoa were the groups with the most species. All ciliates' species are found within Alveolata, while species included in the trophic group of HNF (heterotrophic nanoflagellates) belong to the supergroups Discoba, Stramenopiles, and Holozoa.

Bodo caudatus (6159 ± 4494 ind/mL), *Bodo saltans* (1532 ± 982 ind/mL), and *Spumella termo* (1428 ± 1168 ind/mL) were the most abundant species in HNF. *Actinophrys sol* (480 ± 163 ind/mL), *Trichamoeba osseossacus* (471 ± 790 ind/mL) and *Mayorella microeruca* (377 ± 241 ind/mL) dominated the amoeba and

Table 10.2 Taxonomic list of heterotrophic protists species from the littoral zone of Lake Alchichica according to Adl et al. 2019)

Discoba	**Stramenopiles**	**Alveolata**
Vahlkampfia sp.	*Actinophrys sol*	Ciliophora
Euglenozoa	*Actinosphaerium eichornii*	*Aspidisca cicada*
Anisonema ovale	*Spumella guttula*	*Chilodonella uncinata*
Petalomonas steinii	*Spumella mínima*	*Cinetochimlum margaritaceum*
Notoselenus apocamptus	*Spumella termo*	*Cothurnia* sp.
Kinetoplastia	*Spumella vivípara*	*Cyclidium citrullus*
Bodo caudatus	**Amoebozoa**	*Cyclidium glaucoma*
Bodo globosus	*Amoeba chaos*	*Enchelys simplex*
Bodo mínima	*Trichamoeba osseossacus*	*Holophrya simplex*
Bodo repens	Evosea	*Litonotus fasciola*
Bodo saltans	*Filamoeba nolandii*	*Mesodinium acarus*
Copromonas subtilis	Discosea	*Oxytricha* sp.
Rhyncomonas nasuta	*Mayorella microeruca*	*Spaherophrya soliformis*
Holozoa	*Vexillifera* sp.	*Stylonychia notophora*
Monosiga ovata	**Rhizaria**	*Trochilia minuta*
	Cercozoa	*Uronema* sp.
	Gymnophrys cometa	

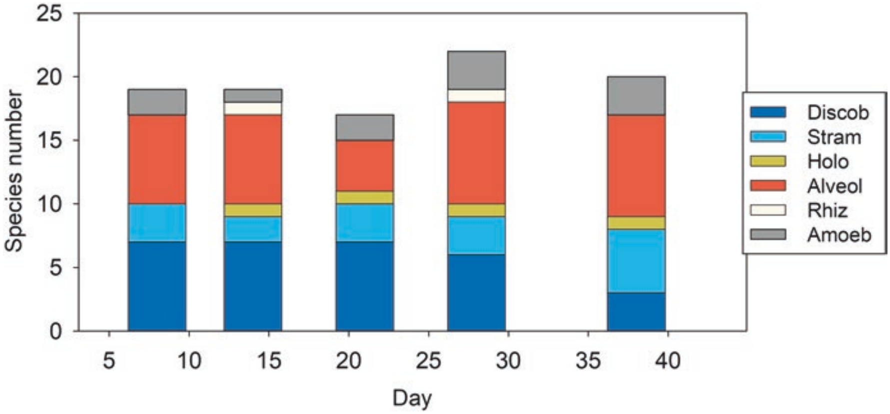

Fig. 10.5 Number of protists species by taxonomic supergroup and sampling day according to Adl et al. (2019)

related groups. In ciliates, *Cyclidium glaucoma* (53 ± 51 ind/mL), *Uronema* sp. (29 ± 31 ind/mL), *Stylonychia notophora* (26 ± 49 ind/mL) and *Trochilia minuta* (21 ± 31 ind/mL).

Theoretically, species number along the colonization process of the PFU must have a positive trend. It did not happen in Lake Alchichica because, at 8 and 14 days, 19 species were observed, but at 21 days, there was a decrease to 17 species. On day 28, an increase to 23 species occurred, and a slight decrease to 20 species on day 38.

10.2.2 Trophic Groups

Figure 10.6 shows the number of species according to their type of feeding (trophic group) throughout the sampling period. Pratt and Cairns (1985) criteria were used for flagellates and amebae, and the ciliates followed the one of Adl et al. (2019). Four trophic groups were found: bacterivores, predators, omnivores, and omnivores-cytrophic. Bacterivores consume bacteria by filtering them from the water; omnivores consume bacteria and other smaller protists, while cytrophic omnivores need to consume other protists to grow, but by consuming them, they also ingest bacteria.

Predators attack their prey, usually other protists or microalgae. From day 8 to 28, bacterivores had the largest number of species, followed by omnivores. However, on day 38, the omnivores equalized the number of bacterivorous.

The composition and dominance of heterotrophic protists in the littoral zone of Lake Alchichica provide valuable information about the biological conditions. The abundance of bacterivorous species indicates the presence of significant amounts of bacteria, which is common in littoral environments due to the fact that there is usually abundant decomposing organic matter (Arndt et al. 2000). This food favors the presence and growth of bacterivorous and detritivorous species of different sizes, among them, the bacterivorous flagellates which are the smallest. In the present study, several genus *Bodo* species, and *Spumella*, small bacterivorous, reached the highest abundances. Other important bacterivores were some small amoebae species such as *Vexillifera* sp. or *F. nolandi*.

The next largest trophic group was the omnivores. This group includes larger amoebae and the vast majority of ciliates. Omnivorous feed on bacteria, but they also

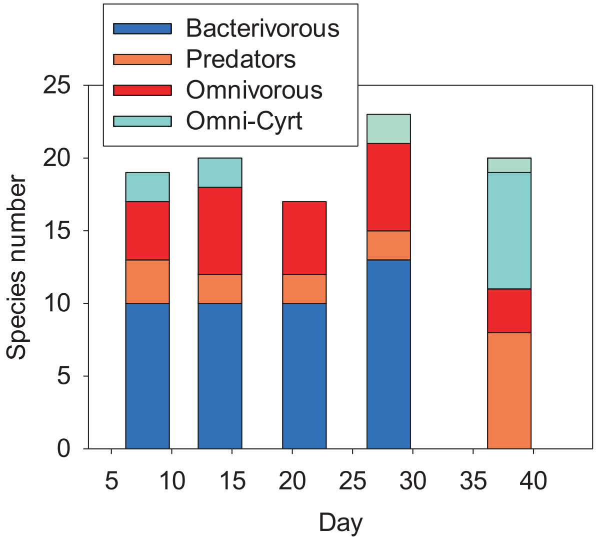

Fig. 10.6 Number of species by trophic group and sampling day in Lake Alchichica

consume other microorganisms such as small cyanobacteria, autotrophic flagellates, HNF, some diatoms, and various other microalgae types. A variant of this group is that of the omnivores-cytrophic, which in order to grow, they must consume protists, commonly flagellated, although they also feed on bacteria (Adl et al. 2019).

Although not very numerous, the predators' group included species from the supergroup Stramenopila (Heliozoa), such as *A. sol* and *A. eichornii*, which are passive predators. In the same case, the ciliated suctor *S. soliformis* is also a passive predator of other ciliates and flagellates. Finally, the ciliate *L. fasciola* is an active predator that detects, attacks, and consumes other ciliate and flagellate species.

The environmental factor that seems to exert the most significant influence on the species richness of the littoral heterotrophic protists of Lake Alchichica is salinity. The lake water has a salinity of 8.5 ± 0.2 g/kg (Vilaclara et al. 1993). At the site where the PFUs were placed, the salinity was 7 ± 0.1 g/kg. This salinity seemed to harm the species richness of protists since in other nearby lakes, with freshwater or considerably less saline, up to 50% more species were observed than in Lake Alchichica (Lugo 1993). Several dominant species in the study, as the HNF *B. saltans* and *R. nasuta,* and the ciliate *C. glaucoma* can occur under both marine and freshwater conditions, but other species have a narrow range of tolerance and salinity may be a limit for their distribution (Arndt et al. 2000; Lynn 2008).

In conclusion, the Lake Alchichica littoral zone's heterotrophic protists have a relevant ecological function as consumers of bacteria and other protists. In turn, they can be consumed by different groups of littoral macroinvertebrates, either directly or indirectly, as components of the organic detritus that constitute several of these invertebrates' food. From the list of littoral fauna groups observed in Lake Alchichica, crustaceans (copepods, ostracods and *Hyalella*), oligochaetes, and nematodes, chironomids could be the protist's predators (Monakov 2003). In this way, littoral heterotrophic protists constitute an energy transfer link from bacteria to a wide variety of macroscopic organisms, which in turn can be the food of fish (Alchichica's silverside), amphibians (Alchichica's axolotl), or even of aquatic birds that live temporarily or permanently in the lake.

10.3 Littoral Diatoms

Alfonso Lugo-Vázquez, María del Rosario Sánchez, Laura Peralta,
Mónica Cuellar, and María Guadalupe Oliva-Martínez

10.3.1 Introduction

In Lake Alchichica, as in other environments, both freshwater and marine and saline, diatoms are essential biological components. In the plankton and the littoral zone, there are numerous species of this group. Diatoms are unicellular or filamentous autotrophic organisms, characterized by presenting a cell wall or frustule made of silicon dioxide. The frustule is formed by two valves (epi and hipovalve) that fit together and joined by a series of bands that form the belt or cingulum. The frustule presents perforations of various forms (striae, pores) or spine-like extensions, which, for a long time, were the basis of the group's taxonomy.

Diatoms are of great importance in the silicon cycle in water bodies and soil. They constitute a fundamental food source for numerous groups of organisms, from protists (ciliates and amoebae) to larger organisms, such as cladocerans and copepods. In the littoral zone of water bodies, they can be the principal food of numerous groups of animals, among them those that make up the meiofauna of sediments, mollusks that scrape them from substrates, or even fish, which consume them together with debris or as epiphytes of plants and algae (Monakov 2003).

Benthic littoral diatoms can form mucilaginous layers on the bottom that help stabilize the substrate and reduce erosion (Grant et al. 1986). In littoral environments, diatoms contribute an essential fraction of primary production, which has been underestimated (Cahoon and Safir 2002), and they constitute the majority of the living organic fraction of sediments. Therefore, they can be considered to constitute most detritivores' food (Admiraal et al. 1984).

As described in detail in Chap. 8 (The Littoral environment), in the littoral area of Lake Alchichica, it is possible to find a wide variety of microenvironments. In the deep (12 m) and rocky area of the littoral, there is a significant growth of the filamentous Chlorophyte *Cladophora* sp. Numerous species of epiphytic cyanoprokaryotes and also some diatoms colonized these filaments (Tavera and Komárek 1996).

In the shallow (<1 m) portion of the litoral zone, the submerged aquatic macrophyte *Ruppia maritima* and the Charophyte *Chara canescens* grow in several places, being substrates where benthic -epiphytic- diatoms grow.

10.3.2 Species Richness

The samples were obtained at eight sites along the lake's perimeter (Fig. 10.7) and three different dates: October 2006, March 2007, and September 2007. The substrates sampled were the submerged aquatic plant *R. maritima* and the charophyte *C. canescens*. Also, where possible, rock scraping or plocon samples were collected. Table 10.3 shows the substrates sampled by season and site. In total, the number of samples analyzed was 32.

In each sampling site and date, water temperature, water conductivity, pH, and dissolved oxygen concentration were measured.

Forty diatom species were found in the eight points sampled in the littoral zone. Table 10.4 shows the list of species. The species number increased in each sampling: 27 species in October 2006, 30 in March 2007, and 36 in September 2007.

Ten species were observed with a frequency ≥75% in the samples obtained (n = 32) during the study (Fig. 10.8): *Navicymbula pusilla, Rophalodia gibberula,*

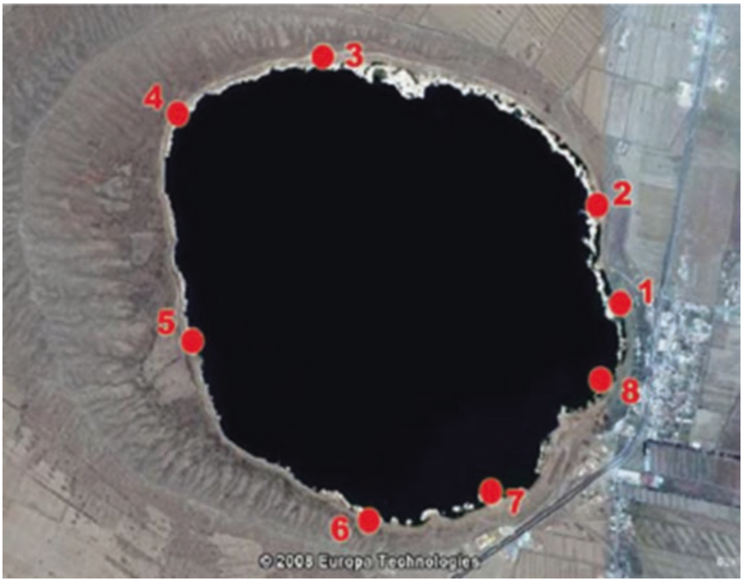

Fig. 10.7 Aerial view of Lake Alchichica showing the sampling site's location

Table 10.3 Substrates sampling for each site and date

Dates/sites	1	2	3	4	5	6	7	8
October 2006	Ep Ru	Ep Cha	El	Pl	Ep Ru El	El Pl	El Pl Ep Ru	El
March 2007	Ep Ru	Ep Cha	El	El	El	Ep Ru Pl	Pl	El
September 2007	Ep Ru	Ep Cha	El	Pl	El	El Pl	Ep Ru Pl	El Ep Ru

Key: Ep: Epiphytic, El: Epilitic, Pl: Plocon, Ru: *Ruppia maritima*, Cha: *Chara canescens*

Gomphoneis olivaceum, Mastogloia smithii, Halamphora veneta, Mastogloia elliptica, *Cocconeis placentula, Surirella striata*, *Anomoeoneis sphaerophora*, and *Navicula cryptocephala*.

The species with a frequency percentage value <10% were *Cocconeis placentula* var. *euglypta*, *Anomoeoneis costata* (both 9.4%) and *Caloneis westii* (3.1%). Most of the species (23 spp.) occurred in the three samplings. In contrast, eight species were found in a single sample: *Hyppodonta* sp. (28.1%) and *Gyrosigma acuminatum* (15.6%) in October 2006. *Anomoeoneis costata* (9.4%) in March 2007. *Cyclotella menenghiniana* (31.2%), *Nitzchia gracilis* (18.8%), *Epithemia sorex*

Table 10.4 Diatom species list from the littoral zone of Lake Alchichica

Achnanthes sp.
Amphora libyca Ehrenberg, 1841
Amphora pediculus (Kützing) Grunow, 1875
*Anomoeoneis costata (*Kützing) Hustedt, *1959*
Anomoeoneis sphaerophora Pfitzer, 1871
Caloneis westii (W. Smith) Hendey, 1964
*Campylodiscus clypeus (*Ehrenberg) Ehrenberg ex Kützing, 1844
Cocconeis placentula var. *euglypta* (Ehrenberg) Grunow, *1884*
Cocconeis placentula var. *lineata* (Ehrenberg) Van Heurck, 1885
Craticula sp.
Cyclotella menenghiniana Kützing, 1844
C*ymbella cistula* (Ehrenberg) O. Kirchner, 1878
Cymbella mexicana (Ehrenberg) Cleve, 1894
Denticula sp.
Diploneis pseudovalis Hustedt, 1930
Entomoneis alata (Ehrenberg) Ehrenberg, 1845
Epithemia argus (Ehrenberg) Kützing, 1844
Epithemia sorex Kützing, 1844
Epithemia turgida (Ehrenberg) Kützing, *1844*
Gomphoneis olivaceum (Hornemann) Ehrenberg 1838
Gomphonema clavatum Ehrenberg, 1832
Gyrosigma acuminatum (Kützing) Rabenhorst, 1853
*Halamphora veneta (*Kützing) Levkov 2009
Hippodonta sp.
Mastogloia elliptica (C. Agardh) Cleve, 1893
Mastogloia smithii Thwaites ex W. Smith, 1856
Navicula cryptocephala Kützing, 1844
Navicula radiosa Kützing, 1844
Navicymbula pusilla (Grunow) Krammer, 2003
Nitzschia communis Rabenhorst, 1860
Nitzschia frustulum (Kützing) Grunow, 1880
Nitzschia gracilis Hantzsch, 1860
Nitzschia vitrea Hantzsch ex Rabenhorst, 1862
Pinnularia brebissonii (Kützing) Rabenhorst, 1864
Pinnularia sp.
Pseudostaurosira brevistriata (Grunow) D.M.Williams & Round, 1988
Rhopalodia gibberula (Ehrenberg) O. Müller, 1895
Stauroneis sp.
Surirella ovalis Brébisson, 1838
Surirella striatula Turpin, 1828

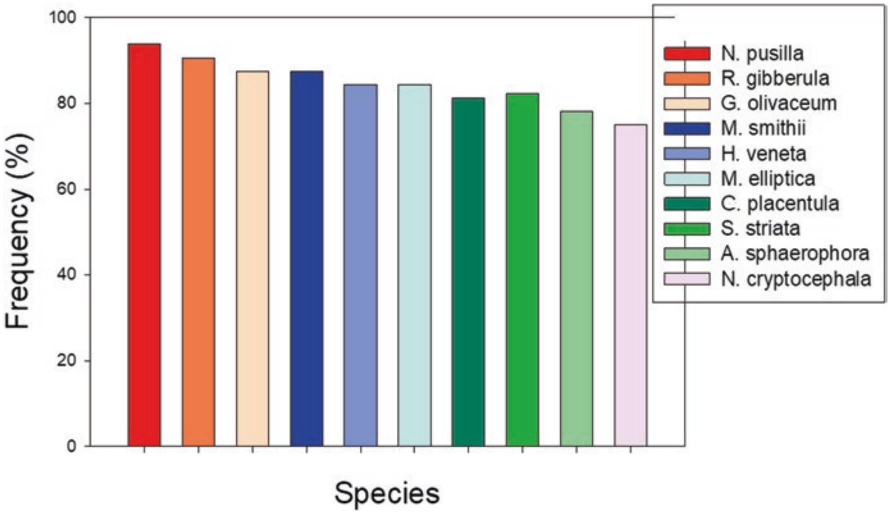

Fig. 10.8 Frequency (%) of the common littoral diatom species in Lake Alchichica

(15.6%), *Cocconeis placentula* var. *euglypta* (9.4%) and *Caloneis westii* (3.1%) in September 2007.

Regarding their spatial distribution, only *G. olivaceum* and N. *pusilla* appeared in the eight sampling sites in October 2006. In March 2007, more species were observed in all the sites: *G. olivaceum* and *N. pusilla*, also *M. elliptica*, *E. alata*, *N. cryptocephala*, *C. placentula* var. *lineata*, *Nitzchia frustulum* and *Epithemia argus*. In September 2007, only three species were present in all sites: *E. argus*, *Rhopalodia gibberula* and *M. smithii*.

Most of the species recorded in the study can live in wide ranges of salinity values, from freshwater environments to marine water. *A. lybica*, *A. sphaerophora*, *C. clypeus*, *E. alata*, *M. smithii*, and *N. communis* have only been found in saline environments. *H. veneta*, *G. olivaceum*, *Hippodonta* sp., *D. pseudovalis* and *R. gibberula* were species with high values of percentage of frequency (Frequency >75%). These are species that develop preferentially in saline environments, being rare in strictly freshwater environments (Hartley 1996; Krammer 2003; Novelo et al. 2007).

The majority of the species found belong to the group of pennate diatoms. *Cyclotella menenghiniana*, a central diatom, was observed in various littoral sites (Frequency 31.2%) only in September 2007. On several occasions, two other species of central diatoms were found in the littoral samples: *Cyclotella alchichicana* and *C. choctawhatcheeana*, which were not included in this study, since they are organisms that arrived from the pelagic zone, where they are common components of phytoplankton (see the chapter on phytoplankton), and their habitat is not the littoral zone.

Most species did not show a preference for some substrate since they grew on *R. maritima*, *C. canescens*, as epilithic, or as part of the plocon. Some exceptions were

C.westii, only observed as epilithic, or *G. acuminatum*, which was only epiphytic; *A. costata*, *E. sorex* and *P. brevissonii* were not observed in the plocon samples.

The environmental conditions measured correspond to those generally observed in the littoral zone and are described fully in Chap. 8. The temperature varied between 16 and 25 °C, the dissolved oxygen between 5 and 13 mg/L, and the pH was basic to strongly basic (8–12 units). During the study, the conductivity range was between 8 (E5 October 2006) and 13 mS/cm (E1, E2, E6, and E7 March 2007). The highest values were associated with decreased water level and salts' concentration in several sampled ponds.

Lake water's electrical conductivity ranges between 12 and 13 mS/cm (Vilaclara et al. 1993). However, due to groundwater entry at various points in the littoral zone, the conductivity may be lower.

10.3.3 Temporal, Spatial, and by Substrate Variation

In Fig. 10.9, the analyzed samples' grouping is observed by time of year, site, and sample type, using the Jaccard index as a similarity value and the UPGMA grouping method. Two groups were evident. The first of them (red box) includes the majority (9) of the sites and substrates from the October 2006 sampling (sampling 1), indicating that the composition of sites 1, 2, 3, 4, and 5 were similar, as well as the epilithic samples from sites 6 and 8 and the epiphytic from site 7. At site 4, which is penultimate to join the group, only a plocon sample was taken (similarity slightly less than 0.5).

In the second group (blue box), the samples from all the sites from the March 2007 sample joined first (sample 2) and then a group of 8 sites from sample 3 (September 2007). Plocon samples from sites 3 and 4 of the third sample are very similar (>0.85) and joined first with the epiphytic sample from station 7, and then with the epilithic sample from site 6, they are then joined with those of the group formed by the pair of plocon samples from sample 2.

Less similar samples, which later joined the previous group, were epilithic from sites 3 and 8 and epiphytic from sites 2, 8, and 5 of the third sample. Most different samples were from sampling date 1: the epilithic and the plocon from site 7, and the plocon from site 6, the latter being the least similar to all the rest. The analysis showed that the most remarkable similarities were temporary. The samples were grouped mainly according to the sampling dates, without the type of substrate from which they were obtained associating them. In some cases, the different substrates of the same site were similar, but in others, they were very different; for example, the epiphytic sample from site 7 of sample 1 had low similarity to the epiphytic and plocon samples from the same site.

The species richness of littoral diatoms of Lake Alchichica, considered a hyposaline lake, was greater than that of the hypersaline Mono lake (Nevada, USA), which only had 30 species (Herbst and Blinn 1998), but less than other hypersaline water bodies such as La Amarga lagoon in Argentina (53 spp.), or the Central Park lake, Turkey, with 126 spp. When Lake Alchichica is compared with freshwater bodies,

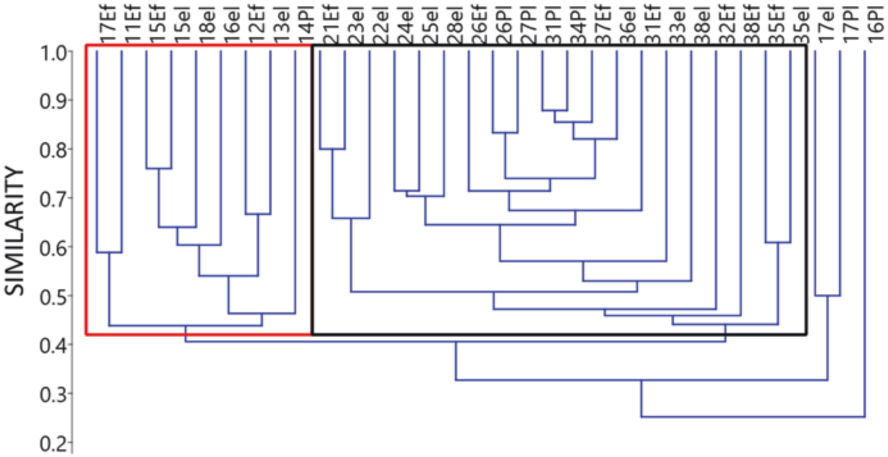

Fig. 10.9 Cluster analysis of Lake Alchichica's diatom species (presence-absence data). Key: First number: sampling number (1–3); second number: sampling site (1–8). Substrates: *Ep* epiphytic, *el* epilithic, *Pl* plocon. Most of the epiphytic samples were from *R. maritima*. Only the epiphytic samples from site 2 are from *C. canescens* (12Ef and 32Ef)

the number of Lake Alchichica diatom species is considerably lower (e.g., Lake Nagpur, India, 92 spp.; Marjal Oliva-Pego, Spain. 51 spp.) (Maidana and Romero 1995; Kaoru et al. 1997; Sarode and Kamat 1980; Cantoral-Uriza and Sanjurjo 2008).

The species richness of littoral diatoms of Lake Alchichica was moderate, with a predominance of species capable of resisting a wide salinity range. However, species with preferentially saline or marine conditions were also present. Except for exceptional cases, no specificity of diatoms was observed for any substrate since most of them were observed indistinctly in several of them. Temporal variation had the most significant influence since the critical factor for grouping the samples was the sampling date. Some of the plocon samples became the ones with the most remarkable difference in species composition. The diatoms of Lake Alchichica seem to be of great importance from the littoral food webs' point of view. They are indeed a very significant food for most of the different groups of macroinvertebrates that inhabit it. Together with the planktonic diatom species, they indeed have a very relevant function within the lake's silicon cycle.

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Chapter 11
Bacterioplankton

Rocío J. Alcántara-Hernández, Miroslav Macek, Jesús Torres-Huesca, Juan Arellano-Posadas, and Patricia M. Valdespino-Castillo

11.1 Study Approaches

11.1.1 Microscopic Techniques (Direct Counts, FISH)

Long-term data on bacterioplankton or heterotrophic (HPP) and autotrophic (APP) picoplankton (microorganisms of <2 µm size) are not available from many lakes; exceptions include Lake Superior (Carrick et al. 2017), Kinneret (Hadas and Berman 1998), Biwa (Nagata 1984; Okuda et al. 2014), Tanganyika (Pirlot et al. 2005), and Kivu (Sarmento et al. 2008). The HPP studies in Lake Alchichica using DAPI direct counts' staining protocol (Porter and Feig 1980) were carried out from 1998 to March 2020 (Peštová et al. 2008; Macek et al. 2009; Hernández-Avilés et al. 2010; Bautista-Reyes 2011; Sánchez-Medina et al. 2016; Macek et al. 2020; Arrellano-Posadas et al. unpublished).

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

M. Macek
Grupo de Investigación en Limnología Tropical, FES Iztacala, Universidad Nacional
Autónoma de México, Tlalnepantla, Estado de México, Mexico
e-mail: mirek@unam.mx

J. Torres-Huesca · J. Arellano-Posadas
Posgrado en Ciencias Mar y Limnología, Universidad Nacional Autónoma de México,
Ciudad de México, Mexico

P. M. Valdespino-Castillo
Molecular Biophysics and Integrated Bioimaging, Lawrence Berkeley National Laboratory,
Berkeley, CA, USA
e-mail: pmvaldespino@lbl.gov

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During the sampling campaigns, it was found that the annual average of bacteria counts (derived from the whole water column sampling depth-weighted averages) was $2.04 \times 10^6 \pm 1.56 \times 10^6$ and 1.69×10^6 cells/mL as the average ± SD and median, respectively. However, excluding high HPP values (over 1×10^7 cells/mL from two samplings in a mixing period), the average changed to $1.93 \times 10^6 \pm 1.03 \times 10^6$ with a minimal change in median (1.67×10^6 cells/mL). By comparison, the sampling layer HPP counts varied between 4×10^5 and 3.26×10^7 cells/mL.

Besides the direct counts, bacterial biomass was analyzed using image analysis (ImageJ, USA with specific macros). As reported in Hernández-Avilés et al. (2012), the representative carbon content per bacterial cell during circulation and in the aerobic layers is 16.6 fg C/cell, while in the anaerobic hypolimnion is 19.4 fg C/cell. A detailed spatial and annual dynamics of HPP is discussed in Sect. 11.2. However, large purple sulfur bacteria were not included in this analysis and will be further discussed in Sect. 11.3.

After a few years, the unspecific direct counts technique was enhanced by implementing FISH (Hernández-Avilés et al. 2010, 2012), and consequently CARD-FISH techniques (Bautista-Reyes 2011; Bautista-Reyes and Macek 2012), which increased the hybridization efficiency (as percentage of bacteria hybridized with a triple EUB cocktail in direct DAPI counts). This implementation allowed complex studies of the prokaryotic composition in Lake Alchichica (period 2008–2009). The hybridization efficiency was approximately 40% in general, but it reached >60% in the well-established circulation. These results suggest that there is a high percentage of unknown microorganisms in Lake Alchichica, especially during the stratification period. Curiously, the highest EUB hybridization was accompanied by the lowest proportion of identified taxa (Bautista-Reyes 2011).

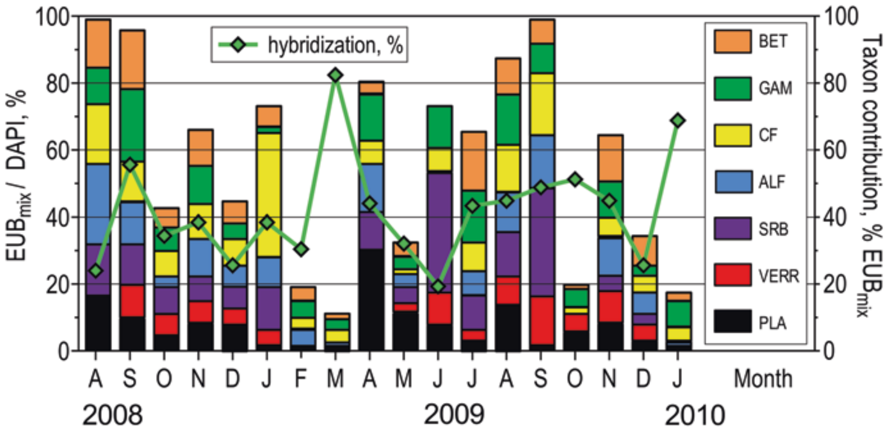

Fig. 11.1 Percentage of hybridized Bacteria (EUB_{mix}) in the FISH-DAPI assays and annual distribution of identified taxa in the Alchichica Lake water column, within EUB hybridized numbers: *BET* Betaproteobacteria, *GAM* Gammaproteobacteria, *CF* Cytophaga-Flavobacteria, *ALF* Alphaproteobacteria, *SRB* Sulfate reducing bacteria, *VERR* Verrucomicrobia and *PLA* Planctomycetes. (Modified from Bautista-Reyes 2011)

The results of CARD-FISH revealed the contribution of diverse aquatic bacterial taxonomic groups, such as Alphaproteobacteria (ALF), Gammaproteobacteria (GAM), Planctomycetes (PLA), and Cytophaga-Flavobacteria (CF) (Fig. 11.1). For example, ALF was the most abundant group in August 2008, but in September 2008 GAM abundance increased. CF dominated in January 2009, whereas PLA dominated the stable stratification. Sulfate-reducing bacteria (SRB), Betaproteobacteria (BET), and GAM were present mainly during stratification. These results also provide insight into the temporal variations of these taxa in Lake Alchichica associated with the hydrodynamic periods, i.e., the physical and chemical changes along the water column.

At the bottom of the metalimnion, which frequently coincided with the oxycline (only layers with DO >0.2 mg/L were integrated), the composition of bacteria showed quantitatively different results (Fig. 11.2). No evident dominance of any bacterial group was observed during the 2008 stratification period but was seen during October when BET dominated. In September 2009, an important contribution of SRB and CF was observed. Alphaproteobacteria (according to other studies, bacteria mainly associated with the genus *Paracoccus*; Hernández-Avilés et al. 2010) became proportionally important. These CARD-FISH results supported the idea that bacteria taxa contribution was continuously changing during the stratification period.

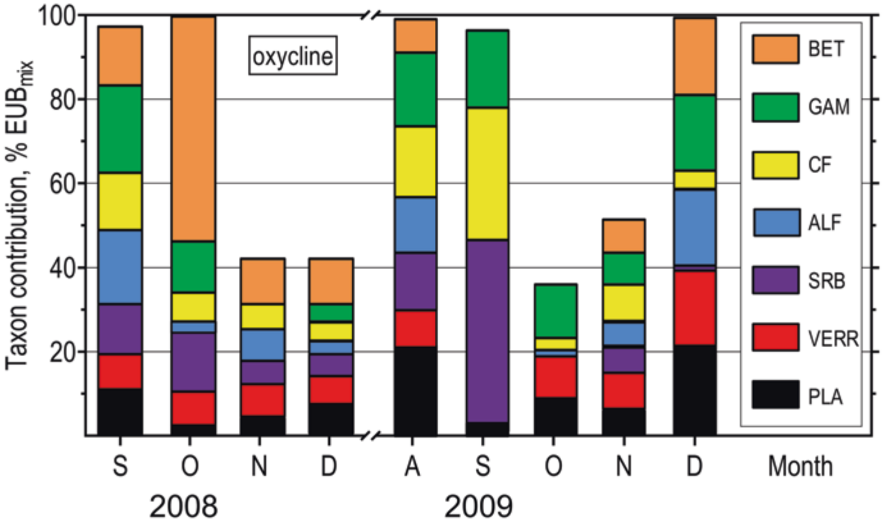

Fig. 11.2 Annual distribution of the identified taxa within EUB hybridized numbers in the oxycline (DO >0 mg/L). *BET* Betaproteobacteria, *GAM* Gammaproteobacteria, *CF* Cytophaga-Flavobacteria, *ALF* Alphaproteobacteria, *SRB* Sulfate reducing bacteria, *VERR* Verrucomicrobia and *PLA* Planctomycetes. (Modified from Bautista-Reyes 2011)

11.1.2 Culture-Independent Gene Marker Surveys

During the past decade (2010–to date), the diversity and metabolic potential of the bacterioplankton was also surveyed using new molecular tools that target gene sequences, particularly 16S rRNA sequences and functional gene markers related to biogeochemical processes. The implementation of new techniques allowed the study of the underestimated bacteria that were not detected by using hybridization approaches (Hernández-Avilés et al. 2010). The next-generation sequencing (NGS) surveys showed that the water column contains several bacteria, with an increasing number with depth (Fig. 11.3a). Further, the number of bacterial and archaeal taxa in the water column is larger during stratification than circulation, as suggested by the CARD-FISH assays (Fig. 11.2; Bautista-Reyes 2011)). For example, there are between 100 and 283 Amplicon Sequence Variants (ASVs) in circulation, whereas

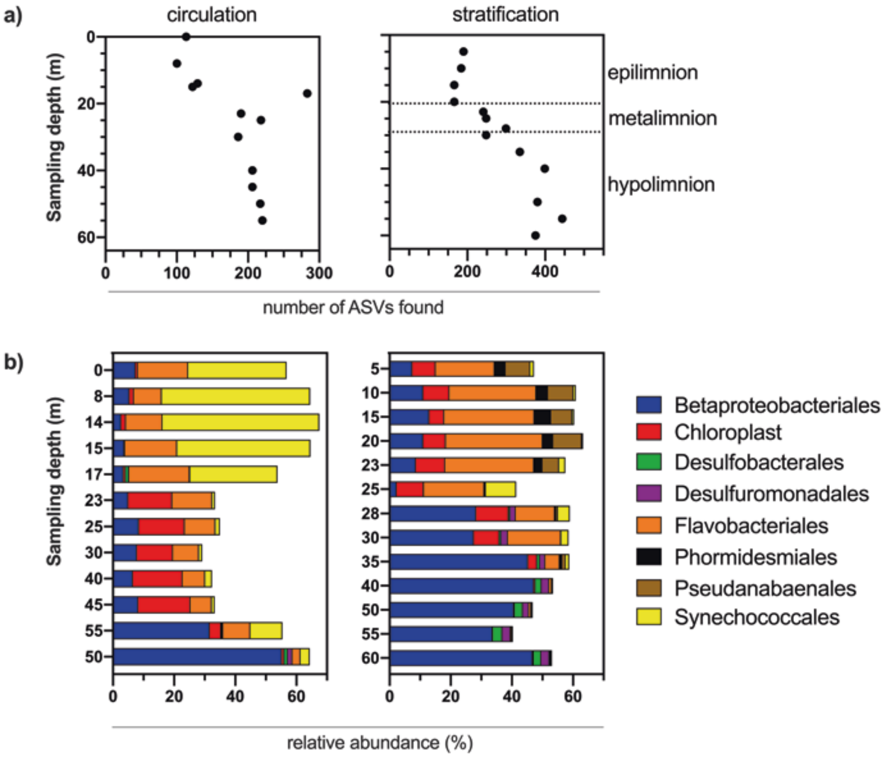

Fig. 11.3 Bacterial survey using the 16S rRNA gene and NGS in Lake Alchichica during the circulation and stratification. (**a**) Number of Amplicon Sequence Variants (ASVs) found in sampling depths. Phylotypes are defined as Amplicon Sequence Variants (ASVs), which are 16S rRNA sequences with 100% nucleotide identity. (**b**) Relative abundance of the main bacterial orders found in the 16S rRNA in the water column, including 16S rRNA sequences related to Chloroplast sequences

in stratification, this number increases to 166–444 ASVs. These variations in the water column are not just in the number of taxa, but also in their taxonomic affiliation (Fig. 11.3b). In circulation, unicellular cyanobacterial belonging to Synechococcales represent 30–60% of the relative abundance, and they are found with Flavobacteriales and diatoms (here mentioned as chloroplasts). However, at the well-established stratification, filamentous cyanobacteria are mostly found in the epilimnion (such as Phormidesmiales and Pseudoanabaenales); whereas some Synechococcales are in the metalimnion (these groups are further considered in Chap. 12, phytoplankton). Despite this high abundance of oxygenic phototrophs, it is also possible to observe diverse bacterial and archaeal taxa, such as Betaproteobacteriales in zones with DO <2 mg/L together with sulfate reducers such as Desulfobacterales and Desulfuromonadales.

Archaea has been also reported in the water column of Lake Alchichica. Hernández-Avilés et al. (2010) found archaeal microorganisms mainly during the stratification in the hypolimnion, yet these results showed low hybridization percentages with the ARCH915 probe. Using the same probe, Bautista-Reyes (2011) and Bautista-Reyes and Macek (2012) found that Archaea exhibited a very low abundance, generally below 5% of direct counts. In contrast, hybridized prokaryotes inside the ciliate cells included up to 10% of Archaea. The presence of archaea has now been confirmed by the 16S rRNA gene sequencing methods. Yet, their relative abundance is relatively low and represents up to 1.2% of the total 16S rRNA sequenced genes. The main microorganisms within this domain belong to the phylum Nanoarchaeaeota, which is also mainly found during the well-established stratification in the hypolimnion. However, Nanoarchaeota were described as interspecies symbionts with other Archaea from geothermal environments (St. John and Reysenbach 2019), yet, their possible host in Alchichica has not been identified.

At the genus level, *Flavobacterium* (order Flavobacteriales) is one of the most frequently found in the epilimnion, whereas *Planktosalinus* is the most abundant genus in the metalimnion. Regarding the order Betaproteobacteriales, the main group was MWH-UniP1, an aquatic group in the epilimnion which is associated with aerobic conditions.

Other gene markers have been used to survey the bacterioplankton in Lake Alchichica. These studies observed the diversity of bacteria related to the N and P cycles (Valdespino-Castillo et al. 2014, 2017; Pajares et al. 2017) and they have reinforced the biogeochemical functions of bacterioplankton in the lake, showing their relevance in elemental cycling. An interesting example is the diversity of microbial ectoenzymes related to phosphorus availability.

The prokaryotic genetic diversity related to the phosphorus cycling has been studied in the water column of Lake Alchichica during the circulation and stratification periods, together with their transcription patterns in a diel cycle (Valdespino-Castillo et al. 2014, 2017). In these studies, the diversity of genes encoding for alkaline phosphatases (*phoX* and *phoD*) and alkaline beta-propeller phytases (*bpp*) were surveyed using specific degenerated primers (reported in Sakurai et al. 2008; Huang et al. 2009; Sebastian and Ammerman 2009). Alkaline phosphatases and phytases are metalloenzymes whose expressions are known to be up-regulated under phosphorus scarcity, although metal ions such as Ca^{+2}, Mg^{+2} and Zn^{+2} act as cofactors of the mentioned enzymes. Lake Alchichica water exhibits a particularly low Ca:Mg ratio and the diversity of these enzymes follows this environmental constraint (Valdespino-Castillo et al. 2014). These enzymes cleave ester and diester bonds to release phosphate from dissolved organic phosphorus (DOP), which is typically the largest fraction of phosphorus in aquatic systems (Dyhrman et al. 2007). Lake Alchichica's endorheic character was considered to study the natural seasonality of DOP utilization potential though microbial markers, finding seasonal changes in the identity of the DOP utilization microbes (Valdespino-Castillo et al. 2014, 2017) which also exhibited diurnal transcriptional patterns. The largest diversity of alkaline phosphatases *phoD* and *phoX* was related to Alpha-, Beta-, and Gammaproteobacteria, in addition to Bacteroidetes. Rhodobacteraceae (Alphaproteobacteria; e.g., *Rhodobacter* or *Paracoccus* genus), in addition to members of Betaproteobacteria: Rhizobiales (e.g., *Mesorhizobium* or *Agrobacterium*) and Burkholderiales (e.g., *Ramlibacter*, *Ralstonia*, and *Cupriavidus*) showed a close affiliation to the sequences found. Both phosphatases studied showed a close affiliation to phosphatases from Actinobacteria (e.g., *Geodermatophilus*, *Streptomyces*, and *Frankia*). Alkaline phosphatase *phoD* and *bpp* phytases were also related to Gammaproteobacteria (e.g., genera *Azotobacter* and *Pseudomonas*). Some *bpp* phytases were affiliated to Flavobacteriales (e.g., *Riemerella*). Flavobacteriales (*Bacteroidetes*) is an order that was later confirmed by 16S rRNA gene surveys as part of the epilimnion community. Finally, transcript sequences of *bpp* were also affiliated to *Scytonema*, a known diazotrophic cyanobacterium. The protein domain DUF839 detected in *phoX* has been recently described in the proteome of radiation resistant bacteria (Vishambra et al. 2017) as part of the proteins from their outer cell, including periplasmic and extracellular proteins. These recent findings converge with previous findings to point to the extracellular allocation (and function) of these enzymes.

11.2 Temporal and Spatial Dynamics of Heterotrophic Picoplankton

The HPP dynamics in Lake Alchichica follows a similar annual pattern, which is clearly linked to the warm-monomictic thermal regime of the lake (i.e., stratification and circulation periods) (Fig. 11.4a). HPP frequently culminates around the onset of- (between the end of December and January) and/or during the turnover (Fig. 11.4a). A second abundance peak is observed after the thermocline stabilization through June–July (maximum column mean 1.82×10^6 to 1.78×10^7 cells/mL, median of 4.11×10^6 cells/mL), which is occasionally higher than the first peak.

There is not a clear pattern in the distribution of HPP throughout the water column (Fig. 11.4b), as it varied notably. It was not proven that bacterioplankton should be concentrated around the bottom of the metalimnion, whereas local drop of

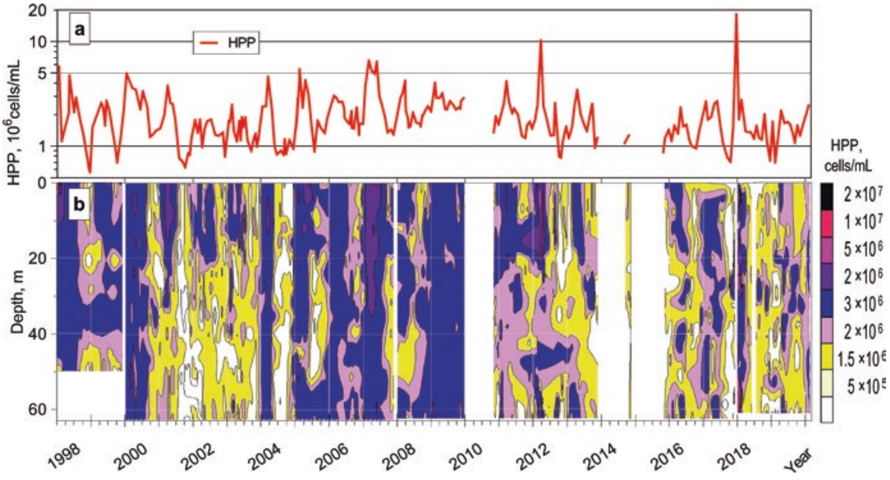

Fig. 11.4 (**a**) Depth weighted average counts of heterotrophic picoplankton, HPP (cells/mL); (**b**) HPP count isopleths (cells/mL)

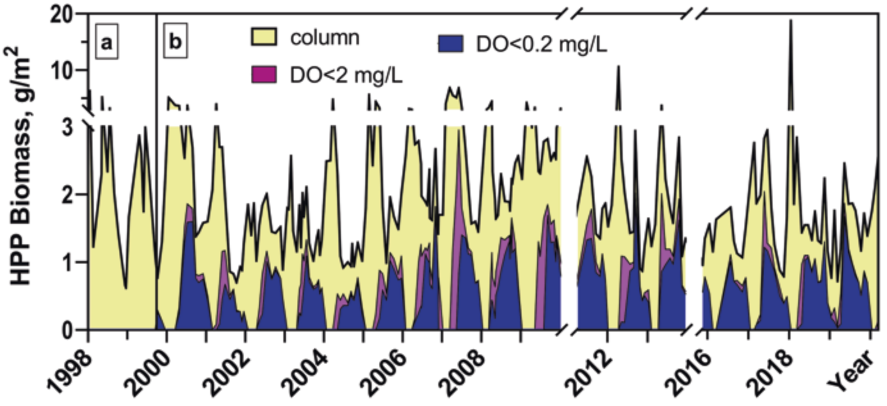

Fig. 11.5 Distribution of the heterotrophic picoplankton (HPP) carbon biomass (g/m^2) within the water column of Lake Alchichica. Total water column (yellow), microaerobic layer (DO <2 mg/L ->0.2 mg/L, violet) and anaerobic (DO <0.2 mg/L, blue) layer. Interval (**a**) represents 1998–2000 where only 5 depths were analyzed thus the oxygen dependent stratification was not evaluated, (**b**) represents a minimum of 10 sampled depths distributed according to the thermal and oxygen stratification

bacterioplankton biomass was observed in the fine scale-sampled upper hypolimnion, along with the peak of ciliate biomass. This behavior could be seen only in a detailed HPP stratification plots (e.g., Chap. 11.3, Fig. 11.8).

The HPP carbon biomass was calculated from the direct counts applying layer specific bacterial cell biomass (Hernández-Avilés et al. 2012). The biomass follows a slightly different pattern than that of direct counts due to the fact that the specific cell biomass is higher in the anaerobic hypolimnion. However, it was sufficient to shift the maximum biomass peak to the early stratification from May to July, even though mixing period maxima were also observed (peaks from 35 to 295 μg/L, median 76 μg/L).

The HPP biomass was also integrated below the surface area (Fig. 11.5) to evaluate the importance of oxygen concentration in the HPP distribution. This exercise shows the relevance of the anaerobic hypolimnion HPP biomass (at DO <0.2 mg/L) within the total column. The anaerobic HPP biomass-contribution ranged from 60% to 70% between August and October, while in the whole stratification period it showed a mean of 42% (carbon).

Due to the observed relevance of the microorganisms and their metabolism in the oxycline, HPP biomass was analyzed in the layer with DO values between 0.2 and 2 mg/L (Fig. 11.5); in this case, the layer contributes in average only 12% to the total column biomass, with a median of 7%. The absolute maxima (up to 60%) were found to be related to the extended oxycline width (plane thermocline up to 8 m but oxycline with a depletion of 0.5 mg/(L m) through up to 10 m) during June–July stratification. The HPP biomass concentrated in the late stratification-oxycline (<2 m during November–December) was not apparently so important.

11.3 Temporal and Spatial Dynamics of Photosynthetic Anoxygenic Bacteria

Lake Alchichica displays a euphotic zone that includes the oxycline and upper anaerobic layers -the top of the hypolimnion- during the well-established stratification when the whole hypolimnion becomes anaerobic (see Chap. 7, physicochemical characteristics). These conditions explain the possible biological sulfate/sulfur reduction to hydrogen sulfide (see Chap. 17, the deep benthic zone). However, possible anoxygenic photosynthetic bacteria (APB) were not noted in the preparations inspected via epifluorescence microscopy using either DAPI staining or FISH techniques (Hernández-Avilés et al. 2010; Bautista-Reyes 2011; Bautista-Reyes and Macek 2012), possible anoxygenic photosynthetic bacteria (APB) were not observed in the preparations inspected via epifluorescence microscopy until 2012. Then, bacteria possessing bacteriochlorophylls were analyzed in the samples harvested on black 1 μm polycarbonate membranes through their infrared fluorescence but deep strata of the hypolimnion were not sampled in detail until 2017. The images were taken with an IR-sensitive camera excluding cyanobacteria and eukaryotic chlorophyll-possessing cells observed in visible color-images using the same filter sets (specific for chlorophyll *a* and phycobilins). The use of a camera was necessary because the IR autofluorescence was not bright enough for direct counting in the microscope (Fig. 11.6). In addition to the IR images, bacterial elemental sulfur deposits were counted in the Quantitative Protargol Stain (QPS) preparations (see Chap. 13) because a silver sulfide precipitate was observed in the cells (Fig. 11.6b).

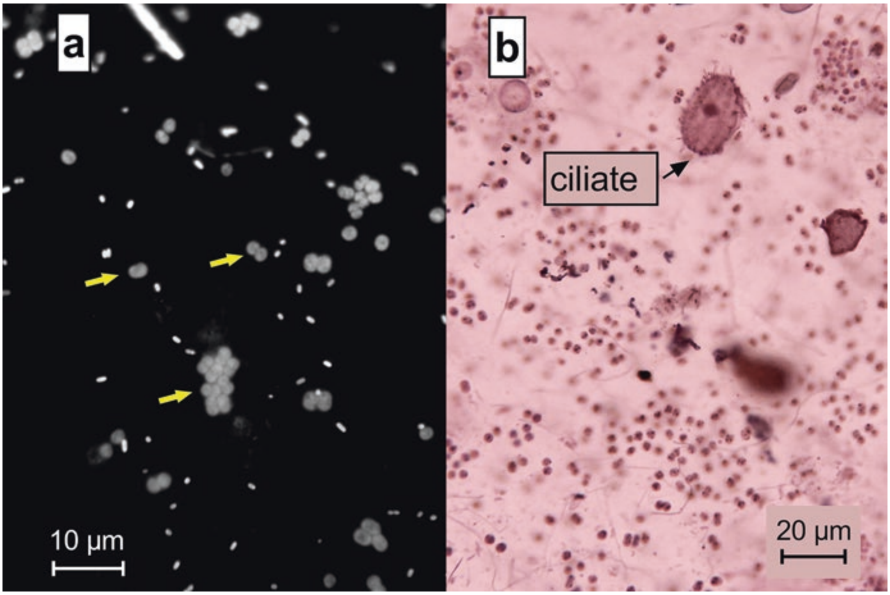

Fig. 11.6 Microscope analysis of anoxygenic photosynthetic bacteria in the water column of Lake Alchichica. (**a**) *Thiocapsa* sp. (marked with yellow arrows) and chlorophyll *a* containing microorganism including picocyanobacteria (bright spots). (**b**) Protargol-stained *Thiocapsa* sp. showing sulfur granules (black spots of silver sulfide) and a scuticociliate

The counts of purple sulfur bacteria (*Thiocapsa* sp.) showed that these microorganisms appear only during the well-established and late stratification (Fig. 11.7). Large *Thiocapsa* sp. was observed generally from July or August until December/January, reaching numbers up to nearly 10^5 cells/mL (Macek et al. 2020; Arellano-Posadas, unpublished). The maxima match with an exhaustion of oxygen and a photosynthetically active radiation (PAR) above 0.1%. The subsequent studies using a 16S rRNA amplicon sequencing strategy confirmed that sulfur oxidizing bacteria mainly belong to the orders Chromatiales and Ectothiorhodospirales, for which the genera *Thiocapsa* and *Thioalkalibrivio*, which are the most visibly abundant. These groups are characteristic of soda lakes (Sorokin et al. 2004; Kompantseva et al. 2007; Baatar et al. 2016).

Thiocapsa sp. direct counts were compared with molecular data using limnologic data as background (Figs. 11.7 and 11.8). In this case, the maximum of *Thiocapsa* sp. counts is found: (i) 2 m below the ciliate maximum biomass (mainly *Euplotes euryhalinus*), (ii) 1 m below the photosynthetic pigments' maximum (i.e., chlorophyll *a* and phycobilins) that matches with that of APP, and (iii) where the Eh reach negative values, and sulfide can be found at an analytically significant concentration. The relative abundance of 16S rRNA sequences related to *Thiocapsa* sp. (and here mentioned as 16S rDNA %) followed roughly the same pattern.

The presence of *Thiocapsa* sp. in a saline, warm monomictic lake such as Alchichica could be explained by its photo/biochemical versatility (van Gemerden

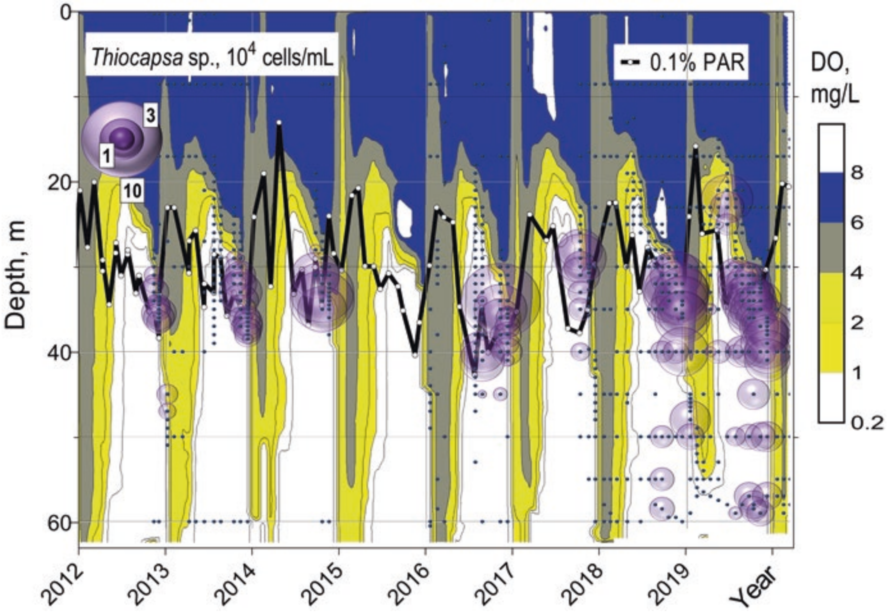

Fig. 11.7 Distribution of the anoxygenic photosynthetic bacteria (*Thiocapsa* sp., cells/mL, purple bubbles) in the water column of Lake Alchichica (2012–2020), quantified by microscopy. (The black dots identify the sampling depths). (Isopleths show the concentration of dissolved oxygen and the thick black line corresponds to 0.1% of photosynthetically active radiation (PAR) in the surface layer)

and Mas 1995; Hemp et al. 2016). This genus is very tolerant to aerobic conditions while it is able to switch between a phototrophic and chemolitotrophic metabolism. Furthermore, this genus was detected as the second most important photosynthetic sulfur bacterium competitive upon sulfide limitation and with higher PAR availability (Avetisyan et al. 2019).

11.4 Conclusions

Microbes, the unseen majority, are responsible for biogeochemical cycling and many other aspects of ecosystems' functioning. Nonetheless, their diversity and ecological properties remain poorly understood. This information is particularly scarce for tropical inland water bodies. The exploration of the microbial communities of Lake Alchichica dating back to the 1990s, constitutes a pioneer example in which spatial and temporal monitoring of the microbial communities is conducted in a deep, tropical lake. Particularly relevant and novel is the exploration of the hypolimnion as a non-homogeneous zone for microbial life. In this sense, the

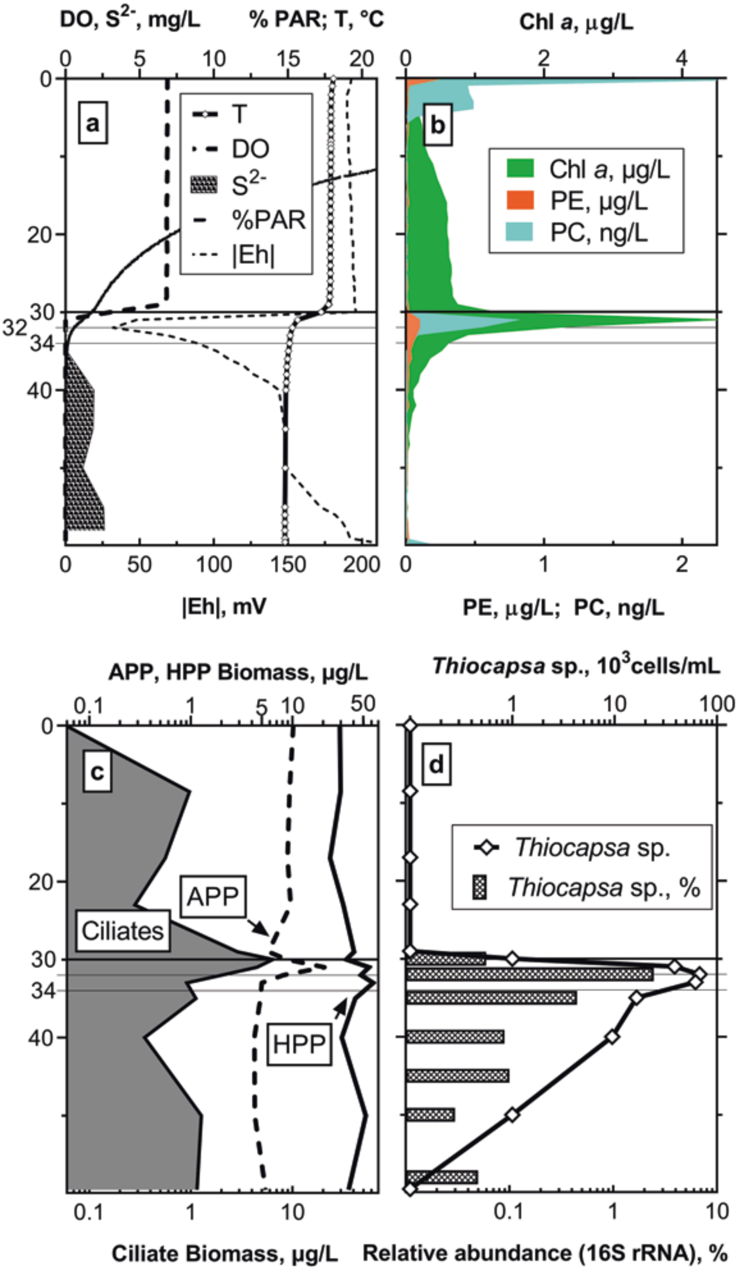

Fig. 11.8 Distribution of photosynthetic anoxygenic bacteria in the water column of Lake Alchichica. (**a**) Limnologic variables in Lake Alchichica (November 15, 2018): Dissolved oxygen (DO), sulfides (S^{2-}), %SPAR, temperature (T), and Redox potential (absolute value, |Eh|. (**b**) Chlorophyll *a*, Chl *a*, phycoerythrin, PE and phycocyanin, PC. (**c**) Biomass of heterotrophic (HPP) and autotrophic (APP) picoplankton, and ciliates; (**d**) Distribution of *Thiocapsa* sp. as direct counts and relative abundance of 16S rDNA sequences. Horizontal lines limit the thermocline and the redox potential drop to negative values

preliminary findings of microbial patterns below the oxygen minimum will contribute to a better understanding of the functioning of the aquatic ecosystem.

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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; Ciros-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

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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 (Sarmento 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 Senerpont 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 Peštová 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 fg/μm^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 fg/cell), lowest in the mixing layer during stratification (epilimnion, 32 fg/cell), and highest in the anoxic hypolimnion (64 fg/cell).

Oliva et al. (2001) and Rosiles-Gonzalez (2005) identified the cyanobacteria composition by their morphology, which has been subsequently acknowledged by Peštová 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 *Synechocysti*s 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 × 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

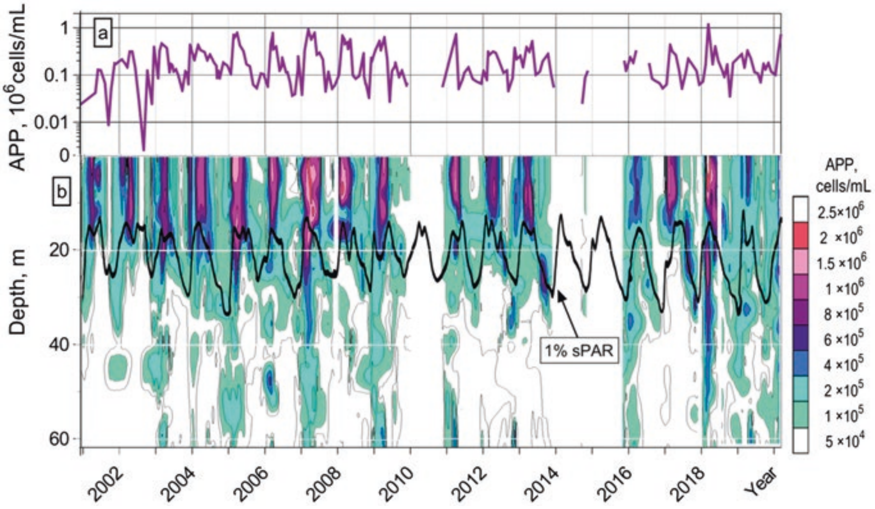

Fig. 12.1 (**a**) Depth weighted average of autotrophic picoplankton, APP (cells/mL). (**b**) Isopleths of APP abundances and the depth of the euphotic zone. (The thick black line corresponds to 0.1% of photosynthetically active radiation (PAR) in the surface layer)

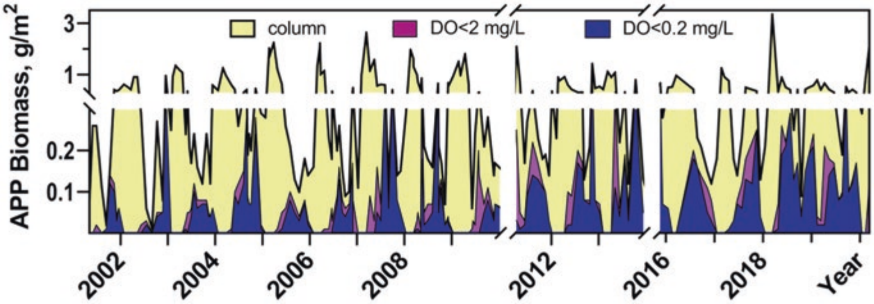

Fig. 12.2 Distribution of the autotrophic picoplankton carbon biomass (g/m^2) within the water column of Lake Alchichica. Total column (column, in yellow), microaerobic layer (DO <2 mg/L, in violet) and anaerobic (0.2 mg/L, in blue) layer

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).

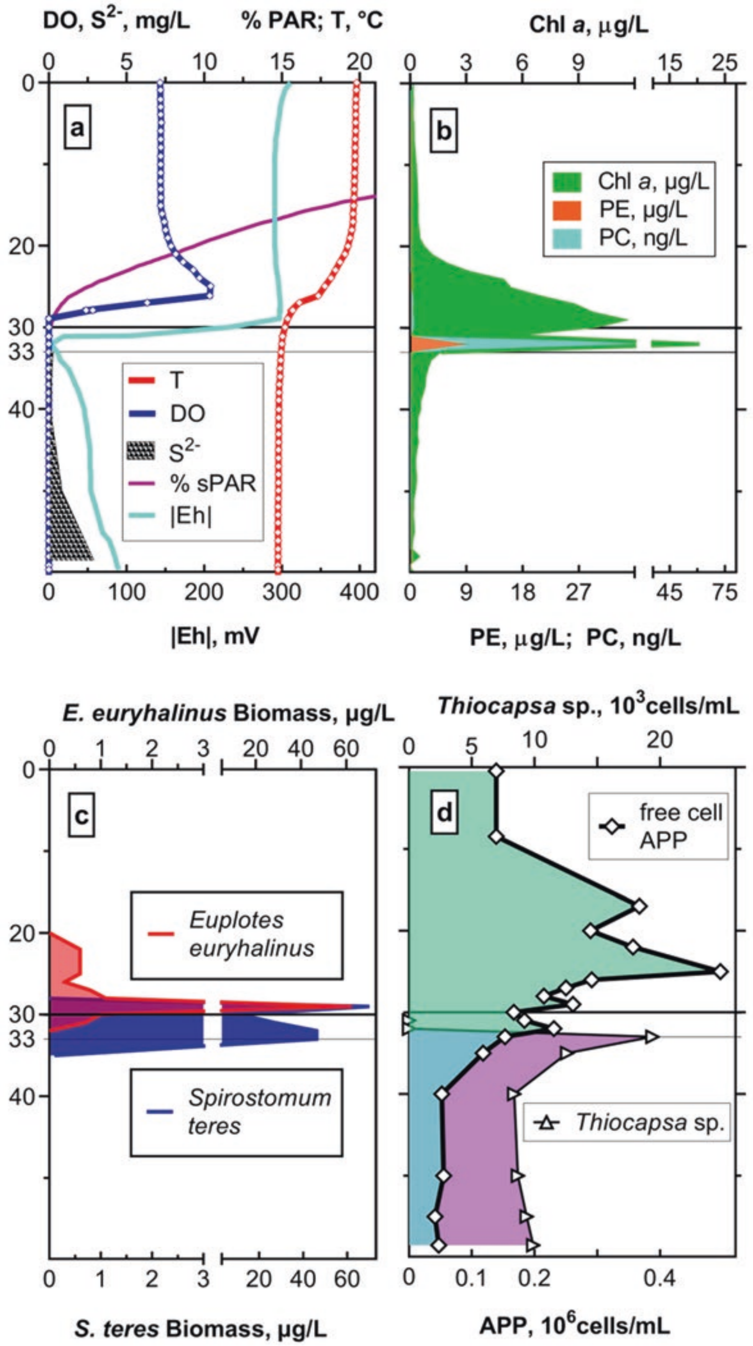

Fig. 12.3 (**a**) Limnological variables in Alchichica, September 2018: Dissolved oxygen, DO; sulfides, S^{2-}; %PAR; temperature, T; and Redox potential (absolute values), |Eh|. (**b**) Chlorophyll-*a*, Chl-a; phycoerythrin, PE; and phycocyanin, PC. (**c**) Distribution of the most biomass-important 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:
Cyclotella alchichicana	M	bio	*Stephanodiscus niagarae* 1; *C. quillensis* 3, 4; *Cyclotella* sp. 6; *C. alchichicana* 7, 10, 11.
C. choctawhatcheeana	N	num	*Cyclotella* sp. 3; *C. choctawhatcheeana* 4, 6, 8, 10.
Chaetoceros elmorei	M	num	*C. similis* 1; *C. elmorei* 3, 4, 6.
Nodularia aff. *spumigena*	M	bio	*N. spumigena* 3, 4, 9; *N.* cf. *spumigena* 2, 5; *N.* aff. *spumigena* 10,12.
Oocystis submarina	M	num	*Oocystis* sp. 1; *O. submarina* 3, 4, 6.
O. parva	N	num	3, 4, 6.
Monoraphidium minutum	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 tychoplankton 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.

Microendemicity 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 cyclicity. 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 (μm^3/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, $N\text{-}NO_3^-$, $N\text{-}NO_2^-$, $N\text{-}NH_3$, and Soluble Reactive Phosphorus, SRP; chlorophyll-*a*, Chlor, µg/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

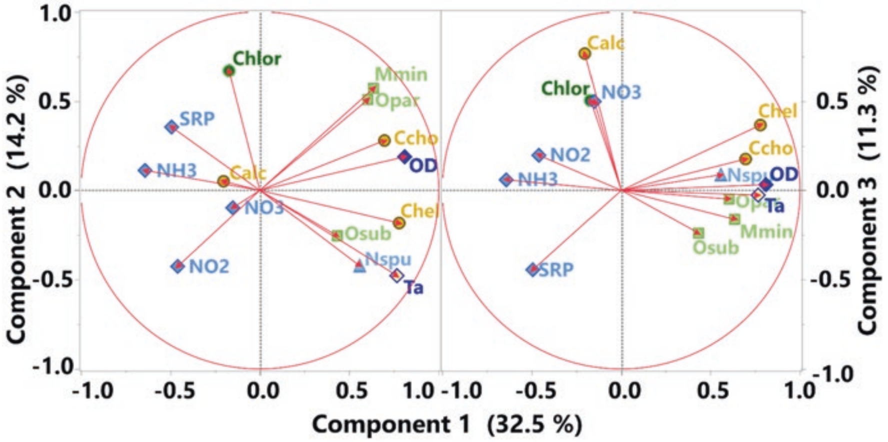

Fig. 12.4 Factorial loading plots of nutrients, chlorophyll-*a*, and the seven main large species: diatoms **Calch** *Cyclotella alchichicana*, **Chel** *Chaetoceros elmorei*, **Ccho** *C. choctawhatcheeana*; cyanobacteria **Nspu** *Nodularia* aff. *spumigena*; chlorophytes **Osub** *Oocystis submarina*,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

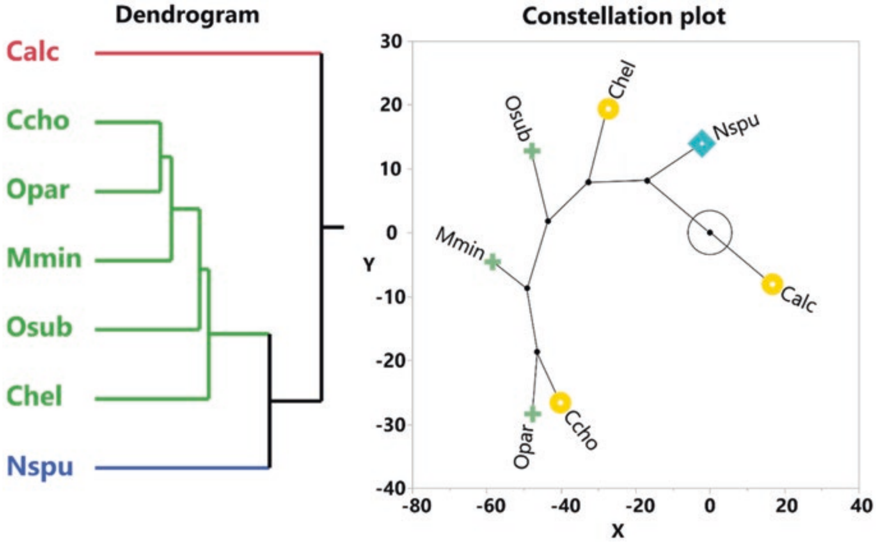

Fig. 12.5 Hierarchical conglomeration (Ward's method). Dendrogram and constellation plot for the biovolumes of the seven most abundant large phytoplankton species of Lake Alchichica. In the constellation plot, yellow circles point to diatoms **Calc** *Cyclotella alchichicana*, **Chel** *Chaetoceros elmorei*, **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; Ciros 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 pelagial 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.

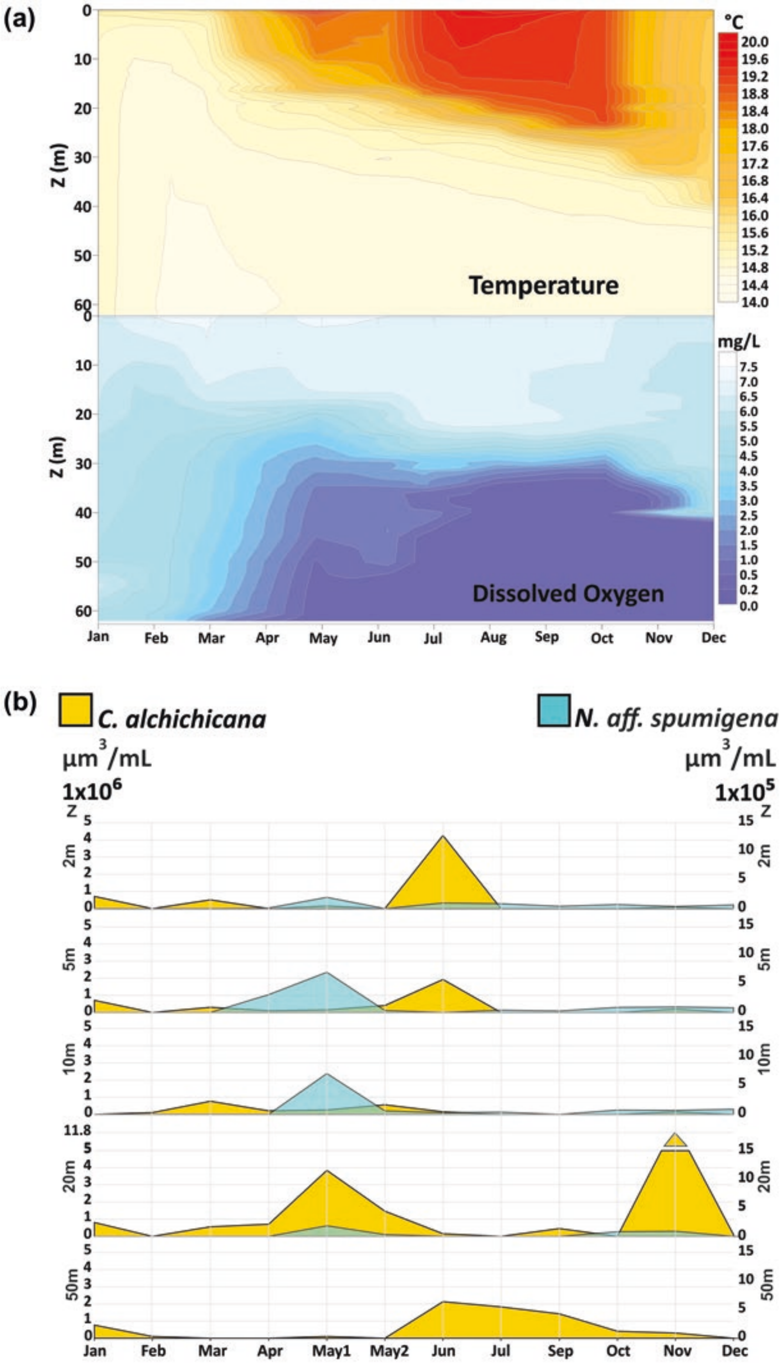

Fig. 12.6 (**a**) Time-depth plots for temperature and dissolved oxygen. (**b**) Comparison of the population biovolume for the two larger phytoplanktonic species (note the difference of an order of magnitude between them)

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Chapter 13
Protozooplankton

Miroslav Macek, Ximena Sánchez-Medina, Gloria Vilaclara, Alfonso Lugo-Vázquez, Fernando Bautista-Reyes, and Patricia M. Valdespino-Castillo

13.1 Introduction

The opinion regarding the importance of protozoa in the plankton mass and energy flows has changed since the 1980s, when the microbial loop concept was formalized (Azam et al. 1983). The relevance of this diverse group within microbial food webs was found to be crucial, particularly in tropical lakes, as defined by Sarmento (2012). Today, protozoan diversity, and their spatial and temporal ecological patterns, remains elusive; annual pattern surveys including protozoan stratification in dark and deep layers of oligotrophic lakes are particularly scarce. Reference studies of freshwater protozoa include those of temperate lakes, such as Traunsee, Austria (Sonntag et al. 2006), and Lake Okaro, New Zealand (James et al. 1995); subtropical lakes, such as Kinneret, Israel (Madoni 1990; Hadas and Berman 1998; Hadas et al. 2014), and Lake Biwa, Japan (Okuda et al. 2014; Nishino 2020); and tropical monomictic lakes (Yasindi and Taylor 2016; Peštová et al. 2008; Tarbe et al. 2011).

In the tropics, Lake Alchichica is the only hyposaline monomictic lake in which long-term and detailed ciliate studies take place. In contrast to other studies, the

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M. Macek (✉) · G. Vilaclara · A. Lugo-Vázquez
Grupo de Investigación en Limnología Tropical, FES Iztacala, Universidad Nacional Autónoma de México, Tlalnepantla, Estado de México, Mexico
e-mail: mirek@unam.mx; vilaclara.gloria@iztacala.unam.mx; lugov@unam.mx

X. Sánchez-Medina · F. Bautista-Reyes
Programa de Posgrado en Ciencias Mar y Limnología, Universidad Nacional Autónoma de México, Ciudad de México, Mexico
e-mail: diffy@comunidad.unam.mx

P. M. Valdespino-Castillo
Molecular Biophysics and Integrated Bioimaging Division, Lawrence Berkeley National Laboratory, Berkeley, CA, USA
e-mail: pmvaldespino@lbl.gov

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exploration of protozoa in Lake Alchichica has included detailed surveys in the vertical axis. By including metalimnetic and hypolimnetic depths, these studies have revealed interesting features of the protozoan ecological niches, e.g., the potential of ciliates to thrive in microaerophilic conditions (Macek et al. 2006, 2008, 2020; Peštová et al. 2008; Bautista-Reyes and Macek 2012; Sánchez-Medina et al. 2016).

13.2 Heterotrophic and Mixotrophic Flagellates

The first analysis of spatial patterns and annual dynamics of nanoflagellates (NF) in Lake Alchichica using DAPI staining (Porter and Feig 1980) covered the period from August 1993 to July 1994 (Lugo-Vázquez 2000). NF counts are shown in Table 13.1; integrated numbers below the area represent a range of 5×10^{10} to 9×10^{10} NF cells/m^2. The maximum counts when considering the whole water column were observed just after water column mixing, however, the numbers dropped in the next circulation period. During the stratification, the maxima were observed in the metalimnion and/or in the top of an anaerobic hypolimnion, whereas flagellates were not abundant in both the epilimnion and the anaerobic hypolimnion (Table 13.1; Fig. 13.1a) Choanoflagellates, heterotrophic chrysophytes (mainly *Spumella*-like), and kinetoplastids (*Rhynchobodo* sp., *Bodo* sp.) were identified in the water column (Fig. 13.2). The possibility that the numbers also include mixotrophic and even autotrophic flagellates was considered. Neither clear seasonal nor stratification patterns were found in analysis of data from the years 2000–2003 (Figs. 13.1b and 13.2). The taxonomic analyses suggest the maximum mixotrophic NF numbers of $>10^4$ cells/mL were observed just after the establishment of the water column stratification (June 2003).

Nanoflagellates were not highly abundant (average 8.3×10^2 cells/mL; Table 13.2) but varied considerably among sampling efforts. The median was nearly the same as that found during the first campaign (5.52×10^2 cells/mL). Spatially, NF were not tightly related to the thermocline position and the column maxima were observed between 10 and 20 m. This result suggests there is an optimum illumination layer (PAR attenuated below 10%), and bacterial abundance did not peak significantly there. On the other hand, flagellate abundance frequently dominated microaerobic and anaerobic conditions (Fig. 13.2).

Table 13.1 The Alchichica nanoflagellates' abundances

Period	Avg	SD	Med	Max	Min
1993–1994	7.12×10^2	6.12×10^2	5.18×10^2	2.95×10^3	7.80×10^1
2000–2003	8.31×10^2	7.86×10^2	5.52×10^2	4.60×10^3	1.53×10^2
2006–2010	8.08×10^2	7.52×10^2	6.01×10^2	4.02×10^3	4.88×10^1

Avg sampling average, *SD* standard deviation, *Med* median, *Max* maximum, *Min* minimum

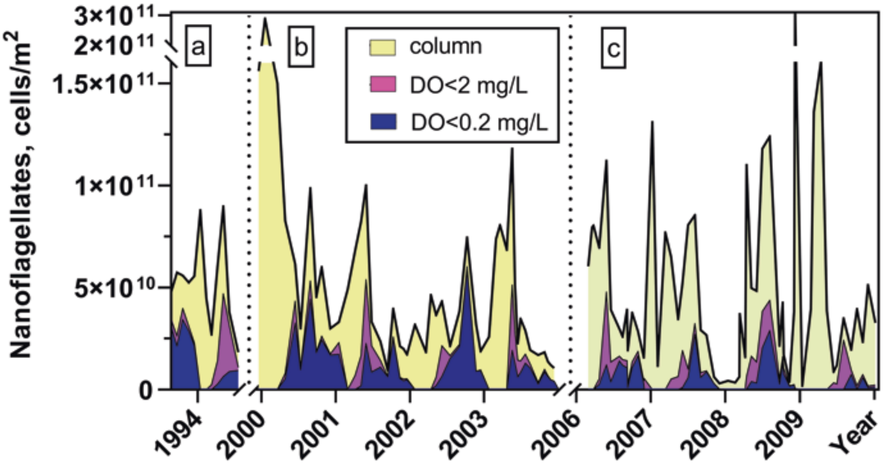


Fig. 13.1 Area-integrated nanoflagellates distribution within the water column layers: anaerobic (DO <0.2 mg/L), microaerobic (0.2–2 mg/L), and the whole water column. (**a**) 1994–1995; (**b**) 2003–2004; (**c**) 2006–2009

Fluorescence microscopy has been used routinely since 2006 to study Lake Alchichica protozooplankton. In this strategy, selective autotrophic pigment observations (filter sets for chlorophyll a and phycobilins) were coupled with analyses of color images (Figs. 13.1c, 13.2, and 13.3). As in the previous study, the nanoflagellates were numerous in anaerobic and microaerobic conditions during the stratification and the annual average did not change significantly. The annual maxima, reaching over 1×10^{11}, and the maximum of about 3×10^{11} cells/m^2, were registered either at the end of stratification or during circulation; minimum numbers were observed when the lake was sampled only during the first days of mixing.

In addition to the above-mentioned heterotrophic NF, autotrophic nanoflagellates with two and sometimes four very long flagella were observed in high numbers in aerobic layers during the well-established stratification (Fig. 13.2). According to the fluorescence observed, their cup-shaped chloroplasts predominantly possessed chlorophyll other than chlorophyll a, and a stigma. Their molecular taxonomy showed their affiliation within Haptophyta: Isochrysidales, possibly *Tisochrysis* sp. (misidentified as *Pyramimonas* sp. in Sánchez et al. 2016).

In general, nanoflagellates proliferated in the euphotic zone of the water column, and once the stratification developed, their numbers decreased steeply in the aphotic zone as dissolved oxygen was exhausted. The highest numbers of pigmented mixotrophic flagellates were observed during the circulation; this occurred at the end of the stratification (from October through December) for the autotrophic flagellates. The highest numbers of strictly heterotrophic nanoflagellates (HNF) were observed at the beginning of the stratification, possibly related to a filamentous cyanobacterium *Nodularia* aff. *spumigena* bloom and its following decomposition. Annual cycle HNF patterns in Lake Alchichica showed similarities to protozoan patterns at the meromictic Lake Pavin, France (Carrias et al. 2016) and with the monomictic

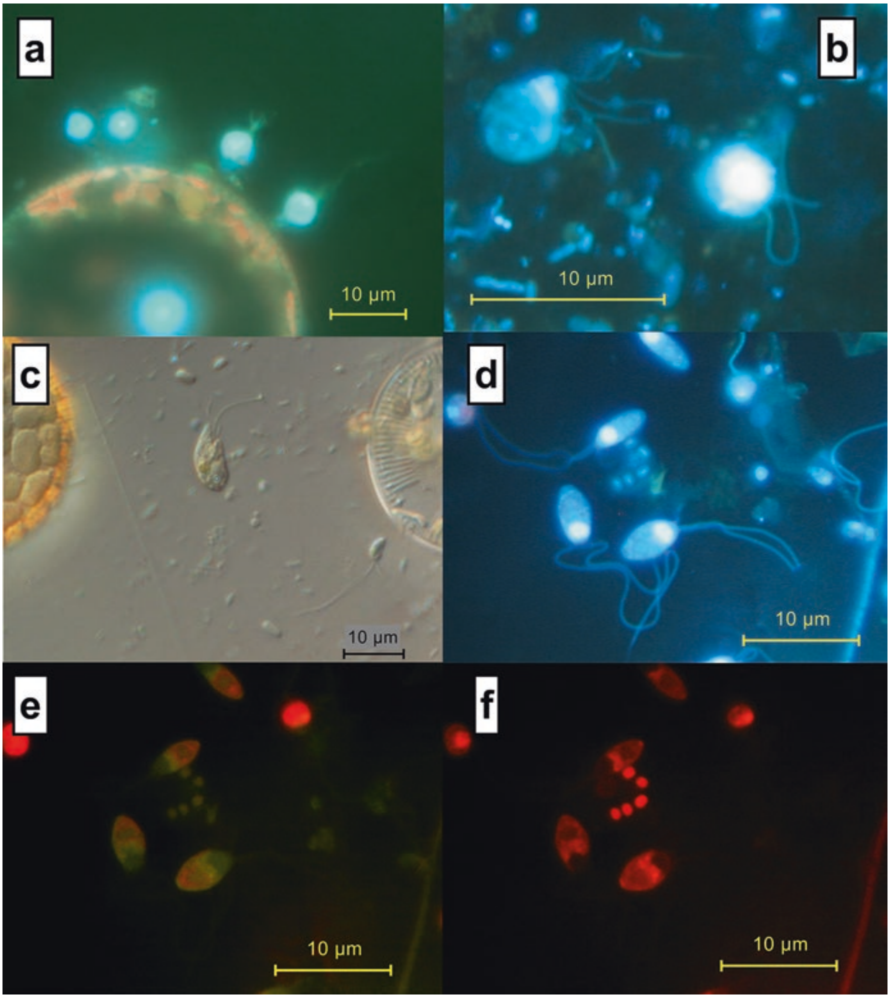


Fig. 13.2 Nanoflagellates of Lake Alchichica. (**a**) Choanoflagellates on *Cyclotella alchichicana* (DAPI); (**b**) cf. *Trimastix* sp. from anaerobic hypolimnion (DAPI); (**c**) *Rhynchobodo* sp. (Nomarski); (**d**–**f**) haptophytes: Isochrysidales, (**d**) DAPI, (**e**) chlorophyll *a* filter set, (**f**) phycobilin filter set

subtropical Lake Kinneret (Hadas et al. 2014). They were also comparable with those of the subalpine monomictic Lake Constance (Cleven and Weisse 2001), and with the very deep tropical Lake Tanganyika (Pirlot et al. 2005). Available data of the monomictic lake Biwa (Nakano et al. 1996) and the meromictic Siberian Lake Shira (Kopylov et al. 2002) showed much higher NF numbers than those found in Lake Alchichica.

The conductivity and ionic composition of the soda Lake Alchichica have been hypothesized as relevant drivers of its protozoan composition. The number of NF

Table 13.2 Revised list of the ciliate species in Lake Alchichica and their distribution within the water column

Identified ciliates		Mixing	Epilimnion	Oxycline	Anaerobic hypolimnion
	Heterotrichea Stein, 1859				
1	*Spirostomum teres* Claparède & Lachmann, 1859			●	●
2	*Stentor multiformis* (Müller 1786) Ehrenberg, 1838			●	●
	Mesodiniidae Jankowski, 1980				
3	*Mesodinium* Stein, 1863	●	●	●	
	Spirotrichea Bütschli, 1889				
4	*Euplotes euryhalinus* Valbonesi & Luporini, 1990	●	●	●	●
5	*Halteria grandinella* (Müller, 1773)	●	●	●	
6	*Uroleptus rattulus* Stein, 1859	●	●	●	
	Armophorea Lynn, 2004				
7	*Brachonella* Jankowski, 1964				●
8	*Caenomorpha* cf. *lauterborni* Kahl, 1927				●
	Haptoria Corliss, 1974				
9	*Actinobolina* Strand, 1928	●	●	●	●
10	*Belonophrya* André, 1914	●	●	●	●
11	*Monodinium* cf. *balbianii* var. *nanum* Fabre-Domergue, 1888	●	●	●	●
12	*Lagynophrya* Kahl, 1927	●	●	●	●
13	*Litonotus* Wresniowski, 1870	●	●	●	
14	*Phialina* Bory de St. Vicent, 1824			●	●
	Suctoria Claparède & Lachmann, 1858				
15	*Sphaerophrya canelli* Clement, 1967	●	●	●	
	Prostomatea Small y Lynn, 1985				
16	*Holophrya* cf. *aklitolophon* Hiller & Bardele, 1988	●	●	●	●
	Plagiopylea Small & Lynn, 1985				
17	*Epalxella* Corliss, 1960				●
	Peritrichia Stein, 1859				
18	*Pelagovorticella natans* Jankowski, 1985	●	●	●	
19	*Rhabdostyla* Kent, 1881				
20	*Vorticella* Linnaeus, 1767	●	●	●	
21	*Vorticella aquadulcis*-complex	●	●	●	
	Scuticociliatia Small, 1967				
22	*Cinetochilum margaritaceum* Perty, 1849	●			
23	*Cristigera* Roux, 1899			●	●

(continued)

Table 13.2 (continued)

Identified ciliates		Mixing	Epilimnion	Oxycline	Anaerobic hypolimnion
24	*Cyclidium* Corliss, 1960	●	●	●	●
25	*Cyclidium glaucoma* Müller, 1773	●	●	●	
26	*Cyclidium porcatum* Esteban, Guhl, Clarke, Finlay & Embley, 1993			●	●
27	*Isocyclidium globosum* Esteban, Finlay & Embley, 1993				●
28	*Pleuronema* Dujardin, 1841 cf. *binucleatum*	●	●	●	
29	*Sathrophilus* Corliss, 1960	●	●	●	
30	*Uronema* Dujardin, 1841	●	●	●	

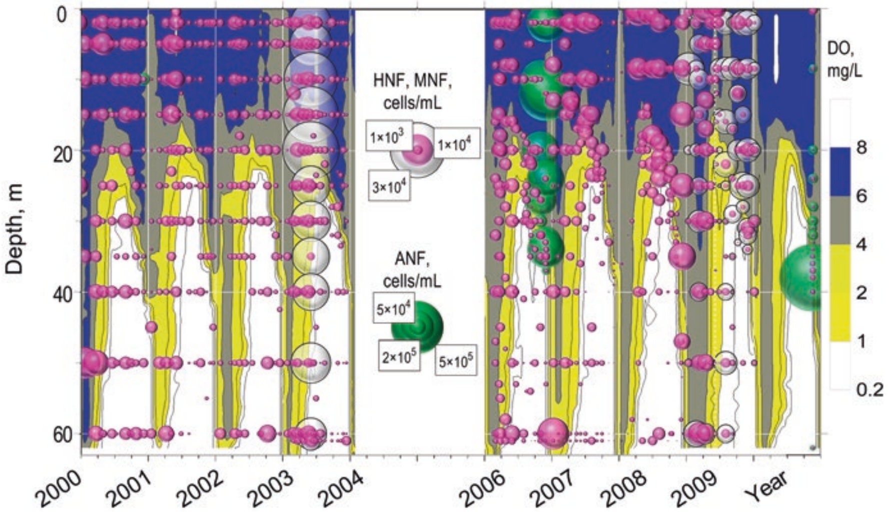


Fig. 13.3 Nanoflagellates' numbers within the water column on the background of dissolved oxygen (DO) isopleths. Heterotrophic, HNF (pink) mixotrophic, MNF (semi-transparent) and autotrophic flagellates, ANF (green)

taxa that are abundant in freshwater systems is comparatively much reduced in Lake Alchichica. As a reference, in Mono Lake, where salinity is high, very small counts of NF have been reported (Davidson and Davidson 2005). Surprisingly, we have not been able to confirm the occurrence of abundant cryptomonads in Lake Alchichica, which were observed typically in meromictic lakes with an anaerobic monimolimnion (Dyer et al. 1986; Massana and Pedrós-Alió 1994; Guhl et al. 1996; Kopylov et al. 2002; Tarbe et al. 2011; Khromechek et al. 2010).

Furthermore, apochlorotic euglenids and/or kinetoplastids were detected in Alchichica. In addition, *Trimastix* sp. and other anaerobic flagellates grew in dialysis experiments implemented in the anaerobic hypolimnion. Using molecular taxonomy, the jakobid anaerobic flagellate *Jakoba* sp. was verified.

13.3 Ciliates as the Dominant Protozooplankton in the Warm Monomictic and Picophytoplankton-Rich Lake Alchichica

In Lake Alchichica, ciliates have been regularly studied with several interruptions since 2003, employing both quantification in DAPI-stained preparations (Porter and Feig 1980) and in quantitative protargol-stain (QPS, Montagnes and Lynn 1993; Skibbe 1994) preparations. Due to the peculiarities of the soda lake water, ciliate fixation and staining protocols had to be modified (cf., Šimek et al. 1995 *vs.* Sánchez-Medina et al. 2016; Macek et al. 2020).

The whole ciliate assemblage has been evaluated in vertical detail of more than ten layers from 2005 to 2009 (Peštová et al. 2008; Bautista-Reyes 2011; Bautista-Reyes and Macek 2012). The most numerically abundant taxon was scuticociliates, exhibiting periodic maxima during the stratification (Fig. 13.4). The depth-weighted column average was 1.2 cells/mL (maximum 16.8; median 0.7 cells/mL). Moreover, peritrichs dominated during circulation with an average abundance of 1.17 cells/mL (maximum 8.35; median 0.62 cells/mL). Halterias were observed without any clear pattern with an average of 0.54 cells/mL (maximum 4.99; median 0.2 cells/mL). During the stratification periods, *Euplotes euryhalinus* (average 0.32; maximum 3.62 cells/mL) peaked in the oxycline or in the upper zone of the metalimnion. *Phialina* sp. (average 0.16; maximum 2.74 cells/mL) and *Holophrya* sp. (average 0.09; maximum 1.59 cells/mL) were also abundant in microaerobic to anaerobic conditions. Additionally, *Mesodinium* sp. was observed occasionally in high numbers (average 0.09; maximum 1.59 cells/mL).

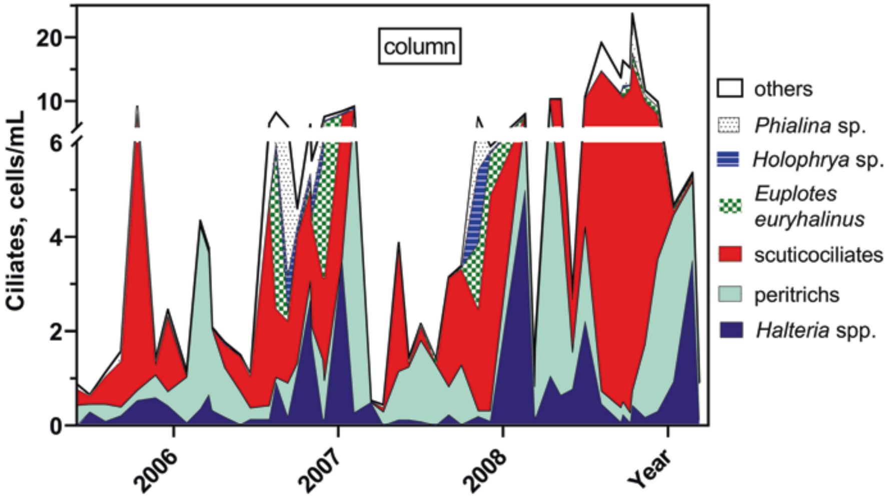


Fig. 13.4 The most numerous ciliate counts in Lake Alchichica 2005–2009

13.3.1 Saline- or Freshwater Communities?

The diversity of ciliates in Lake Alchichica is relatively low compared to other ecosystems. To date, the presence of about 30 ciliate species was confirmed (Table 13.2). In relation with the lake salinity, almost all found species were reported in euryhaline systems (saline lakes and/or seas; Foissner et al. 1999). Instead, some widely distributed oligotrichous ciliates have not been found in Lake Alchichica, such as the genera *Rimostrombidium* and *Limnostrombidium* (e.g., Hecky and Kling 1981; Gasol et al. 1990; Carrias et al. 2001, 2016; Pirlot et al. 2005; Khromechek et al. 2010, 2021); in addition, a very common prostome genus *Coleps*, found in lakes with anaerobic hypolimnion/monimolimnion is also absent (Madoni 1990; Gasol et al. 1990; Camacho et al. 2017; Khromechek et al. 2010, 2021).

Among **heterotrichs**, *Spirostomum teres* (Fig. 13.5a, b) flourished in the oxycline (Chap. 12 Phytoplankton of Alchichica, Fig. 12.3a, c) and just above the bottom of the lake since we started the ciliate monitoring in 2003 (Sánchez-Medina et al. 2016; Macek et al. 2020; misidentified as *Chaetospira* sp. in Peštová et al. 2008, and Bautista-Reyes and Macek 2012). QPS staining observations of the ciliature, membranelles, and morphology of the cytostome depicted a good agreement with the *S. teres* description from both fresh and brackish water (Boscaro et al. 2014). However, the macronucleus, observed with DAPI staining, seemed to be more elongated and curved; an identical pattern was observed within the nearby crater lake La Preciosa *S. teres* population (Macek et al. 2020).

Stentor multiformis was observed only during two occasions at the end of the stratification. The identification should be further confirmed because the cells were not observed alive and the preserved specimens were contracted. The ciliate of Lake Alchichica generally matched with both the general description and ecological characteristics of euryhaline species (Foissner and Wölfl 1994; Thamm et al. 2010). Throughout the whole study we observed a raptorial *Mesodinium* sp. (**SAL** *incertae sedis*), particularly in the aerobic layers (Fig. 13.5e). Due to its minute cell size (from 10 to 20 μm), the species have been rarely identified in the water bodies (e.g., Macek et al. 2006; Sonntag et al. 2006; Hadas et al. 2014; Posch et al. 2015).

The most abundant ciliates within **spirotrichs** were *Halteria grandinella* (Fig. 13.5c, d) and minute *Halteria* sp., which were observed throughout the monitoring of Lake Alchichica (Peštová et al. 2008; Macek et al. 2008; Bautista-Reyes and Macek 2012; Sánchez-Medina et al. 2016). Halterias are one of the most common ciliates in almost all types of environments, including both fresh and brackish waters (e.g., Foissner et al. 1999). *Uroleptus rattulus* was also frequently registered in the epilimnion of Lake Alchichica. The genus is common in brackish water (Foissner et al. 1991), feeding upon algae and possibly bacteria, but ingested algae were not observed in Alchichica.

Euplotes euryhalinus (Fig. 13.5f–h) was identified by Graziano di Giuseppe (University of Pisa; Macek et al. 2019) using a molecular approach; curiously the species has been described from the Ross Sea, Antarctica (Valbonesi and Luporini 1990). The species was first proposed as a mixotrophic *E.* cf. *daidaleos* (Peštová

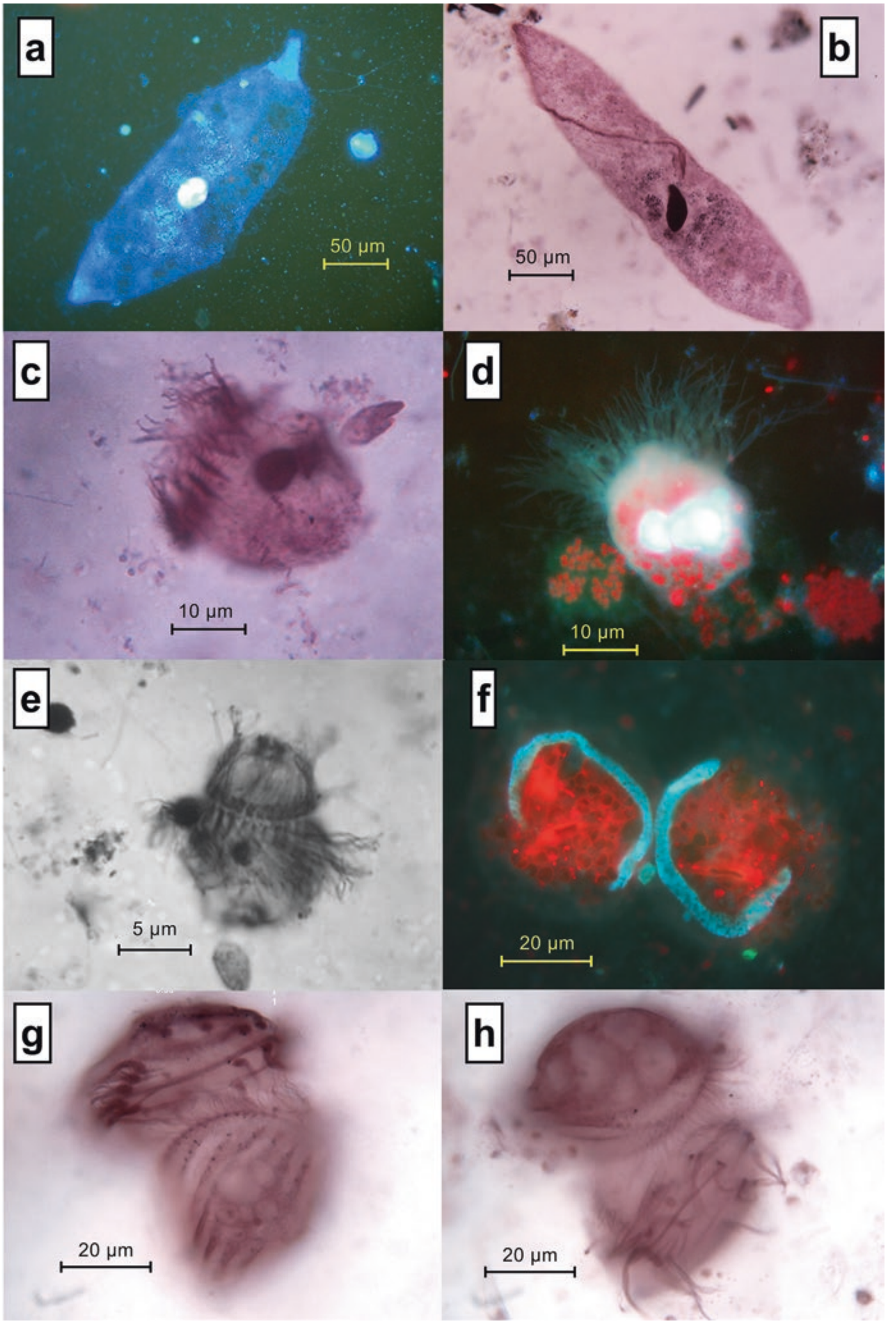


Fig. 13.5 Dominant ciliates of lake Alchichica. (**a**, **b**) *Spirostomum teres* in DAPI and QPS preparations; (**c**, **d**) *Halteria grandinella* in QPS and DAPI (with ingested picocyanobacteria); (**e**) *Mesodinium* sp. in QPS; **(f–h)** *Euplotes euryhalinus* in DAPI (with ingested eukaryotic phytoplankton) and QPS

et al. 2008; Macek et al. 2008), particularly due to the observation of numerous zoochlorella-like cells in the ciliate. However, improved QPS staining confirmed the species *E. euryhalinus* in all analyzed samples from both the surface layer and the ciliate deep maximum below the thermocline.

Peaks of *Euplotes euryhalinus* appeared during well-established stratification with an anaerobic hypolimnion (Macek et al. 2019) at the microaerobic layers (dissolved oxygen (DO) 0.2 to 2 mg/L; see Chap. 12 Phytoplankton of Alchichica, Fig. 12.3a, c). Absolute maximum abundances of over 30 cells/mL were registered during the transition from stratification to circulation (December to January).

Among **armophorids**, the minute *Caenomorpha* cf. *lauterborni* (Fig. 13.6a) appeared periodically at the end of stratification in abundances up to 2 cells/mL in an anaerobic hypolimnion. Its distribution is probably related to the presence of purple sulfur bacteria (Guhl and Finlay 1993). This species has also been reported from marine environments up to 3% of salinity (Kahl 1930–1935). The metopid *Brachonella* sp. (Fig. 13.7b), reported from freshwater to saline environments (Bourland et al. 2017), was rarely observed in the anaerobic hypolimnion of Alchichica.

Litostomatids were represented by several species in Lake Alchichica along the stratification at the oxycline/anaerobic hypolimnion. Some genera detected were *Actinobolina* (Fig. 13.6c) and *Belonophrya* (Peštová et al. 2008; Macek et al. 2008; Bautista-Reyes and Macek 2012; Sánchez-Medina et al. 2016). *Phialina* sp. (Fig. 13.6d) peaked in a narrow layer in anaerobic conditions (Peštová et al. 2008; Macek et al. 2008; Bautista-Reyes and Macek 2012; Sánchez-Medina et al. 2016), as it was found in African soda lakes (Yasindi and Taylor 2016), but not in the water column of Lake Kinneret, which exhibited a similar annual oxycline behavior to that of Lake Alchichica (Madoni 1990). A minute (about 30 μm) *Monodinium* sp. (Fig. 13.6e), which could be identified as *M. balbianii* var. *nanum* (Foissner et al. 1999) was also observed (Peštová et al. 2008; Macek et al. 2008; Bautista-Reyes and Macek 2012; Sánchez-Medina et al. 2016). Due to its minute cell, the ciliate was previously overlooked in the water bodies or combined with *Mesodinium* spp. counts. Another rarely reported species was the minute *Litonotus* sp. (Peštová et al. 2008; Macek et al. 2008; Bautista-Reyes and Macek 2012; Sánchez-Medina et al. 2016). In contrast, *Lagynophrya* sp. (Fig. 13.6f) found in Lake Alchichica (Macek et al. 2006, 2008; Peštová et al. 2008) is a common plankton ciliate (Foissner et al. 1999).

Only one species of **Suctoria** has been recently observed parasiting on *E. euryhalinus* (unpublished) and identified according to Clement (1967) as *Sphaerophrya canelli* (Fig. 13.6g-h). The suctorids detection appears to be species-specific towards *E. euryhalinus.*

Large **prostomatids** that were mixotrophic and/or feeding on algae were observed in Lake Alchichica and identified as *Prorodon*, *Pelagothrix*, and *Holophrya* (Macek et al. 2006, Peštová et al. 2008; Sánchez et al. 2016). However, in the detailed QPS analyses, apparent distinctive phases of the complicated *Holophrya aklitolophon* life cycle were observed (Fig. 13.7a, b). Curiously, the cycle was described in a culture obtained from an axolotl's aquarium (Hiller and Bardele

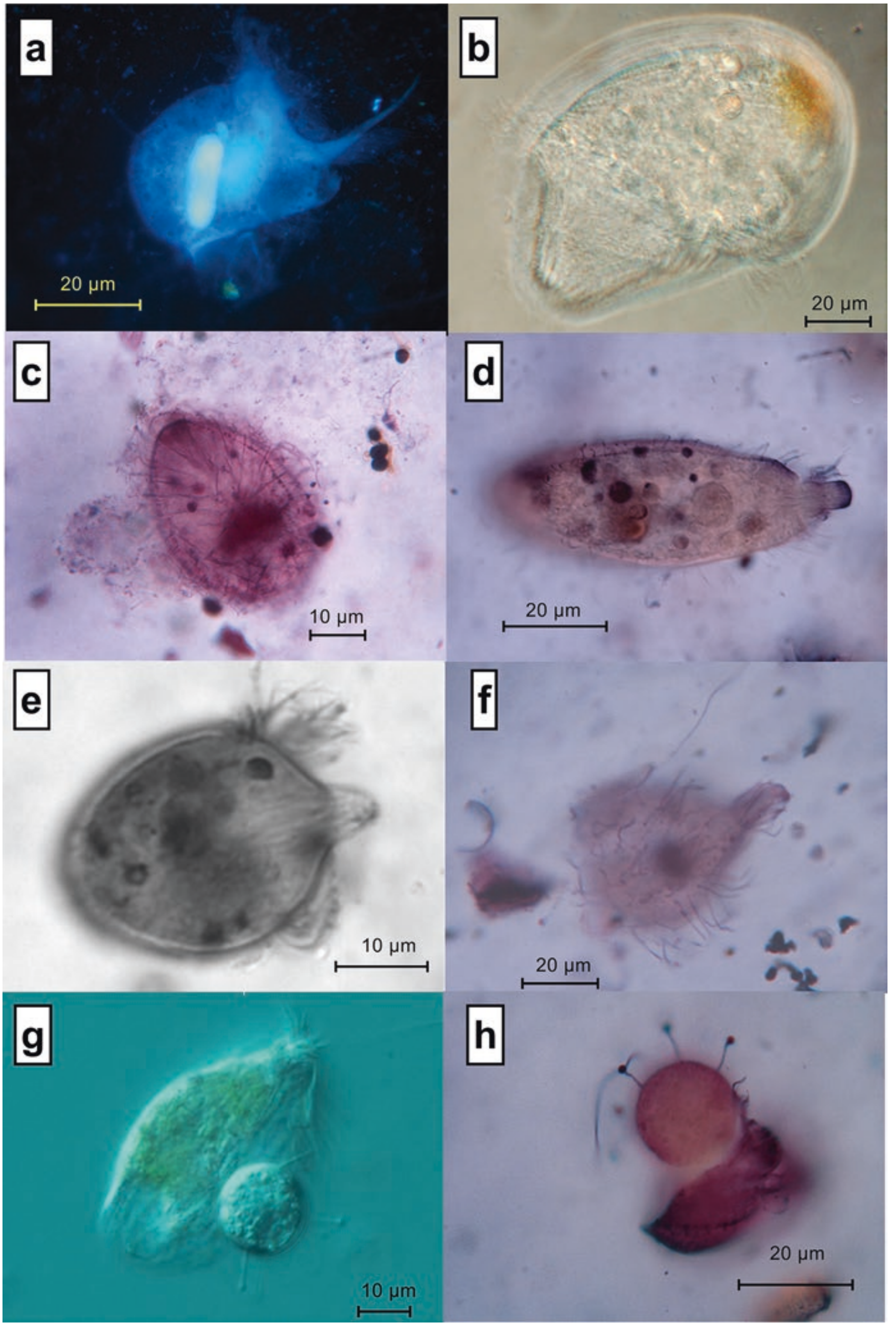


Fig. 13.6 Dominant ciliates of Lake Alchichica. (**a**) *Caenomorpha* cf. *lauterborni* in DAPI preparation; (**b**) *Brachonella* sp. *in vivo* (Nomarski); (**c**) *Actinobolina* sp., (**d**) *Phialina* sp., (**e**) *Monodinium* sp. and (**f**) *Lagynophrya* sp. in QPS; (**g**, **h**) *Sphaerophrya canelli* parasiting *E. euryhalinus in vivo* (Nomarski) and QPS

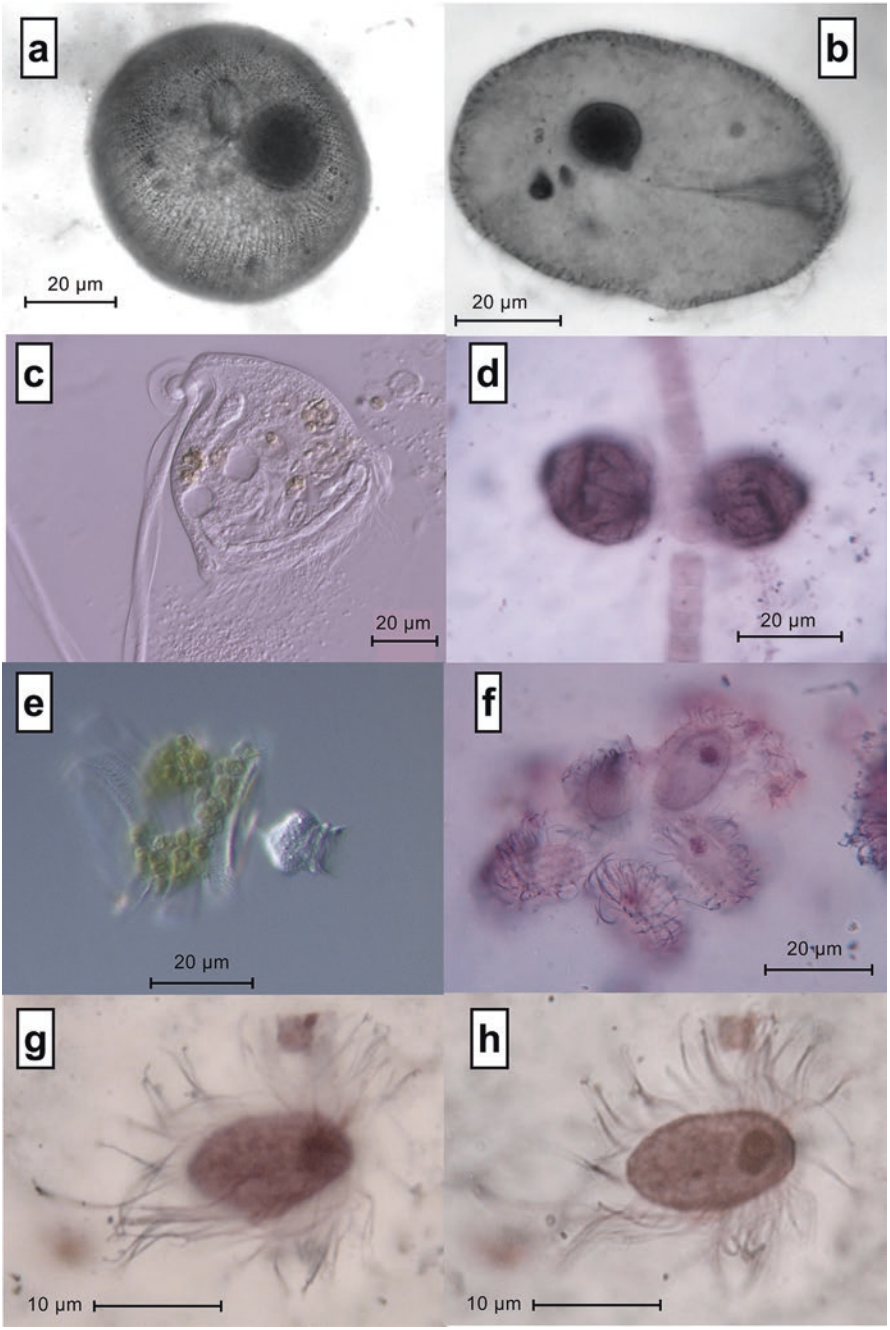


Fig. 13.7 Dominant ciliates of Lake Alchichica. (**a**, **b**) *Holophrya* sp. in QPS preparation; (**c**) Pelagovorticella natans in vivo (Nomarski); (**d** *Vorticella aquadulcis*-complex in QPS (**e**) *Rhabdostyla* sp. *in vivo* (Nomarski); (**f**) abundant scuticociliates and (**g**, **h**) *Cyclidium glaucoma* in QPS

1988; Foissner et al. 1994) and neotenic amphibians axolotls (*Ambystoma taylori*) are common in Lake Alchichica.

The **plagyopylid** *Epalxella* sp., which has been also reported in alkaline and saline African lakes (Ong'ondo et al. 2013), was found at the bottom of the lake (Peštová et al. 2008).

Peritrichs were one of the most important taxa found in Lake Alchichica. During circulation, the unattached *Pelagovorticella natans* (Fig. 13.7c) was distributed throughout the water column, reaching the maximum of 13 cells/mL. Among phytoplankton-attached peritrichs, *Rhabdostyla* sp. (Fig. 13.7e) was the most frequent, colonizing the large diatom *Cyclotella alchichicana* (mainly during the circulation period) and/or the filamentous cyanobacterium *Nodularia* aff. *spumigena*, when it reached the maximum (15 cells/mL). We also found the *Vorticella aquadulcis* complex (Fig. 13.7d), and an unidentified *Vorticella* sp. (resembling *V. picta* but without typical granules on the stalk). For more detailed information on the annual cycle of peritrichs, consult Macek et al. (2008).

The most diverse group of ciliates was **scuticociliates**. Various microaerophilic and anaerobic species are abundant in the metalimnion/oxycline and in the anaerobic hypolimnion/bottom frontiers (Fig. 13.7f–h). Although several species have been identified morphologically, molecular taxonomy is necessary to confirm their identity. Moreover, presumably different stages of the life cycle of microaerobic/ anaerobic scuticociliates species were observed in Lake Alchichica (Sánchez-Medina et al. 2016).

13.3.2 Microaerophilic and Anaerobic Ciliate Assemblages: Are There True Pelagic Ciliates in the Anaerobic Hypolimnion?

Dissolved oxygen concentration (DO) was found to be the best driver of protozoan distribution patterns over the annual cycle. The strict anaerobes, and microaerophilic and aerobic species, were delimited through arbitrary dissolved oxygen concentrations of <0.2, <2, and >2 mg/L, respectively. The relevance of anaerobic species could be better understood by addressing their biomass contribution to the total water column biomass (Fig. 13.8).

The annual ciliate biomass (i.e., organic carbon) peaked at >2 g/m^2 either during the formation of the anaerobic hypolimnion or along the development of the deep chlorophyll maximum. During the stratification, the anaerobic layers harbored about one-half of the total ciliate biomass (average 52.3%, median 50.7%), whereas in the generally narrow microaerobic layers (DO = 0.2 to 2 mg/L), only about one-tenth of the biomass was found (average 17.2%, median 9.6%).

There was a discrepancy between the total ciliate biomass reported in the first studies and the following investigations. Only five sampling depths that could not cover all depths with the different species maxima were considered in early studies (Macek et al. 2006, 2008; Peštová et al. 2008). The later studies of the species level

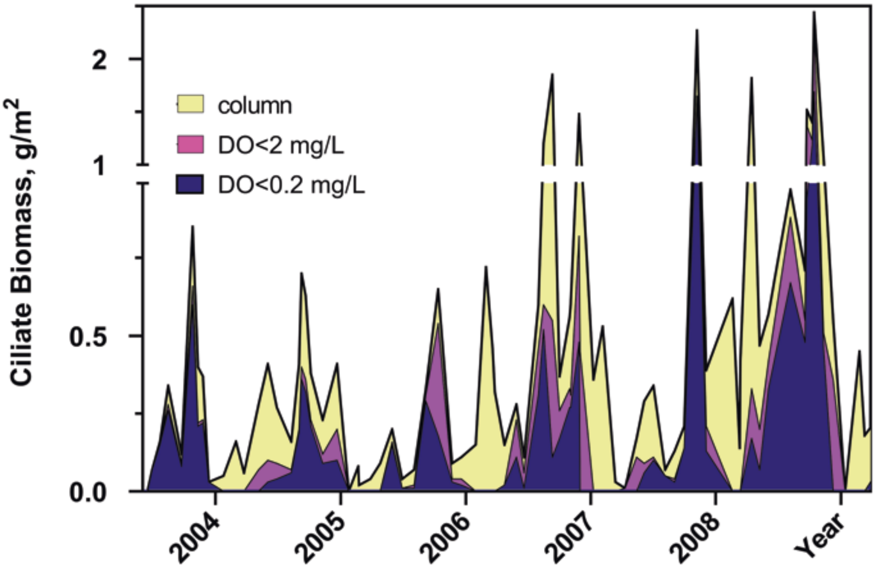


Fig. 13.8 A contribution of anaerobic (DO <0.2 mg/L) and microaerobic (DO <0.2; 2 >mg/L) ciliates to the whole column organic carbon biomass

(Bautista-Reyes and Macek 2012; Sánchez-Medina et al. 2016; Macek et al. 2020) also showed the importance of large ciliates (Fig. 13.9), which appeared to peak in very thin layers, such as *E. euryhalinus* (either in aerobic or microaerobic layers; see Chap. 12 Phytoplankton of Alchichica, Fig. 12.3a, c) and *Phialina* sp. (in anaerobic layers). In addition, anaerobic *S. teres*, *Caenomorpha* sp., and *Brachonella* sp. had not been efficiently quantified until we started to take more samples from the anaerobic hypolimnion. Throughout the stratification period, the anaerobic and microaerobic species prevailed, whereas peritrichs prevailed within the ciliate biomass during the circulation.

General relationships of the ciliate species to DO were evaluated using all of the samples or our databases (2003–2019). The integration of data from more detailed stratification studies (10–20 layers) resulted in a more robust data set to confirm the contribution of microaerophilic/anaerobic species to total biomass (Fig. 13.10). The chosen taxa covered >90% of the total assembled biomass, and their contribution was calculated as an arithmetical average. The contribution of peritrichs to the whole water column biomass was the highest (31%), followed by *E. euryhalinus* and scuticociliates (14.4% and 11.1%, respectively). However, the sum of the average biomasses' contribution of three microaerophilic/anaerobic species reached 21%.

Neither *Holophrya* sp., *Caenomorpha* sp., nor *E. euryhalinus* were observed in >50% of sampled layers (average 14.8%, 9.7%, and 6.3%, respectively) but *Phialina* sp. occurred frequently (average 13.0%, median 2.7%). In contrast, we observed that the *S. teres* peaks were apparently related to oxidized inorganic nitrogen (nitrate and to some extent nitrite concentration; Macek et al. 2020), which could indicate

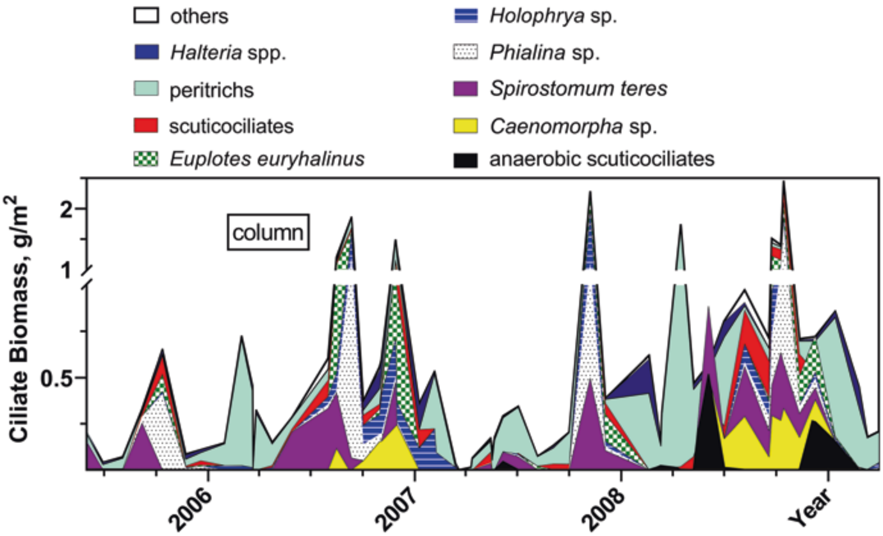


Fig. 13.9 Biomass (organic carbon) contribution of mostly anaerobic (anaerobic scuticociliates, *Caenomorpha* sp., *S. teres*, *Phialina* sp.), anaerobic/microaerobic (*Holophrya* sp.) and mostly aerobic species

an anaerobic nitrate respiration for this ciliate (compare with Psenner and Schlott-Idl 1985).

Within the genus *Cyclidium*, numerous *C. glaucoma* and another *Cyclidium* sp. penetrated deep into the anaerobic hypolimnion. A *Pleuronema* sp.—resembling the *P. binucleatum* described in Hangzhou Bay, China (Pan et al. 2016)—has been previously found, generally above the oxygen limit, and frequently with ingested nanoalgae (e.g., *Monoraphidium*). Among anaerobic species, *Isocyclidium globosum (*Esteban et al. 1993; Esteban and Finlay 1994) and *Cyclidium porcatum* (Clarke et al. 1993) were identified. In Lake Alchichica, the anaerobic scuticociliates were found to be covered by symbionts identified as Bacteria (Fig. 13.11a, b), but which could not be identified as a more specific taxon using CARD-FISH probes (following Jezbera et al. 2005; Bautista-Reyes 2011; Bautista-Reyes and Macek 2012; see Chap. 11 Bacterioplankton). Among the anaerobic life strategies of ciliates, the colonization by ecto- and endosymbionts is the most common (*Cristigera vestita*—Fenchel and Finlay 1991; *Cyclidium porcatum*—Esteban et al. 1993). We have found the same anaerobic scuticociliates depicting intracellular archaea (ARCH915; Bautista-Reyes 2011; Bautista-Reyes and Macek 2012), which were not localized inside vacuoles. These could be archaeal endosymbionts, as has been proven for anaerobic scuticociliates with endosymbiotic methanogens (Fenchel and Finlay 1991; Esteban et al. 1993).

CARD-FISH also showed that Alchichica *Caenomorpha* cf. *lauterborni* possessed possible bacterial endosymbionts localized inside a specific but not food vacuole (Fig. 13.11c, d) that might be related to the activity of a hydrogenosome

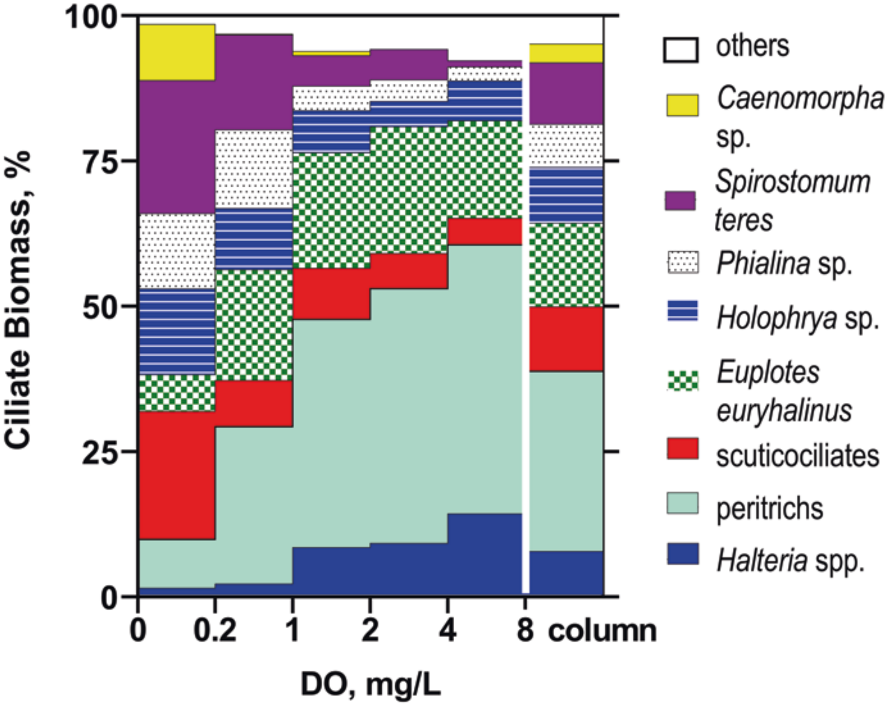


Fig. 13.10 Biomass (organic carbon) contribution of the most important ciliates taxa related to dissolved oxygen concentration intervals and in the whole water column

(Finlay et al. 1991). Archaea and Delta-Proteobacteria (SRB385) were discarded as symbionts but these prokaryotes were observed being ingested inside feeding vacuoles (Bautista-Reyes 2011; Bautista-Reyes and Macek 2012). Similar clusters of bacteria were observed in protargol preparations for *C. medusula* (Li et al. 2017).

13.4 Protozoan Interactions. What We Know About the Protozooplankton Feeding: Predator-Prey Interactions Within Protozooplankton, Prokaryoplankton, and Eukaryotic Phytoplankton

A direct relationship between both mixotrophic and heterotrophic nanoflagellates (HNF) to picoplankton (heterotrophic and autotrophic bacteria) was observed (Fig. 13.12); abundance of HNF was related to that of the prey, i.e., total picoplankton.

The composition of ingested food by phagotrophic nanoflagellates was analyzed using CARD-FISH (Bautista-Reyes 2011; Bautista-Reyes and Macek 2012). Overall, NF were more abundant in the mixing layer and at the upper metalimnion,

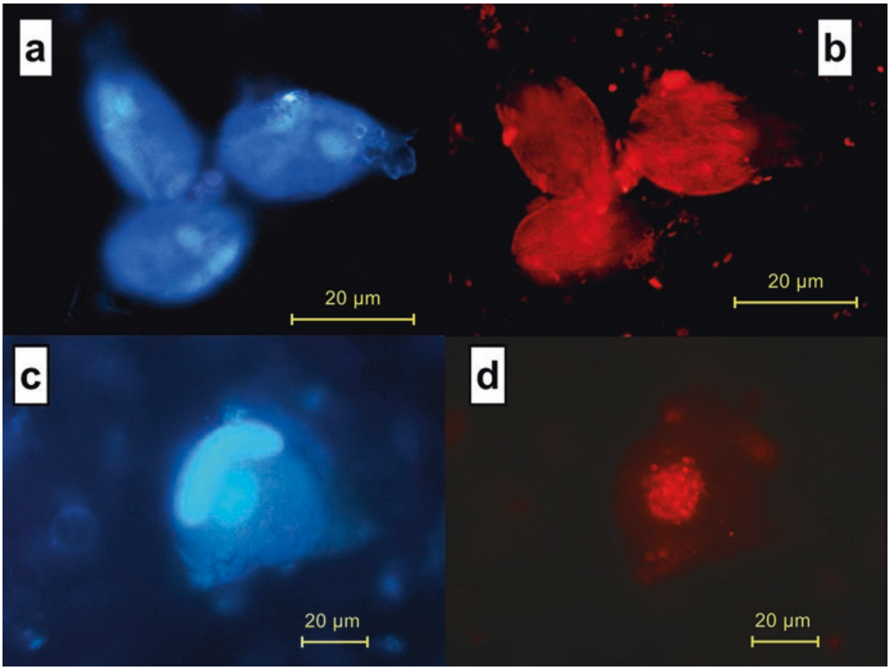
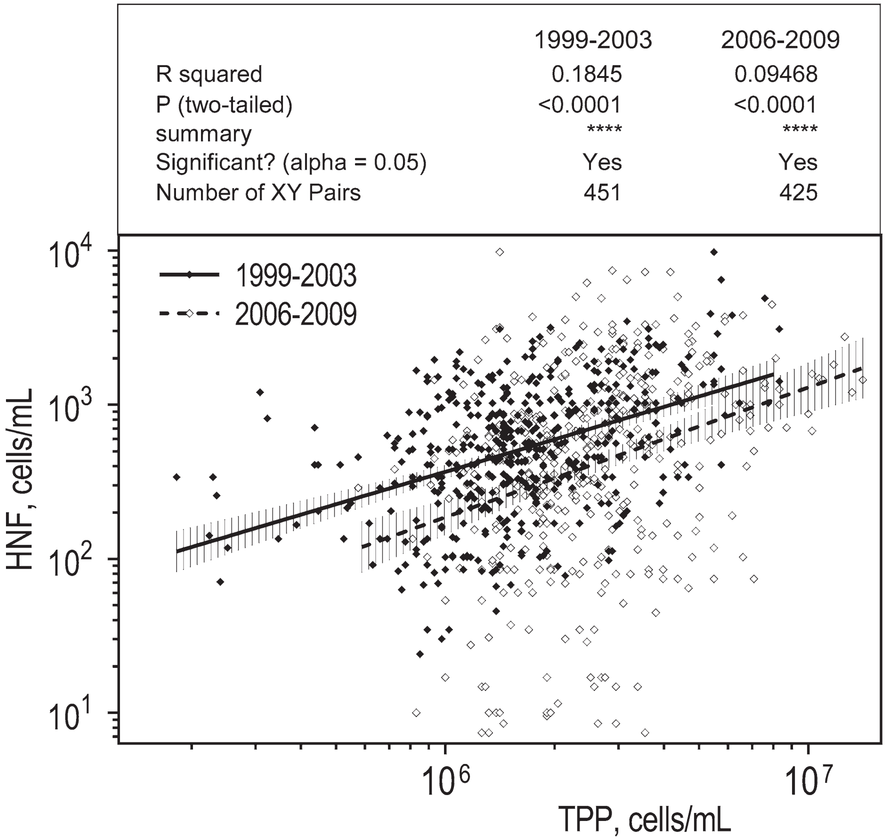


Fig. 13.11 Apparent symbionts of anaerobic ciliates visualized via using CARD-FISH (DAPI and Cy3-EUB probe): (**a**, **b**) scuticociliates covered with ectosymbionts; (**c**, **d**) *Caenomorpha* sp. with the non-food vacuole full with bacteria

resembling the dynamic of the hybridization percentages (see Chap. 11, Bacterioplankton), which were the highest at these layers (sometimes over 30%). The vacuole content of the HNFs showed that flagellates usually have one or rarely two prokaryotic phylogenetic groups as preferred food items, suggesting high selectivity. However, *Spumella*-like flagellates could ingest simultaneously both APP and heterotrophic bacteria of the same size (Fig. 13.13). Picocyanobacteria (APP) selective ingestion was observed during well-established stratification (June and July), and APP numbers were comparatively lower than those in the circulation period.

The ciliate feeding rates were measured upon fluorescently labeled picocyanobacteria, (FLB; Sherr and Sherr 1993), prepared either from pre-filtered (2 μm) natural samples or from cultured *Synechococcus* sp., concentrated by centrifugation (Peštová et al. 2008; Macek et al. 2020). Among typical ciliate picocyanobacteria feeders, peritrichs (detected attached to filamentous cyanobacteria and diatoms), minute spirotrichs *Halteria grandinella*, and scuticociliate *Cyclidium glaucoma* were the most abundant. In contrast, the highest picocyanobacteria uptake of 1300 cells cell^{-1} h^{-1} (in late stratification) was observed in the pelagic (free-swimming) *Pelagovorticella natans.* More picocyanobacteria cells were ingested near the oxycline, where a change of picocyanobacteria pigment fluorescence was also observed (Fig. 13.14).



	1999-2003	2006-2009
R squared	0.1845	0.09468
P (two-tailed)	<0.0001	<0.0001
summary	****	****
Significant? (alpha = 0.05)	Yes	Yes
Number of XY Pairs	451	425

Fig. 13.12 Heterotrophic nanoflagellates (HNF) *vs.* total picoplankton (bacteria + picocyanobacteria) numbers. The two different correlations were obtained related to different methodology employed

By comparison, the calculated uptake rate of picocyanobacteria by *S. teres* did not appear to cover its organic carbon necessities (Macek et al. 2020) and the ciliate had to look for additional nanoplankton feeding. We observed that *S. teres,* in addition to scuticociliates (in particular *Pleuronema* sp.), *Halteria* spp., and *E. euryhalinus,* ingested eukaryotic nanoplankton besides picoplankton. Identified ingested nanoplankton included chlorophytes *Monoraphidium minutum* and *Oocystis parva*, and the minute diatom *Cyclotella choctawhatcheeana*. Ingested purple anoxygenic photosynthetic bacteria (*Thiocapsa* sp.) were also observed in the ciliate samples below the oxycline at the end of the stratification period (when a pronounced depletion of oxygen was registered).

Suctorids and tentacle-bearing ciliates feeding upon other protists were frequently observed in Alchichica. *S. canelli* was found sucking only *E. euryhalinus*

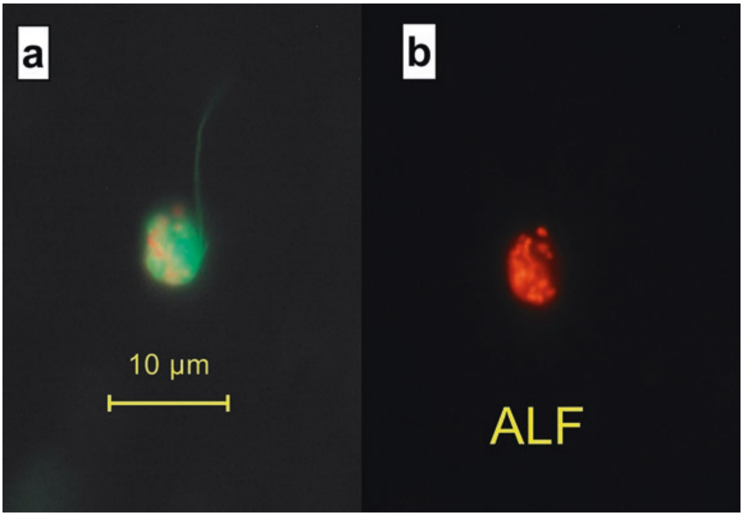


Fig. 13.13 Mixotrophic nanoflagellates (*Spumella*-like chrysomonads): (**a**) ingested picocyanobacteria (DAPI) and (**b**) Alphaproteobacteria (Cy3-CARD-FISH)

cells. Abundant *Actinobolina* sp. and/or *Belonophrya* sp. populations, from hypoxic and upper anaerobic layers, were preferably found feeding via their tentacles. We have not found direct evidence of ingestion of green algae or diatoms.

13.5 Conclusions

Long-term monitoring of Protozooplankton in Lake Alchichica has evidenced the relevance of this group in the plankton microbial food web. Although the diversity of protozoa in Lake Alchichica is relatively low compared to other ecosystems 30 euryhaline ciliate species have been confirmed, being microaerophilic and anaerobic species, biomass-dominating components. Ciliates feeding upon heterotrophic bacteria are periodically abundant: scuticociliates, peritrichs, and *Halteria* spp. Picocyanobacteria is also an important feeding source for almost all of them, including the large, microaerobic/anaerobic heterotrichous ciliate *Spirostomum teres*. Ingested nanophytoplankton appear in the majority of ciliates including small ones (e.g., scuticociliates) but only the spirotrichous ciliate *Euplotes euryhalinus* is evidently selective at feeding on minute diatoms, chlorophytes and cyanobacterial colonies. In addition, strictly anaerobic ciliate species show bacterial ectosymbionts (scuticociliates) or endosymbionts, which occupy special vacuoles (*Caenomorpha* sp.). Among raptorial species, *Phialina* sp. is a typical inhabitant of the anaerobic metalimnetic bottom of Lake Alchichica.

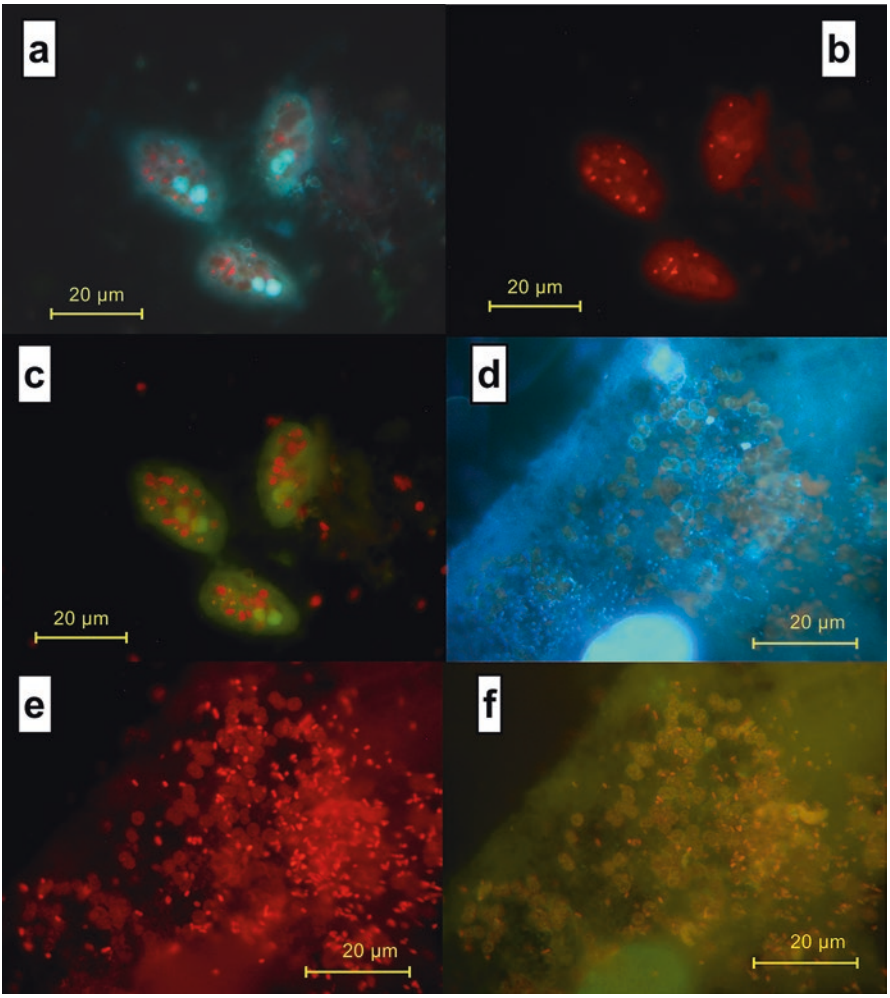


Fig. 13.14 Ciliate feeding behavior. (**a**–**c**) *Pleuronema* sp.: (**a**) ingested picocyanobacteria (DAPI), (**b**) picocyanobacteria (selective filter) and (**c**) chlorophyll *a* containing eukaryotes; (**d**–**f**) *Spirostomum teres*: (**d**) ingested purple sulfur bacteria (*Thiocapsa* sp.) stained with DAPI, (**e**) picocyanobacteria and *Thiocapsa* sp. (phycobilin filter set) and (**f**) absence of chlorophyll *a* containing eukaryotes (chlorophyll *a* filter set)

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Chapter 14
Metazooplankton: The Joys and Challenges of Living in a Saline, Oligotrophic, Warm Monomictic Lake

Elizabeth Ortega-Mayagoitia, José Arturo Alcántara-Rodríguez, Alfonso Lugo-Vázquez, Aideé Montiel-Martínez, and Jorge Ciros-Pérez

14.1 Introduction

For an observer standing on the shores of this lake, contemplating its peculiar beauty, one of the first thoughts that come to mind is that there must be joy in living in Lake Alchichica. Most lakes are small, shallow, unsteady habitats (Schindler and Scheuerell 2002). Aquatic animals must adapt to cope with short-and mid-term chemical and physical fluctuations, including the cyclical absence of water. In contrast, Lake Alchichica is a deep, perennial lake without relevant salinity oscillations. Its massive water content contributes to keeping the temperature within a narrow range throughout the year. Its warm monomictic regime is a repeated event to which life cycles of its inhabitants can be reasonably adjusted. Alchichica seems to be, literally, an oasis in the middle of a desert.

However, the peculiar chemical composition of the water (Chap. 7), the structure and dynamics of the phytoplankton assemblage (Chap. 12), and the interplay of a transparent epilimnion with a dark, anoxic hypolimnion, make Lake Alchichica a challenging environment for metazooplankton populations. In the following pages, we offer a synthesis of our current understanding of the ecological and evolutionary responses of zooplanktonic organisms to this peculiar aquatic system.

E. Ortega-Mayagoitia (✉) · J. A. Alcántara-Rodríguez · A. Lugo-Vázquez · J. Ciros-Pérez
Grupo de Investigación en Limnología Tropical, FES Iztacala. Universidad Nacional Autónoma de México, Tlalnepantla, Estado de México, Mexico
e-mail: eortega@unam.mx; jarturo.alcantara@iztacala.unam.mx; lugov@unam.mx; ciros@unam.mx

A. Montiel-Martínez
Licenciatura en Gestión de Ciudades Inteligentes y Transiciones Tecnológicas, Facultad de Ciencias de la Electrónica, Benemérita Universidad Autónoma de Puebla, Puebla, México
e-mail: aidee.montiel@correo.buap.mx

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14.2 Diversity and Taxonomic Issues

The metazooplankton of Lake Alchichica has a very low species richness. It is dominated by the calanoid copepod *Leptodiaptomus garciai* (Osorio-Tafall 1942). There are two rotifer species, *Brachionus* sp. 'Mexico' and *Hexarthra* cf. *jenkinae*, that are discontinuously present in the water column. The combination of a diaptomid copepod as the dominant taxon plus the presence of a species of *Hexarthra* and a species of *Brachionus* also occurs in other deep, hyposaline environments, like the warm monomictic lakes Walker (Z_{max} = 35 m, TDS: 10.66 g/L) and Pyramid (Z_{max} = 103 m, K_{25}: 8200–8650 μS/cm) in Nevada, USA, and the meromictic lake Shira (Z_{max} = 22 m, TDS: 6.5–23 g/L) in Republic of Khakassia (Cooper and Koch 1984; Galat et al. 1981; Zotina et al. 1999, respectively).

The reduced specific diversity of metazooplankton in Lake Alchichica is likely due to salinity, which constitutes a powerful physiological filter for species richness and functional diversity of metazooplankton (Gutierrez et al. 2018). In addition, the peculiar functional composition and biomass of phytoplankton can, by itself, restrict the establishment of the species present in other lakes of Cuenca Oriental (Hessen et al. 2006). The effect of salinity and the consumer-resource interactions of the three metazooplankton species, and their ecological and evolutive consequences will be described further in this chapter.

14.2.1 Brachionus *sp. 'Mexico'*

The *Brachionus* species that inhabits Lake Alchichica belongs to the *Brachionus plicatilis* complex, a group of at least 15 euryhaline rotifer cryptic species distributed worldwide (Mills et al. 2017). In early scientific literature, it was labeled as *B. rotundiformis* (Sarma et al. 2002), but after its recognition as a bona fide species, and following the current practice among the community of rotiferologists, it beholds the unofficial name of the country where the organisms were first collected: *B.* sp. 'Mexico' (Alcántara-Rodríguez et al. 2012; Mills et al. 2017).

Like other members of this species complex, *B.* sp. 'Mexico' has a smooth pear-shaped lorica, the anterior dorsal margin with three pairs of spines flanking a "U"-shaped sinus. All the spines of the lorica are triangular and similar in size, with a broad base and relatively pointed apices. The size of the lorica of adult females is 211.5 ± 21.2 μm x 143.7 ± 15.5 μm (mean length including spines x width, ± standard deviation, n = 50). Lorica size could be useful, along with morphology, to discriminate *B.* sp. 'Mexico' from other species of the SM clades of *B. plicatilis*, such as *B.* sp. 'Almenara' and *B. ibericus* (Hernández-Lozano 2016).

To date, *B.* sp. 'Mexico' has been found only in three crater lakes: Alchichica and the neighboring Atexcac and La Preciosa, all within the limits of the Oriental Basin. COI gene sequences have unveiled that the three populations compose one monophyletic taxon with four haplotypes. The three populations share only one haplotype, whereas Lake Alchichica hosts three more, making it the most genetically diverse population (Alcántara-Rodríguez et al. 2012).

Regarding the boundaries with phylogenetically close species, an Automatic Barcode Gap Discovery analysis (ABGD) (Puillandre et al. 2012) clustered the COI haplotypes of *Brachionus* sp. 'Mexico' apart from sister clades such as *B.* sp. 'Almenara' and *B. ibericus*. Moreover, laboratory mating trials showed that *B.* sp. 'Mexico' and *B.* sp. 'Almenara' are reproductively isolated from each other at behavioral, prezygotic level, without evidence of hybrid resting egg formation (Alcantara-Rodríguez 2012). This evidence clearly shows that *Brachionus* sp. 'Mexico' is an independent evolving lineage that should be described as a new biological species.

14.2.2 Hexarthra *cf.* jenkinae

The genus *Hexarthra* is an exclusively planktonic taxon whose main diagnostic traits are a triangular body with six robust arm-like appendages with long, pinnate bristles at the tips and foot absent (José de Paggi et al. 2020). Specimens morphologically related to *H. jenkinae* (De Beauchamp, 1932) have been reported to inhabit Lake Alchichica and other neighboring crater lakes (Aljojuca, Atexcac, and Tecuitlapa). However, the common existence of cryptic species in rotifers, the lack of sharp species boundaries, and unsolved phylogenetic relationships within the genus *Hexarthra* prompted us to look for additional evidence to clarify the taxonomic status of these populations.

Bayesian phylogenetic and ABGD analyses, including sequences of the gene COI from Alchichica, Aljojuca, Atexcac and Tecuitlapa populations and other *Hexarthra* species deposited in public databases, revealed that the populations from Oriental Basin lakes belong to two sister clades that probably constitute two distinct species (Fig. 14.1). Unfortunately, there are no publicly available sequences of *H. jenkinae*, so the identity of these clades could not be settled. The clade present in lakes Alchichica, Atexcac, and Aljojuca was labeled as *Hexarthra* cf. *jenkinae* and the other as *Hexarthra* sp. (Tecuitlapa) (Alcántara-Rodríguez 2018). According to the Bayesian phylogenetic tree, their closest relative of both is *H. fennica*. Globally, additional molecular, morphological, and reproductive analysis are needed to assess accurately the phylogenetic relationships within this genus and validate the hypothesis of the existence of cryptic species complexes.

14.2.3 Leptodiaptomus garciai

In 1942, Osorio-Tafall described the calanoid copepod *Diaptomus garciai* (Osorio-Tafall 1942), the first recognized endemic species in Lake Alchichica. Just a few years later, Wilson and Yeatman -without examining biological material- considered

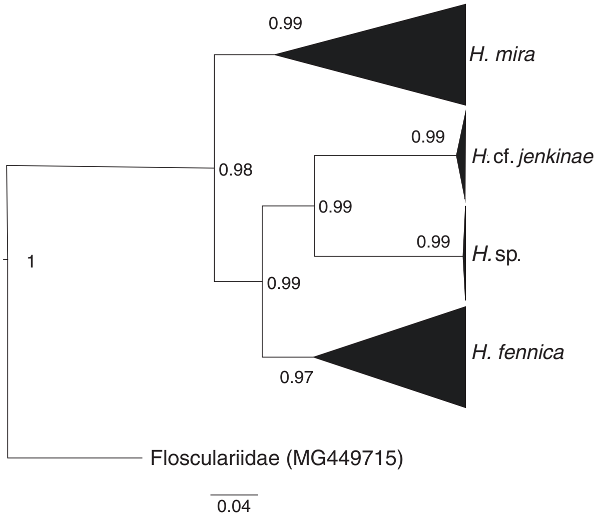

Fig. 14.1 Bayesian phylogenetic tree (chain length = 10,000,000; HKY + G substitution model) for all available COI sequences of the *Hexarthra* genus, including *H.* cf. *jenkinae* (present in lakes Alchichica, Atexcac and Aljojuca) and *H.* sp. (Lake Tecuitlapa). The posterior probability for each clade is shown beside the internal nodes. The scale bar indicates four substitutions per 100 nucleotides

it a synonym of *Diaptomus novamexicanus* Herrick, 1895 (Wilson and Yeatman 1959). However, almost 50 years later, an integrative study performed by Montiel-Martínez et al. (2008) showed that there is enough genetic, ecophysiological, and morphological divergence between the two species to revendicate Osorio-Tafall's taxonomic decision. According to the modern subdivision of the family Diaptomidae, the name of the population inhabiting Lake Alchichica is *Leptodiaptomus garciai.* Up to date, the confirmed distribution of this species is restricted exclusively to Lake Alchichica.

L. garciai is a small, colorless, calanoid copepod (total body size average ± standard deviation; female*:* 960 ± 179 μm; male*:* 910 ± 179 μm; n = 20; see extended data on size plasticity in Sect. 14.7.2). Its morphological features are consistent with *L. novamexicanus*, but there are slight differences in structures related to reproduction. In *L. garciai* males, the length of the lateral process at the antepenultimate segment (19th) of the antennule is less than a half of the penultimate segment (20th). In contrast, the same process in *L. novamexicanus* males from Castle Lake, USA (the closest place to *terra typica*) is more than a half of the length of segment 20th. On the other hand, in females, the process at the right posterior margin of the genital segment is smaller in *L. garciai* than in *L. novamexicanus* (one-third and two-thirds the length of the second urosomite, respectively). This morphological divergence could affect mate recognition and be a prezygotic isolating mechanism (Ohtsuka and Huys 2001). Another prezygotic, ecologically derived barrier between both species is their different tolerance to water salinity, a subject discussed further below.

Regarding molecular divergence, a neighbor-joining tree using a Kimura two-parameter (K2P) distance model applied to sequences of COI, revealed that *L. garciai* is a distinct clade from three Mexican populations of *L. novamexicanus*, with at least 4.4% divergence with its closest relative (Montiel-Martínez et al. 2008). Interestingly, the three populations of *L. novamexicanus* split into two clades, calling for the need for further investigation of the hidden diversity of *Leptodiaptomus* copepods.

Investigating the taxonomic identity of the three metazooplanktonic species of Lake Alchichica revealed that at least two of them (*L. garciai* and *B*. sp. 'Mexico') are endemic, independently evolving lineages. Moreover, using molecular tools to delve into their phylogenetic relationships with other populations and species showed that the diversity of aquatic invertebrates at a regional scale should be much higher than previously assumed.

14.3 Temporal and Spatial Variation

If we were to choose a word to describe the temporal course and spatial distribution of zooplankton in Lake Alchichica, it would be "variability". Each of the three metazooplankton species had different patterns of temporal abundance at seasonal and interannual scales that will be described in this section. The putative mechanisms (tolerance to salinity, resource availability, predation avoidance) behind those patterns will be discussed in the subsequent pages.

For simplicity's sake and taking advantage of the reduced specific richness of the metazooplanktonic assemblage, in the remainder of the chapter, we will name the three species after their generic names: *Hexarthra* (*H.* cf. *jenkinae*), *Brachionus* (*B*. sp. 'Mexico') and *Leptodiaptomus* (*L. garciai*).

14.3.1 Metazooplankton Density

Lake Alchichica is a warm monomictic lake, with a mixing period from late December to March, remaining stratified from April to November (Alcocer et al. 2000). The alternation of mixing and stratification periods strongly influences the development of zooplanktonic populations through changes in the availability of nutrients for phytoplankton and the supply of oxygen for the hatching of resting eggs in deep sediments, among other important ecological effects (Sommer et al. 2012). However, despite the predictable hydrodynamic pattern in Alchichica, data from monthly samplings performed along 5 years (Fig. 14.2 show that there are few repeatable attributes in the temporal dynamics of metazooplankton in this lake, both at seasonal and annual scales.

Regarding repeatable patterns, the three populations of metazooplankton coincided in experiencing wide oscillations in abundance (Fig. 14.2). As observed in

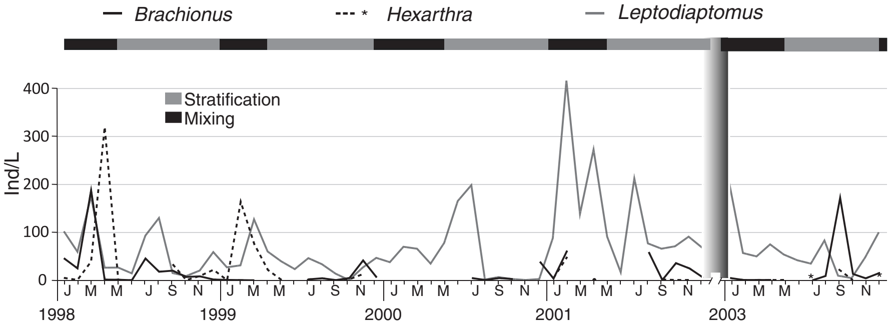

Fig. 14.2 Temporal variation of the monthly average of the metazooplankton abundance in Lake Alchichica (*Brachionus* sp. 'Mexico', *Hexarthra* cf. *jenkinae* and *Leptodiaptomus garciai*), for 1998–2001 and 2003. From 1998 to 2001 the sampling was performed at 2, 5, 10, 20 and 50 m, at daytime (10–16 h). Data from the zone where the metalimnion develops (22–40 m) are available only from 2003. The upper bar shows the approximate span of the stratification and mixing periods of the water column

temperate monomictic lakes (Sommer et al. 2012), the three species usually attained the highest density peak during the mixing of the water column and decreased significantly during the stratification period. However, sometimes another density peak occurred in this period. The highest density observed in a sample was 817 ind/L for *Brachionus* (March), 822 ind/L for *Hexarthra* (April), and 706 ind/L of *Leptodiaptomus* (March), all occurring during 1998. The average density of the three species during the mixing period of the water column (*Brachionus* 21; *Hexarthra* 20 and *Leptodiaptomus* 105 ind/L) also was higher than during the stratification (*Brachionus* 14; *Hexarthra* 11 and *Leptodiaptomus* 56 ind/L), although a U-Mann Whitney analysis indicated that this difference was statistically significant only for *Leptodiaptomus* ($U = 201.5$, $p = 0.0007$).

On the other side, the main difference between the three species is that while the *Leptodiaptomus* population is always present, the rotifer species undergo severe and frequent population crashes, reducing their density to undetectable levels for months or whole years (Table 14.1, Fig. 14.2) (Lugo et al. 1999; Ortega-Mayagoitia et al. 2011).

Concerning the interannual variability, metazooplankton abundance showed wide fluctuations, especially regarding the rotifer species (Table 14.1). In 1998, both rotifer populations reached similar average densities, but the following year, *Brachionus* decreased drastically, and *Hexarthra* was the most abundant rotifer. In 2000, *Hexarthra* was absent in water samples, and *Brachionus* appeared in low numbers only in the second half of the year. In 2001, *Brachionus* populations recovered, but *Hexarthra* continued to be a minor constituent of the metazooplankton assemblage. In contrast, *L. garciai* maintained a more stable annual average (40–63 ind/L), except in 2001, when the annual average doubled the observed in the previous year (Table 14.1).

Table 14.1 Annual average density of the three metazooplanktonic species of Lake Alchichica for 5 years

	B. sp. 'Mexico'		*H.* cf. *jenkinae*		*L. garciai*	
Year	Annual avg.	Range	Annual avg.	Range	Annual avg.	Range
1998	30 ± 52	1–187 (Mar)	36 ± 90	n.d. – 319 (Apr)	61 ± 53	9–175 (Mar)
1999	5 ± 12	n.d. – 42 (Oct)	25 ± 51	n.d. – 164 (Feb)	40 ± 32	1–127 (Mar)
2000	4 ± 11	n.d. – 39 (Dec)	n.d.	n.d.	56 ± 66	1–198 (Jul)
2001	16 ± 24	n.d. – 62 (Feb)	5 ± 14	n.d. – 49 (Feb)	134 ± 113	17–415 (Feb)
2003	24 ± 44	n.d. – 125 (Aug)	4 ± 10	n.d. – 36 (Jun)	63 ± 51	5–201 (Jan)

Annual averages (± standard deviation) and ranges (minimum and maximum monthly averages) of density (ind/L) are shown. Averages were calculated with data from five (1998–2001) or three depths (2003). In *L. garciai*, all developmental stages are shown. For each species and year, the month with the highest average is between parentheses. *L. garciai* values of 1998 were calculated from Lugo et al. (1999), where appears as *L. novamexicanus*; all values of 2003 were calculated from Ortega-Mayagoitia et al. (2011). *n. d.* not detected

Within the top 20 m of the water column, the highest abundance of rotifers and copepods was observed at 10 m during the mixing of the water column. At the beginning of the stratification and later, the abundance peak occurred between 10 and 20 m (Fig. 14.3). This vertical distribution pattern is representative of other years within the sampled period (1998–2001). The distribution of organisms below 20 m was studied in 2003 and is described in the next section.

14.3.2 Metazooplankton Biomass

Data of zooplankton biomass at light hours were obtained at three depths from January 2003 to January 2004 as part of a study of resource limitation and vertical migration (Ciros-Pérez et al. 2015; Ortega-Mayagoitia et al. 2011). The total metazooplankton biomass in Lake Alchichica oscillated from 0.33 to 6.33 mg/L (fresh weight), with an annual average of 1.4 ± 1.5 mg/L. Every month, *Leptodiaptomus* constituted from 69 to 100% of total metazooplankton biomass. The biomass of *Brachionus* was slightly significant only during the stratification period (September) (Fig. 14.4). 2003 was a "typical" year, with the highest total metazooplankton biomass during the mixing of the water column (2.5 ± 2.5 mg/L) and the minimum during the advanced stratification period (0.4 ± 0.3 mg/L) (Fig. 14.4).

Concerning the vertical distribution, the major share of the biomass was distributed in the first 15 m of the water column from January to April (86 ± 11%) and from November onwards (60 ± 30%). The rest of the year (April to September), when light penetration was deeper, the biomass diminished due to the contraction of the *Leptodiaptomus* population. It was mainly allocated between 18–28 m (26 ± 27%) and 30–40 m (45 ± 26%). As we discuss here below, the seasonal deepening of the distribution of metazooplankton biomass in this period is explained by

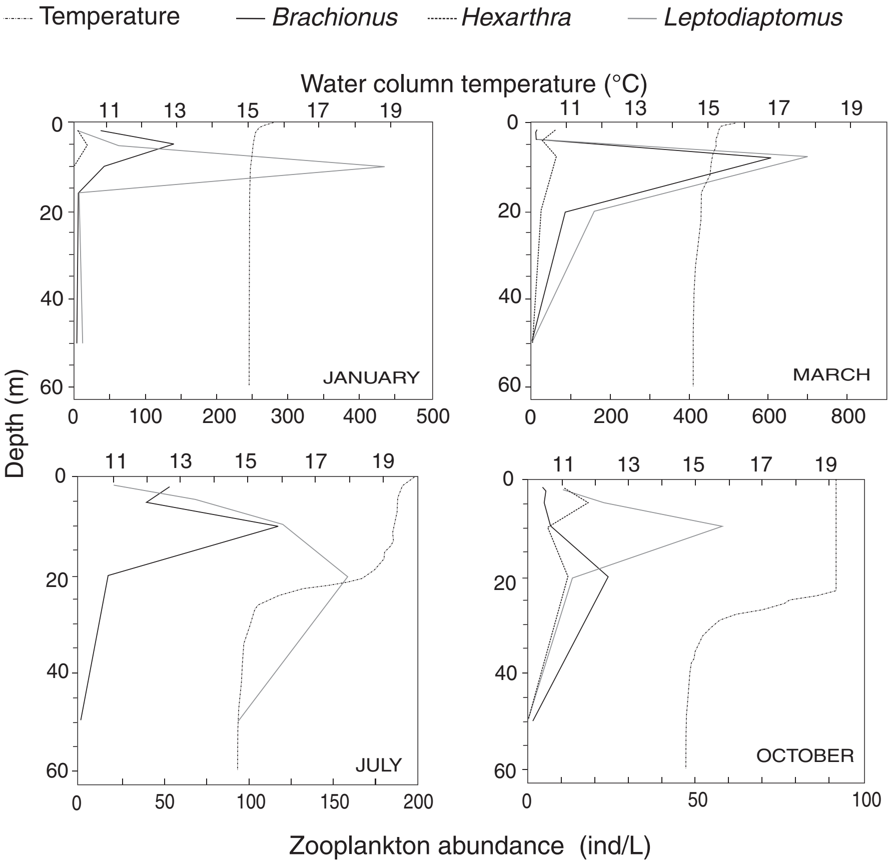

Fig. 14.3 Vertical distribution of the three zooplankton species (*Brachionus* sp. 'Mexico', *Hexarthra* cf. *jenkinae* and *Leptodiaptomus garciai*) and temperature profiles for four dates during 1998. January corresponds to the mixing of the water column, March is at the beginning of the stratification period, July and October reflect the period of well-established stratification. Note the differences in the X-axis scales showing metazooplankton abundance

the diel vertical migration (DVM) performed by late copepodids and adult *Leptodiaptomus* (Ciros-Pérez et al. 2015).

14.4 Facing the Saline Environment

Salinity is considered one of the most significant factors driving the distribution of lacustrine invertebrates, affecting molecular, biochemical, physiological, population and community processes and patterns (Colburn 1988; Williams et al. 1990). The absolute content of dissolved solids and their chemical nature vary widely

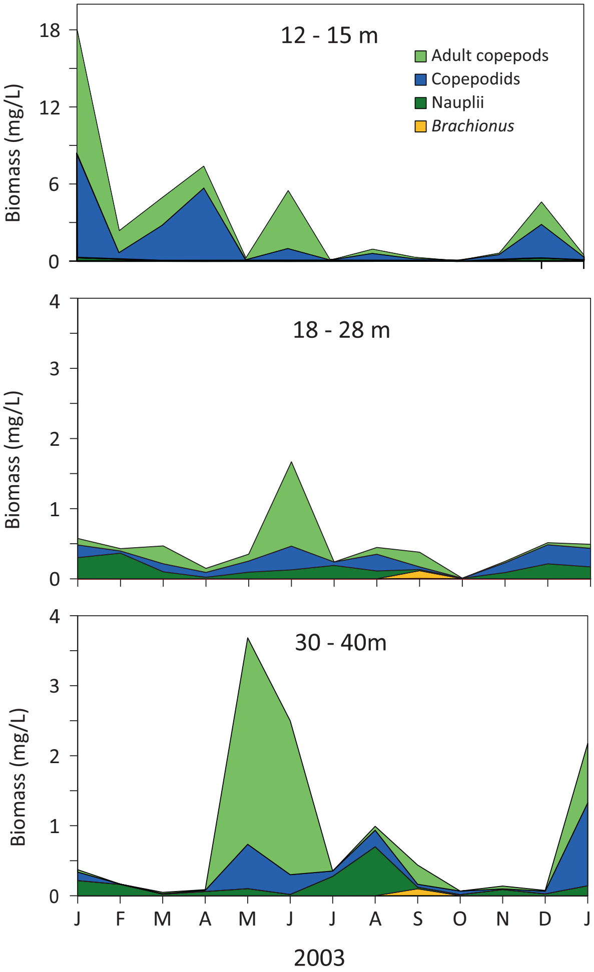

Fig. 14.4 The contribution of *Brachionus* sp. 'Mexico' and *Leptodiaptomus garciai* (nauplii, copepodids and adults) to the metazooplankton biomass (wet weight) from January 2003 to January 2004 at three different strata of the water column. The contribution of *Hexarthra* cf. *jenkinae* is unnoticeable. Biomass of all copepod stages was calculated with length-weight regressions and then multiplied by 10; rotifer biomass was calculated using geometric models and assuming a body density of 1 (Dumont et al. 1975). Note the different scale of the first panel

among continental water bodies, constituting at the same time a filter that shapes community structure (Gutierrez et al. 2018) and a driver of adaptive diversification for zooplanktonic species (Barrera-Moreno et al. 2015).

In ephemeral environments, salinity may experience wide temporal fluctuations, favoring the emergence and maintenance of generalist phenotypes, whereas, in permanent, constant environments, theory predicts the emergence of specialists (Lee and Gelembiuk 2008). Alchichica is a permanent lake with constant salinity close to the range of 5–8 g/L, considered a critical physiological boundary for invertebrates (Khlebovich and Abramova 2000). The latter begs a few questions: are the three populations equally adapted to the local conditions of salinity? Is salinity influencing their population dynamics? What are the evolutive consequences of facing this saline environment?

The rotifer *Brachionus* sp. 'Mexico', which inhabits Lake Alchichica, is also present in the nearby lakes La Preciosa and Atexcac, two crater lakes with lower salinities (1.2 and 6.5 g/L, respectively). However, in contrast to other species of the *Brachionus plicatilis* group that are well adapted to wide salinity ranges (Lowe et al. 2007), the three populations of *B.* sp. 'Mexico' have narrow and differentiated tolerance intervals. Laboratory experiments showed that the best performance of the three populations in important ecophysiological responses like age at sexual maturity and population growth, is at 6.0–6.5 g/L. Organisms were more severely affected by lower (0.1, 1.1, 3 g/L) than by higher salinities (9–12 g/L) (Alcántara-Rodríguez et al. 2012; Sarma et al. 2002). Interestingly, La Preciosa population is the only able to sustain positive growth at 1.1 g/L – its native salinity- (Alcántara-Rodríguez et al. 2012), so it has a wider niche than the other populations. The latter constitutes a case of local adaptation that broadens the range of tolerance to salinity of only one population, likely promoting an asymmetric gene flow between lakes: individuals from La Preciosa eventually could colonize the other two lakes, but individuals from Atexcac and Alchichica could only exchange genes between them.

Most of the 21 species of the genus *Hexarthra* inhabit freshwater bodies, but several species like *H. jenkinae* and H. *oxyuris* have been reported in a broad range of salinities (Gutierrez et al. 2018; Ruttner-Kolisko 1974). The *Hexarthra* species from Lake Alchichica is also found in nearby lakes of lower salinity (Atexcac = 6.5 g/L and Aljojuca = 0.1 g/L), but only the salinity tolerance of the population from Lake Alchichica is known. Sarma et al. (2002) measured its population growth in a gradient from 0.1 to 12 g/L and found that the best performance is at 6 g/L, decreasing significantly at 3 g/L. At 0.1 g/L, organisms died within a week, so we cannot exclude the possibility that the population from Aljojuca has a different tolerance range and even local adaptation to salinity.

The tolerance to salinity of *L. garciai* was tested as part of an integrative approach to elucidating its taxonomic status with respect to *L. novamexicanus* (Montiel-Martínez et al. 2008) (see the previous section on taxonomy). Members of the genus *Leptodiaptomus* have been recorded in a wide range of salinities, but all known populations of *L. novamexicanus* have been found exclusively in freshwater. Survival, somatic growth, mating, egg production, and hatching were tested along a gradient of salinities, including the native conditions of *L. garciai* and a population of *L. novamexicanus* from a freshwater pond (Ixtlahuaca, Estado de México). *L. garciai* was negatively affected by all salinities below 9 g/L. Although some individuals were able to survive, grow, mate and hatch at 2.5 g/L, they did not survive more than 4 days at 0.1 g/L (freshwater). The effects of alternative salinities were harsher for *L. novamexicanus* individuals, as they did not survive long enough above 0.1 g/L to perform any of the corresponding measurements. These results showed that successful population establishment of *L. garciai* in freshwater systems is unlikely and that salinity is an effective prezygotic barrier to reproduction between *L. garciai* and its closest relative identified so far.

Experimental evidence shows that the stable but unique osmotic conditions in Lake Alchichica exert different pressures on the three metazooplanktonic species. Salinity conditions are suboptimal for both rotifer species, limiting their population growth due to a higher energetic investment in osmotic regulation (Lowe et al. 2005). In contrast, *L. garciai* seems to be best adapted to the local salinity, allowing it to allocate a major share of resources to somatic and population growth. This differential adaptation to salinity and physiological adaptation to cope with low food availability, could be one of the keys to explaining the dominance of *L. garciai* in the zooplankton of Lake Alchichica.

14.5 Resource Availability

Food availability for herbivorous zooplankton is directly linked to the dynamics of phytoplankton populations. Lake Alchichica has a peculiar combination of limnological characteristics, including a frequent scarcity of nutrients which determines low biomass of primary producers. Moreover, the temporal abundance and vertical distribution of phytoplankton vary remarkably following the seasonal mixing and stratification of the water column: There is a diatom bloom during the mixing period and a *Nodularia* bloom at the beginning of the stratification, whereas during the well-established stratification, phytoplankton in the epilimnion is scarce, but a deep chlorophyll maximum (DCM) develops in the metalimnion (Adame et al. 2008; Oliva et al. 2001; Chap. 5 in this volume).

As a potential food resource for zooplankton, another relevant feature of phytoplankton is its functional structure. During a study performed in 2003 to assess the resource limitation for zooplankton (Ortega-Mayagoitia et al. 2011), most of the phytoplankton biomass was constituted by the central diatom *Cyclotella alchichicana* (73 ± 26% of total phytoplankton biomass, Fig. 14.5), which is the main component of the winter bloom and the DCM. However, with an average diameter of 45.0 ± 6.5 μm (range 30–72 μm) (Correa-Rizo 2018), this diatom is likely inedible for the small-sized zooplankton species inhabiting Lake Alchichica. The exception are the largest copepod adults that could feed on the smallest cells in winter (see the section on phenotypic plasticity in copepod size; Ortega-Mayagoitia et al. 2018). The potentially edible phytoplankton for rotifers (greatest axial linear dimension, GALD ≤20 μm) constituted the 27 ± 26% of total biomass. It is made up of changing proportions of the chlorophytes *Monoraphidium* spp. and *Oocystis parva*, and the diatom *Cyclotella choctawhatcheeana.* Thus, the expected scenario faced by zooplankton in this lake is one of chronic low availability of resources. This environmental factor could explain the composition and temporal dynamics of the metazooplankton assemblage.

The resource limitation of rotifers was tested with 19 experiments performed along a complete annual cycle, using the natural assemblages of phytoplankton and

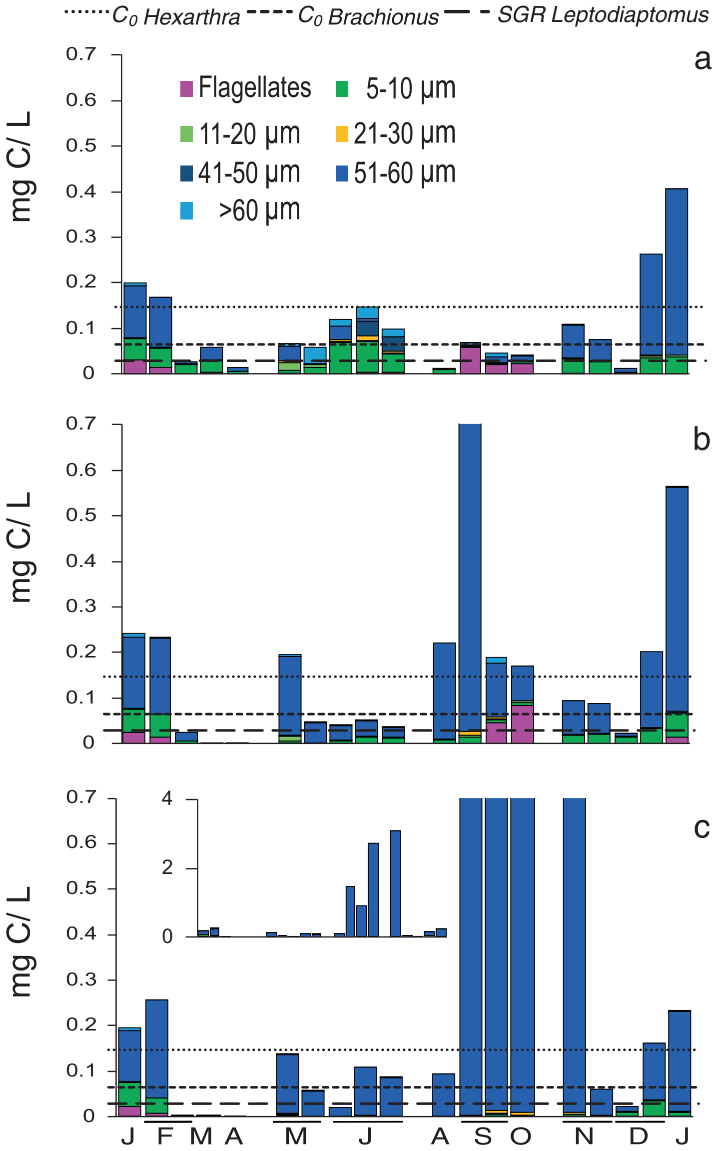

Fig. 14.5 Seasonal abundance of phytoplankton and small heterotrophic flagellates (<10 µm) biomass at three depths in Lake Alchichica from January 2003 to January 2004. **(a)** 12–15 m; **(b)** 18–28 m, and **(c)** 30–40 m. The contribution of different size categories (according to their greatest axial linear dimension) is shown. The diatom *Cyclotella alchichicana* is the main component of the 51–60 µm size category. Horizontal dotted lines show the estimates for the C_0 parameter (see text) for *Brachionus* sp. 'Mexico' and *Hexarthra* cf. *jenkinae* or food concentration at which the specific growth rate (SGR) for *Leptodiaptomus garciai* was still positive. Please, note that the y-axis of panel **c** is cut to 0.7 mg C/L; the inset shows the full scale

zooplankton at three depths of the water column (Ortega-Mayagoitia et al. 2011). *Hexarthra* was present in detectable densities ($\geq$0.2 ind/L) at only eight sampling dates (Figs. 14.2 and 14.4). *Brachionus* was more frequent and abundant. Experiments demonstrated that both species were resource-limited with similar intensity at all tested depths during the mixing and stratification of the water column, irrespective of the total phytoplankton biomass present. Copepods were included in the experiments but owing to the short term of the assays, their results are not reliable.

The competitive capacities of the three metazooplankton species were assessed by measuring the somatic growth rate (SGR) of copepod nauplii and the numerical response of rotifers (to obtain C_0, the food concentration at which population growth equals zero, and r, the specific growth rate). Additionally, the rate of mass loss and the size of usable reserves of the three species were quantified (Ciros-Pérez et al. 2015).

Hexarthra had the highest C_0, followed by *Brachionus* (0.14 ± 0.02 mgC/L and 0.06 ± 0.01 mgC/L, respectively), whereas nauplii maintained a positive SGR even at the lowest food concentration that we explored (0.025 mg C/L). The size of usable reserves of *Leptodiaptomus* nauplii was 1.6 times larger than in *Brachionus*, and in *Brachionus* it was 3.7 times larger than in *Hexarthra*. This pattern was reflected in the rate of body mass loss; thus, when food-deprived, copepods were able to live more than twice than both rotifers (Ciros-Pérez et al. 2015; Fig. 14.6). Finally, *Hexarthra* showed the highest $r_{\max}$, followed by *Brachionus* and then by copepod nauplii ($r_{\max} = 0.79 \pm 0.42, 0.64 \pm 0.07, 0.06 \pm 0.01$, respectively).

These findings indicate that copepods can survive and grow at food concentrations at which both rotifer species would already experience negative growth. Moreover, the capacity of copepods to frugally expend their energetic budget even in case of complete food deprivation contributes to explain their persistence along the year in Lake Alchichica. In contrast, the availability of potentially edible phytoplankton for rotifers is frequently below their minimum requirements, so they are

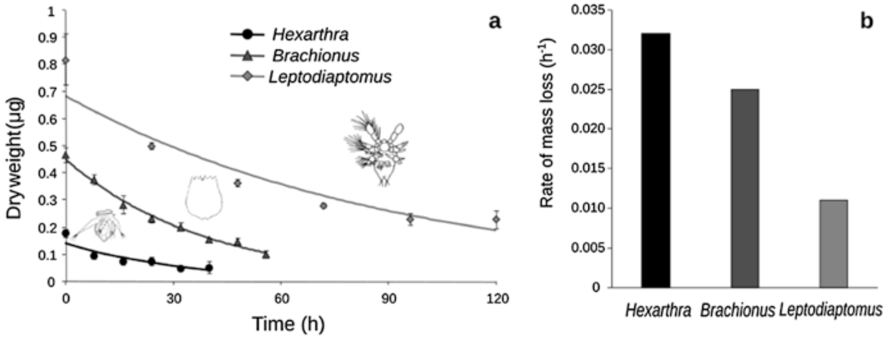

Fig. 14.6 (**a**) Individual body mass of *Brachionus* sp. 'Mexico', *Hexarthra* cf. *jenkinae* and *Leptodiaptomus garciai* vs. starvation time; symbols are average ± SE. (**b**) Rate of mass loss, calculated as the slope of the linear regression of *ln* (body mass) vs. starvation time

more vulnerable to resource limitation and demographic crashes (Fig. 14.5). However, they can take advantage when food availability suddenly increases due to their relatively higher maximum growth rates. It is worth remembering that the salinity of Lake Alchichica negatively affects the growth rate of both *Hexarthra* and *Brachionus* (Alcántara-Rodríguez et al. 2012), contributing likely to their irregular temporal dynamics (Ciros-Pérez et al. 2015; Ortega-Mayagoitia et al. 2011).

The ecophysiological characteristics in the three metazooplankton populations have been selected by the frequent scenario of low availability of food in terms of quantity and/or quality, so an intense competition for resources in Lake Alchichica between the zooplankton species should be the rule.

14.6 On the Avoidance of Light and Visual Predation

The low availability of nutrients in Lake Alchichica translates into a low epilimnetic phytoplankton biomass, allowing deep penetration of light into the water column, especially during the stratification period (Chap. 7). This circumstance entails two survival challenges for metazooplankton: light increases the risk of predation by the planktivorous silverside *Poblana alchichica* (Stich and Lampert 1981) and exposes organisms to harmful UV radiation (UVR, Williamson et al. 2011). Both hazards can be avoided by performing a Diel Vertical Migration (DVM), swimming downwards at dawn, to the spatial refuge provided by deep, cold, and dark waters, returning to epilimnetic/shallow waters to feed at dusk. However, in Lake Alchichica, the hypolimnion is anoxic during most of the stratification period, so the spatial refuge for migrating metazooplankton could disappear, just at the season when light and UVR are more intrusive.

14.6.1 **Leptodiaptomus***: A Normal DVM Pattern Limited by the Anoxic Hypolimnion*

The vertical distribution and movements of metazooplankton were assessed in three seasons with contrasting levels of light penetration, food availability, and fish density. Samplings were performed during the mixing of the water column (January), early stratification (May), and well-established stratification (September) (Ciros-Pérez et al. 2015). As expected in a normal DVM pattern, late copepodid stages and adult copepods -which are the main targets of size-dependent, visual predation-showed intense downward movements at dawn and upward movements at dusk. In contrast, nauplii displayed significant movements only during early stratification. The intensity of displacements, measured using movement traps, was related to the seasonal variation of light penetration: they were less noticeable in January, when light penetration was the lowest due to a diatom bloom, and increased in the well-established stratification, when the euphotic zone was wider, reaching 30 m (Chap. 7). The vertical distribution of organisms, summarised by the Mean Population Depth (MPD) shows that in the first two seasons, the vertical movement of the copepod population allowed many of them to spend the day hours well below the 1% of UVA, UVB and even below the reach of visible light (PAR) (MPD of adults at day hours = 22.4 ± 2.1 m in January and 34.9 ± 2.9 m in June). The extent of the migration performed by *Leptodiaptomus* is much wider than needed to avoid the damaging effects of UVR; thus, the most likely driver is predation evasion (Williamson et al. 2011).

However, during the well-established stratification, adults were found swimming downwards and upwards within the metalimnion with similar intensity at midday (MPD = 23.3 ± 1.3 m). The likely explanation is that even though they were trying to avoid light, the lack of oxygen in the hypolimnion forced them to return to the epilimnion. The result was that copepods were found within the limits of the euphotic zone and UV-A at midday, exposing them to UV-B and predators.

Then, how effective is DVM to avoid light-related risks? DVM seems to be an effective strategy to avoid UVR and light-dependent predation in the first half of the year, but unsuccessful during the well-established stratification and onwards due to the development of hypolimnetic anoxic conditions. Interestingly, the only pelagic predator, *P. alchichica*, seems to avoid light too, because echosounding-based surveys have shown that they are usually distributed below the 1% of PAR (between 25 and 40 m), except when the hypolimnion becomes anoxic (Arce et al. 2011; Ciros-Pérez et al. 2015). This behavior is probably more common than previously thought (Mehner 2012 and references therein). When both fish and copepods coincide within the euphotic zone in late stratification, predators can be more efficient, explaining, at least in part, the repeated scarcity of copepods in this season (Lugo et al. 1999; Ortega-Mayagoitia et al. 2011, Fig. 14.2 this chapter).

14.6.2 **Brachionus** ***and*** **Hexarthra*****: The Law of the Least Effort***

We did not find evidence of DVM in rotifers (Ciros-Pérez et al. 2015). In January, most of the population of *Hexarthra* avoided UVA, UVB, and the euphotic zone, remaining at nearly constant depths during the 24 h cycle (MPD ≈ 22.7 ± 2.1 m). *Brachionus* performed upward movements not associated with DVM, avoiding UVA and UVB, but not the euphotic zone (MPD ≈ 15.0 ± 1.8 m). During the well-established stratification, both rotifer species were confined within the epilimnion, exposed to visible light and UVA (MPD ≈ 22.9 ± 1.2 m for *Brachionus;* ≈ 16.5 ± 1.0 m for *Hexarthra*). Although rotifers did not perform significant vertical movements to evade visual predators, they swam perhaps to maintain a safe position in the water column to avoid damaging UV radiation (Obertegger et al. 2008) and being swept away by gravity. However, when the refuge provided by deep waters was devoid of oxygen, rotifers, like copepods, were forced to remain in the metalimnion and the epilimnion.

Overall, the combination of high solar radiation and transparent water makes the upper zone of Lake Alchichica a risky environment that prompts different strategies in copepods and rotifers. If the water column is oxygenated, both groups of organisms evade the lowest reaches of UVA and UVB; besides, larger stages of copepods migrate further to avoid PAR, likely to reduce the risk of visual predation. However, when the hypolimnion becomes anoxic, neither metazooplankton group is efficiently protected against UVA nor visual predation. Thus, the efficiency of light-avoiding strategies in this lake depends on the interplay of water transparency and oxygen availability in deep layers. The abiotic conditions of Lake Alchichica (oligotrophy, tropicality) combine to expose organisms to unique, conflicting pressures that shape the vertical distribution and temporal dynamics of this aquatic community.

14.7 Lake Alchichica and the Evolution of Life-History Traits

Rotifers and copepods have very different life histories, but share some traits shaped by common selective forces in lacustrine environments. A key feature of the life histories of many aquatic invertebrates is the diapause, an adaptation shared by rotifers and copepods to face seasonal heterogeneity and dispersal in fragmented environments. Another features, like the seasonal influence of temperature on adult size, are better known in copepods than in rotifers. In this section, we discuss how the environmental conditions of Lake Alchichica have impinged the life-history traits of *B.* sp. ‘Mexico’ and *L. garciai*.

14.7.1 Environmental Conditions Favor the Loss of Diapause Propagules

Rotifers and copepods have very different life histories, but share some traits shaped by common selective forces in lacustrine environments. A key feature of the life histories of many aquatic invertebrates is the diapause, an adaptation to face seasonal heterogeneity and dispersal in fragmented environments. In calanoid copepods and most rotifers, the diapause structure is a resting embryo, commonly known as resting egg (Alekseev et al. 2007).

In rotifers and copepods, resting eggs are the result of sexual reproduction. Rotifers usually reproduce parthenogenetically, but under certain stimuli, like population crowding in the genus *Brachionus* (Gilbert 2020), a part of the females produce short-lived males, allowing sexual reproduction (Stelzer and Snell 2003). In calanoid copepods, sexual reproduction is obligate, and the production of resting eggs is attributed to low food availability. It can be triggered by a combination of photoperiod, population density, trophic conditions, and temperature (Alekseev et al. 2007).

Resting eggs produced in the water column sink to the bottom and hatch after months or years, triggered by a proper combination of environmental cues like temperature and light. Because resting eggs accumulate in the sediments, the conditions prevailing in the deep benthos and the littoral zone determine their conservation and hatching. They are, along with water-column predictability, highly relevant factors for the ecological and evolutionary dynamics of metazooplankton populations (García-Roger et al. 2006).

In Lake Alchichica, the sediments of the deep zone are in permanent darkness, at constant, cold (14.5 °C) temperature and under anoxic conditions several months a year. A survey was performed to assess how these factors could affect the diversity, abundance, and viability of the egg bank (Ayala-Arce 2008). The first striking result was that although in the water column the dominant species is *Leptodiaptomus*, only resting eggs from *Brachionus* were recovered. Resting eggs of *Hexarthra* have been found only in the littoral zone (Ayala-Arce 2008). The absence of resting eggs of *Leptodiaptomus* in the sediments is consistent with a year-round study of its reproductive plasticity, where no diapausing structures were observed in 1258 ovigerous females examined (Ortega-Mayagoitia et al. 2018).

The density of the egg bank of *Brachionus* in deep sediments is considerably higher than in the littoral zone (148 ± 6.4 *vs*. 6.8 ± 0.8 eggs/cm^2), probably due to the lack of egg-consuming predators in the former region. However, resting eggs seem to deteriorate relatively soon because, in laboratory assays, only 29% of the eggs in the first 3.5 cm of sediments (age $\leq$10 years) hatched. The density of the egg banks in Lake Alchichica and their deterioration rate seem to be common patterns. Both features fall within the range observed in other water bodies, regardless of whether they are ephemeral or permanent (García-Roger et al. 2006).

Egg hatching in natural conditions was quantified with an *in situ* experiment performed in July–August (2006) and January–February (2007). This study revealed that when the hypolimnion is anoxic, the probability of hatching close to the bottom is unlikely (no hatchings were recorded). The probability improved slightly when oxygen reached the bottom of the lake during the mixing of the water column (~0.2 hatchings/day) (Ayala-Arce 2008; our unpublished results).

Given that resting eggs are linked to sex in rotifers, adverse conditions for conservation and hatching can be selection factors against investing in sexual reproduction in this population of *Brachionus* (Gilbert 2017). A fine-scale assessment of the reproductive patterns of this species in the laboratory showed that within the population, there is significant variability in the propensity to initiate sexual reproduction (Cruz-Cruz 2018). However, all genotypes showed a reduced response to crowding. Even those clones with the highest propensity –those hatched from the egg bank–, required a significantly higher population density to initiate sexual reproduction (mixis threshold = 910–1387 ind/L), compared to other species of the same genus (mixis threshold = 67–170 ind/L; Gilbert 2003; Snell 2017). Considering that the highest population density ever recorded for *Brachionus* in Lake Alchichica is 800 ind/L and that the average population density of *Brachionus* is usually below 200 ind/L (Table 14.1), the demographic conditions triggering the production of resting eggs should be met sporadically.

Suppose the egg bank is composed mainly of individuals with the highest investment in sexual reproduction, and environmental conditions hamper their hatching. In that case, it must follow that the frequency of the genotypes with the lowest investment in sex is higher in the active population in the water column. The latter genetic variants should be further favored by the permanence and predictability of the environment because they may not depend on resting eggs to persist throughout the year. These circumstances are likely leading to the loss of sex by directional selection (Gilbert 2017).

A consequence of the reduced production of resting eggs in rotifers and its probable absence in copepods, is the diminished opportunity for spatial dispersion and genetic flow with populations of other lakes, favoring genetic isolation and lineage divergence (Ortega-Mayagoitia et al. submitted). This circumstance can contribute to the patterns of endemism and local adaptation processes and diversification of metazooplankton in lakes of Cuenca Oriental (Montiel-Martínez et al. 2008; Alcántara-Rodríguez et al. 2012; Barrera-Moreno et al. 2015).

14.7.2 **Leptodiaptomus***: Phenotypic Plasticity to Temperature and Food*

Another way the environment affects life-history traits of zooplankton is by promoting the evolution of phenotypic plasticity, i. e., the production of alternative phenotypes to cope with environmental variability. Historically, it was considered that a temporal variation of at least 14 °C was necessary to stimulate a plastic response in adult copepod size (Riccardi and Mariotto 2000). Therefore, in tropical environments, food availability should be the main driver of adult size and other related traits. In Lake Alchichica, water temperature is relatively stable along a year cycle (the average range of the mixing layer is about 3.2 °C), whereas phytoplankton biomass varies 17-fold (Ortega-Mayagoitia et al. 2018). The effects of temperature and phytoplankton biomass on several life-history traits of *Leptodiaptomus* were tested measuring the natural occurrence of adult female, egg size, clutch size, and hatching success and number of nauplii per clutch during a year (2003–2004) (Ortega-Mayagoitia et al. 2018).

All measured life-history traits except hatching success showed clear seasonal patterns and wide plastic responses (Phenotypic Plasticity Index, Table 14.2). However, although the annual (average) temperature range of the mixing layer was narrow, the mean size of adult females and eggs behave according to the Temperature-Size Rule observed in temperate environments (Angilletta 2009), with the smallest sizes associated to warmer months and the largest during the coldest season (Pearson coefficients between size and water temperature, adult females: $r = -0.940$, $p < 0.001$; eggs: $r = -0.827$, $p < 0.001$).

Table 14.2 Variation and plasticity of life history traits of *L. garciai* (Ortega-Mayagoitia et al. 2018)

Life history trait	Annual average		Month average	
Female length (µm)	*Range*	762–1176	*Minimum*	821 ± 18 (Aug)
	Avg. ± SD	933 ± 83	*Maximum*	1026 ± 51 (Dec)
	n	601	*PPI (%)*	20
Female biomass (µg)	*Range*	41–113	*Minimum*	49 ± 3 (Aug)
	Avg. ± SD	67 ± 14	*Maximum*	82 ± 9 (Dec)
	n	601	*PPI (%)*	41
Egg diameter (µm)	*Range*	75–150	*Minimum*	89 ± 42 (Sep)
	Avg. ± SD	106 ± 16	*Maximum*	131 ± 81 (Mar)
	n	1218	*PPI (%)*	32
Egg biomass (µg)	*Range*	0.2–1.8	*Minimum*	0.37 ± 0.04 (Sep)
	Avg. ± SD	0.7 ± 0.3	*Maximum*	1.17 ± 0.28 (Mar)
	n	1218	*PPI (%)*	68
Clutch size (eggs/ind)	*Range*	1–16	*Minimum*	2.1 ± 0.6 (May)
	Avg. ± SD	4.8 ± 2.4	*Maximum*	9.3 ± 2.0 (Nov)
	n	1258	*PPI (%)*	77
Hatching success (%)	*Range*	0–100	*Minimum*	65 ± 41 (Mar)
	Avg. ± SD	92 ± 9	*Maximum*	98 ± 6 (Sep)
	n	649	*PPI (%)*	n.s.
Nauplii per female	*Range*	1–13	*Minimum*	1.7 ± 0.7 (Apr)
	Avg. ± SD	4.2 ± 2.4	*Maximum*	8.7 ± 2.5 (Nov)
	n	643	*PPI (%)*	80

Female length: cephalothorax plus urosome excluding the furcal rami. Individual female biomass (fresh weight) was calculated using length-weight regressions (Dumont et al. 1975). *PPI* Phenotypic Plasticity Index, calculated according Valladares et al. 2016. *n. s.* non-significant. See further details in Ortega-Mayagoitia et al. (2018)

Clutch size and the number of nauplii per female also showed strong seasonal plasticity, responding positively to the wide variation in total phytoplankton biomass throughout the year (clutch size, $r = 0.644$, $p < 0.018$; nauplii, $r = 0.667$, $p < 0.013$). The ability to adjust the number of descendants according to the abundance of resources could be adaptive. However, more data on the performance of nauplii hatched in different food conditions are needed.

The magnitude of the thermal plasticity of *Leptodiaptomus* in Lake Alchichica was within the range observed in 49 other species of marine and lacustrine copepods from higher latitudes. Therefore, these results showed that absolute thermal plasticity is not related to latitude or annual temperature variation but seems to be more intense in environments of limited temperature variation compared to temperate populations. More data from tropical lakes are needed to assert if this pattern is consistent and if thermal plasticity in copepod size is adaptive.

14.8 Conclusions

Lake Alchichica is a perennial lake with constant salinity and relatively narrow temperature oscillations. These features resemble an oasis in the middle of the desert, offering a constant opportunity of colonization by propagules of planktonic invertebrates transported passively from other lakes, especially from the other seven water bodies that occur in Cuenca Oriental. The regional pool of copepods, rotifers, and cladocerans amounts 86 species. Some of them, like *Mastigodiaptomus* cf. *albuquerquensis* and *Leptodiaptomus* group *sicilis*, have relatively wide salinity tolerance ranges, including the salinity of Lake Alchichica (9 g/L) (our unpublished results; Barrera-Moreno et al. 2015). However, both species are absent in Lake Alchichica, which hosts a specific richness of only three planktonic species. *L. garciai* is found exclusively in Lake Alchichica, whereas the *B*. sp. 'Mexico' and *Hexarthra* cf. *jenkinae* inhabit at least two other neighboring lakes. Then, there must be local, challenging features hampering the establishment of zooplankton species in this lake that, also, could be affecting differently the zooplankton populations that have succeeded in colonizing it.

Field and laboratory experiments have demonstrated that *L. garciai,* is the best-fitted species to the local salinity and the chronic scarcity of food in this waterbody. The phytoplankton in Lake Alchichica has a peculiar functional structure, including a large share of mucilaginous colonies, large-sized diatoms, and filamentous cyanobacteria, which experience wide annual and interannual fluctuations (Chap. 12). *L. garciai* has the lowest requirements of carbon and efficient expenditure of reserves. Although the population growth rate of copepod is not as high as in rotifers, their body size and life cycle are quite plastic, allowing them to exploit the seasonal increases of phytoplankton (including the smallest cells of *C. alchichicana*) to produce more eggs and nauplii. Besides, an energetically efficient adjustment of osmoregulation mechanisms might promote optimal use of resources, explaining its continuous dominance of the metazooplankton assemblage.

Like other crustacean species in transparent lakes, *L. garciai* performs vertical migrations that allow them to evade the damaging effects of UVR and visual predation, explaining their differential vertical distribution throughout the year according to the penetration of light. The biggest challenge appears during the late stratification period when copepods cannot avoid the lower reach of light due to the development of the anoxic hypolimnion. This mismatch is likely responsible for the repeated seasonal population decrease of copepods.

In contrast, Lake Alchichica is a harsher environment for the two rotifer species, which are more restrained by salinity and food limitation. Both live in suboptimal conditions of salinity, negatively affecting their population growth even in food-saturated conditions. Also, the availability of potentially edible phytoplankton is frequently below their minimum growth requirements, setting the stage for recurrent population crashes. On the other side, their relatively high intrinsic growth rates account for sudden, and short-lived density peaks observed irregularly.

As inhabitants of a fragmented landscape, copepods and rotifers rely on the production of resting eggs to disperse elsewhere. Afterward, organisms must withstand the local conditions of salinity to have at least an opportunity to keep stable populations. In the case of *B*. sp. 'Mexico', the permanence and depth of the waterbody and the lack of oxygen in the hypolimnion have promoted the directional selection for loss of sex, reducing their ability to produce propagules. A regional assessment of diversity revealed two other populations of this *Brachionus* species in neighboring lakes. At least in one of them (Atexcac, 6.5 g/L), salinity conditions allow better physiological performance for this rotifer than in Alchichica. Thus, even if similar limnological conditions have promoted the parallel evolution of loss of sex in the three lakes, appropriate conditions of salinity could still allow the maintenance of gene flow between the three populations, although at asymmetrical rates.

On the other hand, *L. garciai* is restricted to Lake Alchichica. This microendemic distribution can result from an extreme adaptation to living in this environment. *L. garciai* could have lost the ability to produce resistant eggs is probably specialized not only to the ionic content of water (9 g/L) but to its singular chemical composition as well. The last argument requires empirical testing but is based on the observation that other *Leptodiaptomus* species distributed in lakes of Cuenca Oriental are under a process of ecological speciation driven by local adaptation to salinity, which functions as an ecological barrier (Barrera-Moreno et al. 2015).

The fact that at least two of the three species of metazooplankton of Lake Alchichica are endemic or microendemic, highlights the evolutionary consequences of the joys and challenges of living in this lake, promoting local adaptation, and hampering the gene flow with other populations. In the long term, these mechanisms can result in diversification and speciation processes, not only for metazooplanktonic species but also for other components of the aquatic biota.

Lake Alchichica is a unique and invaluable environment. Its particular limnological features, spatial closeness to other lakes, and geographical context provide countless opportunities to delve into the factors and mechanisms that shape biological communities and drive evolutionary processes and patterns.

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Chapter 15
Alchichica Silverside

Xavier Chiappa-Carrara, Elsah Arce, Gerardo Pérez-Ponce de León, and Javier Alcocer

15.1 Introduction

Mexico's geological history has profound effects on the ichthyofauna composition of inland waters (Barbour 1973). The diversification of the Mexican inland fish is the product of several factors (Miller 1986), among these: (1) a highly variable physical geography, (2) a wide latitudinal extension, (3) the isolation of the Mesa Central, a large tropical highland plateau, and the fauna of the Lerma River, (4) the adaptation of multiple marine groups to continental waters, and (5) the presence of the largest river system in southeast Mexico, the Usumacinta-Grijalva basin. The atherinopsids case, such as silversides of the genera *Chirostoma* and *Poblana*, represents a local speciation model (Álvarez 1950). Four valid species of *Poblana* are currently recognized, all of them inhabiting aquatic bodies at the north and east of the state of Puebla, each one of them endemic to a single aquatic body: *P. alchichica* in Lake Alchichica, *P. squamata* in Lake Quechulac, *P. letholepis* in Lake La Preciosa, and *P. ferdebueni* in Lake Chignahuapan (De Buen 1945; Álvarez 1950; Froese and Pauly 2019).

X. Chiappa-Carrara (✉) · G. Pérez-Ponce de León
Escuela Nacional de Estudios Superiores Unidad Mérida, Universidad Nacional Autónoma de México, Yucatán, Mexico
e-mail: chiappa@unam.mx; ppdleon@enesmerida.unam.mx

E. Arce
Centro de Investigaciones Biológicas, Universidad Autónoma del Estado de Morelos, Cuernavaca, Morelos, Mexico
e-mail: elsah.arce@uaem.mx

J. Alcocer
Grupo de Investigación en Limnología Tropical, FES Iztacala, Tlalnepantla, Estado de México, Mexico
e-mail: jalcocer@unam.mx

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15.2 Atherinopsidae: *Poblana alchichica*

Within the Atherinopsidae, known as Neotropical silversides (Álvarez 1950), the genus *Poblana* belongs to the subfamily Menidiinae. The common name refers to fish having a silvery lateral line.

The four *Poblana* species have had a controversial taxonomic history and possess identical COI barcodes, suggesting a very recent history of isolation (Valdez-Moreno et al. 2009). De Buen (1945) described *P. alchichica* as a new silverside species collected from Lake Alchichica (Fig. 15.1). Later, Álvarez (1950) and Guerra-Magaña (1986) considered Alchichica's silverside to be a subspecies (*P. alchichica alchichica*). However, Miller (1986), in his study on the origin and geography of the fishes of Central Mexico, and Espinosa et al. (1993), in their list of Mexican freshwater fishes, re-evaluated the specific status of *P. alchichica*.

15.3 Distribution and Abundance

The geographic range of *P. alchichica* is restricted (endemic) to a single locality, Lake Alchichica. Due to its narrow range, it is considered a microendemic species with a limited distribution that reaches <5% of the Mexican territory. Actually, much less since Lake Alchichica's surface area (2.3 km^2) is 0.0001% of the Mexican territory (1,964,375 km^2).

The distribution of *P. alchichica* is divided into two zones of the lake, the pelagic and the littoral zone. The pelagic zone starts at the edge of the stromatolite (tufa) ring to the center, while the littoral zone is considered from the stromatolites to the shoreline of the lake. This uneven distribution within the lake has been described as a donut-like pattern (Arce et al. 2011) since most (>95%) of the fish inhabit the perimeter of the lake close to the tufa ring, accounting for 70% of the total surface area of the lake (Fig. 15.2). Few individuals (<5%) dwelled in the pelagic central zone, which attains 30% of the lake's total surface area.

The bathymetric distribution of *P. alchichica* ranges from the surface to 55 m deep but often not deeper than 40 m (Arce et al. 2011). Although the temperature

Fig. 15.1 The Alchichica silverside, *Poblana alchichica*. (Drawing by Alexis Manuel de la Torre Zavala)

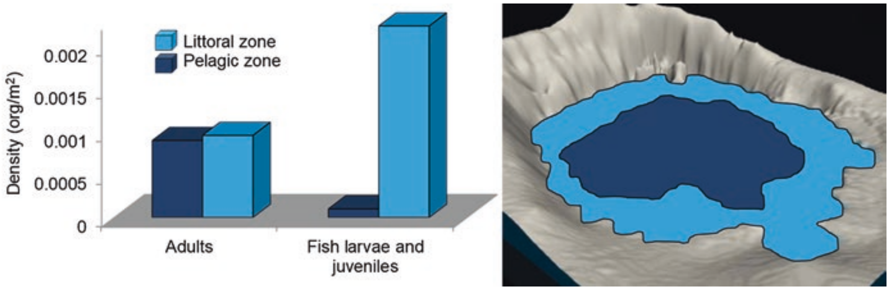

Fig. 15.2 Density and distribution of *P. alchichica* in the littoral and pelagic zones of Lake Alchichica

range found in Lake Alchichica is important to influence *P. alchichica* distribution, the seasonal variations in dissolved oxygen concentration (Woolrich-Piña et al. 2012) seem to play a main role, particularly considering that a deep (below 40 m) anoxic layer develops and persists around six months of the year. Arce et al. (2011) identified this as the principal factor restricting the fish distribution in the lake.

Poblana alchichica is the only zooplanktivorous predator in Lake Alchichica. This fish swims in the shallow, illuminated waters for foraging purposes. Its presence in the pelagic zone is determined by the depth of the photic zone, which reaches between 25 to 40 m, where the illumination conditions are sufficient for efficient foraging (Ciros-Pérez et al. 2015). *Poblana alchichica* has also been observed in deep waters during mixing using echo-sounding techniques.

There is an overlapping distribution in deep waters of the lake between the copepod -*Leptodiaptomus garciai*- and *P. alchichica* during daylight hours (Ciros-Pérez et al. 2015). The overlap suggests that fish can exploit this prey type, and the observed distribution pattern in a dark habitat could enhance their feeding possibilities. Whether this could be explained as a diel vertical migration pattern -DVM- is yet to be elucidated since new data indicate that the vertical distribution of fish does not change during the diel cycle (Arce et al. unpubl.). The decrease of the copepod's abundance during the summer could result from the predatory pressure that *P. alchichica* exerts on this type of prey (Lugo et al. 1999; Ortega-Mayagoitia et al. 2011).

Density values of *P. alchichica* ranged from 0 to 0.0017 org/m^2 (with an average density of 0.0010 ± 0.0007 org/m^2) in the pelagic zone, and from 0.0019 to 0.0044 org/m^2 (0.0032 ± 0.0011 org/m^2) in the perimeter; fish mean density in the basin was 0.0021 ± 0.0015 org/m^2 (Arce et al. 2011; Fig. 15.2). The estimated total abundance of *P. alchichica* was between 16,000 and 21,000 organisms >1 cm in length. Arce et al. (2011) have questioned if these numbers guarantee a healthy and self-sustained population.

Other studies carried out in oligotrophic water bodies showed much higher fish densities. For example, the brown trout -*Salmo trutta*- mean density in Lake Redó, Spain, was 0.0597 org/m^2 (Encina and Rodríguez-Ruiz 2003); the common whitefish *Coregonus lavaretum* density in Lake Paasivesi, Finland, was between 0.026 to

0.053 org/m^2 (Jurvelius et al. 1984); and the density for same species in the Wahnbach reservoir, Germany, was 0.010 to 0.050 org/m^2 (Brenner et al. 1987).

Size class composition of *P. alchichica* differed among the characteristic habitats of Lake Alchichica. In the shallow area between the lake edge and the tufa ring, fish larvae and juveniles (≤36 mm standard length, SL) dominated (≈70% of total abundance). On the contrary, adults (>37 mm SL) dominated (>90%) in the pelagic zone close to the tufa (Flores-Negrete 1998). Unfortunately, the littoral area is continuously being reduced because of declining water levels, thus decreasing habitat availability for the larvae and juveniles of *P. alchichica* to develop.

15.4 Growth and Reproduction

The Alchichica silverside is an iteroparous species. It has two periods of reproduction, one from February to April and the other from July to September, with a spawning peak in March. The egg envelope displays numerous chorionic filaments that adhere to the submerged macrophytes and calcareous tufa deposits (Alcocer et al. 2009). Size at first maturity occurs in individuals of 37 mm SL for males, and of 40 mm SL for females (Flores-Negrete 1998). Maximum recorded fertility is 2423 eggs in a 70 mm SL female (Flores-Negrete 1998).

15.5 Trophic Aspects

Poblana alchichica feeds mainly on benthic macroinvertebrates as chironomid larvae and amphipods (which constitute up to 70% of prey types), and planktonic organisms (accounting for the 30% of the diet) such as the copepod *Leptodiaptomus garciai* (Flores-Negrete 1998). Prey consumption varies according to the seasonal thermal pattern of Lake Alchichica (Flores-Negrete 1998), described as warm monomixis.

During stratification, the stomach contents of *P. alchichica* presented 14 prey types. In general, copepods were the main prey, but their relative abundance varied, increasing their frequency as the fish's size increased. Benthic-related prey types prevailed by number (69.6%) over prey from the plankton realm (28.6%) or even the necton, considering that cannibalized fish were found in the stomach contents (1.8%) (Flores-Negrete 1998).

On the other hand, six prey types were present in the stomach contents of *P. alchichica* during mixing. Chironomid pupae and larvae were the most important prey identified; their numerical contribution increased in larger fish compared to smaller ones. Species characteristic of the benthic habitat predominated (70.4%) over planktonic prey (29.6%).

The diet composition changes as fish grow, affected by morphological changes, particularly the relative increase of the size of mouth and the greater swimming capacity of larger individuals. As fish grows, the intestine's length also increases; the taste organs and the lateral line begin to play an important role in the feeding capabilities of fish at the end of the larval period (Stroband and Dabrowski 1981), producing ontogenetic changes of the feeding habits.

As in the descriptions of the trophic aspects of other atherinopsids (e.g., Gallardo-Cabello 1977; Rauda and García de León 1989), the diversity of prey consumed by smaller *P. alchichica* (feeding mainly on plankton) is lower than the one observed in larger fish (consuming planktonic and benthic organisms, as well as insect larvae and pupae). This differential consumption among size classes is due to the anatomical and ecological niche differences that allow size segregation, reducing competition (Margalef 1983). The trophic plasticity of *P. alchichica* corresponds to a euryphagous organism, capable of taking advantage of the presence of potential prey whose abundance vary according to the seasonal features of the lake.

As in other fish species, the jaw protrusion capacity of *P. alchichica* allows the ingestion of prey by suction, reducing the distance of the predator's approach to its prey (Staab et al. 2012). Furthermore, the mandibular protrusion could also confer another advantage in specific circumstances, such as feeding upon benthic organisms, which constitute the most important prey types of *P. alchichica*.

As mentioned, the hypolimnion (from a depth of 40 m to the bottom) of Lake Alchichica remains anoxic from July or August until late December or early January, when vertical mixing occurs. Anoxia contributes to the regular occurrence of *P. alchichica* in the littoral zone, in contrast to the general behavior of *Chirostoma chapalae*, which lives close to the surface and mid-water of Lake Chapala (Gallardo-Cabello 1977). Furthermore, within the littoral zone, *P. alchichica* is found close to the bottom, in line with the pattern of benthivorous feeding described by Flores-Negrete (1998), which is different from other silversides that are mostly zooplanktivorous.

15.6 Parasites of *Poblana alchichica*

The Alchichica silverside is parasitized by eight helminth parasite species, including two species of trematodes, two cestodes, three nematodes, and one hirudinean. Seven of them are endoparasites, and only one, the hirudinean (leech), is found on the body surface, usually on the fins (Table 15.1). Four studies have documented the helminth parasite fauna of this fish species in the locality to the best of our knowledge. The silverside is infected by two adult parasites and by five larval forms. Four of the larval forms, namely *Posthodiplostomum minimum*, *Tylodelphys* sp., *Eustrongylides* sp., and *Ligula intestinalis*, complete their life cycle when piscivorous birds eat fish.

The first tree species are parasites of ardeids and waterfowl, whereas the tapeworm *L. intestinalis* is exclusively found in crested grebes of the family Podicipedidae. The remaining larval form, the third larval stage of the nematode *Spiroxys* sp., completes its life cycle in turtles or amphibians. Of the seven

Table 15.1 Helminth parasites of *Poblana alchichica* in Lake Alchichica

Parasite	Infection Site	Life-cycle stage	Reference
Trematoda			
Posthodiplostomum minimum (McCallum 1921)	Mesentery	Metacercariae	2, 4
Tylodelphys sp.	Body cavity	Metacercariae	4
Cestoda			
Schizocotyle acheilognati (Yamaguti 1931)	Intestine	Adult	3
Ligula intestinalis (Linnaeus 1758)	Body cavity	Plerocercoid	1, 2, 3, 4
Nematoda			
Rhabdochona canadensis Moravec and Arai, 1971	Intestine	Adult	3, 4
Eustrongylides sp.	Mesentery	Larvae	2
Spiroxys sp.	Mesentery	Larvae	2
Hirudinea			
Myzobdella sp.	Body surface	Adult	3

[1]Pérez-Ponce de León et al. (1992), [2]Pérez-Ponce de León et al. (1996), [3]Flores-Negrete (1998), [4]Moreno-Navarrete and Aguilar-Aguilar (2013)

endoparasite species, two of them (the two species of trematodes) infect the fish via penetration of the larval form (cercariae), released by a mollusk. The remaining five species are trophically transmitted through prey consumption, primarily copepods.

Interestingly, irrespective of the particular physicochemical and ecological conditions and characteristics, no endemic parasites are found in Lake Alchichica. All the parasite species have been previously reported parasitizing other freshwater fish species across central Mexico.

The cestode *Schizocotyle acheilognathi*, the so-called Asian fish tapeworm, in the lake is interesting because this is a co-invasive species in Mexico with an extraordinary ability to adapt to different environmental conditions (Pérez-Ponce de León et al. 2018). The species was first co-introduced in Mexico from China along with the grass carp, *Ctenopharyngodon idella*. Nowadays, the cestode has been found in more than 110 species of freshwater fishes in Mexico, at least in 214 localities all over the country. It is noteworthy that no carps (Cyprinidae) are found in Lake Alchichica; the fact that the tapeworm is present in the lake has to be related to the anthropogenic introduction of other fishes, probably poecilids.

The two species of tapeworms found in the Alchichica silverside, i.e., *S. acheilognathi* and *L. intestinalis* are considered as highly pathogenic parasites that may produce mortalities among host populations, with the Asian fish tapeworm causing severe damages to the intestine of their hosts, whereas the larval form of *L. intestinalis* attains impressive sizes in the body cavity of its intermediate fish host causing extensive systemic pathologies (Choudhury and Cole 2012; Scholz et al. 2012; Woon-Mok et al. 2016; Morlet and Lewis 2019). The transmission of both species of parasites to the fish is via the ingestion of copepods harboring a larval form; however, in *L. intestinalis* the fish act as the second intermediate host because it is an allogenic species with a three-host life cycle, and adults are developed in the intestine of grebes. Instead, *S. acheilognathi* possesses a two-host life cycle and, as an autogenic species, the fish is the definitive host (Fig. 15.3).

Interestingly, *L. intestinalis* was reported in the four studies that have documented the parasite fauna of the silverside (see Table 15.1); it is very commonly found since it has been reported parasitizing up to 95% of the fish (see Flores-Negrete 1998), although in other studies it is not the species reaching the highest prevalence of infection and mean abundance values (see Moreno-Navarrete and

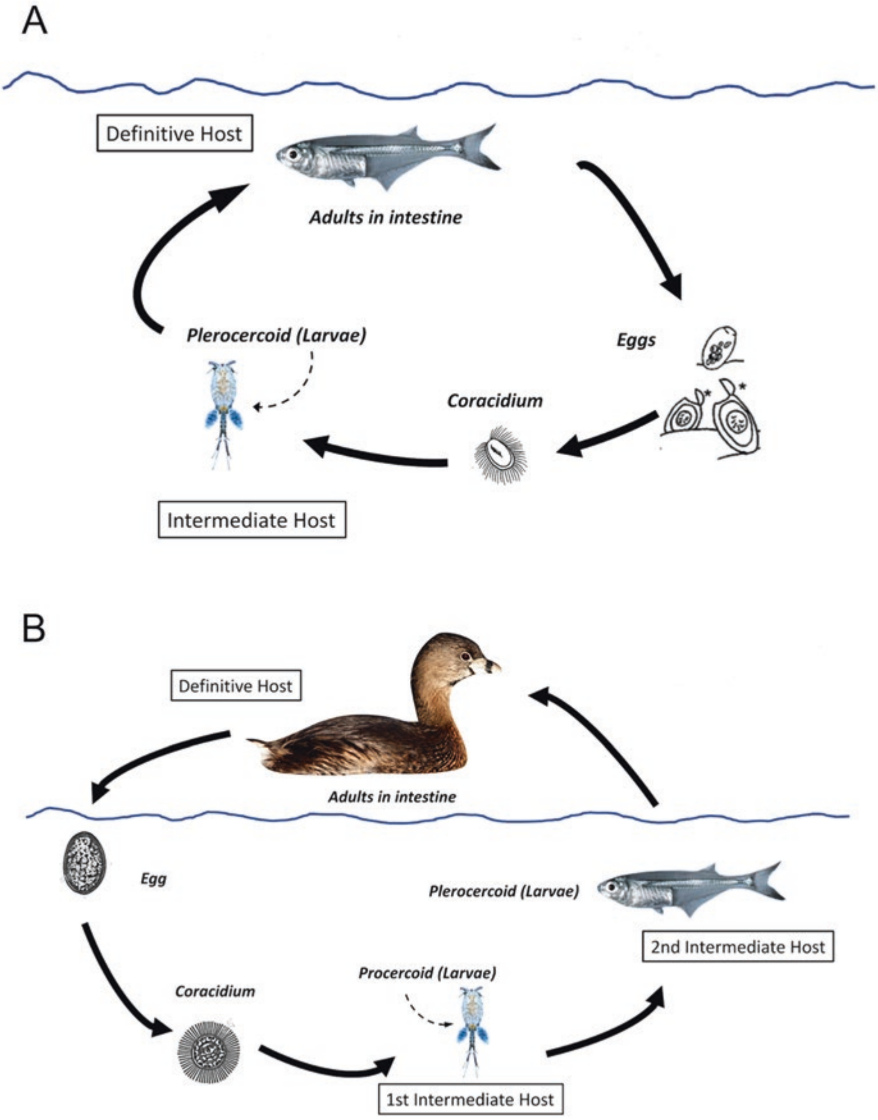

Fig. 15.3 Life cycles of *Schizocotyle acheilognathi* (**a**) and *Ligula intestinalis* (**b**)

Aguilar-Aguilar 2013). This tapeworm is one of the most extensively studied species globally, and it infects mainly freshwater cyprinids, although it has been reported in other fish groups. For instance, in Mexico, this tapeworm has been reported in 14 freshwater fish species belonging to the families Atherinopsidae, Goodeidae, Poeciliidae, and Cyprinidae, mainly distributed in localities across central Mexico. The adult forms have only been reported from the pied-billed greb *Podilymbus podiceps* from Lake Patzcuaro (Pérez-Ponce de León et al. 1992). Because of their large size, plerocercoids of *L. intestinalis* are most likely to produce severe damage to their host, occupying virtually all the body cavity. This species could be regarded as the major threat to the survival of the silverside in Lake Alchichica in terms of their parasite fauna. Some authors noted that the weight of the parasite tissue could be greater than that of the fish tissue (Barus and Prokes 1994). *Ligula intestinalis* exemplifies a case in which parasites cause phenotypic modifications in their hosts, leading to an increased transmission rate and adaptation of the parasite to manipulate the host. Whether or not this is correlated with the selective predation of infected fish by the locality's piscivorous birds is unknown. However, the presence of parasites in the system indicates the dynamic nature of the food web.

15.7 Fishing Technique and Local Consumption

The Alchichica silverside is subject to a local fishery by residents of the area and surrounding communities. The fishery is artisanal and carried out mainly by women who use bedsheets, used as fishing nets, with mesh openings smaller than 1 mm (Fig. 15.4). They capture the fish in the lake's littoral or stromatolite zone, forming groups of fisherwomen, usually three. Two of them carry one end of the bedsheets tied to the ankle to keep it close to the bottom, while the other end is held above the surface. The third person walks in front of the two other fisherwomen carrying a pole with cloth strips tied up at the submerged end of the pole, which "frightens'' and leads the fish to the center of the bedsheet, which ends in a conical shape. It also maintains the arrangement of the net and prevents the escape of fish (Alcocer et al. 2010).

Local people enormously appreciate the silversides for food since they consider *P. alchichica* not as bony as the other *Poblana*. Silversides are prepared after evisceration fried in lard, or in "tamales" grilled on a "comal" within dry corn leaves, seasoned with onion, epazote, chili, and salt.

Fig. 15.4 Artisanal fishery of *P. alchichica*

15.8 Conservation Perspective

The limited distribution of *P. alchichica* places this unique species at risk of extinction due to several anthropic pressures. Local inhabitants use the littoral zone to perform several domestic tasks; detergents and bleaches used to do the laundry are discharged in this zone without control, modifying this critical habitat hence reducing the developmental chances of *P. alchichica*'s larvae and juveniles (Alcocer and Escobar-Briones 2007). Domestic wastewater is being discharged into the lake from nearby houses, and it is highly probable, but not yet evaluated, that pollutants such as pesticides and fertilizers are being supplied into the lake from the surrounding agricultural land as well as petrol from the gas station located in the proximities of the lake.

Local fisherwomen contribute to the risk of extinction of this unique species by overfishing since inadequate nets made from discarded bedsheets are widely used. This efficient fishing gear created by local women has tiny net apertures, allowing the capture of juvenile fish and even larvae. Although there is no information regarding population abundance changes through time, according to the older fishermen, *P. alchichica* population is declining. Captures have been reducing both in number and in fish size.

Over extraction of groundwater for irrigation and water supply to towns and cities is mostly responsible for the lake's desiccation process, although climate change should not be overlooked. Irrigated agriculture is a significant and increasing activity in the basin. Historical aerial photographs reveal a reduction in Lake Alchichica water level. Old high water-level marks are much higher than today's shoreline, causing that a large portion of the tufa deposits, formerly submerged, to be now exposed to sunlight, dry, and deprived of aquatic life (Alcocer and Escobar-Briones 2007). Also, being located at a high altitude (i.e. >2300 masl), the extensive groundwater resources are considered as a potential water source to be transported by gravity to Mexico City (NRC et al. 1995).

Extinction risk is usually correlated with the size of the population and the extension of the distribution range. *P. alchichica* is a species considered at the highest risk of extinction, since its distribution is characterized as *very restricted*. After reviewing the whole set of risk factors such as habitat destruction, unsustainable use, and the presence of parasites, among others, Arce et al. (2011) considered that *P. alchichica* should be changed to the risk category *critically endangered* since it is a species whose distribution area or its population size in the national territory has drastically diminished, putting at risk its biological viability in its natural habitat. This conservation status was finally assessed by the Red List of the IUCN (Gómez-Balandra and Espinosa-Pérez 2019; Lyons et al. 2020).

We urge to put into effect urgent actions to conserve, protect and restore the habitat of *P. alchichica*, such as the reduction of the groundwater over-extraction, implement pollution prevention approaches to decrease the inputs of pesticides and other harmful substances, and a fishing ban in the littoral zone where the reproduction of *P. alchichica* takes place.

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Chapter 16
The Axolotl of Alchichica

**Gabriela Parra-Olea, Rafael Alejandro Calzada-Arciniega,
Víctor H. Jiménez-Arcos, and Omar Hernández-Ordóñez**

16.1 Introduction

The adaptation of amphibians to saline water and the evolutionary processes that lead to it are still poorly understood. The perception that only a few amphibians are tolerant to saline water was generally agreed upon amongst scientists because amphibians are osmotically sensitive due to their highly permeable skin. A recent review (Hopkins and Brodie 2015) showed that 144 amphibian species are tolerant to saline water, from low concentrations up to seawater (35 g/L). Salinity tolerance has evolved repeatedly in amphibians. It occurs in species worldwide; however, only a handful of species evolved into an independent evolutionary unit due to this specialization. Only two amphibian species can constantly inhabit saline waters (Hopkins and Brodie 2015), the Asian frog *Fejervarya cancrivora* and the Mexican salamander *Ambystoma taylori*, the microendemic species inhabiting Lake Alchichica.

Species inhabiting a very narrow geographic distribution are particularly susceptible to any changes in their environment and are extremely vulnerable because their habitats can be lost quickly (Hobohm and Bruchmann 2014). Associated harmful factors to populations' health or permanence over time include habitat loss and modification, pollution, climate change, and the emergence of diseases such as chytridiomycosis. These factors acting alone or synergistically put species with

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G. Parra-Olea (✉) · R. A. Calzada-Arciniega · O. Hernández-Ordóñez
Departamento de Zoología, Instituto de Biología, Universidad Nacional Autónoma de México, Ciudad de México, Mexico
e-mail: gparra@ib.unam.mx; omar.hernandez@ib.unam.mx

V. H. Jiménez-Arcos
Laboratorio de Herpetología Vivario de la FES Iztacala, Universidad Nacional Autónoma de México, Tlalnepantla, Estado de México, Mexico
e-mail: victorhja@iztacala.unam.mx

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restricted distributions, such as most salamanders in Mexico, at great risk of extinction (Vié et al. 2008).

The chytrid fungus *Batrachochytrium dendrobatidis* has been linked to the severe amphibian declines observed worldwide starting in the 1980s. *Batrachochytrium dendrobatidis* affects adult amphibians' keratinized skin, causing an osmotic imbalance that can cause death to the organisms. The emergence of chytridiomycosis caused the population declines and extinction of almost 200 species of amphibians. Chytrids themselves are susceptible to several environmental factors which allow them to grow successfully in the amphibian host, such as pH, temperature, salinity, and oxygen concentration, among others (Gleason et al. 2008). Several authors (Chukanhom and Hatai 2004; Gleason et al. 2006; White 2006) have suggested that chytrids cannot grow in saline estuaries; chytrids spores die after prolonged exposure to high levels of salinity above 5%. However, there are reports of salt-tolerant species being positive for *B. dendrobatidis* (Groner and Relyea 2010; Tatarian and Tatarian 2010; Sztatecsny and Glaser 2011). More than 100 species of amphibians have tested positive for the *B. dendrobatidis* in Mexico, including *A. velasci* from Quechulac, one of the freshwater crater lakes near Lake Alchichica (Frías-Álvarez et al. 2008; Basanta et al. 2020).

16.2 Amphibians from Lake Alchichica and Nearby Zones

The amphibian fauna of Lake Alchichica and nearby zones (>6 km ratio) is composed of nine species (three salamanders and six frogs). Camarillo (1998) published the first species checklist of amphibians from the crater lakes of the Cuenca Oriental, where he reported two species of *Ambystoma* (*A. taylori* and *A. velasci*) and one Leopard Frog (*Rana spectabilis*). Cuellar et al. (1996) described a microendemic species of frog from Lake La Preciosa, also known as "Las Minas", *Rana chichicuahutla* belonging to the *Rana berlandieri* species group. Lake La Preciosa is 3.5 km S from Lake Alchichica. Two more anurans have been collected in the vicinity of Lake Alchichica, the frogs *Spea multiplicata* and *Incilius occidentalis* (GBIF 2021). In 2018, two coauthors (RACA and VHJA) collected a specimen of *Pseudoeurycea* sp. (Plethodontidae) in nearby xerophytic scrub. Finally, according to the IUCN Red List distribution maps, two tree frogs (Hylidae: *Hyla eximia* and *H. plicata*) could potentially occur in this area (IUCN 2020b, c). Most of the amphibian species in Lake Alchichica and nearby zones have a wide distribution along the Trans-Mexican Volcanic Belt and Mexican Plateau (Frost 2021). Only *A. taylori, R. chichicuahutla,* and the undescribed species of *Pseudoeurycea* are endemic to a very small area within the Cuenca Oriental.

Even though amphibian's diversity in the Cuenca Oriental is low, even if compared with other arid regions of Mexico, it brings a unique opportunity to develop amphibian studies from ecological and evolutionary perspectives, from paedomorphic salamanders inhabiting saline waters to tropical salamanders and anurans in arid environments. Human activities threaten the survival of their populations or the entire species; therefore, we consider that it is necessary to implement conservation and restoration actions and develop better practices in using natural resources by local communities.

16.3 Aquatic Salamanders of the Genus *Ambystoma*

> *Dr. Hobart Smith and I visited Lake Alchichica in 1932, but because of the salinity of the water, we made no effort to collect salamanders, presuming that they could not occur* (Taylor 1943).

Professor Edward Harrison Taylor and Hobart Muir Smith, founders of the modern era of herpetology in Mexico, met each other in 1932. That year, they visited Lake Alchichica. However, being aware of the lake's salinity, they did not make any effort to try to collect amphibians in the place (Taylor 1943). Years later, E.H. Taylor received two ambystomatid larvae and one transformed adult from Mr. Dyfrig McH Forbes. The larvae were from Lake Alchichica, and the transformed adult was found outside of the water, a few hundred yards from the lake. In 1940, Taylor and Smith revisited Lake Alchichica and collected two salamander larvae found dead on the shore. Subsequently, in 1941, Taylor collected more larvae from the rim of Lake Alchichica in the shallow waters, where, as he mentions, probably the salamanders came from the deeper water to feed (Taylor 1943). The neotenic larvae were used as paratypes, while the transformed adult was the holotype of *Ambystoma subsalsum,* a new species described by Taylor in 1943.

Forty years later, Ronald A. Brandon suspected that the larvae from the lake and the transformed individual (paratypes and holotype) in which Taylor based the description of *A. subsalsum* were not conspecific. Brandon looked over the larvae collected by R.G. Altig from Lake Alchichica and transformed and larvae from the lake's vicinity and other localities in Tlaxcala and Hidalgo. Brandon and colleagues (Brandon et al. 1982) concluded that the neotenic salamanders from lake Alchichica including immatures and neotenic adults used by Taylor as paratypes of *Ambystoma subsalsum,* represent a different species from the transformed individuals collected outside of Alchichica (including the holotype of *A. subsalsum*). Considering that, they described a new species named *Ambystoma taylori* in honor of Professor Edward H. Taylor, a neotenic species, endemic to Lake Alchichica. They also concluded that the revised specimens from the plains in vicinities of Alchichica and those from Tlaxcala and Hidalgo agreed with the holotype of *Ambystoma subsalsum*. However, all the reviewed populations except the one from Lake Alchichica were then named *Ambystoma tigrinum* (subspecies *A. t. velasci*), given *Ambystoma tigrinum velasci* was described before *A. subsalsum*, the latter became a synonym of *A. t. velasci*, which posteriorly was recognized as a species (*Ambystoma velasci*) (Shaffer and McKnight 1996).

Webb resurrected the name *Ambystoma subsalsum* in 2004 based on color pattern and assigned it to some scattered populations in Puebla, Durango, Zacatecas, San Luis Potosí, and Aguascalientes, while also suggested that some populations from Nuevo León and Guanajuato states might belong to this species. Even though *Ambystoma velasci* is a species complex, this resurrection has not been considered for most of the literature because of the highly variable color variation in the complex and the absence of molecular data supporting this decision. Nevertheless, *Ambystoma subsalsum* has been occasionally mentioned in publications as state lists. We consider *Ambystoma taylori* a neotenic species distributed exclusively in Lake Alchichica and all other Ambystomatid salamanders from the Cuenca Oriental, including the other crater lakes, as *Ambystoma velasci*.

16.3.1 **Ambystoma taylori** ***Brandon, Maruska, and Rumph, 1982***

Ambystoma taylori (Fig. 16.1) is a relatively large paedomorphic salamander closely related to the populations of *A. velasci* in the eastern Mexican plateau (Shaffer and McKnight 1996) and other species such as *A. mexicanum*, *A. dumerilii,* and *A. ordinarium* (Shaffer 1984; Weisrock et al. 2006). Individuals of >70 mm are considered mature. Little is known about the species, including any ontogenetic change or differences due to sexual dimorphism. To obtain additional data regarding the sexual size dimorphism in recent surveys, digital calipers were used to measure the distance from the tip of the snout to the posterior angle of the vent (SVL), tail length (TL), head width (HW), and the weight of 20 females and 22 males, all of them mature organisms. There are significant differences between males and females in the SVL, with females being larger than males (Table 16.1). The selection in fecundity could explain the differences in SVL, where females could mature many eggs, increasing their reproductive success. The largest SVL size (119.27 mm) is slightly larger than the 115 mm reported previously for the species (Brandon et al. 1982). The ground color of the species is described from golden to canary yellow to subdued yellowish tan, and in the dorsum and the sides of all the body, it has dark maroon spots. The species do not usually transform in metamorphosed adults; however, some have transformed in captivity (Brandon et al. 1982).

A recent study using DNA data from *Ambystoma* populations present in crater lakes Alchichica, Quechulac, La Preciosa, Atexcac, and Tecuitlapa showed that the population of *A. taylori* is a closed genetic deme that does not have immigrants from the surrounding lakes. However, the genetic diversity found in the species indicates that the population is large and that it has not experienced drastic reductions (Percino-Daniel et al. 2016). The above is likely the result of the particular chemical conditions found in Lake Alchichica, such as the salinity. Perhaps the organisms from other nearby lakes may not tolerate such salinity. Similarly, the high adaptation of *A. taylori* to Alchichica conditions could have been fundamental for its speciation.

Fig. 16.1 Top: Juvenile of *A. taylori* recorded in the stromatolite's cavities at 27 meters depth. (Photo taken by Luis A. Martínez). Bottom: Two adult specimens of *A. taylori* showing color variation. (Photo taken by Victor H. Jimenez-Arcos)

Table 16.1 Morphometric data. Average values ±1 standard error and the minimum and maximum in parentheses. SVL (snout vent length). With these data and using the Mann-Whitney U because the data do not meet the normality test females are significantly larger in SVL (U = 129.00; P = 0.02)

	SVL	Tail length	Head width	Weight
Females (*n* = 20)	89.65 ± 3.77 (63.21–119.27)	60.82 ± 3.88 (34.79–88.92)	23.80 ± 1.25 (17.04–33.93)	30.66 ± 5.05 (10.62–80.67)
Males (*n* = 22)	80.90 ± 3.03 (60.8–118.67)	56.05 ± 2.83 (39.63–89.80)	21.07 ± 0.75 (15.98–29.99)	19.82 ± 2.59 (8.70–56.51)

16.3.2 Ambystoma velasci *Dugès, 1888*

Ambystoma velasci is a transforming species of *Ambystoma* and one of the most widely distributed amphibians in Mexico. It is endemic to the country and occurs from the Sierra Madre Occidental in Chihuahua's northern state through the Central Plateau, The Sierra Madre Oriental, and the southernmost part of the Trans Mexican Volcanic Belt in the state of Veracruz. *Ambystoma velasci* is a large species of a facultative paedomorphic salamander. The paedomorphic adults' range in size between 85 and 106 mm SVL, with the metamorphosed organisms being smaller (Ramírez-Bautista et al. 2009). The aquatic larvae and the paedomorphic adults can be yellow, golden-yellow brown, brown-olive, or dark brown with or without small black or brown dots in the body, while metamorphosed adults could be from light brown to black in the background with large cream blotches in the body, head, and tail. Also, some individuals are dark brown in the background with dots or blotches cream or dark brown all over the body. Along with its distribution, the species inhabit different types of vegetation such as temperate forests (pine and oak forests), grasslands, and xerophytic scrub (IUCN 2020d; GBIF 2021). Unlike other *Ambystoma*, *A. velasci* dwells in different kinds of water bodies, small mountain streams, lakes, dams, ponds, puddles, marshes, and artificial water bodies used to store water which has allowed them to survive in highly transformed landscapes (Contreras-Calvario et al. 2021). The species is listed as Least Concern by the IUCN Red List (IUCN 2020d). However, it is included in the Mexican Norm of species at risk under the category of special protection (Pr, Protección Especial in Spanish; SEMARNAT 2019).

16.4 *Ambystoma velasci* in the Cuenca Oriental

The populations of *Ambystoma velasci* in the Cuenca Oriental correspond to the southeastern portion of the distribution of the species where scarce records are known (IUCN 2020d; Contreras-Calvario et al. 2021). The low availability of water in the basin, which is an arid region (see Chap. 6, meteorological regime and local climate), restricts the presence of amphibians to scarce water bodies. However, *Ambystoma velasci* is known from various sites of the Cuenca Oriental, where it has been recorded at different stages (eggs, juveniles, gilled, and metamorphosed adults). Aquatic individuals have been collected or observed in the Lake Totolcingo and Lakes Quechulac, La Preciosa, Atexcac, Tecuitlapa and Aljojuca, and other localities near Lake Alchichica (Brandon et al. 1982; Arriaga Cabrera et al. 2000; Percino-Daniel et al. 2016).

The characteristics of the water bodies used by the species in the Cuenca Oriental differ drastically from each other, from shallow water bodies as Totolcingo to dug wells, irrigation systems, and deep crater lakes. The maximum salinity recorded for a waterbody used by the region's species is Lake Atexcac with 7.4 g/L. Transformed adults have been recorded about a few hundred yards from Lake Alchichica, as described by Taylor (1943) and from Rancho San Antonio and Rancho el Riego, 6 km N and 5 km E from Lake Alchichica, respectively (Brandon et al. 1982). Particularly in the Cuenca Oriental, transformed adults are dark lead color with cream spots (see Chap. 24, Alchichica: traditions, myths, and legends), and the paedomorphic and larva are yellow gold with brown dots (Brandon et al. 1982).

Molecular data has shown that this taxon is a polytypic group where some populations of *Ambystoma velasci* are highly distinctive from each other, in most cases being more closely related to other species than to each other (Shaffer and McKnight 1996, Weisrock et al. 2006; Recuero et al. 2010; Everson et al. 2021). *Ambystoma* populations from the Cuenca Oriental except Lake Alchichica are supposedly *A. velasci*. Molecular data (Percino-Daniel et al. 2016) showed that the salamander population from saline Lake Atexcac is also a closed genetic deme without gene flow from the other lakes. On the other hand, populations from the freshwater lakes Quechulac, La Preciosa, and Tecuitlapa have continuous gene flow amongst them. Several molecular markers (mitochondrial and nuclear genes) and modern techniques such as next-generation sequencing have been used trying to elucidate the taxonomy and phylogenetic structure of *A. velasci* (Weisrock et al. 2006; Recuero et al. 2010; Everson et al. 2021). All of them show the same lack of monophyly for the taxon, resulting from its recent diversification along the Trans-Mexican Volcanic Belt.

16.5 Conservation of *Ambystoma* Species in the Cuenca Oriental

Both, *A. velasci* and *A. taylori*, are included in the Mexican Norm of species at risk under the category of special protection (Pr, Protección Especial in Spanish; SEMARNAT 2019) (see Chap. 21, conservation actions). Species that are under special protection are considered within this category because factors are threatening their viability or the survival of some of their populations. In contrast, in the IUCN Red List *A. velasci* is listed as Least Concern (IUCN 2020d), while *A. taylori* is evaluated as critically endangered (IUCN 2015).

The ecological data essential to estimate population trends obtained with systematic surveys have not been performed for *Ambystoma taylori*, as with many other salamanders in Mexico. However, field observations during surveys in the lake from 1940 and 1980 bring insights into the population status and behavior in the better conservation conditions in which the lake and the region were at that time. Taylor tells this scene during his surveys in Alchichica "could be collected at night (individuals of *A. taylori*) when they came to the surface and seemingly fed at the edge of the lake. They could be seen in quantity with the light of a gas lantern" (Brandon et al. 1982). Ronn G. Altig mentioned that in 1970 the salamanders were common among the bottom vegetation of a shoreline shelf about 0.5 m deep. A bit later, Brandon, in 1980, found that the salamanders were very common to see during night surveys in shallow pools among rocky outcrops at 6 to 10 meters offshore, just before the lake plunged. A first deeper survey at night with the use of scuba diving equipment was done in July 1981. In that survey, some salamanders were seen at 4 to 5 meters, and many as 20 were seen at 12 m depth.

Regarding the populations of *Ambystoma velasci* outside of the crater lakes, it is known that the species has been exploited for human consumption, specifically in Lake Totolcingo. Despite its large size, from the last decades, the capture of specimens has been depleted due to the lake's desiccation (Arriaga Cabrera et al. 2000). Furthermore, the land-use change to agriculture and other human activities potentially restricted the species to the largest water bodies and limited transformed individuals' movements.

The potential presence of *B. dendrobatidis* parasitizing *Ambystoma* was investigated in samples of *A. taylori* (Lake Alchichica) and *A. velasci* (Lake Atexcac). Real-time PCR investigated the current and historical *B. dendrobatidis* prevalence and infection load in *A. taylori* and *A. velasci*. All our samples for *A. taylori* and *A. velasci* came out negative for *B. dendrobatidis*, probably due to the combined effects of the environmental conditions (i.e., salinity) found in the lakes are acting as a refuge as it has been proposed for other species (Stockwell et al. 2015) or simply that these two populations are not susceptible to the infection by *B. dendrobatidis*. We did not test the frog species inhabitant of Cuenca de Oriental for the presence of *B. dendrobatidis*. However, there are reports of all of them except *R. chichicuahutla* tested positive for *B. dendrobatidis* in other regions of the country (Frías-Álvarez et al. 2008; Cortes-Garcia 2014; García-Feria et al. 2017), so we know they are either susceptible to the infection or carrier of the pathogen. Although *B. dendrobatidis*' presence was not found in Lake Alchichica and Atexcac, monitoring of the presence of pathogens in the species of the Cuenca Oriental should be maintained.

16.6 Other Amphibians of the Oriental Basin

16.6.1 Incilius occidentalis *(Camerano, 1879)*

Incilius occidentalis is a robust species of medium size toad that could reach 65 mm SVL. It has well-developed parotoid glands and cranial crests. The dorsum's coloration is variable from grey to brown and has two paravertebral bands surrounded by green or brown blotches. Its ventral surface is white or cream with dark blotches (Ramírez-Bautista et al. 2009). This toad is endemic to Mexico. Its distribution comprises large regions of the north, center, and south of the country. It inhabits temperate and xerophytic vegetations and wetlands. This species could be seen more often at night near water bodies in natural or modified environments. In the Cuenca Oriental, it has been recorded near Lake Alchichica, and most of the Cuenca Oriental is considered within the distribution range proposed by the IUCN Red List

(IUCN 2020a). Regarding its conservation status, the species is not considered under threat by the IUCN, and it is not in the Mexican Official Norm for species at risk (SEMARNAT 2019).

16.6.2 Hyla eximia *Baird, 1854*

A small species of frog of about 32.5 mm SVL. This species has small forelimbs and hindlimbs with small adhesive discs. In the dorsum, its coloration is light green, but some individuals are dark green or brown olive. Usually, the dorsum has many blotches of different sizes that could be arranged longitudinally. A dark band extends laterally from the tip of the snout through the nostril, eyes, and tympanum to the side of the body (Ramírez-Bautista et al. 2014; Hernández-Salinas et al. 2018). The species is endemic to Mexico and is distributed in the Sierra Madre Oriental, the Central Plateau, and the Trans-Mexican Volcanic Belt. The species uses distinct habitats such as temperate forests, grasslands, xerophytic scrub, and wetlands. The region of Cuenca Oriental is within the proposed distribution of the species by the IUCN (2020c); however, they have not been collected in Lake Alchichica (GBIF 2021). The species has been evaluated as Least Concern by the IUCN Red List (IUCN 2020c), and it is not present in the Mexican Official Norm of species at risk (SEMARNAT 2019).

16.6.3 Hyla plicata *Brocchi, 1877*

This species is a small frog very similar to *Hyla eximia*; however, this species reaches 47 mm of SVL. Their hindlimbs and forelimbs are small but more robust than *H. eximia*. Also, his adhesive disks are small compared with other hylid frogs. The dorsum color could be light or dark green. Some individuals could present dark blotches, in general, less conspicuous than in *H. eximia* but most commonly forming a dorsolateral band. A dark brown band extends from the tip to the snout to the groin (Ramírez-Bautista et al. 2009; Ramírez-Bautista et al. 2014). This frog is endemic to Mexico and is distributed in the Trans-Mexican Volcanic Belt and the Sierra Madre Oriental (Ramírez-Bautista et al. 2009). This species' habitat is restricted to temperate forests where it can be found in the woodland or associated with small ponds or streams. Its estimated distribution area extends throughout the Cuenca Oriental; however, there are no museum records from the region (IUCN 2020b; GBIF 2021). The species is listed as Least Concern by the IUCN Red List (IUCNb 2020b). However, it has been included in the Mexican Official Norm of species at risk as a threatened species (Amenazada in Spanish; SEMARNAT, 2019).

16.6.4 Rana chichicuahutla *Cuellar, Méndez-De La Cruz, and Villagrán-Santa Cruz, 1996*

This frog could be considered a large-sized species since the only known female reaches 86 mm of SVL (Cuellar et al. 1996). This frog species is lime-green on the dorsal surface, having dorsal spots with smooth borders and evident yellow-green halos. Different from other leopard frogs, the skin of its back has few tubercles. A distinct character is their light brown dorsolateral folds raised prominently (Cuellar et al. 1996). The distribution of the species is restricted to the state of Puebla, where it is only known from Lake La Preciosa and its surrounding shore located 3.5 km S from Lake Alchichica in the Cuenca Oriental. The species is not included in the Mexican Official Norm of species at risk (SEMARNAT 2019). However, the frog has been evaluated as a Critically Endangered species by the IUCN Red List mainly because of its small distribution and the deterioration of the quality of the habitat due to human activities as agricultural development, which also caused a decrease in the water level in the lake in the last decades (IUCN 2020f).

16.6.5 Rana spectabilis *Hillis and Frost, 1985*

A medium-sized frog, smaller than 70 mm of SVL. The color of the species could be from metallic green to green-yellow in the dorsum. The blotches in the dorsum could be brown or copper and are surrounded by dark brown. The ventral surface is pale yellow or cream with grey mottling (Ramírez-Bautista et al. 2014). The species is endemic to Mexico and is well distributed from the Central Plateau and the Trans-Mexican Volcanic Belt and through the interior highlands of the Sierra from Hidalgo to the Central Valleys of Oaxaca (IUCN 2020e). The species uses diverse vegetation types such as temperate forests, tropical deciduous forests, and mesquite grasslands within its distribution. While the Cuenca Oriental is within the estimated distribution area of the IUCN, the only known records from the Cuenca Oriental correspond to specimens collected in 1979 from Lake Quechulac. These specimens collected before *R. chichicuahutla* was described were identified as *Rana spectabilis*, however, there is an absence of other records in the region (*e.g.*, within a 30 km diameter; Cuellar et al. 1996; GBIF 2020). We highlight the need for a taxonomic revision of these specimens to confirm their presence in the region. The species is considered as Least Concern by the IUCN Red List (IUCN 2020e) and is not present in the Mexican Official Norm of species at risk (SEMARNAT 2019).

16.6.6 **Spea multiplicata** ***(Cope, 1863)***

This toad reaches 58 mm of SVL. It could be green-greyish or brown with multiple obscure blotches and tubercles in the dorsum. The color of the ventral surface is cream or grey. Forelimbs and hindlimbs are short and robust. It has a conspicuous elongate inner black metatarsal tubercle in the hindlimbs (Ramírez-Bautista et al. 2014). Its distribution comprises the central south of the United States and the Chihuahuan desert, the central Plateau, and the Trans-Mexican Volcanic Belt (Santos-Barrera et al. 2010). The species inhabits temperate forests and xerophytic scrubs. Particularly in the Cuenca Oriental, the species has been recorded in grasslands and farming lands (Castañeda-Hernández, 2009). Also, this species' specimens have been collected from 5 km west of Lake Alchichica (GBIF 2021). Regarding its conservation status, the species is considered as Least Concern by the IUCN Red List (Santos-Barrera et al. 2010) and is not present in the Mexican Official Norm of species at risk (SEMARNAT 2019).

16.6.7 **Pseudoeurycea** ***sp.***

Specimens of an undescribed species of the genus *Pseudoeurycea* were collected by VHJA and RACA in 2018. *Pseudoeurycea* sp. is a large salamander compared with other species of the genus *Pseudoeurycea*. A phylogenetic analysis locates this species within the *Pseudoeurycea gadovii* species group (unpublished data; Parra-Olea 2002). Further analyses are needed to confirm the molecular distinctiveness and a latter formal description to name this species. This salamander has been recorded beneath rocks in xerophytic scrub vegetation. The presence of a plethodontid salamander within this region is a remarkable record not only for the genus but also for the tropical plethodontids (Bolitoglossini) which ecological requirements, especially of humidity, restrict the distribution of almost all of the known species to less extreme environments as a temperate forest, cloud forest, and tropical forest. This population's conservation status is critical due to the modification of the landscape by human activities in the area where it has been recorded.

16.7 Discussion

16.7.1 Amphibians of the Cuenca Oriental

The Cuenca Oriental is a large (~5000 km^2), high altitude (2300–2500 m a.s.l. at the basement), endorheic basin. A relatively low number of species occur in this large area, not surprising given the meager precipitation and the surrounding xerophytic scrub vegetation. Published molecular data show that all of these *Ambystoma* populations belong to a closely related group of species hard to differentiate molecularly but with little or no migration or genetic mixing between the two saline lakes (Alchichica and Atexcac), nor between the saline and the freshwater lakes (Quechulac, La Preciosa, Tecuitlapa; Percino-Daniel et al. 2016). Differently, there is genetic mixing between the three freshwater lakes. This observed pattern results from the relative recency of the evolutionary radiation that gave rise to all species of *Ambystoma* along the Trans-Mexican Volcanic Belt (Shaffer and McKnight 1996; Weisrock et al. 2006).

Rana chichicuahutla is known only from two specimens that have gone missing. During our first prospective field trip to Lake Alchichica, we conducted a night survey (between 19:00 and 21:00 hrs) around the shoreline of Lake La Preciosa to collect individuals, but we could not find any individuals. This species requires special attention, and research must be done to investigate their natural history, conservation status, and phylogenetic relationships. *Pseudoeurycea* sp. extends the ecological niche of the tropical salamanders. This highlights the plasticity of the genus *Pseudoeurycea,* which has enabled species within it to adapt from almost sea level to above 4000 m. Ecological and physiological studies, which have been rare until now in the plethodontids, are needed to investigate the sensitivity of this population to an imminent increase of temperature caused by climate change.

Spea multiplicata and *Incilius occidentalis* commonly occur in a wide range of arid and semi-arid habitat types as long as breeding pools exist. These two species are of the least concern due to their extensive distribution in Mexico, and they seem to be quite abundant in the rainy season. *Hyla eximia* and *Hyla plicata* in the Cuenca Oriental might occur in the coniferous forests found at higher elevations in the basin boundaries.

16.7.2 Amphibian Declines, and **Ambystoma taylori**

There has been a general decline in amphibians worldwide (Houlahan et al. 2000). The ultimate causes of this decline are unknown, although in many cases, the proximate causes responsible for the local extinction of the species are usually known (Blaustein and Wake 1990; Wake 1991). In the case of species of the genus *Ambystoma*, it is known that overexploitation for commercial purposes or local consumption, coupled with contamination, fragmentation, and transformation of the landscape due to the intensification of anthropogenic activities, has had negative impacts on dispersal, genetic flow, and the persistence of wildlife populations and has led to the majority of Ambystomatidae species being in some category of extinction risk.

According to the initial studies of *A. taylori* in 1980 by Brandon and colleagues, this species seemed to be abundant at the time. However, by 1986 the abundance had started to decrease as reported by Calderón and Rodríguez (1986). According to these authors, the place's inhabitants indicated that the abundance of salamanders had decreased. However, they could still be observed at night, especially in the rainy season from May to August. Even though *Ambystoma taylori* is still present in the lake and seems abundant at certain depths (25 m), some population changes are evident, even compared to the 2013 surveys. In 2013 we found individuals at 12 m, while in 2020 and 2021 our surveys reported a single dead organism at 20 m depth and individuals started to abound at 25 meters and deeper. Surveys in 2013 and 2020 were performed at the end of the warm, rainy season (September and October), while the 2021 survey was performed at the end of the cold season (March). In all of the surveys, there were no organisms close to the surface at night. It is important the establishment of a long-term program to monitor and evaluate the demographic patterns along the seasons as well as to identify the factors that are generating the changes in the vertical and horizontal distribution of the population.

16.7.3 Chytridiomycosis

Chytridiomycosis has been recognized as one of the causative agents of many amphibian populations decline worldwide. A cross-reference of the literature for amphibian species with tolerance to saline water and the global database for *B. dendrobatidis* (Bd-maps.net Olson et al. 2013) showed that out of the 144 salt-tolerant species reported by Hopkins and Brodie (2015), over 40 of them have tested positive for *B. dendrobatidis*. These species range in their tolerance to salinity from as low as 1 g/L in *Triturus marmoratus*, to as high as 35 and 39 g/L in *Pelobates cultripes* and *Rana berlandieri* respectively, with *A. taylori* falling in the lower end with 8.3 g/L found in Lake Alchichica. Most of the *B. dendrobatidis* -positive saline tolerant species occur in different localities ranging from freshwater to saline water. It is unknown the salinity conditions for the localities where they tested positive for *B. dendrobatidis*. However, one confirmed study shows the presence of *B. dendrobatidis* in populations of *Bufo calamita* in saline water (Bramwell 2011). In Bramwell's study, even though *B. dendrobatidis* is present in saline water, there is a clear *B. dendrobatidis* infection pattern and salinity where frogs from saline ponds exhibited weaker infections compared to those from freshwater ponds (Bramwell 2011).

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Chapter 17
The Deep Benthic Zone

Javier Alcocer, Elva Escobar, Luis A. Oseguera,
and María del Carmen Hernández

17.1 Introduction

Deep tropical lakes are warm monomictic, displaying a single predictable annual period of deep mixing or complete overturn, circulating in association with the hemispheric winter (Lewis 1983). The tropics' mixing season may be as short as a month or six weeks, which implies an extended stratification period (Lewis 1996). A lengthy stratification period coupled with comparatively hypolimnetic higher temperatures has important limnological implications. Higher temperatures hold less dissolved oxygen, increase the velocity at which sediments reach a negative redox potential, and, together with the accelerated bacterial metabolic rates, lead to oxygen depletion, regardless of the tropical lake's trophic state.

During stratification, when oxygen cannot be renewed either by photosynthesis or by mixing, the biochemical oxygen demand of the deep waters leads to oxygen depletion and even anoxia (Lewis 1987). Soon after the onset of the stratification, the hypolimnion becomes anoxic and remains so long as the lake's stratification persists.

J. Alcocer (✉) · L. A. Oseguera
Grupo de Investigación en Limnología Tropical, FES Iztacala,
Tlalnepantla, Estado de México, Mexico
e-mail: jalcocer@unam.mx; loseguera@unam.mx

E. Escobar
Unidad Académica de Ecología y Biodiversidad Acuática, Instituto de Ciencias del Mar y
Limnología. Universidad Nacional Autónoma de México., Ciudad de México, Mexico
e-mail: escobri@cmarl.unam.mx

M. d. C. Hernández
Programa de Posgrado en Ciencias del Mar y Limnología, Universidad Nacional Autónoma
de México, Ciudad de México, Mexico

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Benthic communities have an essential role in the structure and function of aquatic ecosystems, e.g., through connecting lake habitats (benthic-pelagic coupling) by exchanging energy, mass, and nutrients. However, anoxia could limit or prevent this interchange, particularly in the tropics, where, as mentioned, anoxia frequently is long-lasting. On the contrary, completely overturn of the water column brings back favorable conditions to the deep benthos opening an ecological niche with no or almost no competition or predation (and frequently with abundant fresh food supply coming from the winter diatom bloom) to those organisms able to take advantage of this newly available habitat.

The benthic community's biomass has been identified as an essential factor in understanding seasonal patterns and energy fluxes in food webs (Rigler and Downing 1984). The deep zone of a lake depends on the contributions of the littoral and pelagic zones and, the greater the depth, the organic matter that reaches the bottom is less in quantity and quality (Prat and Rieradevall 1998). The exported organic matter increases the food supply but decreases the dissolved oxygen concentration (Jørgensen and Revsbech 1985). Due to low oxygen availability and habitat homogeneity (Cleto-Filho and Arcifa 2006) the deep benthic community has been defined as simple.

17.2 Deepwater Physical and Chemical Properties

While most deepwater environmental characteristics remain quite similar along the year, for example, water temperature (14.5 ± 0.1 °C, see Chap. 7, physicochemical characteristics, Fig. 7.8), pH (9.17 ± 0.14), and electrical conductivity (13.6 ± 0.7 mS/cm), others change widely (Acosta et al. 2017; Hernández-Fonseca et al. 2013).

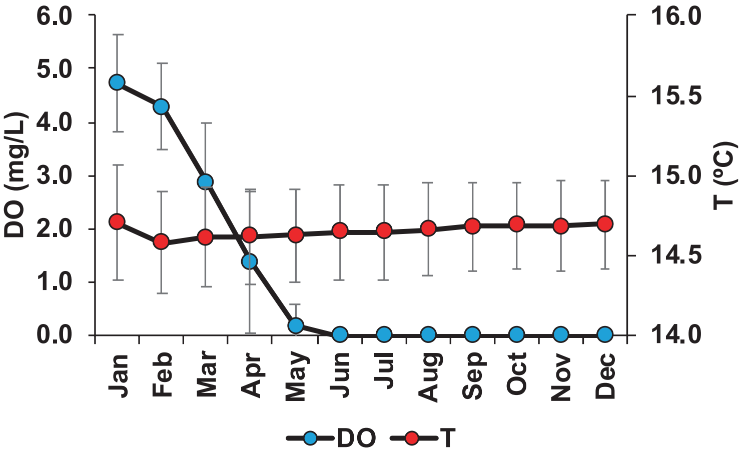

Fig. 17.1 Dissolved oxygen (DO) concentration and temperature (T) (average ± standard deviation) in the bottom (deepest 5 m) water stratum of Lake Alchichica

Essential is the dissolved oxygen concentration. The lake bottom remains oxygenated while mixing, while the deep anoxia starts soon after the lake stratifies and remains so along the stratification season (Fig. 17.1, see Chap. 7, physicochemical characteristics).

Another factor that varies with stratification is hydrogen sulfide (H_2S). During circulation and at the onset of stratification, H_2S is absent. However, soon after the deep benthic layer becomes anoxic, the concentration of H_2S increases progressively from 0.14 mg/L in June until reaching its maximum concentration in December with 4.28 mg/L.

In addition to the lower DO solubility in the relatively higher temperatures of tropical lakes, Adame et al. (2008) mentions the winter diatom bloom deposition largely explained the early anoxia found in Lake Alchichica deep waters. Higher temperatures foster remineralization of organic matter in bottom waters and sediments, leading to prompt deep benthic anoxia. Álvarez-Sánchez et al. (2015) found the bacterial density at the sediments ranged between 5.32 and 16.71×10^9 cell/cm^3 of sediment, while biomass fluctuated between 57 and 187 μg C/cm^3 of sediment. The highest density and biomass were found during the mixing period -along with the diatom bloom sedimentation- and diminished during the stratification.

17.3 Deep Sediment Characteristics

Differently from the littoral sediments, deep surface sediments of Lake Alchichica are quite homogeneous (Hernández et al. 2015), clayey silts (sands 4%, silts 72%, clays 23%), with a high content of organic matter (35 ± 3%, 29–42%) and carbonates (14 ± 4%, 6–25%). Chl-a concentrations in the surface sediment ranged from 144 to 492 mg/m^2 with an average value of 271 ± 71 mg/m^2.

Chl-a concentrations in the surface sediment over 5 years (2003–2007) remained similar ($p > 0.05$); however, within each annual cycle, the concentration during the early stratification, just after the end of the winter diatom bloom, was significantly higher ($p < 0.05$) compared with the rest of the year (Alcocer et al. 2012, 2014).

Particulate organic carbon (POC) concentration found in the surface sediments averaged 36.3 ± 18.0 g/m^2 with a range of 17.1 to 86.5 g/m^2 (Alcocer et al. 2012) or 25 ± 12 mg/g d.w. with a range of 12 and 60 mg/g d.w. (Alcocer et al. 2014). The POC concentration in the deep, surface sediments of Lake Alchichica is high compared with other aquatic systems of a similar or even greater (meso and eutrophic) trophic condition than oligotrophic Lake Alchichica. The dominance of large size phytoplankton (e.g., *Cyclotella alchichicana*) favors its exportation below the thermocline (Adame et al. 2008; Ardiles et al. 2012) and not recycling in the euphotic zone as in most oligotrophic aquatic bodies dominated by small phytoplankton, which explains the larger POC concentrations (Alcocer et al. 2012).

The temporal POC dynamics displayed a larger accumulation during the early stratification period, resulting from the sedimentation of the winter diatoms bloom during the circulation period (Alcocer et al. 2012, 2014). Oseguera et al. (2011)

found a similar temporal dynamic in total particulate matter fluxes where the more significant fluxes were related to diatom blooms. Adame et al. (2008) identified a biennial cycle in Lake Alchichica phytoplanktonic Chl-a with years with a lower concentration of Chl-a associated with diatom blooms less intense and shorter duration, alternating with years with higher concentrations of Chl-a related to more intense and longer diatom blooms. Sedimentary POC displayed the same biennial pattern coupled with more intense and more prolonged diatom blooms followed by weaker and shorter diatom blooms (Alcocer et al. 2012).

17.4 Deep Benthos

17.4.1 Structure: Composition and Richness

The species richness of the deep benthic community of Lake Alchichica is two species, both are new species described for the lake, and both are seemingly microendemic to Lake Alchichica. The first one is the chironomid midge *Chironomus alchichica* (Acosta et al. 2017), and the second one the ostracod clam shrimp *Candona alchichica* (Cohuo et al. 2017).

Chironomus alchichica larvae are relatively small with a complete, non-retractable cephalic capsule on the thorax, well chitinized, with opposable sensory structures, oral apparatus, and jaws. The larva has long ventral tubules of the eighth segment, two lateral shorter tubules in the abdomen's seventh segment. The head is relatively light in color, without spots on the clypeal part and barely colored gluttony. The central tooth is trifid on the chin. The fourth lateral tooth is shorter than the fifth. The ventromedial plate is smooth in the middle. The epipharyngeal comb does not have smaller teeth intercalated between regular teeth. The jaw has three internal teeth, the third being lighter in color than the other two. The pupa has a single row of hooks in the second segment. The size is less than 10 mm, the thorax with some granulations, and segment IV's pleura does not have lateral spines. In segment III, the spinules of the tergith diminish in size from posterior to anterior.

Candona alchichica reproduces sexually and exhibits a well-defined sexual dimorphism evident in the shape of the soft parts of the body, size, shape, and fine details of the leaflets. The shells are globular, translucent white that allow the disclosure of yellow-orange soft parts in living organisms. Females are smaller in length, height, and carapace width, unlike males, who are more robust considering the same dimensions. The organisms inhabiting the deep benthos tend to be smaller ($p < 0.05$) than those of the littoral zone in some anatomical features, both in the valves and in some appendages. The number of eggs in ovigerous females is higher in the deep population ($p < 0.05$) than in the littoral. An important aspect is that the organisms in the deep zone have developed a thicker abductor muscle ($p < 0.05$). This trait may be the result of an anatomical adaptation so that a hermetic seal occurs when conditions become unfavorable (anoxia).

According to frequency (92%) and abundance (98%), *Candona alchichica* is the dominant taxon at the deep benthos. *Chironomus alchichica* is a rare species with low abundance (2%) and low frequency (12%).

17.4.2 Distribution and Seasonal Variations (Abundance and Biomass)

Candona alchichica inhabits the deep zone (50–62 m) of Lake Alchichica all year around. Differently, *Chironomus alchichica* is also present in the deep zone of Lake Alchichica but just as long as the deep benthic zone remains oxygenated.

Hernández et al. (2014, 2015) found the average density of the deep benthic macroinvertebrate community was 1197 ± 1976 ind/m^2 (274 ± 154 ind/m^2 to 3629 ± 3564 ind/m^2). *Candona alchichica* averaged 1169 ± 1970 ind/m^2 (98%), while *Chironomus alchichica* 28 ± 146 ind/m^2 (2%). The deep benthic macroinvertebrate community's average biomass was 16.13 ± 30.81 mg C/m^2 (5.90 ± 3.39 mg C/m^2 to 65.22 ± 95.85 mg C/m^2). *Candona alchichica* contributed notably to 11.12 ± 12.94 mg C/m^2 (71%), while *Chironomus alchichica* with 4.92 ± 27.33 mg C/m^2 (29%). Density and biomass showed significant differences ($p < 0.05$) both spatially and temporarily; density and biomass increased from the central zone towards the shoreline, while April–May showed the highest values of density and biomass (Fig. 17.2).

The existence of benthic macroinvertebrates in the deep benthic zone of Lake Alchichica is favored during the circulation period when the deep zone offers favorable conditions as the presence of dissolved oxygen and a large quantity of fresh and high-quality food (settling diatoms from the winter diatom bloom). Opposite, they are severely affected by the prolonged anoxia that is generated along the stratification period, associated with the presence of high concentrations of toxic H_2S (up to 4.28 mg/L).

17.4.3 Population Structure

Candona alchichica

Candona alchichica juveniles and adults (females and males) inhabit the deep benthic zone of Lake Alchichica. Juveniles were more abundant with 69% (818 ± 1974 ind/m^2), followed by females with 22% (249 ± 266 ind/m^2) and, finally, males with 9% (96 ± 111 ind/m^2). The density of the various stages was significantly different ($p < 0.05$). There is a differential distribution, with the highest density closest to the shoreline while the lowest in the deepest central zone. Juveniles and females showed their highest density in March with 2844 ± 4091 ind/m^2 and 426 ± 319 ind/m^2, respectively, while the males in July with 178 ± 207 ind/m^2.

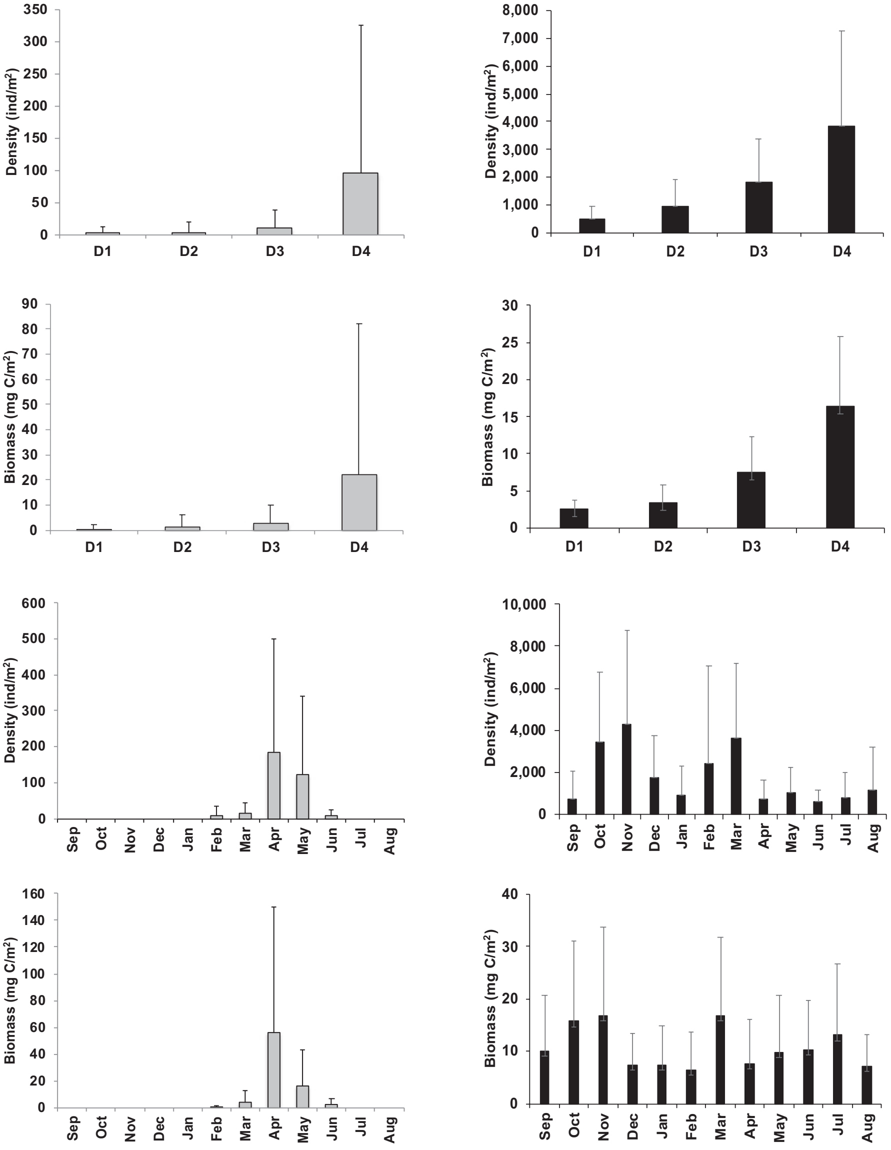

Fig. 17.2 Spatial [from de center (D1) towards de coastline (D4)] and temporal distribution of *Chironomus alchichica* (gray) and *Candona alchichica* (black) density and biomass at Lake Alchichica deep benthos profound zone (≥50 m)

Chironomus alchichica

Chironomus alchichica displayed three benthic larval stages (II, III, and IV). The second and third instars were scarce, contributing less than 30% of the total larvae density. In contrast, the fourth stage was the most abundant with 90%. *Chironomus alchichica* length ranged from 1.22 to 14.67 mm. The most significant growth appears to occur during stage IV. The range of this stage varies from 10.01 to 14.67 mm. Some specimens at this stage had already developed some pupal structures. *Chironomus alchichica* larvae are present along the whole circulation period. At the onset of the stratification, larval density decreased markedly. Stage IV showed a continuous distribution during the circulation season. The monthly frequency distribution for each larval stage suggests *Chironomus alchichica* completes an entire generation in the deep zone.

17.4.4 Strategies for Coping with Anoxia

Hernández et al. (2014, 2015) found both benthic species have chosen different strategies to take advantage of the benefits offered by the deep benthic zone of Lake Alchichica, a practically uninhabited habitat, with a large amount of fresh food, essentially without competition and deprived of predators. To inhabit this zone, the organisms must cope with a “hostile” environment, the hypolimnion, that becomes anoxic and rich in H_2S as soon as the lake stratifies. In this sense, each species has had to develop a strategy to cope with environmental conditions to maintain its population and survive.

Chironomus alchichica pupate and emerges *in masse* once it detects hypoxic conditions. Simultaneously, *Candona alchichica* enters diapause/latency in the juvenile stage as an adaptive survival strategy until the oxygenation conditions are restored. Therefore, the benthic macroinvertebrates structure in the deep benthic zone is largely controlled by the availability of dissolved oxygen.

Chironomus alchichica is an opportunist species that colonize the deep zone only temporarily during circulation. The larvae migrate from the littoral zone to the bottom, finding available space and sufficient fresh food to reach their optimal development. Once they reach maturity (stage IV) and detect low oxygen concentrations, they “escape” from the sediment, emerging seasonally. Therefore, it is a species that responds to the environmental stress of the deep zone at the beginning of the stratification period. It has developed a swimming capacity that allows it to escape these conditions. The low concentration of oxygen and the presence of high concentrations of H_2S are factors that are lethal for the *Chironomus alchichica* larvae.

Candona alchichica has a short life cycle, with the rapid development of organisms to reach a resistance stage such as A-2 larvae and the production of resistance eggs. The life cycle is governed by the limiting factors that are generated in the background (anoxia and high concentrations of H_2S), which has made the species develop an adaptive strategy to colonize this habitat. All the stages of *Candona* *alchichica* are active during the period of circulation, while in the period of stratification, anoxia and the presence of H_2S affect the population entirely, generating a massive death of stages, except A-2 larvae, which remains in a latent state until the next period of circulation.

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Chapter 18
Lake Metabolism

Javier Alcocer, Luis A. Oseguera, Daniel Cuevas-Lara, Sandra Guadarrama-Hernández, and Benjamín Quiroz-Martínez

18.1 Introduction

Primary production (PP) is a measure of inorganic carbon's incorporation rate during photosynthesis and is carried out by all organisms that synthesize organic matter (OM): algae and bacteria. A part of the produced OM maintains the metabolism itself (gross primary production, GPP), and another part transforms into biomass (net primary production, NPP). This last type is the source of trophic energy for the entire ecosystem (Roldán Pérez and Ramírez Restrepo 2008).

There are many literature concepts to describe primary production indices (PP) and respiration (R) at the ecosystem level. Gross Primary Production (GPP) is defined as the total autotrophic transformation of inorganic carbon to organic carbon forms, regardless of its destination. Respiration in the ecosystem (R) is the total oxidation of organic carbon to inorganic carbon by heterotrophic and autotrophic organisms (Cole et al. 2000; Lovett et al. 2006).

Aquatic ecosystems where photosynthesis exceeds plankton's total respiration ($P > R$) are completely autotrophic, produce oxygen and organic matter, and act as

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J. Alcocer (✉) · L. A. Oseguera
Grupo de Investigación en Limnología Tropical, FES Iztacala, Universidad Nacional Autónoma de México, Tlalnepantla, Estado de México, Mexico
e-mail: jalcocer@unam.mx; loseguera@unam.mx

D. Cuevas-Lara · S. Guadarrama-Hernández
Programa de Posgrado en Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México, Ciudad de México, Mexico
e-mail: biossandy@ciencias.unam.mx

B. Quiroz-Martínez
Laboratorio de Ecología Numérica y Análisis de Datos, Unidad Académica Ecología y Biodiversidad Acuática. Instituto de Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México, Ciudad de México, Mexico
e-mail: bquirozm@cmarl.unam.mx

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CO_2 sinks. On the contrary, aquatic ecosystems where respiration exceeds photosynthesis ($P < R$) are net heterotrophs, and by consuming organic carbon emit-sources- CO_2 into the atmosphere (Carignan et al. 2000). On the other hand, nutrient enrichment can cause a lake to go from heterotrophic to autotrophic, favoring GPP more than R. However, external inputs of dissolved organic matter increase R, and the resulting light attenuation reduce GPP.

On a global scale, the GPP:R ratio and net primary production (NPP) help better understand the carbon cycle globally and explain the aquatic ecosystems' role as atmospheric CO_2 sources or sinks (del Giorgio and Duarte 2002).

PP and R are dynamic and diverse environmental factors interact to regulate the phytoplankton growth in time and space. These factors include light, temperature, pH, and nutrient availability (Lampert and Sommer 2007; Edding et al. 2006). Since most phytoplanktonic organisms do not live for more than 1 day, GPP and NPP variate in response to diurnal light cycles. However, monthly, seasonal, and annual variations can show changes in the ecosystem's structure and the different phytoplankton groups' activity (Smith and Hollibaugh 1997; del Giorgio and Duarte 2002; Ask et al. 2009).

Various studies (e.g., Lewis 1996) show essential differences in the fundamental processes -primary production among them- between temperate and tropical lakes. These differences derive from the fact that in tropical latitudes: (a) annual solar radiation is higher, (b) there is less variation in solar radiation, and (c) a diminished Coriolis effect. Of great relevance to PP are particularly its interactions with radiation and temperature. Most of the research on PP and R in aquatic ecosystems has been done in temperate latitudes (79%), with much fewer studies in subtropics (10%), tropical (8%), and arctic (3%) (Staehr et al. 2012a). However, the available information suggests that tropical lakes are more efficient at generating phytoplankton biomass than temperate ones (Lewis 1996).

Among the studies carried out in tropical environments, even fewer have been conducted in deep and oligotrophic lakes (e.g., Carignan et al. 2000; Staehr et al. 2012b). Studies carried out in tropical lakes are still scarce worldwide and practically unknown for Mexican lakes, both deep and shallow.

Chlorophyll-a (Chl-a) is widely used as a biomass indicator in phytoplankton productivity and biomass estimates (Reynolds 1984). Also, Chl-a is directly related to the lake's total primary production (Melack 1976). Light, temperature, and nutrients are often referred to as the most important variables affecting Chl-a concentration and dynamics, and phytoplankton species composition and size spectrum (Pollingher 1986; Talling and Lemoalle 1998).

The fluctuations of these variables largely explain the Chl-a dynamics. Nonetheless, the variability depends on the considered time scale (Reynolds 1984). For example, long-term variations, which may be determined by climate, cause changes in the phytoplankton composition; annual oscillations are capable of producing seasonal changes in the community's composition and productivity, which, to a certain extent, can be repeated in successive years. On a smaller scale, daily fluctuations in the physical environment (thermal structure or solar radiation) affect existing populations.

18.2 Primary Production and Respiration

Primary productivity (PP) in Lake Alchichica has been measured through two different approaches: (a) the light and dark bottles method (Wetzel and Likens 1991) by measuring *in situ* changes in dissolved oxygen, and (b) the Chamberlin et al. (1990) empirical equation relating *in situ* natural fluorescence of chlorophyll-a to the photosynthetic rate (Kiefer and Chamberlin 1989).

18.2.1 The Light and Dark Bottles Method

Primary production was measured in the euphotic zone (Z_{EU}) since no photosynthetic activity occurs below it. Average gross primary productivity (GPP) was 110 ± 86 mg $C/m^3/d$, while net primary productivity (NPP) was 15 ± 143 mg $C/m^3/d$. During the mixing period, high PPB and PPN values were observed along the Z_{EU}. The maximum values were found at 5 m with 277 and 243 mg $C/m^3/d$, respectively. The highest GPP (488 mg $C/m^3/d$) and NPP (304 mg $C/m^3/d$) values of the annual cycle were recorded at the onset of the stratification period. Unlike the circulation season and early stratification, where higher PP values were recorded in the upper layer, during the well-established stratification, the maximum PP values were observed in the metalimnion (GPP 148 mg $C/m^3/d$; NPP 122 mg $C/m^3/d$) associated with the deep chlorophyll maximum, DCM (Fig. 18.1).

The annual mean of the integrated GPP and NPP per unit area considering the Z_{EU} was 2915 ± 796 mg $C/m^2/d$ and 842 ± 2296 mg $C/m^2/d$, respectively. Throughout the annual cycle, four well-defined peaks were observed. The first peak (GPP: 3496 mg $C/m^2/d$; NPP: 2322 mg $C/m^2/d$) was found at the beginning of the circulation period in January. The second peak was at the early stratification, in May for GPP (3782 mg $C/m^2/d$) and in June for NPP (2758 mg $C/m^2/d$). The third peak took place during the well-established stratification (October) with 3433 mg $C/m^2/d$ for GPP and 3163 mg $C/m^2/d$ for NPP. At the late stratification and the onset of the circulation period (December), GPP was 4195 mg $C/m^2/d$, and NPP was 2592 mg $C/m^2/d$. The NPP showed negative values in February (−579 mg $C/m^2/d$), April (−2914 mg $C/m^2/d$) and November (−4100 mg $C/m^2/d$) indicative the lake's role as carbon source (Fig. 18.2).

According to Oseguera et al. (2015), the variation of GPP and NPP throughout the year associates with the main phytoplankton events, which are closely related to the lake's hydrodynamics. During the circulation period, the high PP values associate with nutrient availability leading to the winter diatom bloom. During mixing, neither nitrogen nor phosphorus is limiting the PP (Ramos-Higuera et al. 2008), which favors the diatom bloom, where *Cyclotella alchichicana* dominates the phytoplankton biomass (Oliva et al. 2001).

At the beginning of the stratification, an increase in the integrated per unit area PP mirrors the *Nodularia* aff. *spumigena* (Oliva et al. 2001, 2009) bloom. Unlike

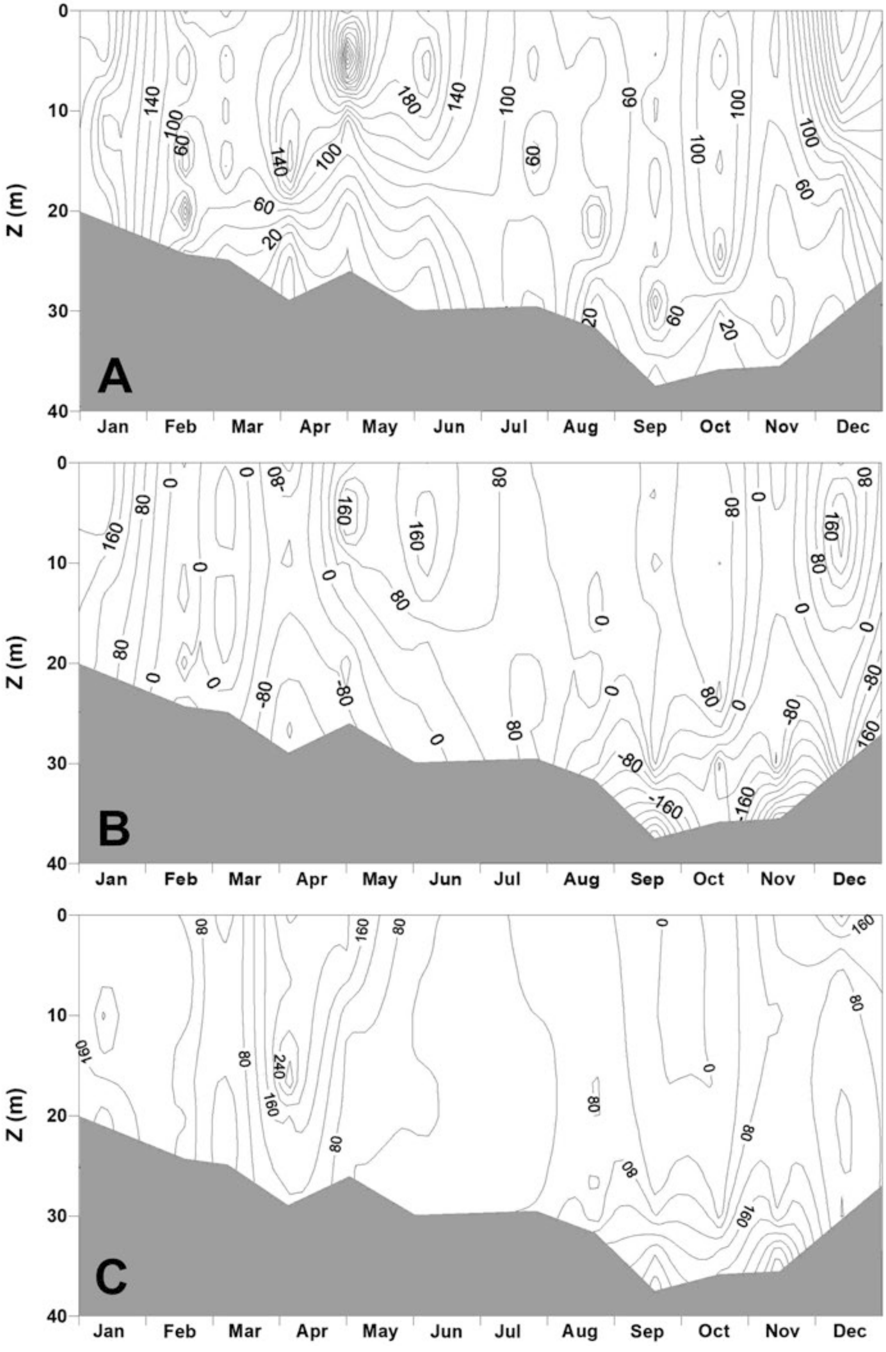

Fig. 18.1 Depth-time diagram of the GPP (**a**), NPP (**b**), and R (**c**) (mg C/m^3/d) in Lake Alchichica. The gray area represents the aphotic zone (<0.1% PAR)

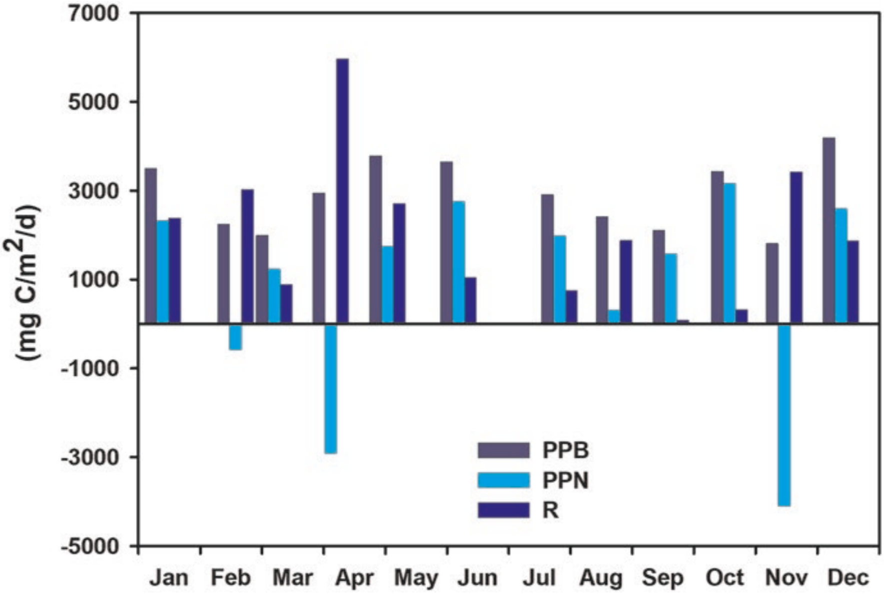

Fig. 18.2 Temporal variation of the integrated PPB, PPN and R per unit area (mg C/m^2/d) in Lake Alchichica

the circulation period where the PP is carried out more or less homogeneously throughout the water column, the PP associated with the cyanobacteria bloom is located in the water column's upper layer. While phosphorus is still available, but nitrogen is already depleted, the nitrogen fixing *N.* aff. *spumigena* remain close to the surface to fix atmospheric nitrogen.

The increase in integrated per unit area GPP during the well-established stratification was associated with the presence of a deep chlorophyll maximum (DCM), which develops at the metalimnion, right at the bottom of the Z_{EU}. Diatoms, mostly *C. alchichicana* but also *C. choctawhatcheeana* composed the DCM. These diatoms take advantage of the nutrients that diffuse from the hypolimnion into the metalimnion through the turbulence generated by internal waves.

Like PP, R varied along the water column and throughout the year. The annual average was 78 ± 75 mg C/m^3/d. During the circulation and along the Z_{EU}, R values ranged between 60 and 225 mg C/m^3/d. The maxima were found at the beginning and the end of the stratification with values above 200 mg C/m^3/d. In January and February, in the mixing season, R reached values above the general mean throughout the Z_{EU} (Fig. 18.1). The average value of integrated per unit area R was 2029 ± 1642 mg C/m^2/d, with three peaks along the year associated with the NPP negative values (Fig. 18.2). The first peak was in February with 3028 mg C/m^2/d, while in April, R recorded 5996 mg C/m^2/d, which is twice the value of the circulation and the highest of the whole year. The third peak and second in magnitude was in November (3421 mg C/m^2/d) at the end of the stratification season.

The February R peak is mainly attributed to the presence of large quantities of the copepod *Leptodiaptomus garciai*, coupled with the diatom bloom (Lugo et al. 1999; Ortega-Mayagoitia et al. 2011). The increase of zooplankton explains the November R peak as found in other lakes (from del Giorgio and Peters 1993; from del Giorgio and Williams 2005), and the oxidation of hypolimnetic organic matter. *L. garciai* in Lake Alchichica is at the bottom of the epilimnion, and the rotifer *Brachionus plicatilis* group in the metalimnion (Ortega-Mayagoitia et al. 2011), right where the DCM is developing. A share of the organic matter generated by the phytoplankton at the DCM is oxidized *in situ*, while other is exported down to the bottom of the lake (Ardiles et al. 2012).

The GPP: R ratio had an annual average of 4.39 ± 6.84 without a clear temporal pattern. GPP: R ratio indicates to be predominantly autotrophic (GPP > R), with a positive annual NPP indicating the lake's role as CO_2 sink 75% of the time (Oseguera et al. 2015).

18.2.2 *In situ Natural Fluorescence Method*

Overall, phytoplanktonic PP in Lake Alchichica ranges from 0.1 mg C/m^3/h in deep waters to 101.6 mg C/m^3/h at 5 m depth into the euphotic zone. Annually, the PP shows two periods in the water column (Fig. 18.3). The first period (from January to June) has a higher gradient of PP rate decrease with depth than the second period.

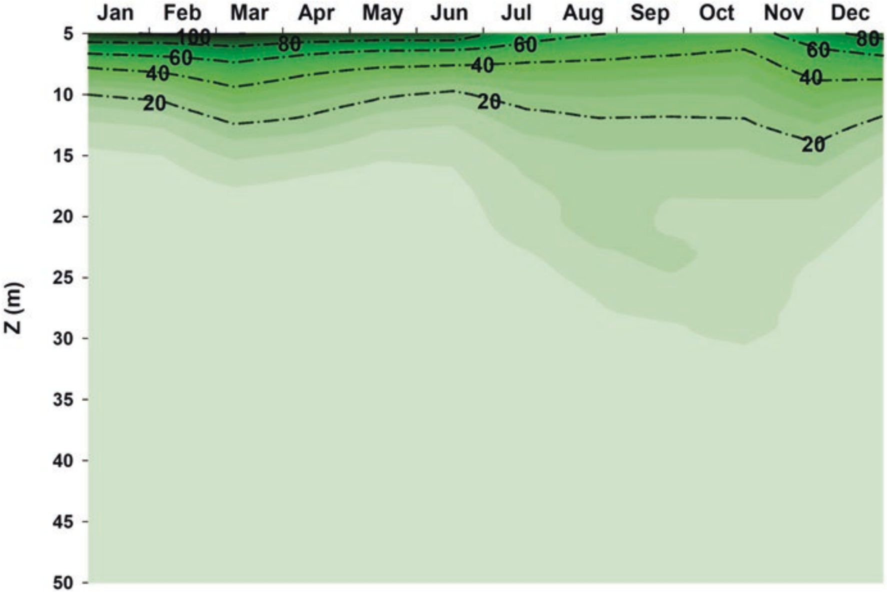

Fig. 18.3 Depth-time diagram of phytoplankton PP rate (mg C/m^3/h) in Lake Alchichica

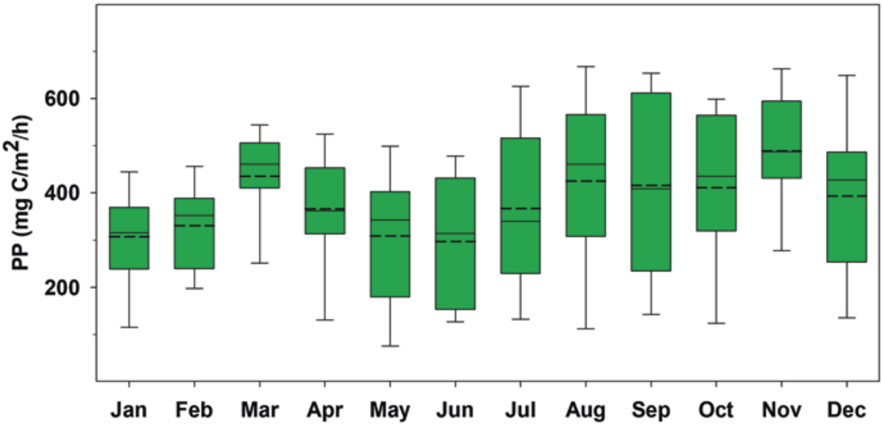

Fig. 18.4 Water column integrated phytoplankton PP in Lake Alchichica. Out of the box: Whiskers are 90 and 10th percentiles. Within the box: straight and short lines are median and mean, respectively

For instance, the rates surpass 5 mg C/m^3/h in the first 15 m of depth until ≈100 mg C/m^3/h in 5 m. In the second period (from July to November), the rates above 5 mg C/m^3/h distributed up to 30 m, but the rates observed in 5 m are below 75 mg C/m^3/h.

The water-column phytoplanktonic PP values per unit-area (m^2) in Lake Alchichica averages 379 ± 151 mg C/m^2/h (50–700 mg C/m^2/h). The values show two periods of highest PP rates (Fig. 18.4): the first one in March (396 ± 72 mg C/m^2/h) corresponding to the end of the winter diatom bloom, and the second one spans from August to November (411 ± 160 to 489 ± 120 mg C/m^2/h) resultant from the DCM develop throughout the well-established stratification.

18.2.3 Long-Term Phytoplankton Primary Production

Long-term limnological investigations allow us to understand better the functioning of aquatic ecosystems (Larson et al. 2007). The long-term monitoring of phytoplankton's primary production (PP) allows evaluating a single but complex variable, the lakes' trophic status evolution (Goldman 1988, 1990). Fluctuations in the food web structure and climate change partially explain long-term variation in phytoplankton PP (e.g., Goldman et al. 1989). Although climate change seems to be the primary source of phytoplankton PP variations in lakes, the mechanisms involved are still unknown (Darchambeau et al. 2014; Franchini et al. 2017).

Phytoplankton PP in Lake Alchichica is stable and relatively predictable in the long-term (Fig. 18.5). Phytoplankton *in situ* photosynthetic rates recorded monthly from 1999 to 2014 ranged between 50.4 and 700.6 mg C/m^2/h (378 ± 144 mg C/m^2/h), without significantly increasing nor decreasing trends (Cuevas-Lara et al. 2016).

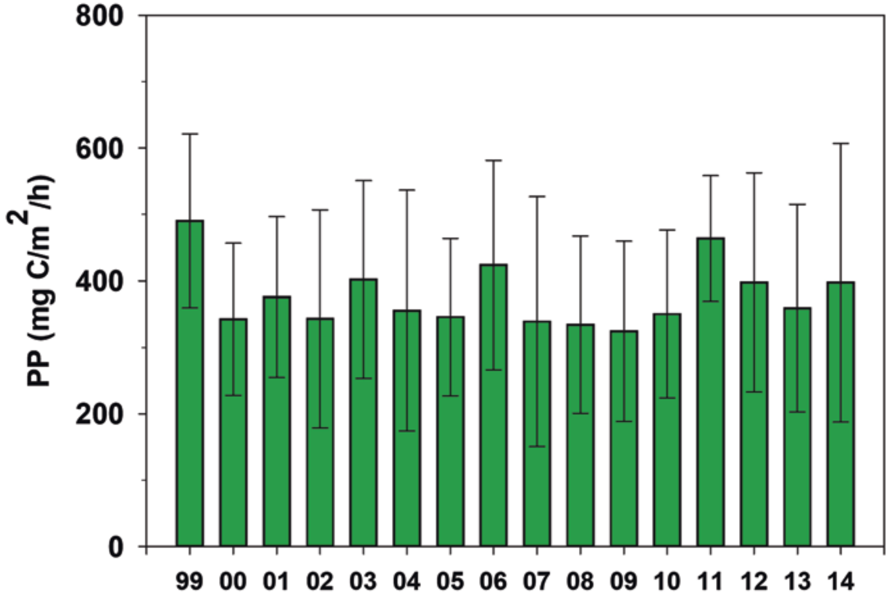

Fig. 18.5 Long-term (1999–2014) water-column integrated phytoplankton PP rates in Lake Alchichica (annual average ± standard deviation)

18.3 Chlorophyll

The study of Chl-a concentration, vertical distribution, and temporal dynamics in Lake Alchichica has been evaluated through two different methods: a) *in situ* natural fluorescence of the Chl-a (PNF-300, Biospherical Instruments, and b) *in vitro* determination on acetone-extracted Chl-a (EPA method 445.0, Arar and Collins 1997).

18.3.1 In Situ *Natural Fluorescence*

Gonzáles-Contreras et al. (2015) found employing *in situ* natural fluorescence profiles, the average water column integrated Chl-a concentration was 28.29 ± 11.54 mg/m^2. The months with the highest Chl-a concentration were January (39.93 ± 15.17 mg/m^2) and September (37.01 ± 14.88 mg/m^2). Higher Chl-a (above the average) concentrations were found from January to March and September to December. From April to August corresponded the lower (below the average) Chl-a concentrations (Fig. 18.6).

The high Chl-a concentration during the mixing period (January–March) is related to the winter diatom (mostly *Cyclotella alchichicana*) bloom. The minor increase in Chl-a concentration between May and June corresponded to the spring N-fixing cyanobacteria (*Nodularia* aff. *spumigena*) bloom at the onset of the

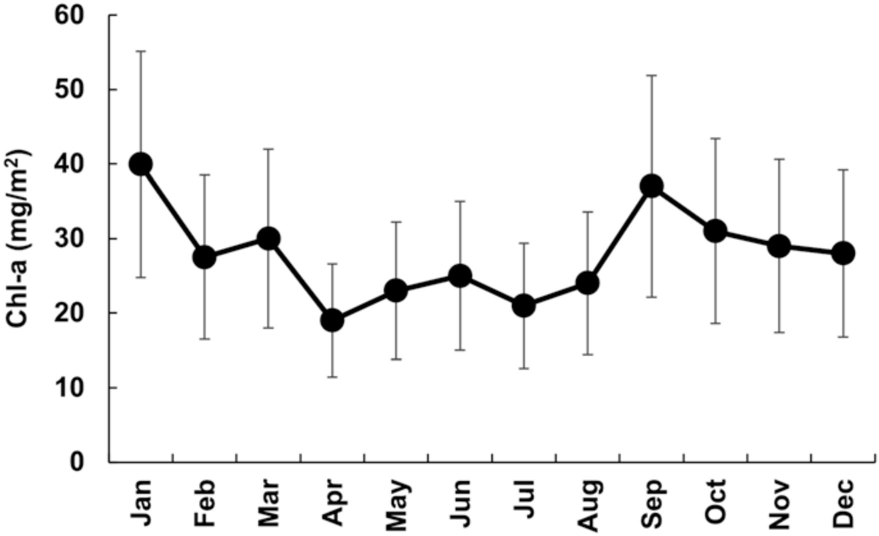

Fig. 18.6 Water-column integrated Chl-a concentration in Lake Alchichica

stratification period. The high Chl-a concentration found from September to early December corresponded to a deep chlorophyll maximum (DCM) developed at the metalimnion during the well-established and part of the late stratification periods. This is the general recurrent annual pattern tightly associated with the warm monomixis thermal type, which defines the lake's hydrodynamics (mixing and stratification periods). Although there were interannual variations, Gonzáles-Contreras et al. (2015) found no other interannual patterns or cycles than the described annual cycle, nor trends along the 12 years analyzed.

Lake Alchichica displays three different Chl-a vertical (water column) distribution patterns corresponding to the three Chl-a concentration peaks along the annual cycle (Gonzáles-Contreras et al. 2015). (a) nearly homogeneous distribution along the water column during the mixing period when the winter diatom bloom takes place; (b) highly concentrated close and at the surface layer during the onset of the stratification period, while the cyanobacterial bloom progresses; and (c) concentrated at the metalimnion during the well-established and late stratification periods, when the DCM develops (Fig. 18.7).

18.3.2 Extracted Chl-a

Adame et al. (2008) found Chl-a concentration in Lake Alchichica averages 4.2 ± 4.2 μg/L. The highest concentration in the mixing season was 18.6 ± 3.9 μg/L, up to 12.3 μg/L in the surface waters associated to the cyanobacterial spring bloom, and up to 17.2 μg/L (average 3.6 ± 3.2 μg/L) at the DCM along the stratification.

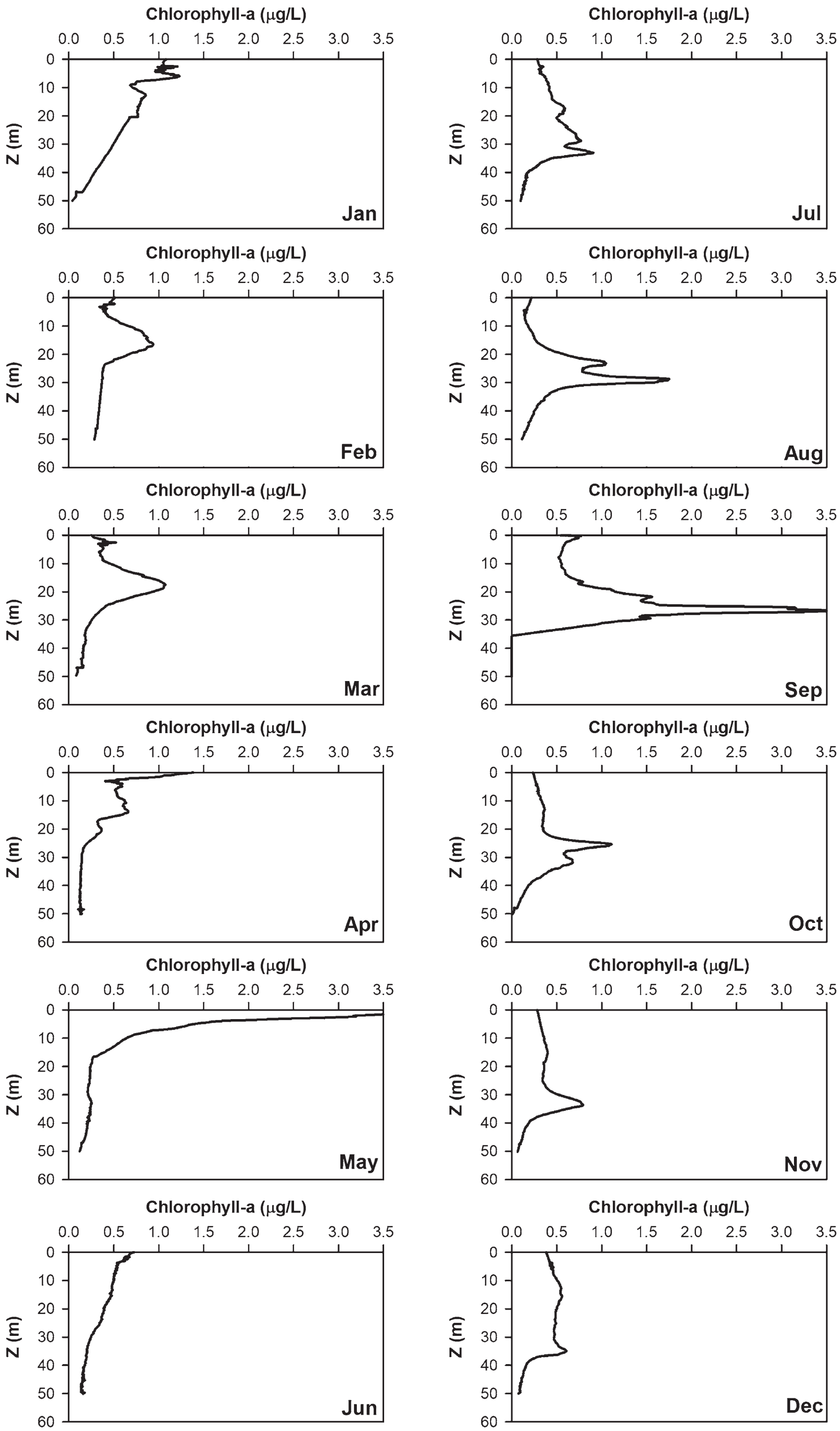

Fig. 18.7 Temporal dynamics of Chl-a profiles in Lake Alchichica

Chl-a concentration in the Z_{MIX} averaged 5.11 ± 4.67 μg/L, 9.8 ± 4.7 μg/L during the mixing season, while 2.5 ± 1.8 μg/L along the stratification.

Oliva et al. (2001) and Macek et al. (2009) reported similar and low Chl-a concentrations (<4–5 μg/L), with exceptional punctual augments up to ~20 μg/L. Moreover, these authors mentioned that the highest Chl-a concentrations along the annual cycle are composed of the diatoms *Cyclotella alchichicana* and *C. choctawhatcheeana* in the mixing period, the cyanobacteria *Nodularia* aff. *alchichica* at the onset of the stratification, and the diatoms *C. alchichicana* and *Chaetoceros elmorei* at the DCM throughout the stratification.

18.3.3 The DCM

Oligotrophic, transparent lakes -such as Lake Alchichica- develop deep chlorophyll maxima (DCM) while stratified. The DCM definition is the depth interval in which the maximum concentration of chlorophyll is found, usually located at the metalimnion or close to the top of the hypolimnion, far from the surface (Camacho 2006). The DCM in Lake Alchichica locates at the metalimnion or even on the top/ceiling of the hypolimnion. The planar DCM usually couples with the planar thermocline. The planar DCM is found below Z_{EU} (1% of the surface PAR, SPAR) most of the time, with an average of 0.6 ± 0.8% and ranging between 0.01% and 2.1% SPAR. Seemingly unusual, below the 1% SPAR DCMs has already been reported elsewhere (e.g., Pinel-Alloul et al. 2008).

The DCM in Lake Alchichica is usually present from June (end of the early stratification) to November (end of the late stratification); however, the duration varies yearly. The Chl-a concentration of the DCM respecting the total water column Chl-a concentration ranged from 24% to 96% (68 ± 18%). On an annual basis, the DCM accumulated Chl-a concentration averages 25.3 ± 8.6% of the total annual Chl-a concentration; a similar percentage is contributed by the accumulated Chl-a concentration of the winter diatom bloom during the mixing period with 24.4 ± 14.9%.

The DCM shape is not always a sharp peak within a narrow depth interval but distributed over a wider layer; in this case, the term deep chlorophyll layer (DCL) seems to be more appropriate (Pilati and Wurtsbaugh 2003). The DCM in Lake Alchichica varies in depth, width, and concentration along the stratification period displaying both shapes, DCM and DCL (Fig. 18.8).

Usually, a DCM consists of only one or a few phytoplankton species, whose population densities are extremely high compared to their epilimnetic abundance (Gasol et al. 1992; Miracle et al. 1992); which in Lake Alchichica is composed by *Cyclotella alchichicana* (mostly), and *C. choctawhatcheeana* (a minor proportion) (Ortega-Mayagoitia et al. 2011).

Specific Chl-a profiles display not one but two peaks of different magnitude composing the DCL. Sometimes, the first peak is larger than the second (Fig. 18.7,

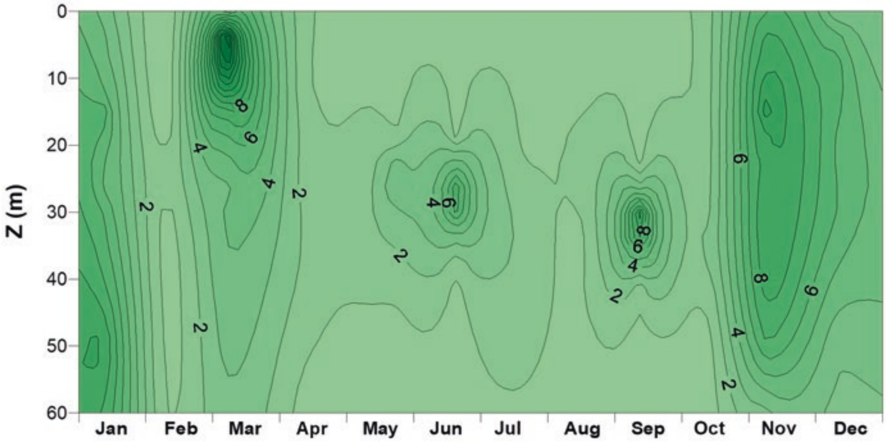

Fig. 18.8 Depth-time diagram of chlorophyll-a concentration in Lake Alchichica

October), but sometimes the second peak is larger than the first one (Fig. 18.7, August). Presumably, both peaks could be integrated by different dominant species growing better under different environmental conditions. Nonetheless, further analyses are needed to confirm or reject this assumption.

18.3.4 Size-Fractionated Chlorophyll

Oliva et al. (2001) found small-size chlorophytes and cyanobacteria (*Monoraphidium minutum*, *Oocystis parva*, *Synechocystis aquatilis*) numerically dominate the phytoplankton of Lake Alchichica over the annual cycle. However, algae ≥20 µm contributes 73 ± 26% of the total phytoplankton biomass (Ortega-Mayagoitia et al. 2011).

The Chl-a concentration corresponding to the large size phytoplankton fraction (LChl-a) follows closely the same pattern as the total Chl-a concentration (TChl-a) (Fig. 18.9), mirroring its dominance (Adame et al. 2008). LChl-a reached a maximum average concentration of 8.7 ± 4.8 µg/L in January during the mixing period. LChl-a concentrations remained above the average (2.7 ± 3.4 8 µg/L) while mixing and below the average during the stratification. LChl-a concentration at the epilimnion was lower (1.6 ± 1.6 µg/L) than at the metalimnion (2.2 ± 2.0 µg/L), and hypolimnion (2.7 ± 3.4 µg/L). The similar concentration at the meta and hypolimnion suggests continuous sedimentation of phytoplankton from the metalimnion (i.e., DCM) to the lake's bottom, as later confirmed by Ardiles et al. (2012) through evaluating the diatom fluxes to the bottom of Lake Alchichica.

Differently, the Chl-a concentrations of the small size phytoplankton fraction (SChl-a) remains low and relatively constant throughout the year (0.7 ± 0.8 µg/L). SChl-a was mostly limited to the upper layer. In the same way as the TChl-a and LChl-a concentrations, SChl-a concentrations remained above the annual average

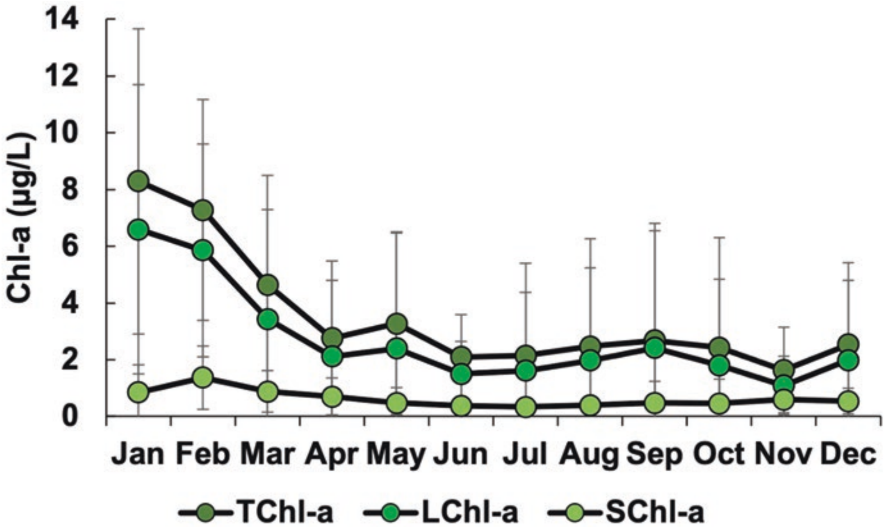

Fig. 18.9 Total and size-fractionated Chl-a concentration in Lake Alchichica. (TChl-a = total chlorophyll-a, LChl-a = large-size fraction chlorophyll-a, SChl-a = small-size fraction chlorophyll-a

while mixing and below the average along the stratification. The dynamics of the SChl-a was not related to the lake's hydrodynamics, opposite to the LChl-a, which is primarily determined by the warm monomictic thermal pattern of the lake (Adame et al. 2008). In summary, LChl-a dominated along the annual cycle by contributing with 80% (65 to 89%) of TChl-a, while SChl-a composed the remained 20% (11 to 35%) (Fig. 18.10).

18.4 New and Regenerated Production

Dugdale and Goering (1967) introduced the concepts of new (P_{NEW}) and regenerated production (P_{REG}) associated with the origin of the nitrogen source available for phytoplankton in the euphotic zone (Z_{EU}). P_{NEW} is the primary production that uses nutrients from sources outside the Z_{EU}, particularly from the upwelling of deep waters. However, nutrients can also come from allochthonous sources, both terrestrial and atmospheric.

P_{NEW} depends on advective processes associated with circulation, where nutrients derived from the remineralization of organic matter in deep water (e.g., hypolimnion) are transported to the Z_{EU} through mixing vertical of the water body. In contrast, P_{REG} uses the nutrients derived from organic matter that was metabolized by organisms and returned to the water column within the Z_{EU}. The primary source

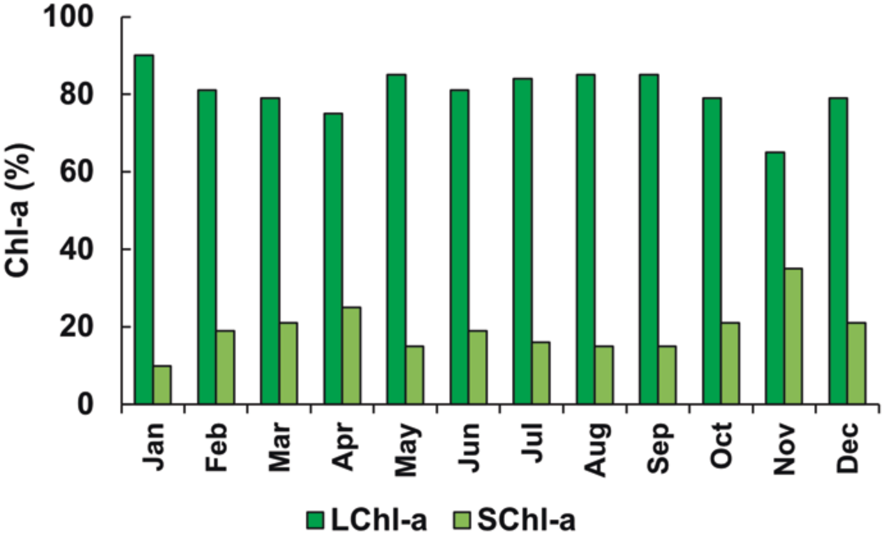

Fig. 18.10 Percentual contribution of the large (LChl-a) and small (SChl-a) size phytoplankton fractions Chl-a concentration in Lake Alchichica

of N used by phytoplankton for P_{NEW} is nitrite (NO_3^-), while that of P_{REG} is mainly ammonium (NH_4^+).

As mentioned, PP in Lake Alchichica (Fig. 18.11) is tightly coupled with the lake's thermal/hydrodynamic stages corresponding to the warm monomictic type (i.e., mixing, early stratification, well-established stratification, late stratification). In December, the Z_{MIX} expands by eroding the thermocline and releasing the nutrients trapped in the metalimnion stimulating diatom to bloom (P_{REG}). The remineralization of organic matter in the hypolimnion throughout the stratification season enriches the hypolimnion in nutrients, distributed to the whole water column in January along the lake mixing process (P_{NEW}). In addition to the resuspension of nutrients from deep water, the nutrient input to the surface by dustfall increase in the cold and dry season. However, the enhancing of PP by dustfall is minor ompared with the PP enhanced by resuspension in the lake (Oseguera et al. 2011).

At the early stratification period (April to June), a short-lived cyanobacterial (*Nodularia* aff. *spumigena*) bloom develops. The diatom bloom development along the mixing period exhausted nutrients in the Z_{MIX}, particularly N, favoring the N-fixing cyanobacteria to bloom by consuming the remaining P and fixing atmospheric N_2. Once stratified, PP on the Z_{MIX} relies primarily on regenerated nutrients (P_{REG}).

Throughout the well-established stratification and most of the late stratification periods, Lake Alchichica develops a deep chlorophyll maximum (DCM) from July to November, which reaches the maximum intensity between September and November. The development of the DCM and its location at the metalimnion implies an injection of nutrients from the hypolimnion -remineralized- (P_{NEW}), which reach

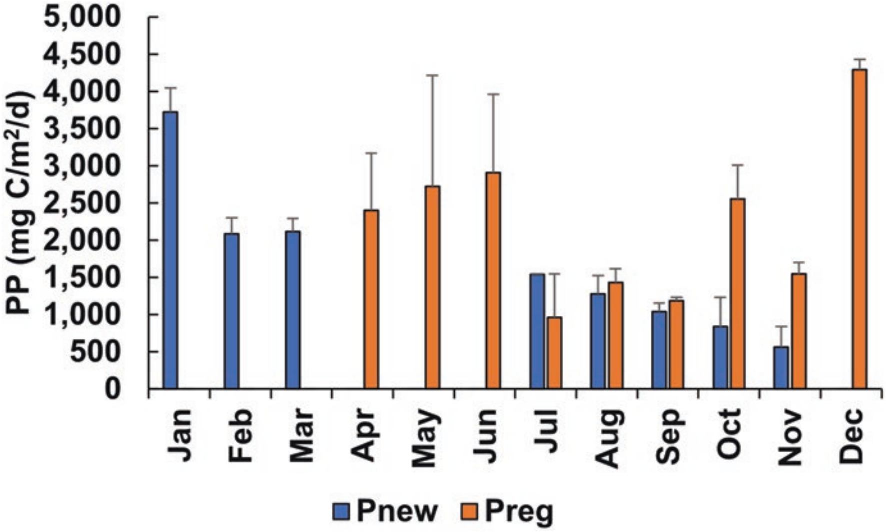

Fig. 18.11 New (P_{NEW}) and regenerated (P_{REG}) phytoplankton primary production (average ± s.d.) in Lake Alchichica

the metalimnion via the turbulence generated by the presence of internal waves that in Lake Alchichica reach 1.4 m in amplitude (Filonov and Alcocer 2002). Nonetheless, organic matter is recycled at the metalimnion providing an alternative nutrient source (P_{REG}) (Fig. 18.11).

As expected, the highest P_{NEW} (>2000 mg C/m^2/d) occurs during the mixing period and diminishes the rest of the year. Differently, P_{REG} becomes significant from the early to the late stratification fluctuating from >2000 mg C/m^2/d in early and late stratification to <2000 mg C/m^2/d in the well-developed stratification (Alcocer and Oseguera 2018).

In summary, during the lake's mixing period, the P_{NEW} dominates the total PP since it takes advantage of the nutrients regenerated in the hypolimnion during the stratification period (Fig. 18.12). On the other hand, when the lake is stratified, the thermocline's presence constitutes an insurmountable barrier for exchanging nutrients, so these are depleted in the epilimnion (Z_{MIX}); the organic matter that is deposited to the bottom, remineralizes releasing nutrients that concentrate in the hypolimnion. However, the transparent waters of Lake Alchichica allow light reaching the metalimnion. Then a DCM develops by taking advantage of both nutrient sources (Fig. 18.12): (a) those regenerated in the hypolimnion that reaches the metalimnion through the turbulence generated by the internal waves (P_{NEW}), and (b) nutrients released from the *in situ* organic matter remineralization (P_{REG}). In December, by the end of the stratification period, the thermocline's fast erosion releases nutrients trapped at the metalimnion (P_{REG}), inducing the onset of the diatom bloom (Fig. 18.12).

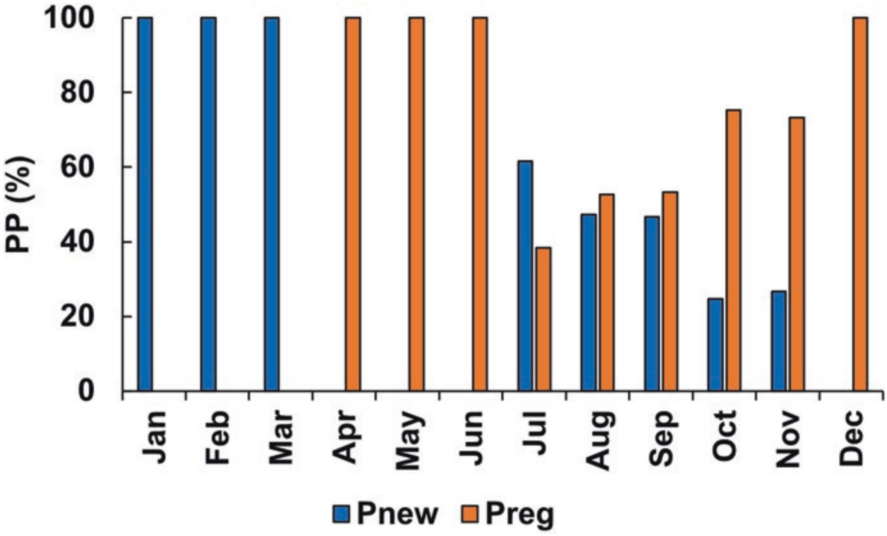

Fig. 18.12 Percentual contribution of new (P_{NEW}) and regenerated (P_{REG}) phytoplankton primary production in Lake Alchichica

18.5 Nutrient Limitation of Primary Productivity

The phytoplankton of the majority of tropical lakes show pronounced seasonal changes which generally correspond to variations in precipitation, runoff, or vertical mixing of the lake, variables that directly influence the concentration of nutrients. The recycling of nutrients depends, mostly, on the mixing process (regeneration in the mixing layer, regeneration in the sediments in contact with the layer of mixing, and transfer of nutrients to the mixing layer from the water column below the mixing layer), which controls, for a nutrient load and a given hydraulic residence time, nutrient availability (Lewis 1996).

Nitrogen and phosphorus are the leading nutrients limiting phytoplankton growth in aquatic ecosystems. Although the role of phosphorus and eutrophication is well-known in temperate lakes, there is evidence suggesting nitrogen limitation is more important and widespread in tropical lakes (e.g., Talling and Talling 1965; Talling and Lemoalle 1998). Lewis (2002) examines the causes for the high frequency of nitrogen limitation in tropical lakes; among them are the higher hypolimnetic temperatures, lower hypolimnetic oxygen holding capacity and duration of stratification, prompt onset and long-lasting anoxia, and higher metabolic (microbial) and denitrification rates compared to temperate lakes.

Ramos-Higuera et al. (2008) found nutrient enrichment experiments on samples of the mixing period of Lake Alchichica did not significantly modify the phytoplankton growth. Differently, the phytoplankton in samples from the stratification period grew better on the nitrogen enrichment treatments. The N:P ratio in the Z_{MIX}

of Lake Alchichica ranges 0.2–1.7 during the stratification period suggesting nitrogen is the most likely limiting nutrient of phytoplankton growth. The nutrient enrichment experiments confirmed that nitrogen is the limiting nutrient of phytoplankton growth in Lake Alchichica.

Also, Lake Alchichica displays some nitrogen-deficiency indicators in tropical lakes mentioned by Lewis (2002), like the recurrent bloom of the heterocystous nitrogen-fixing cyanobacteria *Nodularia* aff. *spumigena* at the onset of the stratification period and prolonged episodes of low DIN:SRP ratios.

Ramírez-Olvera et al. (2009) carried out monthly nutrient enrichment experiments on Lake Alchichica, revealing both nitrogen and phosphorus alternate in limiting the phytoplankton growth along the year. It seems such alternation in the limiting nutrient relies on the combination of natural (lying on young volcanic terrains rich in phosphorus) and anthropic (surrounding by agricultural activities with nitrogen fertilization) influences. In brief, phosphorus limited phytoplankton growth most of the time (5 months), followed by nitrogen (4 months), while there was co-limitation in 3 months.

The absolute concentrations and the stoichiometric ratios in Lake Alchichica show nitrogen as the general limiting nutrient and a high probability of nitrogen plus silicates co-limitation. The potential silicate limitation occurs from October to February, at the end of the late stratification and most of the mixing period, along with the diatom bloom. The potential nitrogen limitation is in March and April, at the end of the mixing and the onset of the stratification periods, along with the N-fixing cyanobacteria bloom. Nutrient enrichment experiments, including the three nutrients, phosphorus, nitrogen, and silicates, showed the nitrogen plus phosphorus and nitrogen plus phosphorus plus silicates treatments induced the highest increases in phytoplankton biomass. Not a single nutrient by itself but only the combination of the two or three nutrients could stimulate phytoplankton growth in the bioassays.

Silicates are seldom considered an essential phytoplankton growth-limiting nutrient, particularly in tropical lakes where silica concentration is usually higher than in temperate lakes since the higher tropical temperatures increase silicates' weathering. However, in diatom-rich lakes, silicate could play the central role in controlling phytoplankton growth. Nonetheless, the ratio of silicates to phosphorus or nitrogen is more important than the absolute concentration of silicates (Lewis 1996). Such seems to be the case in Lake Alchichica, where Adame et al. (2008) found Si:N ratio plays an important role in controlling the magnitude of the winter diatom bloom in Lake Alchichica.

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Chapter 19
Lake Food Webs

Elva Escobar and Javier Alcocer

19.1 Introduction

Lewis (1987, 1996) accounts for relevant differences between temperate and tropical lakes implicating tropical food webs (e.g., more efficient in producing phytoplankton biomass on a given nutrient base, inefficient in passing primary production to the highest trophic levels). Further, Sarmento (2012) found microbial food webs in tropical lakes are especially relevant because it is highly active in extended periods of time, and picocyanobacteria seem to be more abundant and persists for longer periods.

Changes in the lake's hydrodynamic conditions leading to shifts in species structure (e.g., algal composition) and its abundance can change the carbon flux rates (Macek et al. 2009). How planktonic species respond to temperature change and the lake's stratification patterns can lead to community structure shifts, trophic mismatch within the food web, and changes in the flux of organic matter to the neighboring ecosystems in the lake (littoral zone and deep benthos). Then, expected changes associated with global and climate change require understanding how food quantity and quality structure the lake communities and the food web structure. Food webs are important for predicting climate change impacts (IPCC 2019) and forecasting life shifts in a lake.

E. Escobar (✉)
Unidad Académica de Ecología y Biodiversidad Acuática, Instituto de Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México, Ciudad de México, Mexico
e-mail: escobri@cmarl.unam.mx

J. Alcocer
Grupo de Investigación en Limnología Tropical, FES Iztacala, Universidad Nacional Autónoma de México, Tlalnepantla, Estado de México, Mexico
e-mail: jalcocer@unam.mx

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Differences in quantity and quality of the food supply in Lake Alchichica's communities lack updated direct evidence. This knowledge gap limits the understanding of how food supply influences the biodiversity patterns of the lake ecosystem and carbon cycling. Different reports recorded the food-web mediated export of biogenic carbon in Lake Alchichica and how hydrodynamic control defines the species composition (Ortega-Mayagoitia et al. 2011) and carbon fluxes (Oseguera-Pérez et al. 2013). Also, experimental work described the food selectivity based on size, recognized the physiological limits imposed by hypoxia/anoxia and the ultraviolet radiation on pelagic species (Ciros-Pérez et al. 2015). Escobar Briones et al. (1998) described the main organic carbon pathways for the pelagic and littoral systems in Lake Alchichica.

19.2 The Water Column

The pelagic food web is simple, comprising few species (Escobar Briones et al. 1998). The phytoplankton size structure defines three main carbon flux pathways driven by seasonal hydrodynamics along a continuum of conditions from mixing to stratification (Alcocer et al. 2008) and turnover times from long-lived to short-lived organic carbon pools, respectively. In Lake Alchichica, the pathways are (a) remineralization within the bacteria-microzooplankton -microbial- loop (Peštová et al. 2008; Macek et al. 2009; Bautista-Reyes and Macek 2012), (b) food-web transfer of primary production with potential downward flux (Ortega-Mayagoitia et al. 2011; Ciros-Pérez et al. 2015), and (c) the sinking to the deep sediments of ungrazed phytoplankton as particulate organic carbon (POC) or export (Alcocer et al. 2008), related to size, unpalatability, aggregation, vertical migration of zooplankton and their excretion (Escobar Briones et al. 1998).

19.2.1 Microbial Loop

Picoplankton dynamics display a temporal pattern (Peštová et al. 2008; Macek et al. 2009; Bautista-Reyes and Macek 2012). Increasing numbers associated with the mixing and early stratification periods (see Chaps. 7, 11 and 13). The number of cells within the water column is high, even during the long period of anoxia (Macek et al. 2009). Autotrophic picoplankton (APP) contributes ≥30% to total picoplankton (TPP) and is composed dominantly of unicellular picocyanobacteria; picoeukaryotes are below the detection limit. The picophytoplankton biomass contribution to the total chlorophyll-a concentration is 27.7% on average (Adame et al. 2007).

Ciliated peritrichs followed by minute spirotrichs (particularly *Halteria grandinella*) often numerically dominated the ciliate assemblage and emerged as the most efficient picocyanobacteria feeders observed in the surface layer at the end of the mixing period during the development of diatoms (*Cyclotella alchichicana*) and the

Nodularia aff. *spumigena* bloom (Peštová et al. 2008). *Euplotes euryhalinus* was important picocyanobacteria and their colonies' grazers above the oxycline (Macek et al. 2019). Scuticociliates (mainly *Cyclidium glaucoma* and anaerobic species) were the numerically dominant picoplankton consumers within the hypolimnetic assemblages (Bautista-Reyers and Macek 2012). The ciliate *Spirostomum teres* feeds on both picocyanobacteria, purple sulfur bacteria (*Thiocapsa*), and eukaryote phytoplankton (the chlorophytes *Monoraphidium minutum* and *Oocystis* sp., small diatoms *Cyclotella choctawhatcheeana*) in the metalimnion and anoxic hypolimnion (Macek et al. 2020). Protozooplankton species feed upon both heterotrophic and autotrophic picoplankton (Bautista-Reyes and Macek (2012).

Generally, protozooplankton feeding activity is significant during the mixing period (in particular, peritrichs colonizing phytoplankton species) and the stratification, localized above and below the metalimnion. Microaerophilic and anaerobic species play an important role (Sánchez-Medina et al. 2016; Macek et al. 2019, 2020). There is a close relationship between the picoplankton, the lake's hydrodynamics, and protist consumers' presence (see Chaps. 11, 12 and 13).

The production of dissolved organic carbon (DOC) by phytoplankton and inorganic nutrients is expected to be the most critical bottom-up controlling factor for bacterioplankton. Picoplankton maxima appear to be associated with particulate matter resembling clay particles (Macek et al. 2009). APP increase as a result of succession and competition with filamentous cyanobacteria *Nodularia* aff. *spumigena* that constitute the second phytoplankton bloom at the onset of the stratification period (Oliva et al. 2001).

19.2.2 Microbial-Herbivorous Food Web

Phytoplankton is relatively poor (Oliva et al. 2001, see Chap. 12). The chlorophytes *Monoraphidium minutum*, *Oocystis parva*, and picocyanobacteria are the most abundant species in cell numbers. The large centric diatom *Cyclotella alchichicana* contributes to most biomass throughout the year (Oliva et al. 2006), followed by *C. choctawhatcheeana* and *Chaetoceros elmorei* (Oliva et al. 2001). *C. alchichicana* is the principal component of the winter diatom bloom and the deep chlorophyll maximum (DCM) at the metalimnion during the stratification period. It contributes to most POC sinking to the deep sediments (Ortega-Mayagoitia et al. 2011). The $\leq$20 μm phytoplankton fraction consists of the chlorophytes *Monoraphidium* spp., the diatom *C. choctawhatcheeana,* and the picocyanobacteria; small colonies of the mucilaginous chlorophyte *Oocystis parva* occur during the early stages of the stratification (Ortega-Mayagoitia et al. 2011).

The calanoid copepod *Leptodiaptomus garciai*, the rotifers *Hexarthra jenkinae,* and *Brachionus* group 'Mexico,' as well as small heterotrophic flagellates (<10 μm) are the dominant zooplankton components that control and modulate phytoplankton by herbivory (Ortega-Mayagoitia et al. 2011). The zooplankton copes with food scarcity in the water column (a minor amount of small-size edible phytoplankton). Although primary producers are available in large amounts, the species are not palatable for most zooplankton species (e.g., *Nodularia* aff. *spumigena* and other large filamentous cyanobacteria are inedible or with an indigestible mucilaginous envelope) or are segregated by their large size (*C. alchichicana*).

The major challenges for the zooplankton in the epilimnion (Ciros-Pérez et al. 2015) include, in addition to the seasonal and spatial resource availability or limitation (Ortega-Mayagoitia et al. 2011), a risk from predators (i.e., the one-third of the *Poblana alchichica* population that dwells in the pelagic zone) and exposure to damaging ultraviolet radiation (UVR) at the epilimnion. Although diel vertical migration seems to be mostly related to predation avoidance, migration to deep waters also protects copepods from the UVR deleterious effects.

Internal waves (see Chap. 6) promote nutrient pulses which in turn foster food availability (e.g., algae, protozoans, and bacteria), while physiological rates and size are some of the copepods and rotifers responses to famine in the water column (Ortega-Mayagoitia et al. 2011; Ciros-Pérez et al. 2015). Biogenic carbon can be transformed in the microbial loop, consumed, and transferred within the herbivorous food chain within the lake's euphotic zone.

The silverside *Poblana alchichica* are visual predators; carbon stable isotope values recognize them as top pelagic predators (Escobar Briones et al. 1998). Fish remain preferentially in the top of the metalimnion where they feed on zooplankton (see Chap. 15) and avoid being exposed to UVR and waterfowl seasonally visiting the lake.

19.3 Pelagic-Benthic Coupling

Winter mixing promotes turbulence and nutrient availability, favoring the development of a diatom bloom composed mainly by the large diatom species *Cyclotella alchichicana*. Most of this bloom could not be consumed by the metazooplankton and sinks in mass and further deposit in the deep benthic zone (Alcocer et al. 2008). In lakes, massive phytoplankton export has important consequences for nutrient recycling, predator-prey interactions, and the food web's structure and stability. Particulate organic carbon (POC) fluxes in Lake Alchichica (see Chap. 7) fluctuate between 116 and 621 mg/m^2/d (Oseguera et al. 2011; Oseguera-Pérez et al. 2013).

A *Nodularia* aff. *spumigena* bloom developed at the surface waters during the early stratification period. A small portion of this biomass (14% as POC) sinks to the deep sediments but mostly (86% as POC) is wind-transported to the littoral zone (Fig. 19.1) without an apparent effect on the pelagic food chain (Alcocer et al. 2008, 2012; Oseguera et al. 2013).

Stratified most of the year, the sinking of the winter diatom bloom generates hypolimnetic anoxia and prevents the establishment and development of a deep benthic faunal community. The estimated sedimentation rate is 44 μm/s reaching the

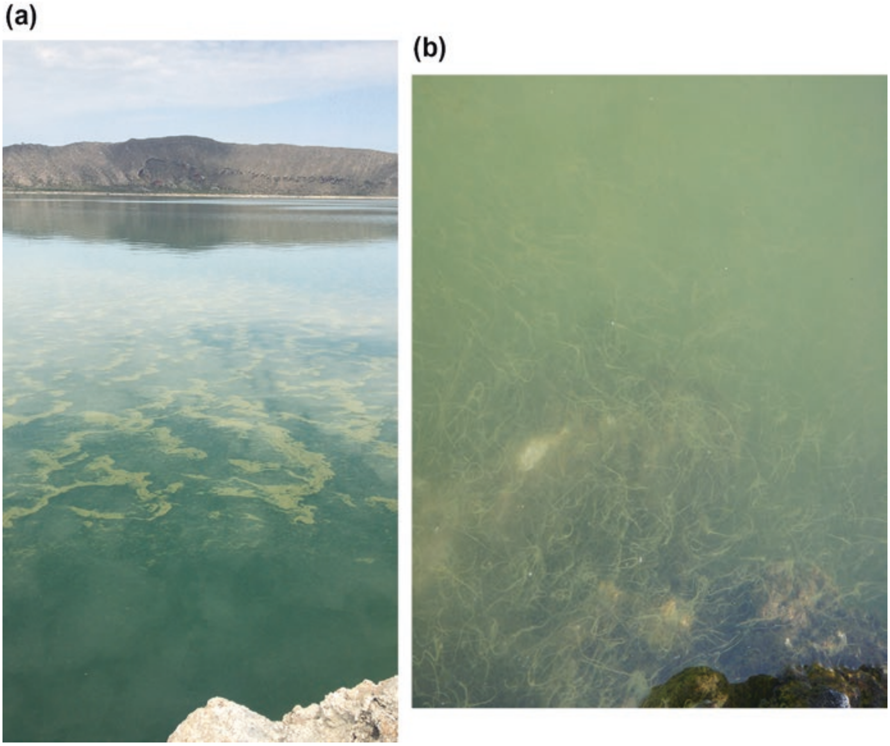

Fig. 19.1 *Nodularia* aff. *spumigena* bloom wind-blown to the littoral zone of Lake Alchichica. (Photographs by Javier Alcocer)

from the euphotic zone down to the lake bottom in 15 days or more, depending on its integration in the food web. Biogenic carbon is exported below the thermocline by sinking not-consumed large phytoplankton cells, and probably copepods fecal pellets from the pelagic herbivorous food web (Alcocer et al. 2008).

Carbon stable isotope results showed that the pelagic environment was more carbon depleted than the littoral (Escobar Briones et al. 1998) and confirmed that *N.* aff. *spumigena* biogenic carbon is not transferred within the pelagic food web (Fig. 19.2). The source endpoint in the simplified pelagic community is the diatomaceous phytoplankton (Escobar Briones et al. 1998).

Mostly *Cyclotella alchichicana* and a small proportion of *Nodularia* aff. *spumigena* are the two biogenic carbon sources contributing to the pelagic-benthic coupling (Escobar Briones et al. 1998); their sinking and deposit support the deep benthic community growth for a short period but also triggers oxygen consumption processes that lead to hypoxia and further anoxia most of the year (Alcocer et al. 2008).

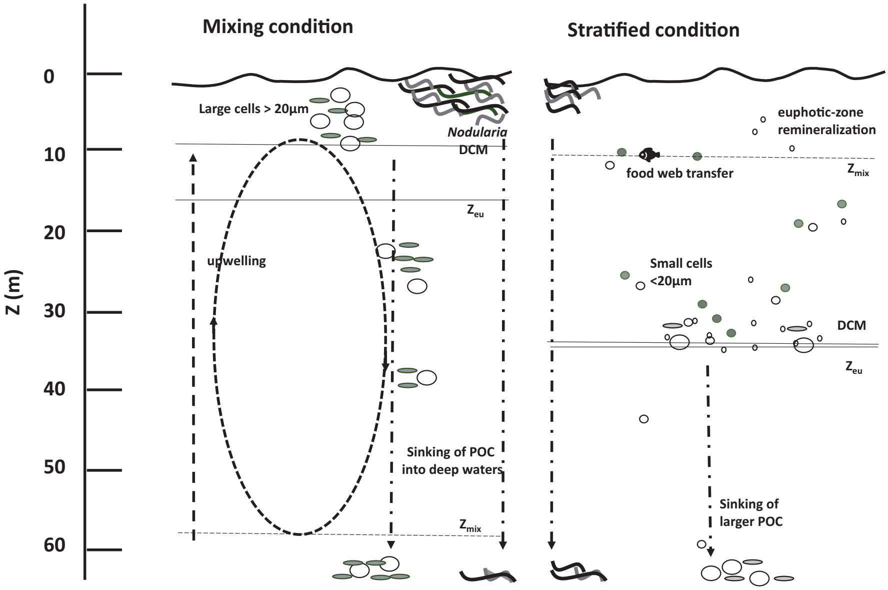

Fig. 19.2 Biogenic carbon pathways in Lake Alchichica as controlled by hydrodynamic conditions. [Abbreviations used: *Z(m)* depth in m, *DCM* Deep Chlorophyll Maximum, Z_{eu} Euphotic zone, Z_{mix} Mixing layer]

19.4 The Deep Zone

In Lake Alchichica, the deep benthos is inhabited by two species: a chironomid midge (*Chironomus alchichica*) contributing with the most significant biomass, until emerging at the onset of the anoxia in the deep zone (Hernández et al. 2014), and an ostracod clam shrimp (*Candona alchichica*) contributing with the largest numbers and undergoing a period of suspended development (diapause) throughout the unfavorable anoxic conditions (Alcocer et al. 2012; Hernández et al. 2014).

As mentioned, through the benthic-pelagic coupling, the winter diatom and the early spring *Nodularia* aff. *spumigena* blooms (Alcocer et al. 2015) represent the arrival of an abundant food supply benefiting the deep benthic community for a few months before the setting of hypolimnetic anoxia (Hernández et al. 2014). Both species take advantage of the lack of competition and predation in the deep benthic zone and use this habitat temporarily to feed, grow and reproduce before the onset of anoxia. The strong dissolved oxygen gradients promote bacteria's temporal development in the sediment (Álvarez-Sánchez et al. 2015). In other deep lakes, chironomids of the deep benthos have been recorded to energetically rely on CH_4-derived carbon from methanotrophic bacteria (Frossard et al. 2015).

19.5 Littoral Zone

The littoral zone of Lake Alchichica is a more complex and productive system than the pelagic (Alcocer et al. 1993). It displays a high habitat diversification and holds a rich species composition (Lugo et al. 1993; Alcocer et al. 1998; see Chap. 8) and is supported by diverse primary energy sources (primary producers: epiphytes, macrophytes, and autochthonous and allochthonous detritus).

Carbon stable isotope results from the littoral community show that the macrophyte *Ruppia maritima* starts the detritus carbon pathway (Escobar Briones et al. 1998). The highly diverse littoral community (see Chap. 10) is represented by gastropods (*Physa* sp.), amphipods (*Hyalella azteca*), corixids (*Krizousacorixa tolteca*), and odonates (*Enallagma praevarum*) as the dominant components. Escobar Briones et al. (1998) found it is largely sustained by *Chladophora* spp. and other epiphyte species.

Littoral benthic macroinvertebrates trophic guilds recognize herbivorous, detritivores, predators, and filter feeders (Pérez-Rodríguez et al. 2013). Each guild's biomass varies spatially and temporally with vegetation coverage and organic matter content in the sediments (see Chaps. 8 and 10).

The silverside *P. alchichica* is a first-level carnivore that feeds on chironomids and amphipods in the littoral zone (Alcocer et al. 2009). These results corroborate Flores Negrete (1998) findings on *P. alchichica* diet based on stomach contents that recorded a mixed diet dominated by benthic macroinvertebrates prey (70%) and a lower proportion of zooplankton (30%), suggesting silversides move between the littoral and the pelagic zones to feed. The cestode *Ligula intestinalis* parasites a

Fig. 19.3 *Nodularia* aff. *spumigena* decomposing at the littoral zone of Lake Alchichica. (Photograph by Luis A. Oseguera)

large number of *P. alchichica*. *L. intestinalis* shows similar carbon stable isotope values as its host.

Often reported as herbivorous, the corixid *K. tolteca* has a carbon stable isotope value as a primary carnivore feeding on protozoa, microscopic metazoans, but also on algae and debris (Escobar Briones et al. 1998). No allochthonous sources, including the wind-transported input of *Nodularia* aff. *spumigena* to the littoral zone seemed to influence the littoral food web directly. The littoral detritus from both the macrophyte *R. maritima* and *N. spumigena* mostly remains in the littoral zone, contributing to carbon storage (Fig. 19.3).

If littoral detritus is transported to deep sediments, it could contribute to more extended carbon storage and increased oxygen consumption for remineralization. In contrast to deep temperate lakes (Pal et al. 2015), the lateral transport of *Nodularia* from the littoral zone into the deep benthos has not been documented in Lake Alchichica. Littoral phytodetritus from detached or decaying macrophyte and *Nodularia* accumulated by the wind in the lake margins move downslope, where they decompose in the deep lake or are buried in the sediments as occurs in Crater Lake, Oregon (Dymond et al. 1996). All three zones, pelagic, littoral and deep benthos, are interconnected through the transport of algae (herbivorous food chain) and detritus (detritivores food chain) in the lake (Fig. 19.4).

The salamander *Ambystoma taylorii* is a top carnivore feeding on atherinid fish and benthic invertebrates in the littoral zone. Seasonal visiting aquatic waterfowl may feed on *P. alchichica* and invertebrates in the littoral zone. The carbon stable isotope values of the littoral zone are more enriched than the pelagic (Escobar Briones et al. 1998).

19.6 Conclusions

Three interconnected districts described the food web in Lake Alchichica: the pelagic, deep lake, and littoral zones. The pelagic and the deep benthic zones food webs are simplified, composed by few species. Primary producers are partitioned by their size structure, leading to three carbon flux pathways (microbial loop, herbivorous food-web transfer, and export to deep sediments of ungrazed phytoplankton), and by turnover times that change with the seasonal hydrodynamics (mixing and stratification) in a food-limited food web. Pelagic-benthic coupling supports the deep benthic community feeding on the freshly exported diatoms to deep sediments until the onset of anoxia. The littoral zone is a more complex and productive system defined by higher diversity and trophic options. It is connected to the pelagic zone through the *Nodularia* bloom exportation, which is wind-transported into the littoral zone contributing to the detritus food web. There is scarce information on the lake's food web structure and flow, with only one study based on stable isotope analysis and a few studies that provide stocks and fluxes.

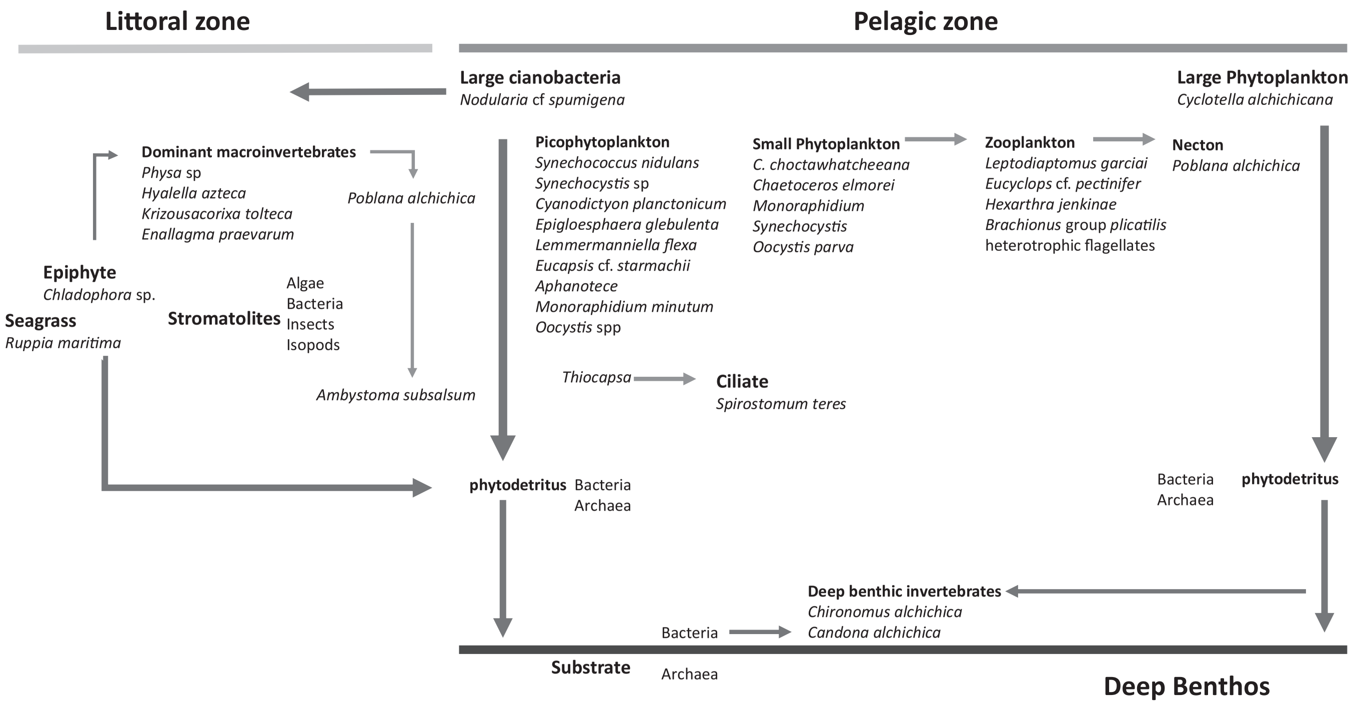

Fig. 19.4 Lake Alchichica pelagic, deep benthic, and littoral food web interconnectivity

19.7 Next Steps

Future studies on Lake Alchichica food web need to be focus on the function of the lake ecosystem as follow.

(a) describe the role of detritus in both the littoral and deep benthos zones
(b) depict the stromatolite cosmos and associated life, its connectivity to the pelagic and littoral zones, the changes with depth and desiccation
(c) illustrate the deep pelagic and benthic food web
(d) trace food uptake isotopically by labeling the food in pulse-chase experiments to experimentally delineate trophic pathways and identify the taxa that dominate and initiate food uptake from differing food sources
(e) explain the role of vertebrates (silverside, salamander, and waterfowl) and the use of the pelagic and littoral ecosystem energy resources
(f) clarify the autotrophic, chemoautotrophic, and detritus carbon pathways in the pelagic and benthic ecosystems

This information is required to reveal the carbon budgets and fluxes, ecological forecasting models to define pollution and global and climate change scenarios, and the stable isotopic signatures. Food webs in Lake Alchichica acquire particular importance in the future when evaluating the climate change impacts that can lead to community shifts, carbon flux changes, and loss of ecosystem services.

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Chapter 20
Diversity and Endemisms

Elizabeth Ortega-Mayagoitia, Gloria Vilaclara,
Rocío J. Alcántara-Hernández, and Miroslav Macek

20.1 Introduction

The total number of species and the number of exclusive, endemic species inhabiting a geographic area or even a single environment are two fundamental elements in the sphere of management and conservation policies. For example, biodiversity hotspots are relatively small areas where species richness and endemism levels are high, and organisms are facing a strong threat of habitat loss (Reid 1998). Therefore, the biological diversity inventory is a mandatory first step that in a relatively small and geologically young lake such as Alchichica could resemble a simple task. However, it has been a quite complex and slow process.

20.2 Diversity and Endemic Species: A Fascinating, Never-Ending Story

The number of species that a single lake can host depends on several factors acting at different temporal and spatial scales. These factors range from local interactions such as competition and predation to long-term continental processes such as

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

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

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glaciation, speciation/extinction rates, and dispersal barriers originated by plate tectonics (Brönmark and Hansson 2005). Further, inside a lake itself, the environment is not homogeneous, and there are species with different adaptations to exploit different ecological opportunities. Usually, the littoral zone is the most heterogeneous due to the physical structures produced by riparian and submerged vegetation, different kinds of sediments, and substrates, among others. It hosts a higher number of species compared to the water column (Schindler and Scheuerell 2002). However, the diversity observed in the water column may increase when including detailed analyses of microstratified, microaerobic, and anaerobic zones of the water column, with plenty of resource-rich niches controlled by the position of thermocline, as well as the anoxic hypolimnion (see Chap. 11 Bacterioplankton and Chap. 13 Protozooplankton).

In Lake Alchichica, an additional element increases the environmental complexity, enhancing species richness. The ring of tufa (i.e., stromatolites) circling the littoral zone, which creates small, isolated ponds, offers a myriad of microhabitats itself, and forms high vertical, underwater walls (see Chap. 10, The littoral community, and Chap. 22, Microbialites: diversity hotspots in the Mexican Plateau).

There is, however, another factor that heavily influences the number of species we know in each environment: the human factor. Each human scholar has the free will to choose the biological group she/he will investigate. Some biological groups are more attractive than others, producing an uneven understanding of the different branches of the tree of life. Also, and for practical uses, each scholar decides what a species is, how to name it, how to classify it, and how, when, and where to look for it. Inadvertently, such decisions are strongly impinged not only by personal and academic backgrounds but by technical advances and even by philosophical and sociopolitical settings.

Throughout the years, the practice of identifying species within each biological group has evolved at a different pace and followed slightly different paths due to the available technology. For hundreds of years, the best-studied species were animals, land plants, and fungi, which were defined mainly in terms of morphological discontinuities (Paterlini 2007). The number of records of these three groups in current electronic catalogs of life is a testimony of this historical bias. However, thanks to the advent of the microscope first and molecular tools more recently, life has revealed an astonishingly diverse microbial treasure: the immense majority of life forms on Earth are eukaryotic single-celled species (traditionally called protists), Bacteria, and Archaea (Burki et al. 2020; Yilmaz et al. 2014). Although in many groups, identifications still rely heavily on morphological characters, the biologist's toolkit nowadays can include cultures, molecular markers, ecophysiological experiments, and reproductive compatibility trials.

Following this historical path, the first records of the biological diversity in Lake Alchichica were animals and were based mainly on morphological characters. The copepod *Leptodiaptomus* (*Diaptomus*) *garciai* (Osorio-Tafall) and the silverside *Poblana alchichica* De Buen were described according to the current systematic standards and announced as new species in 1942 and 1945, respectively (Osorio-Tafall 1942; de Buen 1945; see also Chap. 14, Metazooplankton, and Chap. 15, Alchichica silverside). These two cases illustrate how systematics and personal points of view influence the perceived diversity and endemicity in an environment.

As early as 1953, Wilson and Yeats decided that the copepod inhabiting Alchichica was a population of the North American *Diaptomus novamexicanus* and considered *D. garciai* a synonym, extending the ecological range of the freshwater copepod to saline waters (Wilson and Yeats 1953). Later, when the genus *Diaptomus* underwent a major systematic revision and was split into smaller genera, it was assigned to *Leptodiaptomus*. Thus, the first paper on the ecology of the population inhabiting Alchichica was published as *L. novamexicanus* (Lugo et al. 1999). More than 50 years later, a study applying COI barcoding, reproductive trials, and eco-physiological tests showed that despite morphological differences are subtle, the copepod from Alchichica, now *Leptodiaptomus garciai,* was a valid name assigned to a species that is genetically, reproductively, and ecologically isolated from *L. novamexicanus* (Montiel-Martínez et al. 2008). Although he used only morphological traits, Osorio-Tafall was right from the start.

The silverside *Poblana alchichica* has been the subject of several studies regarding its taxonomic status and diversification patterns in Atherinidae in North America. There are other silversides in the neighboring lakes that were initially recognized as different, microendemic species: *P. letholepis* Alvarez, 1950 in Lake La Preciosa and *P. squamata* Alvarez, 1950 in Lake Quechulac. The status of the three species has been controversial because others have qualified their morphological divergence as non-significant, and their COI sequences are identical (Valdez-Moreno et al. 2009). Attending these criteria, they have been considered conspecific (*P. alchichica* with three subspecies) or members of the genus *Menidia*, given their low COI divergence with *M. menidia*. Later phylogenetic studies have shown that all members of the genus *Poblana* do form a monophyletic group closer to *Chirostoma* than to *Menidia*. However, the proper delimitation of the three genera and species within *Poblana* still awaits clarification (Bloom et al. 2009).

Meanwhile, the three species with their original names are regarded as valid in FishBase (Froese and Pauly 2020). To summarize, the story goes like this: the number of fish species in the three crater lakes went from three new species belonging to a new genus to a single species with three sub-species belonging to a pre-existing, widely distributed genus. In the end, the original taxonomic assignment prevailed, but the story is far from concluded.

From the early studies of the 1940s to recent years, the number of species found in Alchichica increased as new generations of researchers interested in the littoral, the stromatolites, the pelagic, and deep benthic zones (see next section). Remarkably, several species that in the subsequent decades would be recognized as new, endemic species, initially were misidentified: the now emblematic diatom *Cyclotella alchichicana* Oliva et al. 2006 was first identified as *Stephanodiscus niagarae* (Arredondo et al. 1984) or *Cyclotella quillensis* (Oliva et al. 2001); the rotifer *Brachionus* sp.

'Mexico' that inhabits Alchichica, Atexcac and La Preciosa (Alcántara-Rodríguez et al. 2012) appeared in a paper as *Brachionus rotundiformis* (Sarma et al. 2002); the insect *Chironomus alchichica* Acosta & Prat, 2017 was incorrectly identified as *Chironomus stigmaterus* (Alcocer et al. 2016); the ostracod *Limnocytherina axalapasco* Cohuo-Durán, Pérez & Karanovic (2014) was in a first moment confounded with *Limnocythere inopinata* (Hernández et al. 2010). Sometimes the discovery they were new, endemic species came after an observation during the peer-review process, or with a newcomer looking for cryptic diversity, or simply a well-trained eye that was able to see beyond the -apparently- obvious.

Other species have been uncovered straightforwardly, thanks to easily observable traits like in the case of the amphipod *Caecidotea williamsi* Escobar-Briones & Alcocer 2002, or by the intervention of young specialists as happened with *Candona alchichica* Cohuo, Hernández, Pérez & Alcocer (2017), or by renowned authorities in the field, like the description of *Cletocamptus gomezi* Suárez-Morales, Barrera-Moreno & Ciros-Pérez (2013), and the cyanobacterial species *Entophysalis litophila, E. atrata, Chamaesiphon halophilus, Heteroleibleinia profunda, Mantellum rubrum* and *Xenococcus candelariae* Tavera & Komárek (1996), and *Gloeomargarita litophila* Moreira et al. (2017).

Overall, up to date, there are 18 recognized endemic species (7 cyanobacteria, 11 eukaryotes) inhabiting Lake Alchichica (16 exclusive, 2 shared with neighboring lakes), but we can foreshadow that the list will grow in the short term. Systematic studies have invigorated recently with the use of molecular markers, as part of a polyphasic approach to uncover the diversity of prokaryotes in Alchichica (Aguila et al. 2021; Moreira et al. 2017; Chaps. 11 and 22, Bacterioplankton and Microbialites: Diversity hotspots in the Mexican Plateau). An ongoing project on metabarcoding suggests that there are nearly 8600 Amplicon Sequence Variants (ASVs of the 16S rRNA gene with 100% sequence identity) related to Bacteria and Archaea (unpublished data). These data suggest that from these sequences, 14 Archaea and 544 Bacteria genera are present in the sediment, microbialites, and water samples from the littoral and pelagic zones of Lake Alchichica. However, most of the sequences cannot be assigned at the genus level, leaving a considerable task pending identifying Lake Alchichica prokaryotes by polyphasic approaches in the future.

The preceding paragraphs show that knowing how many species there are in a lake is an arduous process. New, endemic species are frequently overlooked, and their status can be controversial. With such considerations in mind, we present the most comprehensive list ever published of the known specific diversity of Lake Alchichica.

20.3 How Many Species Do We Know in Lake Alchichica?

The species list that closes this chapter gathers the species richness of Lake Alchichica, known after 80 years of research. Most species have appeared previously in peer-reviewed papers, and others are mentioned for the first time in the preceding chapters of this book.

Modern systematics pursues a unified three-domain taxonomy, making classification consistent with phylogeny (Yilmaz et al. 2014). To organize the species list in a coherent whole, we adopted the phylogenomic classification framework of the SILVA rRNA database project (Yilmaz et al. 2014), which integrates the classification system of Eukarya proposed by Adl et al. (2005, 2012, 2019). Within the framework of the phylogenomic approach of Adl et al. (2019), the classification of unicellular organisms is well resolved. However, inevitably we had to draw upon the most recent Linnean-based classifications to integrate the names of Metazoa (animals) and Streptophyta (charophytes and plants) species. Current supraspecific classification, valid/correct binomina, and authorities were confirmed in Catalogue of Life (https://www.catalogueoflife.org/), World Register of Marine Species (http://www.marinespecies.org/), AlgaeBase (https://www.algaebase.org/) and the SILVA database (https://www.arb-silva.de/), using the version 138 released in November 2020.

Although some biological groups still await proper study (birds, fungi, parasites of invertebrates, etc.), the known biological diversity of Lake Alchichica encompasses distant branches of the three domains of life: Bacteria (37 genera and species reported), Archaea (8 genera identified) and Eukarya (196 genera and species), rendering a list of 241 taxa identified thus far. Inevitably, the length and composition of the list show not only the outcome of natural processes, but the expertise and experience of the researchers attracted to Lake Alchichica, in addition to the array of tools they had applied.

The task of comparing the taxonomic richness in the three domains of life is not straightforward due to the different species concepts and tools applied in each field (de Queiroz 2007). In prokaryotes, 18 bacterial and archaeal genera were detected exclusively with metabarcoding techniques. The remaining prokaryotes and eukaryotes were diagnosed with morphological or polyphasic approaches.

The most integral project for surveying Bacteria and Archaea in Lake Alchichica includes samples from the sediments, microbialites, and water column, all of them collected during the stratification period of the lake (unpublished data). Most of the identified bacterial taxa are Cyanobacteria (89%), with minor proportions of Bacteroidota and Proteobacteria (5.5% each). Members of the phylum Cyanobacteria are the most often identified due to their biogeochemical functions (C and N fixation) and relative abundance in the lake (see Chaps. 11 and 12). Archaeal diversity and its taxonomic affiliation are just being explored. In this case, the phylum Euryarchaeota was the most represented with 75% of the ASVs.

Table 20.1 Specific richness (S) of eukaryotic supergroups found in Lake Alchichica

	S	%
TSAR	96	49.0
Amorphea	73	37.2
Archaeplastida	12	6.6
Discoba	11	5.6
Haptista	1	0.5
Cryptista	1	0.5
Incertae sedis	1	0.5
Total	196	

In Eukarya, the supergroup TSAR is by far the most diverse (Table 20.1). The largest share are ciliates (42) and diatoms (45). The second most important supergroup is Amorphea, which includes 66 metazoan species (animals). In Archaeplastida, six species are embryophytes (plants). Interestingly, 63% of all Eukarya species here reported are protists (unicellular eukaryotes), constituting a more balanced view of the actual distribution of life forms across the eukaryotic tree of life (Burki et al. 2020).

Concerning habitats, 150 species are considered exclusively littoral and amount a significant proportion of taxa (62%), as expected due to the heterogeneous composition and morphometry of Lake Alchichica. The reported taxa found in the microbialites constitute nearly 58% of the prokaryotic diversity. In Chap. 10 (The littoral benthic community), the number of species, including macroinvertebrates, protozoans, and diatoms, is considered moderate compared to other lakes. In contrast, the pelagic environment is inhabited by 53 species (22%), a number considered low regarding phytoplankton (15 species, Chap. 12, Phytoplankton of Alchichica), ciliates (25 species, Chap. 13, Protozooplankton), metazooplankton (3 species, Chap. 14), fish (1 species Chap. 15, Alchichica silverside). The parasites of the silverside *P. alchichica* amount to 4% of the species.

20.4 Concluding Remarks

Given the relatively low species richness in Lake Alchichica, the number of endemic species is a striking and attractive attribute. This geologically young (13.3 to 6.3 ka) and small (2.4 km^2) lake holds a known overall richness of 241 taxa (Tables 20.2 and 20.3), among which 18 (7.5%) are endemic (Tables 20.2 and 20.3). Given the disparity in the sampling effort and the identification methods employed across biological groups, this figure is relative. For example, if only plants and animals were considered, endemicity rises to 14% (total richness = 73; endemic = 10). Even more, if we use the common approximation of focusing on particular taxa, the share of endemicity soars: if only vertebrates are accounted (*P. alchichica*, and *A. taylori*), then 100% of species are endemic; four out of six species (67%) of crustaceans thus far recorded (*C. williamsi*, *L. garciai, C. gomezi, C. alchichica*) are also exclusive of this lake. As more unique, endemic eukaryotic and especially prokaryotic taxa are found, species richness and global endemicity indicators will surely rise.

Another interesting indicator of the importance of endemic species in Lake Alchichica is that endemic species do not restrict to a single group but belong in several distant branches of the tree of life, including bacteria, diatoms, crustaceans, insects, and vertebrates. Additionally, they are present in – or even dominate – every functional community and possess unique biological or ecological features: the only pelagic predator, *P. alchichica* is endemic, as are the two main components of the plankton biomass: the copepod *L. garciai* and the diatom *C. alchichicana* (Chaps. 14 and 12, respectively). The amphipod *C. williamsi* is the first asellid recorded in saline environments and is highly specialized in inhabiting crevices in the stromatolites (Escobar-Briones and Alcocer 2002). *G. litophila*, associated with the microbialites, was the first known cyanobacterium with intracellular carbonate inclusions (Moreira et al. 2017). The salamander *A. taylori* is a model for the evolution of obligated paedomorphy (Percino-Daniel et al. 2016). The list goes on.

The evolution of neoendemic species is favored by high diversification rates, limited dispersal capabilities, and local conditions hampering the invasion of cosmopolitan taxa (Martens and Segers 2014). In Lake Alchichica, the study of the evolutionary processes behind endemicity began just a few years ago. As far as we know, the peculiar ionic conditions and geographical isolation could have played a key role in the diversification process, promoting local adaptation and genetic isolation from other populations (Percino-Daniel et al. 2016; Bloom et al. 2013; Chaps. 12, Phytoplankton of Alchichica, and Chap. 14, Metazooplankton). Moreover, ionic conditions also seem to restrict the establishment of species from geographically close lakes. To acquire a better understanding of these diversification processes, we should extend our efforts to, at least, the neighboring lakes. Surely, they will provide many answers and, we hope, new questions, so we can continue this never-ending story.

Finally, it is important to note that all this exciting effort to discover the wonders still hidden in Alchichica may be dramatically interrupted by the increasing threats to the conservation of the lake habitats and, with it, the peculiar biota adapted to this unique environment (see Chap 5, Hydrogeology and Hydrochemistry, and Chap. 21, Conservation actions).

Table 20.2 Main Archaea and Bacteria detected in Lake Alchichica

ARCHAEA	Habitat	Identified by
● Archaea		
● ● Altiarchaeota (Silva rRNA database project)		
● ● ● Altiarchaeia		
● ● ● ● Altiarchaeales		
● ● ● ● ● Altiarchaeaceae		
Candidatus Altiarchaeum	Sed	M
● ● Crenarchaeota (Silva rRNA database project)		
● ● ● Nitrososphaeria		
● ● ● ● Nitrosopumilales		
● ● ● ● ● Nitrosopumilaceae		
Candidatus Nitrosotenuis	Sed	M
● ● Euryarchaeota (Silva rRNA database project)		
● ● ● Methanobacteria		
● ● ● ● Methanobacteriales		
● ● ● ● ● Methanobacteriaceae		
Methanobacterium	Sed	M
● ● ● Thermococci (Silva rRNA database project)		
● ● ● ● Methanofastidiosales		
● ● ● ● ● Methanofastidiosaceae		
Candidatus Methanofastidiosum	Sed	M
● ● ● Methanomicrobia (Silva rRNA database project)		
● ● ● ● Methanomicrobiales		
● ● ● ● ● Methanocorpusculaceae		
Methanocalculus	Sed	M
● ● ● ● ● Methanoregulaceae		
Methanolinea	Sed	M
● ● ● Methanosarcinia (Silva rRNA database project)		
● ● ● ● Methanosarciniales		
● ● ● ● ● Methanosaetaceae		
Methanosaeta	Sed	M
● ● ● ● ● Methanosarcinaceae		
Methanolobus	Sed	M
BACTERIA		
● Bacteria		
● ● Bacteroidota (Silva rRNA database project)		
● ● ● Bacteroidia		
● ● ● ● Flavobacteriales		
● ● ● ● ● Flavobacteriaceae		
Flavobacterium	P	M
Planktosalinus	P	M
● ● Cyanobacteria		
● ● ● Cyanobacteriia (Silva rRNA database project)		

(continued)

Table 20.2 (continued)

●●●●Cyanobacteriales		
●●●●●Cyanobacteriaceae		
Chroococcus sp.	Mi, Sed	PA, M
●●●●●Nostocaceae		
Calothrix sp.	Mi	M
Calothrix cf. *parietina* Thuret ex Bornet & Flahault 1886	Mi	PA
Nodularia sp.	P, Sed	M
Nodularia aff. *spumigena* Mertens ex Bornet & Flahault 1888	P	PA
Rivularia sp.	Mi	M
Rivularia cf. *haematites* C. Agardh ex Bornet & Flahault 1886	Mi	PA
Trichormus sp. Tavera & Komárek 1996	Mi, P	PA
●●●●●Phormidiaceae		
Tychonema sp.	Sed, Mi	PA, M
●●●●●Xenococcaceae		
Chroococcidium sp.	Mi	PA
Chroococcidium gelatinosum Geitler 1933	Mi	PA
Myxosarcina sp.	Mi	PA
Xenococcus sp.	Sed, Mi	M
* ***Xenococcus candelariae* Tavera & Komárek 1996**	E	PA
●●●●Eurycoccales		
●●●●●Eurycoccales *Incertae Sedis*		
Candidatus Gloeomargarita	Mi	M
* ***Gloeomargarita lithophora* Moreira et al. 2017**	Mi	PA
●●●●Phormidesmiales		
●●●●●Nodosilineaceae		
Haloleptolyngbya sp.	Mi	PA
Halomicronema sp.	Mi	PA, M
Leptolyngbya sp.	Mi, Sed	PA, M
Nodosilinea sp.	Mi, Sed	PA, M
●●●●Pseudanabaenales		
●●●●●Pseudanabaenaceae		
Pseudanabaena sp.	P	M
●●●●Synechococcales		
●●●●●Cyanobiaceae		
Cyanobium/Synechococcus sp.	P, Mi, Sed	PA, M
Prochlorococcus sp.	Mi	PA
Synechocystis sp.	P	M
●●●●Thermosynechococcales		
●●●●●Acaryochloridaceae		
Acaryochloris sp.	Mi	M

(continued)

Table 20.2 (continued)

●●● Cyanophyceae (Algaebase)		
●●●● Chroococcales		
●●●●● Chroococcaceae		
Chroococcus schizodermaticus West 1892	Mi	PA
* ***Entophysalis atrata*** **Tavera & Komárek 1996**	Mi, P	PA
* ***Entophysalis lithophyla*** **Tavera & Komárek 1996**	Mi, P	PA
●●●● Synechococcales		
●●●●● Chamaesiphonaceae		
* ***Chamaesiphon halophilus*** **Tavera & Komárek 1996**	E	PA
●●●●● Merismopediaceae		
Eucapsis cf. *starmachii* Komárek & Hindák 1989	Mi, P	PA
* ***Mantellum rubrum*** **Tavera & Komárek 1996**	E	PA
●●●●● Synechococcaceae		
Epigloeosphaera cf. *glebulenta* (Zalessky) Komárková-Legnerová 1991	P	PA
Lemmermanniella cf. *flexa* Hindák 1985	P	PA
●●●●● Synechococcales *Incertae sedis*		
* ***Heteroleibleinia profunda*** **Tavera & Komárek 1996**	E	PA
●● Proteobacteria		
●●● Alphaproteobacteria		
●●●● Rhodobacterales		
●●●●● Rhodobacteraceae		
Paracoccus sp.	P	M, PA
●●● Gammaproteobacteria		
●●●● Chromatiales		
●●●●● Chromatiaceae		
Thiocapsa sp.	P	M, PA

The list includes species reported and identified by polyphasic approaches [see references and Chap. 12], while other genera have been detected by metabarcoding of the 16S rRNA gene (V4 region) (unpublished data). The classification system is according to the SILVA rRNA database project (https://www.arb-silva.de/) (v138, release 11–2020), and those species not found in the Silva database project are according to the Algaebase (https://www.algaebase.org/). For further information on the ecology and occurrence of these species, please refer to the corresponding chapters of this book.

Habitat, P: pelagic, Sed: sediment, Mi: littoral microbialite, E: Epiphyte. Identified by M: metabarcoding, PA: polyphasic approach. Endemic species are in bold characters and an (*)

Table 20.3 Eukaryotic diversity in Lake Alchichica

TSAR	Habitat
● Stramenopiles Patterson 1989, emend. Adl et al. 2005	
●● Gyrista	
●●● Ochrophyta	
●●●● Chrysista	
●●●●● Chrysophyceae	
●●●●●● Ochromonadales	
Ochromonas sp.	P
Spumella (*Monas*) *guttula* (Ehrenberg, 1830)	L
Spumella (Monas) *minima* (Meyer, 1897)	L
Spumella (Monas) termo (Müller) Tanichev, 1993	L
Spumella (Monas) vivipara (Ehrenberg) Kent, 1881	L
●●●● Diatomista	
●●●●● Diatomeae	
●●●●●● Bacillariophytina	
●●●●●●● Mediophyceae	
●●●●●●●● Chaetocerotophycidae	
Chaetoceros elmorei Boyer, 1914	P
●●●●●●●● Thalassiosirophycidae	
* ***Cyclotella alchichicana*** **Oliva et al., 2006**	P
Cyclotella choctawhatcheeana Prasad, 1990	P
Cyclotella group *meneghiniana* Kützing, 1844	L
●●●●●●● Bacillariophyceae	
●●●●●●●● Fragilariophycidae	
Pseudostaurosira brevistriata (Grunow) D.M.Williams & Round, 1988	L
●●●●●●●● Bacillariophycidae	
Achnanthes sp.	L
Amphora libyca Ehrenberg, 1841	L
Amphora pediculus (Kützing) Grunow, 1875	L
*Anomoeoneis costata (*Kützing) Hustedt,1959	L
Anomoeoneis sphaerophora Pfitzer, 1871	L
Caloneis westii (W. Smith) Hendey, 1964	L
*Campylodiscus clypeus (*Ehrenberg) Ehrenberg ex Kützing, 1844	L
Cocconeis placentula var. *lineata* (Ehrenberg) Van Heurck, 1885	L
Cocconeis placentula var. *euglypta* (Ehrenberg) Grunow, *1884*	L
Craticula sp.	L
Cymbella cistula (Ehrenberg) O. Kirchner, 1878	L
Cymbella mexicana (Ehrenberg) Cleve, 1894	L
Denticula sp.	L

(continued)

Table 20.3 (continued)

TSAR		Habitat
	Diploneis pseudovalis Hustedt, 1930	L
	Entomoneis alata (Ehrenberg) Ehrenberg, 1845	L
	Epithemia argus (Ehrenberg) Kützing, 1844	L
	Epithemia sorex Kützing, 1844	L
	Epithemia turgida (Ehrenberg) Kützing, 1844	L
	Gomphoneis olivaceum (Hornemann) Ehrenberg, 1838	L
	Gomphonema clavatum Ehrenberg, 1832	L
	Gyrosigma acuminatum (Kützing) Rabenhorst, 1853	L
	Halamphora sp.	P
	Halamphora veneta (Kützing) Levkov, 2009	L
	Hippodonta sp.	L
	Mastogloia elliptica (C. Agardh) Cleve, 1893	L
	Mastogloia smithii Thwaites ex W. Smith, 1856	L
	Navicula cryptocephala Kützing, 1844	L
	Navicula radiosa Kützing, 1844	L
	Navicymbula pusilla (Grunow) Krammer, 2003	L
	Nitzschia vitrea G. Norman, 1861	L
	Nitzschia communis Rabenhorst, 1860	L
	Nitzschia frustulum (Kützing) Grunow, 1880	L
	Nitzschia gracilis Hantzsch, 1860	L
	Nitzschia vitrea Hantzsch ex Rabenhorst, 1862	L
	Pinnularia sp.	L
	Pinnularia brevissonii (Kützing) Rabenhorst, 1864	L
	Rhopalodia gibberula (Ehrenberg) O. Müller, 1895	L
	Stauroneis sp.	L
	Surirella ovalis Brébisson, 1838	L
	Surirella striatula Turpin, 1828	L
● ● ● Actinophryidae		
	Actinophrys sol Ehrenberg, 1830	L
	Actinosphaerium eichornii (Ehrenberg) Stein, 1857	L
● Alveolata Cavalier-Smith 1991		
● ● Dinoflagellata		
● ● ● Dinophyceae		
● ● ● ● Peridiniphycidae		
● ● ● ● ● Peridiniales		
	aff. *Parvodinium*	P
● ● Ciliophora		
● ● ● Postciliodesmatophora		
● ● ● ● Heterotrichea		
● ● ● ● ● Spirostomidae		
	Spirostomum teres Claparède & Lachmann, 1859	P

(continued)

Table 20.3 (continued)

TSAR	Habitat
●●●●●Stentoridae	
Stentor multiformis (Müller,1786) Ehrenberg 1838	P
●●●Intramacronucleata	
●●●●SAL (Spirotrichea (S), Armophorea (A) and Litostomatea (L))	
●●●●●Mesodiniidae Jankowski, 1980. *Incertae sedis*	
Mesodinium sp.	P
Mesodinium acarus Stein, 1863	L
●●●●●Spirotrichea	
●●●●●●Euplotia	
●●●●●●●Euplotida	
●●●●●●●●Aspidicidae	
Aspidisca cicada (O.F. Müller, 1786)	L
●●●●●●●●Euplotidae	
Euplotes euryhalinus Valbonesi & Luporini, 1990	P
●●●●●●Perilemmaphora	
●●●●●●●Hypotrichia	
●●●●●●●●Stichotrichida	
●●●●●●●● ●Halteriidae	
Halteria grandinella (Müller, 1773)	L, P
●●●●●●●● ●Oxytrichidae	
Oxytricha sp.	L
Stylonychia notophora Stokes, 1885	L
●●●●●●●● ●Uroleptidae	
Uroleptus rattulus Stein, 1859	P
●●●●●Lamellicorticata	
●●●●●●Armophorea	
●●●●●●●Metopida	
●●●●●●●●Metopidae	
Brachonella sp.	P
●●●●●●●Caenomorphidae	
Caenomorpha cf. *lauterborni* Kahl, 1927	P
●●●●●●Litostomatea	
●●●●●●●Haptoria	
●●●●●●●●Lacrymariidae	
Phialina sp.	P
●●●●●●●●Didiniidae	
Monodinium cf. *balbianii* var. *nanum* Fabre-Domergue, 1888	P
●●●●●●●●Pleurostomatida	
●●●●●●●● ●Litonotidae	
Litonotus sp.	P
Litonotus fasciola (Müller, 1773)	L

(continued)

Table 20.3 (continued)

TSAR	Habitat
●●●●●●●●Spathidiida	
●●●●●●●● ●Actinobolinidae	
Actinobolina sp.	P
Belonophrya sp.	P
●●●●●●●● ●Enchelydae	
Enchelys simplex Kahl, 1926	L
●●●●●●●● ●Trachelophyllidae	
Lagynophrya sp.	P
●●●●CONTHREEP (Colpodea (C), Oligohymenophorea (O), Nassophorea (N), Phyllopharyngea (P), Prostomatea (P), and Plagiopylea (P)	
●●●●●Phyllopharyngea	
●●●●●●Subkinetalia	
●●●●●●●Cyrtophoria	
●●●●●●●●Chlamydodontida	
●●●●●●●● ●Chilodonellidae	
*Chilodonella uncinata (*Ehrenberg, 1838)	L
●●●●●●●●Dysteriida	
●●●●●●●● ●Dysteriidae	
Trochilia minuta (Roux, 1899) Kahl, 1931	L
●●●●●●●Suctoria	
●●●●●●●●Exogenida	
●●●●●●●● ●Podophryidae	
Sphaerophrya canelli Clement, 1967	P
Sphaerophrya soliformis Lauterborn, 1908	L
●●●●●Prostomatea	
●●●●●●Prorodontida	
●●●●●●●Holophryidae	
Holophrya cf. *aklitolophon* Hiller & Bardele, 1988	P
Holophrya simplex Schewiakoff, 1893	L
●●●●●Plagiopylea	
●●●●●●Plagiopylida	
●●●●●●●Epalxellidae	
Epalxella sp.	P
●●●●●Oligohymenophorea	
●●●●●●Peritrichia	
●●●●●●●Sessilida	
●●●●●●●●Epistylididae	
Rhabdostyla sp.	P
●●●●●●●●Vorticellidae	
Pelagovorticella natans Jankowski, 1985	P
Vorticella sp.	P
Vorticella aquadulcis – complex	P
●●●●●●●●Vaginicolae	

(continued)

Table 20.3 (continued)

TSAR	Habitat
Cothurnia sp.	L
●●●●●● Scuticociliatia	
●●●●●●● Philasterida	
●●●●●●●● Uronematidae	
Uronema sp.	L, P
●●●●●●● Pleuronematida	
●●●●●●●● Cyclidiidae	
Cristigera sp.	P
Cyclidium sp.	P
Cyclidium glaucoma Müller, 1773	L, P
Cyclidum citrullus Cohn, 1865	L
Cyclidium porcatum Esteban, Guhl, Clarke, Finlay & Embley, 1993	P
Isocyclidium globosum Esteban, Finlay & Embley, 1993	P
●●●●●●●● Pleuronematidae	
Pleuronema sp.	P
●●●●●● Scuticociliatia	
●●●●●●● Loxocephalida	
●●●●●●●● Cinetochilidae	
Cinetochilum margaritaceum Perty, 1849	L, P
●●● Intramacronucleata	
Sathrophilus sp.	P
● Rhizaria Cavalier-Smith 2002	
●● Cercozoa	
Gymnophrys cometa Cienkowski, 1876	L
HAPTISTA	
● Haptista Cavalier-Smith 2003	
●● Haptophyta	
●●● Prymnesiophyceae	
●●●● Isochrysidales	
aff. *Tisochrysis*	P
CRYPTISTA	
● Cryptista Adl et al. 2019	
●● Cryptophyceae	
●●● Cryptomonadales	
Cryptomonas sp.	P
ARCHAEPLASTIDA	
● Chloroplastida Adl et al. 2005	
●● Chlorophyta	
●●● Ulvophyceae	
Cladophora sp.	L
●●● Trebouxiophyceae	

(continued)

Table 20.3 (continued)

TSAR	Habitat
Monoraphidium dybowskii (Woloszynska) Hindák & Komárková-Legnerová, 1969	P
Monoraphidim minutum (Naegeli) Komárková-Legnerová, 1969	P
Oocystis parva West & G.S. West, 1898	P
Oocystis submarina Lagerheim, 1886	P
Picochlorum sp.	P
●●Streptophyta	
●●●Phragmoplastophyta	
●●●●Charophyceae	
Chara canescens Loiseleur, 1810	L
●●●●Embryophyta	
●●●●●Magnoliopsida	
●●●●●●Poales	
●●●●●●●Cyperaceae	
Amphiscirpus nevadensis (S. Wats.) Oteng-Yeb., 1974	L
Cyperus laevigatus Linnaeus, 1771	L
Eleocharis dombeyana Kunth, 1837	L
●●●●●●●Juncaceae	
Juncus arcticus Willd., 1799	L
Juncus sp.	L
●●●●●●Alismatales	
●●●●●●●Ruppiaceae	
Ruppia maritima Linnaeus, 1753	L
AMORPHEA	
●Tubulinea Smirnov et al. 2005	
●●Elardia	
●●●Euamoebida	
Amoeba sp.	L
Trichamoeba osseosaccus Schaeffer, 1926	L
●Evosea Kang et al. 2017	
●●Variosea	
●●●Filamoeba	
Filamoeba nolandii Page, 1967	L
●Discosea Cavalier-Smith et al. 2004, sensu Smirnov et al. 2011	
●●Flabellinia	
●●●Dermamoebida	
Mayorella microeruca Bovee, 1970	L
●●●Dactylopodida	
Vexillifera sp.	L
●Holozoa Lang et al. 2002	
●●Choanoflagellata	

(continued)

Table 20.3 (continued)

TSAR	Habitat
●●●Craspedida	
●●●●Salpingoecidae	
Monosiga ovata Kent, 1878	L, P
Monosiga sp.	P
●●Metazoa	
●●●Bilateria	
●●●●Arthropoda	
●●●●●Malacostraca	
●●●●●●Amphipoda	
●●●●●●●Hyalellidae	
Hyalella azteca Saussure, 1858	L
●●●●●●Isopoda	
●●●●●●●Asellidae	
*** *Caecidotea williamsi* Escobar-Briones & Alcocer, 2002**	Mi
●●●●●Hexanauplia	
●●●●●●Calanoida	
●●●●●●●Diaptomidae	
*** *Leptodiaptomus garciai* (Osorio-Tafall, 1942)**	P
●●●●●●Harpacticoida	
●●●●●●●Canthocamptidae	
*** *Cletocamptus gomezi* Suárez-Morales, Barrera-Moreno & Ciros-Pérez, 2013**	L
●●●●●Ostracoda	
●●●●●●Podocopida	
●●●●●●●Candonidae	
*** *Candona alchichica* Cohuo, Hernández, Pérez & Alcocer, 2017**	L, DB
●●●●●●●Limnocytheridae	
*** *Limnocytherina axalapasco* Cohuo-Durán, Pérez & Karanovic, 2014**	L
●●●●●Insecta	
●●●●●●Ephemeroptera	
●●●●●●●Baetidae	
Callibaetis montanus Eaton, 1885	L
●●●●●●Odonata	
●●●●●●●Aeshnidae	
Rhionaeschna dugesi (Calvert, 1905)	L
●●●●●●●Coenagrionidae	
Enallagma praevarum Hagen, 1861	L
●●●●●●Hemiptera	
●●●●●●●Corixidae	
*** *Krizousacorixa tolteca* Jansson, 1979**	L

(continued)

Table 20.3 (continued)

TSAR	Habitat
●●●●●●●Naucoridae	
Ambrysus sp.	L
●●●●●●●Notonectidae	
Buenoa sp.	L
●●●●●●Trichoptera	
●●●●●●●Limnephilidae	
Grensia sp.	L
●●●●●●●Leptoceridae	
Oecetis sp.	L
●●●●●●●Hydroptilidae	
Oxyethira sp.	L
●●●●●●●Polycentropodidae	
Polycentropus sp.	L
●●●●●●Coleoptera	
●●●●●●●Dytiscidae	
Hydroporus sp.	L
Laccodytes sp.	L
●●●●●●●Chrysomelidae	
Donacia sp.	L
●●●●●●●Hydrophilidae	
Berosus sp.	L
Tropisternus sp.	L
●●●●●●●Staphylinidae	
Stenus sp.	L
●●●●●●Diptera	
●●●●●●●Chironomidae	
Apedilum elachistus Townes, 1945	L
Chironomus sp.	L
*** *Chironomus alchichica* Acosta & Prat, 2017**	L, DB
Cryptochironomus fulvus gr. Johannsen, 1905	L
Cricotopus (Cricotopus) triannulatus Kieffer, 1909	L
Dicrotendipes neomodestus (Malloch, 1915)	L
Labrundinia pilosella (Loew, 1866)	L
Limnophyes sp.	L
Micropsectra sp. 1	L
Micropsectra sp. 2	L
Paratanytarsus sp.	L
Procladius sp.	L, DB
Psectrocladius sp.	L
Psectrotanypus sp.	L
Stictochironomus sp.	L
Tanypus (*Apelopia*) sp.	L

(continued)

Table 20.3 (continued)

TSAR	Habitat
●●●●●●●Ceratopogonidae	
Culicoides occidentalis sonorensis Jørgensen, 1969	L
●●●●●●●Culicidae	
Culex sp.	L
●●●●●●●Ephydridae	
Ephydra hians Say,1830	L
●●●●●●●Stratiomyidae	
Stratiomys sp.	L
●●●●Nematoda	
●●●●●Enoplea	
●●●●●●Triplonchida	
●●●●●●●Tobrilidae	
Neotobrilus sp.	L
Semitobrilus sp.	L
Tobrilus sp.	L
●●●●●Chromadorea	
●●●●●●Rhabditida	
●●●●●●●Hoplolaimidae	
Hoplolaimus sp. 1	L
Hoplolaimus sp. 2	L
●●●●●●●Rhabdochonidae	
Rhabdochona canadensis Moravec & Arai, 1971	Po
●●●●●●●Gnathostomatidae	
Spiroxys sp.	Po
●●●●●●Chromadorida	
●●●●●●●Cyatholaimidae	
Paracyatholaimus sp.	L
●●●●●●Monhysterida	
●●●●●●●Xyalidae	
Daptonema sp.	L
Monhystera sp.	L
●●●●Annelida	
●●●●●Clitellata	
●●●●●●Haplotaxida	
●●●●●●●Naididae	
Limnodrilus hoffmeisteri Claparède, 1862	L
Tubifex tubifex (Müller, 1774)	L
●●●●●●Rhynchobdellida	
●●●●●●●Glossiphoniidae	
Glossiphoniidae sp.	L
Helobdella stagnalis (Linnaeus, 1758)	L

(continued)

Table 20.3 (continued)

TSAR	Habitat
●●●●●●● Piscicolidae	
Myzobdella sp.	Po
●●●● Mollusca	
●●●●● Gastropoda	
●●●●●●● Physidae	
Physa sp.	L
●●●● Platyhelminthes	
●●●●● Trematoda	
●●●●●● Diplostomida	
●●●●●●● Diplostomidae	
Posthodiplostomum minimum (McCallum, 1921)	Po
Tylodelphys sp.	Po
●●●●● Cestoda	
●●●●●● Bothriocephalidea	
●●●●●●● Bothriocephalidae	
Schizocotyle acheilognati (Yamaguti, 1931)	Po
●●●●●● Diphyllobothriidea	
●●●●●●● Diphyllobothriidae	
Ligula intestinalis (Linnaeus, 1758)	Po
●●●● Rotifera	
●●●●● Eurotatoria	
●●●●●● Flosculariaceae	
●●●●●●● Hexarthridae	
Hexarthra cf. *jenkinae* (Beauchamp, 1932)	P
●●●●●● Ploima	
●●●●●●● Brachionidae	
*** *Brachionus* sp. ‘Mexico’**	P
●●●● Chordata	
●●●●● Actinopterygii	
●●●●●● Atheriniformes	
●●●●●●● Atherinopsidae	
*** *Poblana alchichica* de Buen, 1945**	L, P
●●●●● Amphibia	
●●●●●● Caudata	
●●●●●●● Ambystomatidae	
*** *Ambystoma taylori* Brandon, Maruska & Rumph, 1982**	L, P
DISCOBA	
● Discoba Simpson in Hampl et al. 2009	
●● Heterolobosea	
●●● Tetramitia	
●●●● Eutetramitia	

(continued)

Table 20.3 (continued)

TSAR		Habitat
● ● ● ● ● Vahlkampfidae		
	Vahlkampfia sp.	L
● ● Euglenozoa		
● ● ● Euglenida		
● ● ● ● Heteronematina		
	Anisonema ovale Klebs, 1883	L
	Petalomonas steinii Klebs, 1893	L
	Notoselenus apocamptus Stokes, 1884	L
● ● ● Kinetoplastea		
● ● ● ● Metakinetoplastina		
● ● ● ● ● Neobodonida		
	Rhynchobodo sp.	P
	Rhynchomonas nasuta Klebs, 1892	L
● ● ● ● ● Eubodonida		
	Bodo caudatus (Dujardin) Stein, 1878	L
	Bodo globosus Stein, 1878	L
	Bodo minima Klebs, 1892	L
	Bodo repens Klebs, 1892	L
	Bodo saltans Ehrenberg, 1838	L
***Incertae sedis* EUKARYA**		
	Copromonas subtilis Dobell, 1908	L

Species organization follows the classification system of Eukarya by Adl et al. (2019), with supergroups as defined in Burki et al. (2020): TSAR (telonemids, stramenopiles, alveolates, Rhizaria), Haptista, Cryptista, Archaeplastida, Amorphea and Discoba. [Habitat: Pelagic (P), Littoral zone (L), Deep benthos (DB), Mi (Microbialites), parasites of *Poblana alchichica* (Po)]. Endemic species are in bold characters and an (*). For further information on the ecology and occurrence of these species, please refer to the corresponding chapters of this book

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Chapter 21
Conservation Actions

Elva Escobar, Verónica A. Arellano-Peralta, Verónica Aguilar-Sierra, and Javier Alcocer

21.1 Introduction

Protecting the biodiversity of epicontinental water bodies is of overall importance, especially those isolated from surface connections, and often supports unique taxa or high biodiversity (Scheffer et al. 2006). The conservation objectives should focus on protecting the lake and incorporating the watersheds and the possible forms of freshwater connectivity involved in protection policies (McCullough and Skaff 2019).

Two-thirds of the Mexican territory has an arid and semi-arid climate. The conservation of inland aquatic resources in this region should be a national priority since these ecosystems are highly susceptible to human disturbance, and they respond drastically even to small changes in hydrology (Calderón-Aguilera et al. 2012).

E. Escobar (✉)
Unidad Académica de Ecología y Biodiversidad Acuática, Instituto de Ciencias del Mar y Limnología. Universidad Nacional Autónoma de México, Ciudad de México, Mexico
e-mail: escobri@cmarl.unam.mx

V. A. Arellano-Peralta
Independent Environmental Consultant, Tlalpan, Ciudad de México, Mexico

V. Aguilar-Sierra
Comisión Nacional para el Conocimiento y Uso de la Biodiversidad (CONABIO), Tlalpan, Mexico
e-mail: vaguilar@conabio.gob.mx

J. Alcocer
Grupo de Investigación en Limnología Tropical, FES Iztacala, Universidad Nacional Autónoma de México, Tlalnepantla, Estado de México, Mexico
e-mail: jalcocer@unam.mx

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Numerous scientific investigations on Lake Alchichica show its ecological uniqueness and importance for Mexico and the world's aquatic biodiversity. Such studies are the basis for initiating conservation actions for both the lake and the hydrological basin as a single unit. However, the government must pay attention to the surface (watershed) and groundwater since this is the main water supply to Lake Alchichica.

21.2 Background Studies

The first scientific document on Lake Alchichica describes the diaptomid copepod *Leptodiaptomus garciai* (Osorio-Tafall 1942), a new and dominant zooplankton species in the pelagic zone of the lake (Montiel-Martínez and Ciros-Pérez 2019); the status of this species was further validated by Montiel-Martínez et al. (2008). A new species of neotenic salamander inhabiting Lake Alchichica, *Ambystoma subsalsum*, was described by Taylor (1943). Brandon et al. (1981) reclassified and renamed the endemic salamander as *Ambystoma taylori*.

De Buen (1945) described a new atherinopsid fish locally known as "charal". The silverside *Poblana alchichica* turns out to be endemic to Lake Alchichica (Alcocer et al. 2010). It was reclassified as the subspecies *Poblana alchichica alchichica* by Álvarez (1950) and Guerra Magaña (1986), and subsequently declassified by Espinosa et al. (1993) as *P. alchichica*. Jansson described in 1979 a new littoral species of hemipteran aquatic insect of the Corixidae family (backswimmers) in Lake Alchichica, *Krizousacorixa tolteca*, that is also endemic (Kato et al. 2019).

Escobar-Briones and Alcocer (2002) described a new species of isopod crustacean in Lake Alchichica, *Caecidotea williamsi*, associated to the microbialites (Alcocer and Escobar-Briones 2007). The species is endemic and the only isopod species inhabiting epicontinental saline waters in America (Escobar and Alcocer 2019). A new diatom -golden algae- species, *Cyclotella alchichicana*, was described from the pelagic zone of Lake Alchichica by Oliva et al. (2006). It was recognized recently as endemic to Lake Alchichica (Oliva et al. 2019).

A new endemic harpacticoid copepod, *Cletocamptus gomezi*, was described by Suárez et al. (2013), inhabiting specific littoral benthic habitats in Lake Alchichica (Alcocer et al. 2015). The ostracod (seed shrimps) *Limnocytherina axalapasco*, new species inhabiting Lake Alchichica and nearby Lakes Quechulac and La Preciosa was described by Cohuo et al. (2014). Later on, another ostracod, *Candona alchichica*, was described as a new and endemic species to Lake Alchichica (Cohuo et al. 2017). The latter species occurs from the littoral down to the deep benthos (Hernández et al. 2014).

Acosta et al. (2017) described a new species of midge, the dipteran insect *Chironomus alchichica* endemic to Lake Alchichica, inhabiting from the littoral down deep benthos. Emblematic to Lake Alchichica is a semi-closed ring of microbialites on its periphery. Their appearance is rocky and has a carbonated

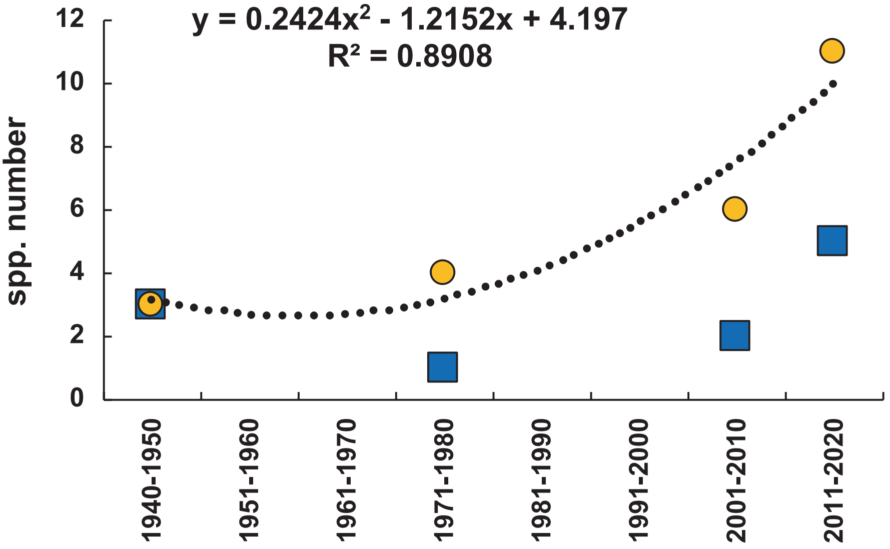

Fig. 21.1 Timeline of new species description in Lake Alchichica. (Blue squares = newly described species, orange circles = accumulated new species)

composition. They are associated with cyanobacteria (Valdespino-Castillo et al. 2019), among which a newly described species by Moreira et al. (2017) is *Gloeomargarita lithophora*, which turns out to be also a new gender, new family (Gloeomargaritaceae), and a new order (Gloeomargaritales).

The number of new species described from Lake Alchichica is increasing exponentially (Fig. 21.1); it is most likely that many more species will be described as taxonomists work with the different taxa encountered in multiple sampling programs. For example, the nitrogen-fixing cyanobacteria *Nodularia* aff. *spumigena* is most likely a new yet undescribed species for Laker Alchichica (Vilaclara and Oliva 2019). Scientific evidence shows that a planktonic rotifer originally named *Brachionus plicatilis* is a new but yet-to-be-described species that also inhabit the neighboring Lakes Atexcac and Queculac. Another planktonic rotifer, originally named *Hexarthra jenkinae* could also be a new species, but the lack of molecular evidence prevents it from being certain (see Chap. 14, metazooplankton).

21.3 Endemism and Conservation

Endemic species in saline, high altitude, endorheic crater lakes such as Lake Alchichica face challenging dispersal barriers. Although endemism characterizes many lakes (Martens, 1997), endemic species are at the greatest risk of extinction from anthropogenic threats and climate change (Thomas 2011).

Table 21.1 New species described for Lake Alchichica

Family	Species	Author
Xenococcaceae	*Xenococcus candelariae*	Tavera & Komárek (1996)
Gloeomargaritaceae	*Gloeomargarita lithophora*	Moreira et al. (2017)
Chroococcaceae	*Entophysalis atrata*	Tavera & Komárek (1996)
Chroococcaceae	*Entophysalis lithophyla*	Tavera & Komárek (1996)
Chamaesiphonaceae	*Chamaesiphon halophilus*	Tavera & Komárek (1996)
Merismopediaceae	*Mantellum rubrum*	Tavera & Komárek (1996)
Synechococcales	*Heteroleibleinia profunda*	Tavera & Komárek (1996)
Stephanodiscaceae	*Cyclotella alchichicana*	Oliva et al. (2006)
Diaptomidae	*Leptodiaptomus garciai*	Osorio-Tafall (1942)
Brachionidae	*Brachionus* sp. Mexico	*
Canthocamptidae	*Cletocamptus gomezi*	Suárez et al. (2013)
Candonidae	*Candona alchichica*	Cohuo et al. (2017)
Limnocytheridae	*Limnocytherina axalapasco*	Cohuo et al. (2014)
Asellidae	*Caecidotea williamsi*	Escobar-Briones and Alcocer (2002)
Corixidae	*Krizousacorixa tolteca*	Jansson (1979)
Chironomidae	*Chironomus alchichica*	Acosta & Prat (2017)
Atherinidae	*Poblana alchichica*	De Buen (1945)
Ambystomatidae	*Ambystoma taylori*	Brandon et al. (1981)

*Declared new species by Alcántara et al. (2012), confirmed in Mills et al. (2017), but yet to be formally described

Lake Alchichica represents ~0.0001% of the Mexican territory (Cohuo et al. 2017). Most of the new species described for Lake Alchichica show restricted occurrence and fall within the category of microendemic according to MER ("Method for evaluating the risk of extinction of wild species in Mexico") developed by Tambutti et al. (2001). Species inhabiting this lake encounter diverse threats that allow classify them as extremely vulnerable. Table 21.1 lists the new species described for Lake Alchichica up to date.

21.4 Priority Hydrological Regions (RHP-CONABIO)

Human activities threaten the integrity of the epicontinental inland systems and their biological diversity (Arriaga Cabrera et al. 2000). The lack of a spatial planning exercise has led to frequent conflicts among users and species conservation. Water quality deterioration and depletion of the available surface and groundwater resources point out that the continental waters are not unlimited. Within this context, the National Commission for the Knowledge and Use of Biodiversity (CONABIO) initiated in 1998 the program Mexico's Priority Hydrological Regions (RHPs, in Spanish) to develop a reference framework to contribute to the conservation and sustainable management of the inland water environments (Arriaga Cabrera et al. 2000).

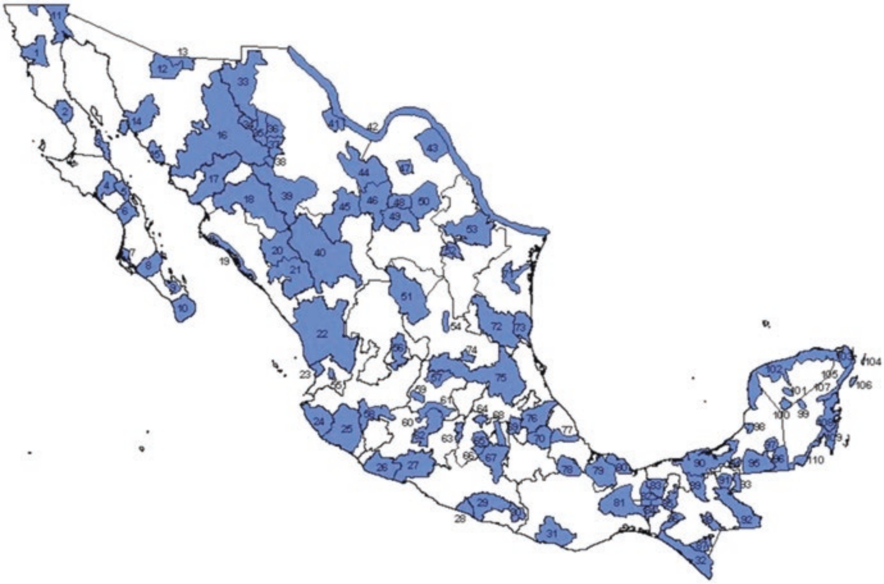

Fig. 21.2 Priority Hydrological Regions of Mexico established by CONABIO. (RHP 70 = Oriental basins, where Lake Alchichica locates)

The RHPs were selected for their biological richness, level of knowledge, current and potential use, impacts on biodiversity, ecosystem services, and conservation efforts, using the hydrological basin as the analysis unit (Arriaga Cabrera et al. 2000). Maps of the Mexican territory were made for top priority areas concerning biodiversity, resource use, lack of information, and conservation potential. The process included the elaboration of technical file cards for each RHP. Cards' information considered geology/edaphology, water resources, biodiversity, resources and their uses, economic aspects, conflicts, and recommendations on research and conservation.

The RHPs are a synthesis of the water resources' actual situation associated with top priority areas considering biodiversity. Among the 110 RHPs, Oriental basin is RHP number 70 and covers 4982 km^2 (Fig. 21.2). The Oriental basin classifies as RHP based on the biodiversity and the relevance of its surface and underground hydrological resources. It includes diverse water bodies within the endorheic basin. Among them: a) lakes Alchichica, San Luis Atexcac, La Preciosa, Quechulac, Aljojuca, San Miguel Tecuitlapa, Totolcinco, Tepeyahualco, Totolango and Ovando, b) rivers, streams and springs La Caldera, Xonecuila, Quetzalapa, Piedra Grande, El Carmen, Vicencio, Ojo de Agua, Lara Grajales, and c) groundwater.

Lake Alchichica embodies unique ecological characteristics with a high degree of endemism and particular physiography due to microbialites deposits produced by the intense biogenic activity. The most significant problems in the RHP 70 include environmental modification, deforestation, overexploitation of groundwater, wind erosion, salinization of soils and water contamination by litter and agrochemicals and introduced species for aquaculture (Arriaga Cabrera et al. 1998).

21.5 Long-Term Ecological Research Network

Lake Alchichica is limnologically monitoring since 1998 (Alcocer 2019). The Red Mex-LTER is the Mexican branch of the International Long-Term Ecological Research Network (ILTER), allowing valuable latitudinal intercomparisons (Alcocer and Bernal 2009).

The objective of ILTER is to understand the long-term environmental changes of the planet through long-term scientific research generating ecological databases of the ecosystems under study. The thematic areas develop in the Alchichica Group are: 1) patterns and control of primary productivity in ecosystems, 2) patterns and control of the dynamics of water, carbon, and nutrients in ecosystems, 3) effect of climate change in the structure and functioning of ecosystems, 4) the role of biodiversity in the structure and functioning of ecosystems, and 5) patterns and frequency of disturbances in ecosystems.

21.6 Protected Species

The aquatic biodiversity of Lake Alchichica is seriously threatened, mainly since the water level in the lake is decreasing rapidly. Lake Alchichica water supply comes predominantly from groundwater (see Chap. 5, hydrochemistry). With the water level decrease, all the recently described species, all adapted to the lake and unique evolutionary history, could promptly disappear from the planet. The constant and increasing decrease in the lake's water level is the result of complex environmental problems. The constant and increasing decrease in the lake's water level is the result of complex environmental problems. Despite this critical situation, of the total number of new species described for the lake up to date, eleven, the majority new to science and considered microendemic, only two are protected by the Official Mexican Standard NOM-059-SEMARNAT-2010 (DOF 2010; in Mexico), and by the IUCN Red List of Threatened Species. The two species are the following (Table 21.2, Fig. 21.3 and 21.4):

Recently (October 2020), The Commission for the Environment, Sustainability, Climate Change and Natural Resources of the Chamber of Deputies, H. Congreso de la Unión, the Mexican Government, exhorted the Secretary of the Environment and Natural Resources (SEMARNAT) to undertake the relevant actions to

Table 21.2 Protected species according to NOM-059-SEMARNAT-2010 and the IUCN Red List of threatened species

Species	Common name	NOM-059[a]	IUCN[b,c]
Poblana alchichica	Achichica silverside	Threatened	Critically endangered
Ambystoma taylori	Taylor's salmander	Subject to special protection	Critically endangered

[a] NOM-059-SEMARNAT-2010, [b] Gómez and Espinosa 2019, [c] IUCN SSC Amphibian Specialist Group 2015

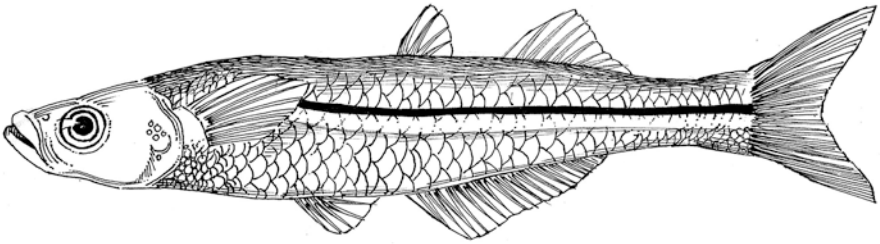

Fig. 21.3 *Poblana alchichica*. (Original drawing by Alexis Manuel De la Torre Zavala)

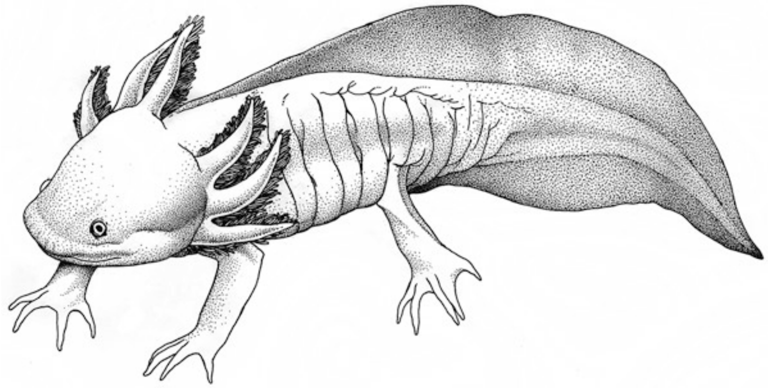

Fig. 21.4 *Ambystoma taylori.* (Original drawing by Edgar M. Caro Borrero)

guarantee the protection, preservation, and propagation of the different *Ambystoma* ("ajolote") species included in the NOM-059-SEMARNAT-2010, as well as their habitat (Cámara de Diputados LXIV Legislatura. H. Congreso de la Unión, México 2020).

The water quantity and quality deterioration of Lake Alchichica is a consequence of the accelerated development of rural and urban settlements, and the growing anthropic activities (e.g., agriculture) in the Serdán-Oriental basin. Habitat deterioration threatens species with a protected status, namely *Ambystoma taylori* and *Poblana alchichica* survival. The unplanned development and incentives for irrigation agriculture and industrial expansion (e.g., pig and poultry farms, automobile industry) lead to organic and inorganic pollutants, and the water level depletion of the former abundant aquifers (Woolrich-Piña et al. 2017). The decrease of the water level OF Lake Alchichica leads to habitat loss in the littoral zone with changes in the physical and chemical composition that threat the aquatic biota and the conservation efforts required (Woolrich-Piña et al. 2012, 2017).

In addition to the already mentioned anthropic threats to Lake Alchichica, reduced population, inbreeding, the loss of habitat, impinge in the genetic condition and exposes *Ambystoma taylori* with further risk This salamander is paedomorphic, holding lower genetic diversity, vulnerable to the effects of gene drift and inbreeding. The loss of genetic diversity in such a small and isolated populations will decrease the fitness and adaptive potential and increase the species' likelihood to extinction (Parra-Olea et al. 2012). Currently, the greatest threat to natural, wild populations of this paedomorphic salamanders is its habitat modification and loss, including alteration in the hydrology, integration of pollutants that act at the cellular and organismic, reproductive and growth levels. In addition, the introduction of alien species, the overexploitation of species, and incidence of disease (Parra-Olea et al. 2012) will affect its survival. Dyer (1984) and Michaels et al. (2016) reported the death of some individuals of *A. taylori* through the infestation of the nematode *Hedruris siredonis* in the digestive tract, they consider it an early warning system of the presence of pollution acting on the population's health.

The decline in the world's amphibian population is one of the best documented indicators of the loss of biodiversity on our planet, particularly, Mexican amphibians are seriously threatened (Wilson et al. 2013). The Mexican Government began the "Programa de Acción para la Conservación de las Especies (PACE)" (Action Program for Species Conservation) in 2018. "PACE *Ambystoma*" includes the species *A. taylori* (SEMARNAT 2018) and is part of the *Biodiversity Conservation and Management axis of the CONANP (National Commission of Protected Natural Areas) 2040 strategy,* with strategic goal of developing and implementing action programs for the recovery of species at risk. This program is related with the Natural Protected Areas Management Programs and supports itself in diverse instruments, including citizen involvement programs. The general objective of "PACE *Ambystoma*" applies comprehensive strategies for the conservation of axolotl and allow increasing knowledge of the species, strengthening management measures for their sustainable use and preventing and mitigating possible threats to the species and their habitats. The conservation strategies are the following (SEMARNAT 2018):

1. Population management and protection
2. Integrated landscape management
3. Conservation and management of species at risk
4. Conservation economics
5. Evaluation and operation of the program

The EDGE (Existence, Evolutionarily Distinct and Globally Endangered species) program is another global conservation initiative focused specifically on threatened species, which are unique and irreplaceable from the world's natural heritage and that is applied in Alchichica. The goal of EDGE is to catalyze conservation actions and ensure that local stakeholders, governments, and national and international conservation organizations take ownership of these species and commit to ensuring their future survival (https://www.edgeofexistence.org/). The EDGE project for *Ambystoma taylori*, "Action Plan for the Conservation of the Alchichica axolotl (*Ambystoma taylori*)" (Hernández-Díaz et al. 2020) seeks to achieve the following objectives in a 5 to 10 years' time. The goals are:

1. A permanent monitoring program of the axolotl population and its habitat
2. Create an axolotl assurance colony

3. Protect and restore the ecosystem in the areas surrounding the other nearby crater lakes (La Preciosa and Quechulac)
4. Involve the local community in conservation actions for the axolotl and its habitat.
5. Reduce litter and sewage in Lake Alchichica and its surroundings
6. Reduce pollution from vehicles moving along the highway near Alchichica
7. Regulate the extraction of water in the area to reduce its impact

21.7 Protected Natural Area

In November 2018, the Alchichica, La Preciosa, Quechulac, and Atexcac lakes were declared by the government of the State of Puebla in Mexico, as a Protected Natural Area (PNA) in the form of a State Park, with the name "Lagos de Tepeyahualco and Guadalupe Victoria" (POEP 2018). (Fig. 21.5).

The PNA polygonal area covers a total of 38,183.69 hectares and a perimeter of 281.84 km. It partially includes two municipalities: Tepeyahualco and Guadalupe Victoria. The PNA "core zone" is made up exclusively of the four crater lakes: Alchichica, La Preciosa, Quechulac, and Atexcac, occupying 417.68 ha constitutes 1.09% of the PNA. The "buffer zone" is made up of the land region and the El Salado (Tepeyahualco) wetland and comprises most of the 37,766.01-ha surface, that is, 98.91% of the total polygonal (POEP 2018).

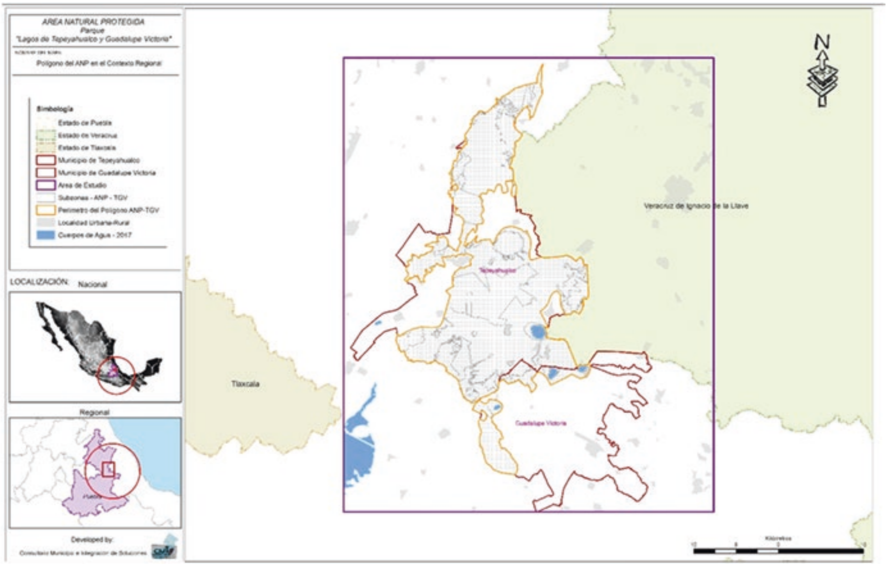

Fig. 21.5 Polygonal of the Protected Natural Area "Lagos de Tepeyahualco and Guadalupe Victoria"

In the PNA, there is five terrestrial ecosystems representative of the State's ecological and biogeographic regions: pine forest, pine-oak forest, táscate forest, rosetophilous desert scrub, and halophilic grassland. It also includes the aquatic ecosystems (four crater lakes and the El Salado wetland). Together, they host at least 34 flora and fauna species included in some risk category of the Official Mexican Standard NOM-059-SEMARNAT-2010, many of them being endemic or microendemic.

The reasoning for the PNA declaration (Informe Técnico Justificativo, Secretaría de Desarrollo Rural, Sustentabilidad y Ordenamiento territorial del Estado de Puebla 2018) include the following statements.

- Five different and representative ecosystems are holding numerous endemic and/or protected species.
- The landscape and ecological value of the bodies of water, which allow the scientific study of ecosystems and endemic species, unique on the planet.
- The microbialites ring of Lake Alchichica, considered unique and one of the oldest life records on the planet (see Chap. 22, microbialites).
- Large wetlands representing important reproduction, nesting, feeding, and protection areas for local and migration aquatic birds.
- The biological relevance of ecosystems recognized in the scientific field at the national and international level.
- The ecological importance of groundwater resources (see Chap. 5, hydrochemistry).
- The City of Cantona, an important archaeological and cultural site from the late pre-classic (200 BC) (see Chap. 1, Lake Alchichica: history and human settlement).

Although the Protection of the Natural Environment and Sustainable Development Law of the State of Puebla establishes the general guidelines for the management, use, exploitation, and legal restrictions of the PNA, the specific Management Program of the ANP is lacking. There is an absolute vacuum of administration and authentic protection of the PNA. Not having a PNA Management Program is especially problematic considering the complex environmental problems that threaten the area.

21.8 Environmental Issues

21.8.1 Modification of the Water Dynamics of the Basin

There is a significant problem of land-use changes from forests to agriculture, cattle raising, and urban development. The replacement of deep-rooted natural vegetation by grasslands and cultivable species with shallow roots has resulted in a change in local hydrology in the region, causing increased water evaporation from the soil and its consequent salinization. Runoff water has washed these soils, and sediments have settled in the basin's lakes (Alcocer et al. 2004). Also, these activities have changed drainage patterns in the area, increasing sediment loads from runoff. The formation of grazing paths and breaking the protective surface crusts of the soil by cattle have caused their compaction in the tracks and their erosion in degraded areas (Alcocer et al. 2004).

In the past, there were numerous streams and springs in the region that, despite their temporality, provided a source of fresh water for the local inhabitants (Knoblich 1973). However, with the population growth and urban settlements, the diversion of tributaries, and the intensive use of water resources, many surface water bodies have entirely disappeared (Reyes 1979). In others, such as the El Salado wetland (Tepeyahualco), the water volume decrease has caused a reduction in the lacustrine area and the lakebed exposure to the elements. The wind usually carries sediments and salts from the soil and from the exposed lakebed to other parts of the basin, increasing dust deposits in the region (Alcocer et al. 2004).

The greatest management challenge facing the PNA, which seriously threatens the survival of the aquatic biodiversity of both Lake Alchichica and the rest of the crater lakes and wetlands, is the groundwater overexploitation for agricultural irrigation. Agriculture is a fundamental and growing activity in the basin. Historically, it depended exclusively on rainfall; however, irrigation with groundwater has replaced rainwater irrigation (Alcocer et al. 2004). The sprinkler irrigation in the central part of the basin is very inefficient and inappropriate since it takes place in hours of high insolation in a dry climate, which generates a significant loss of water by evaporation and, consequently, a greater demand for the water resource (Alcocer et al. 2004). Thus, the PNA Management Program should include alternative agricultural irrigation methods that allow saving the resource more efficiently and sustainably. It is also crucial that the cultivable species selected are preferably native or with low agricultural irrigation needs.

Groundwater overexploitation has caused a decrease in the crater lakes water level; the shallow littoral areas that provided refuge for biota (resident and migratory waterbirds, larvae, and juveniles of fish, and various microorganisms) have disappeared. The shoreline is already impacted, threatening biological conservation (Alcocer et al. 2004). In Lake Alchichica, previously submerged microbialites have been exposed and have died, with the consequent loss of microhabitats (Escobar and Alcocer 2002).

The water level in Lake Alchichica is most likely decreasing due to current climatic conditions that significantly favor evaporation over precipitation and groundwater input. However, evidence suggests that groundwater exploitation this "natural" process (Silva-Aguilera and Escolero 2019; see Chap. 5, hydrochemistry).

The impacts on the dynamics of the basin's hydric resources have caused an increase in the lakes' salinity, which has caused chemical, physical, and biological changes in these bodies of water. The rise in salinity exceeds the salts' solubility capacity, which precipitates, altering the remaining solution's ionic composition (see Chap. 5, hydrochemistry). The elevation of salinity decreases the solubility capacity of oxygen. These alterations also have consequences in the aquatic biota, causing the more salinity-tolerant species to predominate (Alcocer et al. 2004).

21.8.2 Pollution

Some crater lakes of the PNA (particularly Lake Alchichica) are the object of interest for local and foreign tourism due to their outstanding scenic beauty and are visited continuously without control or regulation. This free tourist activity generates litter inside and outside the water bodies (Romero et al. 2020). Litter is visible in the lakes, cans, bags, containers, and in general, a whole series of wastes. Locals use soaps, detergents, and bleaches for personal hygiene and laundry along the crater lakes' littoral zone. Although garbage cleaning brigades have been organized in Lake Alchichica, these are neither regular nor permanent (Hernández-Díaz et al. 2020). Construction of some latrines made small changes since direct sewage discharge resulted from the scarcity or non-existence of wastewater collection systems nor treatment plants in the neighboring municipalities (Romero et al. 2020).

21.8.3 Introduction of Exotic Species and Extraction of Biota

The government and locals promoted the introduction of exotic fish species (*Oncorhynchus mykiss*, the rainbow trout) in Lakes Quechulac and La Preciosa for food (in cages) and tourism (recreational fishing); the possible adverse effects on native and endemic biota are unknown (Romero et al. 2020). Extraction of locally endemic species is usual. The microendemic and protected silverside *Poblana alchichica* sustains a local fishery for feeding purposes. Extraction of the endemic and protected salamander *Ambystoma taylori* for scientific purposes is frequent (Alcocer et al. 2004). Silversides and salamander's extraction take place as well in other crater lakes of the area. Another usual practice activity is bird hunting in Lake Alchichica and the other close by lakes (Romero et al. 2020).

21.8.4 Lake Alchichica Menaces

Diverse potential and real natural and anthropic impacts threaten the permanence of Lake Alchichica and its aquatic biota. Threats related to climate change, extraction activities, and exploitation activities (Fig. 21.6).

Expected impacts are as follow (e.g., Alcocer et al. 1998, 2004; Arriaga Cabrera et al. 1998; Alcocer 2019 also see Chap. 4, recent climate, and Chap. 5, hydrochemistry). However, most of these expected impacts and threats have not been

Fig. 21.6 Potential and proven human impacts and threats in Lake Alchichica

measured/proven, nor evaluated the impact degree or the effects on the loss of species and habitats or ecosystem change.

1. Environmental changes associated with climate change leading to a decrease in the water level of the lake.
2. Diversion of lake water for use in irrigation, road building, and industry reduces the lake volume, loss of littoral lake habitats, and associated biological diversity and the services these provide to local communities.
3. Cutting political boundaries leads to difficulties in reaching consensus among diverse citizenries and decision-making.
4. Spring desiccation, reduced natural -free- water supply promoting the use of bottled water affecting the family economy and increasing litter
5. Pollutants (agrochemicals) from industry, gas station leaks, farms, and underground sewage input threaten contaminants, resulting in biodiversity loss.

6. Unconnected local sanitation systems and household runoff led to sewage input and eutrophication of the lake littoral habitats and the potential transfer of human diseases to aquatic life.

21.9 Conservation Prospects

Two years have passed since the PNA State Park “Lagos de Tepeyahualco and Guadalupe Victoria” was declared. Nonetheless, no conservation measures have been carried out on Lake Alchichica or any other PNA water bodies. The absence of conservation actions is a consequence of the lack of a Management Program for the PNA. Although the PNA decree is an encouraging fact, the lack of a Management Program prevents to the fulfillment of conservation objectives. The Management Program is the guiding instrument for planning and regulation, which establishes the activities, actions, and basic guidelines for the PNA management and administration.

It is important to emphasize that the surface and underground water resources of the PNA and the entire basin are seriously threatened (see Chap. 4, recent climate, and Chap. 5, hydrochemistry). There is an urgent need to apply sustainable water use strategies in the basin since the rate of degradation of its epicontinental aquatic resources and its drying trend is accelerated. The increasingly hotter and drier local climate, water scarcity, dust storms, deforestation, overgrazing, overexploitation of aquifers, and salinization of soils, derived from poor irrigation practices, have induced severe erosion processes and widespread desertification in the basin (Alcocer et al. 2004).

The PNA Management Program, therefore, is essential because, even though the basin has been classified as a closed area for groundwater extraction since 1954 and categorized as a Priority Hydrological Area by CONABIO since 1998 (Arriaga Cabrera et al. 2000), no management has been carried out for the sustainable use of groundwater (Alcocer et al. 2004, Romero et al. 2020).

The conservation of the unique biodiversity of Lake Alchichica, the rest of the lakes, and all the ecosystems involved in the state PNA “Lagos de Tepeyahualco and Guadalupe Victoria” requires a comprehensive vision of the conservation of the aquatic resources of the basin. The preservation of the endemic species can only be possible if the entire habitat is conserved, which necessarily involves the rest of the native species and the whole ecosystem’s specific environmental conditions. Conservation efforts should focus on managing the drainage basin, both superficial and underground since the fundamental water supply source for Lake Alchichica and the other crater lakes is underground. The generation of strategies focused on the conservation of ecosystems, their restoration, and sustainable use of resources in the short, medium, and long terms require the involvement of all social sectors: local population, industry, academia, Non-Governmental Organizations (NGOs), and municipal, state, and federal governments.

21.10 Rationale for Prioritizing Biodiversity Conservation

Biodiversity, endemism, and vulnerability are only some of the criteria recognized in conservation. Lake Alchichica belongs to a crater lake district that harbors numerous endemic species. Microbialites and littoral vegetation provide critical habitats for endemic fish, crustaceans, insects, and another biota that feed the amphibian, the silverside fish, and the migrating birds. The lake springs, slowly disappearing, support small terrestrial mammals, reptiles, and another biodiversity. The lake's biodiversity is central to the lives of local communities' economy that border the lake.

Lake Alchichica delivers diverse ecosystem services to the local economy. Among these services provided, there are food and water, materials (wood, vegetation), weekend and seasonal tourism, inspiration, swimming, diving, boating, hiking, birdwatching, and also significant is the blue carbon storage capacity by the littoral vegetation and microbialites.

These ecosystem services that Lake Alchichica provides to the watershed should be further assessed along with the lake processes to understand the cost of its loss better if conservation does not occur. Although conservation initiatives in Lake Alchichica have acquired an increased interest in the last decade (e.g., Premio a Investigación Científica en Conservación Biológica 2016, Anfibios de Puebla, "Por Amor al Planeta," VW) the lake's critical role as the provider of ecosystem services and biodiversity continues to be invisible to the conservation funding programs. Some actions are required to make biodiversity visible to conservation. Here is a list of potential activities as an example.

1. A complete list of the species occurring in Lake Alchichica ecosystems and habitats. The lake harbors many species, the sum of existing diversity in the water column, the interface water sediment, the vegetation, the superficial sediment, and the microbialites. The latter will require applying new State of the art tools (i.e., as recorded in other lakes, Sherbakov 1999) to describe this undescribed diversity due to the difficulties in the taxonomic literature and the limited number of experts.
2. Biodiversity monitoring by ecosystem or habitat. A large number of samples have been collected for the past 22 years in Alchichica. It is necessary to document the species composition, richness, and variability in time and space to understand the variability in time and space and define the best conservation strategies.
3. Essential environmental variables and biodiversity data in open access data repositories and databases and FAIR principles. Data from Lake Alchichica require being findable, accessible, interoperable, and reusable to deliver new and transformative knowledge that can support conservation and ensure that essential data are collected and retained and made accessible for analysis application current and future users.
4. Engage stakeholders and holders and traditional and local knowledge of the lake. Engaging in dialogue with the organizations interested in conserving biodiversity should help find solutions through new strategies to significant threats

to the lake and its vulnerable biota. The traditional and local knowledge of lake conservation will be a challenge but will make a transformative change if achieved.

5. Explore dialogue with stakeholders to develop a spatial management plan. Conserving the lake should consider watershed maps and conservation strategies for the water resource in the entire watershed. The recorded threats to the lake are challenging and require political will, funding, and time.

21.11 Conclusions

Lake Alchichica biodiversity is unique, the lake's geographical location and changes in the lake district increase its vulnerability to effects of human disturbance in synergy with climate change. The rate of description of new species that started in 1941 is steep and rising suggesting that many more will be discovered in the next years. Microendemism is explained by the lake's saline nature and its occurrence in high altitude and an endorheic basin where the unique species challenge dispersal barriers and the risk of extinction. The three conservation criteria (uniqueness, vulnerable habitat and species and uniqueness) have led to actions that seek to protect the lake and species in an integrative way including the NOM-059-SEMARNAT-2010 and the IUCN Red List of threatened species protection status. Other conservation actions include that Lake Alchichica and three lakes in the lake region were declared "Lagos de Tepeyahualco and Guadalupe Victoria" State Park Protected Natural Area in 2018 supported in the lake's attributes, aquatic and terrestrial life and the existing archaeological and cultural assets. Conservation measures are pending due to the lack of a Management Program and prevents the fulfillment of conservation.

Lake Alchichica Long-Term Ecological Research monitoring program has recognized that water quality, and surface and groundwater depletion result in environmental stress. With 22 years of samples and diverse monthly environmental measurements an increase in litter, sewage, introduction of exotic species, extraction of biota, extraction and exploitation have been observed but requires systematic documenting. The lake's biodiversity is central to the economy of local communities. It provides food and water, materials (wood, vegetation). Visitors benefit from tourism aquatic activities and inspiration from outdoor sports and birdwatching. In addition, the lake's blue carbon storage capacity requires assessment jointly to the impacts to help understand the cost of its loss of this and other services. Different actions are required to engage the local community to preserve the lake's integrity and biota with support of stakeholders.

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Chapter 22
Microbialites: Diversity Hotspots in the Mexican Plateau

Patricia M. Valdespino-Castillo, Bernardo Águila, Jesús Torres-Huesca, Carla M. Centeno, Jesus Martínez-Díaz, Margarita Reyes-Salas, Sonia Angeles-García, Yislem Beltrán, Rocío J. Alcántara-Hernández, Hoi-Ying N. Holman, and Luisa I. Falcón

22.1 Overview

Microbialites have been called "texcales" in Mexico since pre-Hispanic times. In the native Náhuatl language, this word translates to "rocks", they also have been called tufa, stromatolites, or bacterial reefs. Similarly to corals, a thin living surface in submerged microbialites mediates the precipitation, cementation, and accretion of sediments, minerals, and organic matter, forming massive mineral rock-like structures. In these microbial reefs, or microbialites, biomineral formation is mediated mainly by prokaryotes. In Lake Alchichica ("the place of bitter water" for locals), some of these massive structures have emerged because the lake's water

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P. M. Valdespino-Castillo (✉) · H.-Y. N. Holman
Molecular Biophysics and Integrated Bioimaging, Lawrence Berkeley National Laboratory, Berkeley, CA, USA
e-mail: pmvaldespino@lbl.gov; hyholman@lbl.gov

B. Águila
Posgrado en Ciencias Biológicas, Universidad Nacional Autónoma de México, Ciudad de México, Mexico

Laboratorio de Ecología Bacteriana, Instituto de Ecología, Campus Yucatán, Universidad Nacional Autónoma de México, Municipio de Ucú, Yucatán, Mexico

J. Torres-Huesca · J. Martínez-Díaz
Posgrado en Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México, Ciudad de México, Mexico

C. M. Centeno
Baden Powell School, Atizapán de Zaragoza, Mexico
e-mail: ccenteno@badenpowell.edu.mx

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level has been decreasing in the last decades. Today, living microbialites develop from the lake surface, forming a ring of white stones (Fig. 22.1) which extend along the litoral and reach a depth of 40 meters. These white constructions, a major tourist attraction of Mexico, turn brown-green as they get closer to the water. The dark color is the pigment of the live rock-building microbial communities. Scientists have shown that these organo-sedimentary structures are the result of interactions between aquatic microorganisms and their geochemical environment. Microbialites have also been called tufa, stromatolites, or bacterial reefs.

The singular panorama offered by the microbialites of this turquoise lake has fascinated travelers over the years. Besides travelers, scientists have been attracted to these “uncommon” bioconstructions. While the formation of the sedimentary structures was long attributed to “blue-green algae”, today we know that diverse microbial consortia populate microbialites (Kaźmierczak et al. 2011, Couradeau et al. 2011, Centeno et al. 2012, Saghaï et al. 2015). These numerous microbes are actively doing photosynthesis and fixing nitrogen (Falcón et al. 2002, 2020; Beltrán et al. 2012) and are models to understand microbially mediated mineral formation (e.g., Valdespino-Castillo et al. 2018). These benthic structures allow the establishment and development of many other species. This chapter explores these organo-sedimentary structures in detail, the geochemical features that explain their presence and their role as biodiversity hotspots.

22.2 Research History

The geochemistry of the lake and other biological compartments was studied long before the availability of technical advancements to study the biological component within microbialites. While geochemical features of Lake Alchichica are summarized in Chap. 5 (Hydrochemistry of Lake Alchichica and its drainage basin) three features of the lake are crucial to explaining the presence of microbialites: (a) clear

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M. Reyes-Salas · S. Angeles-García
Electronic Microscopy and Microanalysis Laboratory & LANGEM. Instituto de Geología, Universidad Nacional Autónoma de México, Ciudad de México, Mexico
e-mail: adelars@unam.mx

Y. Beltrán
Instituto de Ciencias Del Mar y Limnología, Unidad Académica de Sistemas Arrecifales, Universidad Nacional Autónoma de México, Mexico City, Mexico

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

L. I. Falcón
Laboratorio de Ecología Bacteriana, Instituto de Ecología, Campus Yucatán, Universidad Nacional Autónoma de México, Municipio de Ucú, Yucatán, Mexico
e-mail: falcon@ecologia.unam.mx

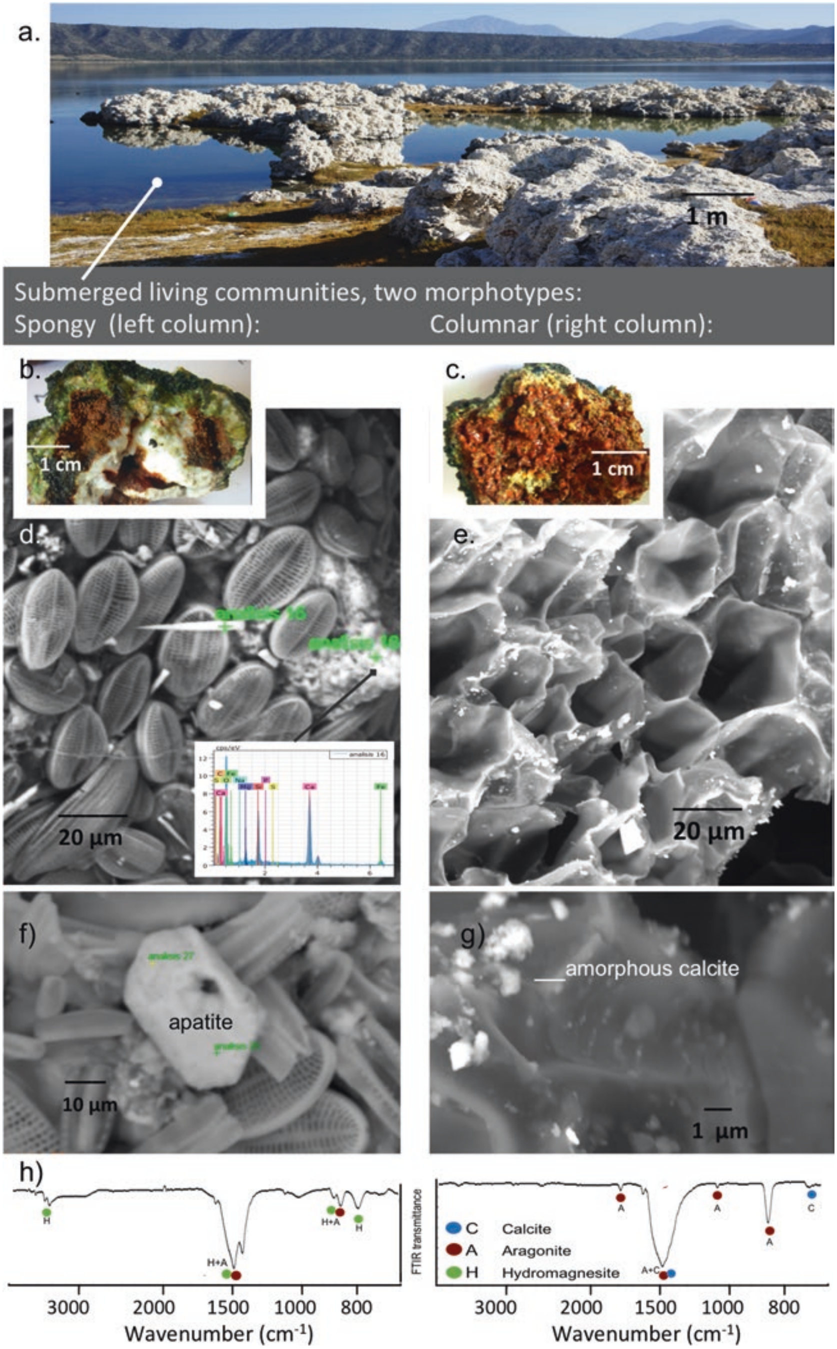

Fig. 22.1 Lake Alchichica microbialites: left = spongy, right = columnar morphotypes. From top to bottom (**a**) field view, cross-section of spongy (**b**) and columnar (**c**) morphotypes. SEM-EDS

oligotrophic waters allowing light penetration, (b) availability of major anions including bicarbonate (HCO_3^-) and sulfate (SO_4^{-2}) and major cations such as Na^+, Ca^{+2} and Mg^{+2}, and; (c) relatively high alkalinity contributing to chemical species availability and thermodynamically favoring biomineralization; these features have been documented largely in Chap. 5 (Hydrochemistry of Lake Alchichica and its drainage basin). The geochemical survey of volcanic lakes of Mexico published by Armienta et al. (2008) and other studies (see chapters 5, Hydrochemistry of Lake Alchichica and its drainage basin, and 7, Physicochemical characteristics) also account for the hyposaline character of the lake's water, depicting a high Mg:Ca ratio when compared to lakes worldwide.

Lake Alchichica held scientists' attraction in the '70s and '80s; limnologists, geologists, and protistologists often studied the lake to hypothesize about life in the past. The microbial communities related to microbialites were not studied until the '90s. As a Ph.D. student advised by J. Komarek, R.L. Tavera published a fine description of the cyanobacterial components populating the mineral bioconstructions (Tavera and Komárek 1996). The reader should consider that the Nostocales cyanobacterial cells studied by these authors populated the surface of the microbialites. Unlike many other smaller microbes, Nostocales cyanobacteria are ~10 by 50 μm, and therefore, their details were accessible under a benchtop optical microscope. Besides describing the cyanobacterial components and their taxonomy, these authors pointed out the coexistence of two different microbialite morphotypes within the lake. One was called spongy because of its round microstructure, and the second one, columnar, because of its vertically disposed microstructure (Fig. 22.1). Kaźmierczak et al. (2011) provided a comprehensive examination (e.g., age, structure, and mineralogy) of Lake Alchichica's microbialites and morphological and molecular analysis of the living cyanobacterial mats. Further, Couradeau et al. (2012) reported a unicellular cyanobacterium associated to carbonate mineral precipitations in Lake Alchichica's microbialites which is proposed to form amorphous carbonate inclusions intracellularly. This cyanobacterium is proposed to be *Gloeomargarita lithophora* (Moreira et al. 2017), and further studies are needed to understand its phylogeny and natural history.

Over the years, microbial systematics studies have provided direct evidence of high microbial diversity in these assemblages. Like ocean reefs, microbialites contribute to the formation of micro-habitats along the littoral zone, populated by mollusks, arthropods, protists, helminths, fishes, amphibians, and other organisms (see Chaps. 10, 11 and 12 of this book). This aquatic diversity has led to the growing recognition of the lakes of the Central Highlands of Mexico as biodiversity hotspots,

Fig. 22.1 (continued) micrographs and elemental analyses of (**d**) spongy, showing amorphous calcite formations often surrounded by benthic diatoms, and (**e**) columnar microbialites depicting a hexagonal-based aragonite structure. At higher magnification, (**f**) fluorohydroxyapatite crystals were detected in the spongy morphotype, and (**g**) amorphous precipitations of 1 μm over honeycomb-like aragonite structure in the columnar morphotype. (**h**) SR-FTIR spectral signals of main carbonates of spongy and columnar microbialites: aragonite, calcite, and hydromagnesite (for details, see Valdespino-Castillo et al. 2018) areas that are extremely important for biodiversity conservation (Valdespino-Castillo et al. 2019). Many prokaryotes in Lake Alchichica microbialites have no parallel in the current databases. Likewise, eukaryotic organisms related to Alchichica microbialites exhibit a high endemism (as seen in chapters 16, Alchichica axolotl, 20, Diversification and endemisms, and 21, Conservation actions). Diversity indices of Shannon and Chao (6.1 and 6.3; 2026 and 2271 for spongy and columnar types, respectively) have been reported by Centeno et al. 2012) and indicate a high degree of prokaryotic diversity in these assemblages. DNA sequences and taxonomic assignment of Bacteria and Archaea in Alchichica microbialites can be found in GenBank under NCBI BioProject PRJNA418176 (BioSamples: SAMN08017101 and SAMN08017098). Pyrosequences were deposited in the Sequence Read Archive (SRA, NCBI), under BioProject SRA040061. Information regarding the most abundant prokaryotic phyla can be found in Centeno et al. (2012). By comparing microbial composition from five different Mexican sites, Centeno et al. reported that the most abundant phyla for all these locations was Proteobacteria (~ 31–42%; where Alpha > Beta > Gamma > Deltaproteobacteria), followed by Cyanobacteria (overall range 1–24%). Notably, cyanobacterial abundance in Alchichica was the highest. Microbial phyla with medium abundance in the Mexican microbialite survey were Planctomycetes (5–11%), Verrucomicrobia (3–8%), Bacteroidetes (4–8%), Acidobacteria (1–2.4%), Chloroflexi (1–2.4%) and Firmicutes (1–3%). Phyla with low abundance included Actinobacteria, Nitrospira, Chlamydiae, Spirochaetes, Chlorobi, Fusobacteria, and Gemmatimonadetes. The challenges of extracting total DNA from these complex mineral mixtures have been discussed in Gómez-Acata et al. (2019).

22.3 Microbialite Microbiology: Microbialites Are Active Communities

As a M.S. student, LI Falcón provided the first physiological evidence that these microbial consortia were metabolically active, performing N_2 fixation in rates that averaged 3 μM N_2 m_2 h^{-1}, with higher rates in the spongy compared to the columnar forms. The evidence of activity (Falcón et al. 2002) broke skepticism and was a first step for the research she has led on the microbialites of Lake Alchichica. N_2 fixation was further related to specific microbes (*nifH*), mostly within cyanobacterial Nostocales (Beltrán et al. 2012). Basal-heterocyst cyanobacteria seem to be a key component of this process in Alchichica microbialites.

The microbial components of microbialites were first described by Couradeau et al. (2011) and Centeno et al. (2012) using next-generation sequencing methods. These studies showed a diverse community, which varied along a depth gradient up to 14 m (Couradeau et al. 2011). Centeno et al. (2012 and 2016) suggested that the microbial composition of Alchichica microbialites was taxonomically similar to microbialites from other regions of Mexico but intriguingly richer in cyanobacteria.

The cross-system comparison included microbialites from coastal and inland karstic locations: Bacalar, Muyil, and Cuatro Cienegas Basin. Microbialite communities among systems shared taxonomic features, and the main prokaryote groups were generally Proteobacteria, Cyanobacteria, Planctomycetes, and Verrucomicrobia. Archaea seemed to be less abundant in the microbialites studied, whereas the main phyla were Euryarchaeota and Crenarchaeota. Centeno et al. (2012) also identified conductivity, pH, and nitrate availability as the ambient environmental factors significantly related to microbial communities' differences.

22.4 Microbialites in Deep Waters

As explained in Chap. 5 (Hydrochemistry of Lake Alchichica and its drainage basin), Lake Alchichica is one of Mexico's deepest lakes (z_{max} = 60 m). While the lake's shallow environment harbors at least two visually recognizable types of microbialites, these comprise a continuum that extends to depths of ~ 40 m. The microbial composition and the characteristics of these microbialites constitute an intense subject of research. Couradeu et al. (2011) reported a shift in the composition of Cyanobacteria with depth, where Pleurocapsales increased in abundance at 14 m. A similar pattern was reported by Águila (2018) and Águila et al. (2021). Furthermore, deeper microbialites harbor a larger diversity of Actinobacteria and Firmicutes than surface structures (Couradeau et al. 2011).

22.5 Cyanobacteria: Main Components of Microbialites

In Alchichica microbialites, cyanobacterial taxa showed a depth distribution pattern (Kaźmierczak et al. 2011; Saghaï et al. 2015; Águila et al. 2021). Dominant cyanobacterial taxa of different depths are shown in Fig. 22.2. These authors suggested that filamentous Synechococcales (*Haloleptolyngbya* sp., *Leptolyngbya* sp., *Nodosilinea* sp. and *Oculatella* sp.) with Nostocales (*Rivularia* sp. and *Calothrix* sp.) were major components for microbialites developing at a depth of 3 m. *Nodularia* sp. was only present in winter but was not a central component of microbialites. Unicellular Synechococcales (*Acaryochloris* sp., *Cyanobium* sp. and *Prochlorococcus* sp.) strongly associated to deep-water (20 and 30 m) microbialites. Most importantly, Chroococcales (*Entophysalis* sp.) and Pleurocapsales (*Chroococcidium* sp. and *Myxosarcina* sp.) were common in all microbialites; their abundance increased at a depth of 20 m. The study of *Entophysalis* sp., *Chroococcidium* sp., and Myxosarcina sp. has provided significant insights into the depth-related pigments diversity and photosynthetic activity in spongy microbialites. Pleurocapsales have also been described for microbialites of Lake Pavilion in Canada (Russell et al. 2014), Highborne Cay in the Bahamas (Mobberley et al. 2015), being dominant in some dome-shaped microbialites of Lake Dziani-Dzaha

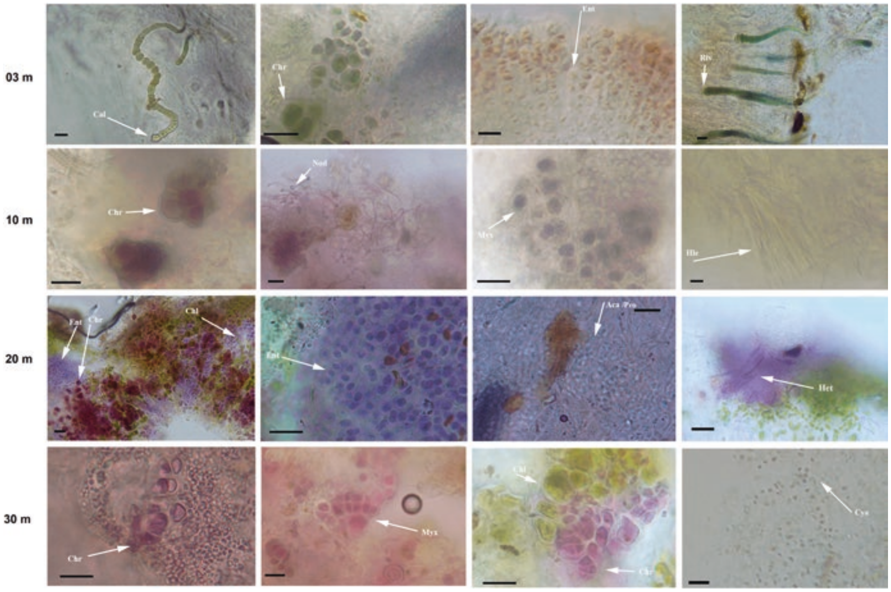

Fig. 22.2 Optical microscopy of cyanobacteria in microbialites. For 3 m: *Calothrix* (Cal) filaments were scarcely found, *Chroococcidium* showed a green morphotype (Chr), *Entophysalis* (Ent) showed a red morphotype, and *Rivularia* (Riv) colonies were found abundantly in the exterior of microbialites. For 10 m: *Chroococcidium* exhibited a violet morphotype, *Nodosilinea* (Nod) was abundant in the exterior of microbialites, *Myxosarcina* (Myx), and *Haloleptolyngbya* (Hal) were also present. For 20 m: a consortium of *Entophysalis* with purple morphotype, *Chroococcidium*, and a Chlorophyte (probably *Cladophora*) were common, there were also cells of *Acaryochloris* or *Prochlorococcus* (Aca/Pro) and filaments of *Heteroleibleinia* (Het). For 30 m: *Chroococcidium* and *Myxosarcina* were found abundantly, as well cells of *Cyanobium* (Cya) Scale Bar = 10 µm

in Mayotte (Gérard et al. 2013). The endolithic ecology of Pleurocapsales probably depends on low light conditions; nonetheless, the difficulty of culture isolation has made this group of cyanobacteria historically understudied (Brito et al. 2017). Since their role in mineral precipitation and photosynthesis in Alchichica microbialites appears to vary with depth, more research is needed to untangle the specific roles of the different cyanobacterial components of these structures (Águila et al. 2021).

22.6 Biomineral Structures

Lake Alchichica is a maar alkaline and saline system with a relatively recent history (see Chap. 5, Hydrogeology and Hydrochemistry). To understand their fossilized biosignatures, Kaźmierczak et al. (2011) studied microbialites mineral composition, texture, and isotopic composition. They used U-Th radiometric dating on both stromatolite-types. Their results suggested the formation of the different microbialite morphotypes might be related to distinct stages of lake hydrogeology, which could explain the difference in mineral composition in both morphotypes, where the spongy types were composed mainly of hydromagnesite with an admixture of huntite and calcite, and dating to ~ 2800 years B.P. Meanwhile, the columnar-types were composed of aragonite and an admixture of Mg-calcite, dating to ~ 1100 years B.P.

Structural microbialite surface minerals were primary carbonates, mainly exhibiting micrometric-scale micric, amorphous precipitations (Fig. 22.1b, c). As reported in Valdespino-Castillo et al. (2018), microarchitectural observations showed that benthic diatoms (and silicification potentially) might play a role in building micrometric environments in the surface of the microbialites (Fig. 22.1b, d), which needed further clarification. A regular honeycomb-like structure of hexagonal caveats was observed at the columnar type's surface, where aragonite was the main mineral found. Other minerals were also formed, for example, apatites (Fig. 22.1c) as detected by SEM-EDS microscopy-spectroscopy (Fig. 22.1d).

A novel bioimaging strategy was developed and applied to characterize living cells and biogeochemical systems at microscale (Holman et al. 2010; Probst et al. 2013, 2014; Valdespino-Castillo et al. 2018). Synchrotron infrared spectromicroscopy was used to characterize minerals and biomass of live microbialites from various locations. Infrared spectral features of the carbonates reported in Valdespino-Castillo et al. (2018) included generalized hydromagnesite signals, aragonite, and calcite (Fig. 22.2h), but also spatially segregated calcite with traces of strontium and siderite.

Microbialites from Lake Alchichica have inspired many geo-microbiologists to investigate how aquatic biological diversity is structured and maintained (Couradeau et al. 2011; Centeno et al. 2016). By using novel strategies of microscopy and chemical imaging techniques, Gérard et al. (2013) linked the potential formation of aragonite to Pleurocapsales cyanobacteria in microbialites from the depths of 20 m. Kaźmierczak et al. (2011) and Valdespino-Castillo et al. (2018) reported that calcite nucleation on surface layers of microbialites is spatially related cyanobacterial filaments. Deeper analyses of the microbialites open new questions and challenges to the study of these communities.

22.7 Biogeochemical Cycles

The potential role of nitrogen and phosphorus as the nutrients limiting the productivity of lake Alchichica has been documented in different studies (e.g., Ramírez-Olvera et al. 2009; see Chap. 7). Therefore, the role of microbes in nitrogen and phosphorus biogeochemical cycling has been extensively explored in Lake Alchichica. Different studies reveal that microbialites harbor a significant genetic diversity potential for N and P remineralization (Valdespino-Castillo et al. 2014, 2017; Alcántara-Hernández et al. 2017). Recent studies document the genetic potential of microbialites associated with sulfur cycling (Torres-Huesca, in preparation). A general scheme of the main biogeochemical transformations in microbialites as detailed by the bacterial genes explored is shown in Fig. 22.4.

22.7.1 Nitrogen Cycling

The work of Alcántara-Hernández et al. (2017) analyzed the diversity associated with N cycling by coupling genomic characterization and expression patterns of nitrogenase (*nifH*), ammonia monooxygenase (amoA), nitrite oxidoreductase (*nxrA, nxrB*), hydrazine oxidoreductase (*hzo*), and nitrite (*nirS* and *nirK*) and nitrous oxide (nosZ) reductases. Alcántara-Hernández et al. (2017) showed that the genetic potential for N_2 fixation, ammonia oxidation, anammox, and denitrification was present in the microbialites of Alchichica. The taxonomic affiliation of the amplicons is shown in Fig. 22.3 for each step of the nitrogen cycle. However, compared to the transcriptomic signal, the main metabolism expressed was N_2 fixation linked to Nostocales cyanobacteria.

22.7.2 Phosphorus Cycling

Dissolved organic phosphorus (DOP) is usually the most abundant and largely uncharacterized fraction of phosphorus in aquatic environments (Kolowith et al. 2001; Dyhrman et al. 2007). To make phosphorus available from this fraction, microbes harbor diverse strategies such as using pH-dependent (acid or alkaline)

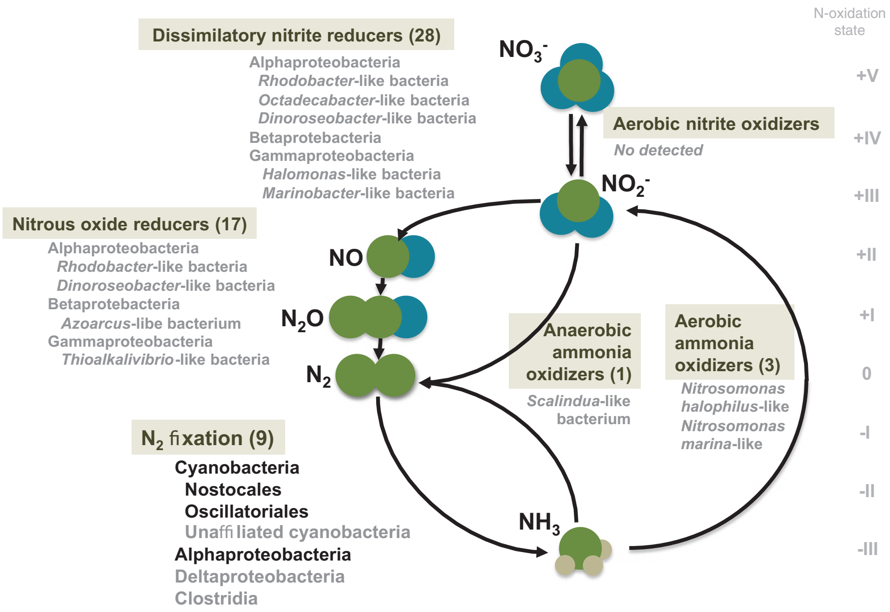

Fig. 22.3 N-cycling genetic markers and their taxonomical affiliation detected in microbialites of Lake Alchichica (Alcántara-Hernández et al. 2017)

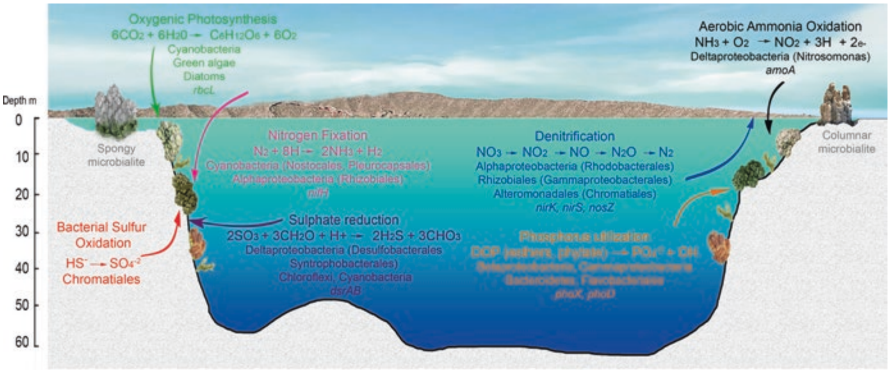

Fig. 22.4 A general scheme of the role of microbialite microbes in biogeochemical transformations is shown. Biogeochemical pathways equations are simplified and shown along with their prokaryotic signals in microbialites, including taxonomic affiliation and genes. For example, Alphaproteobacteria and Cyanobacteria are main participants in carbon and nitrogen fixation. Alpha- Beta- and Gamma-proteobacteria are main participants in organic phosphorus utilization (contributing to phosphate availability). Additionally, Deltaproteobacteria, Chloroflexi, and Cyanobacteria are relevant taxa in sulfate reduction, and finally, Gammaproteobacteria in sulfur oxidation

phosphatases to release orthophosphate or polyphosphate chains from organic matter phosphate esters (Ruttenberg and Dyhrman 2005). Phytate or phytic acid is another molecule that may be abundant in DOP of aquatic environments due to plant debris runoff (Suzumura and Kamatani 1995). Some microbes can release orthophosphate from phytate using phytases. A diverse set of beta-propeller phytase (BPP) markers were detected in microbialites and bacterioplankton of Lake Alchichica. In their studies, Valdespino-Castillo et al. (2014, 2017) found the pool of alkaline phosphatases (AP) *phoA* and *phoD*, as well as beta-propeller phytases (3-phytase, BPP) was higher in microbialites than in bacterioplankton. This P remineralization potential was taxonomically related to Alpha-, Beta-, and Gamma-proteobacteria. Compared with other AP surveys, this taxonomic affiliation is similar among systems exhibiting contrasting environmental characteristics (e.g., trophic state, phosphorus condition, the concentration of Zn^{+2}, Mg^{+2}, and Ca^{+2}, metal cofactors of these type of enzymes) (Valdespino-Castillo et al. 2014). The diversity of BPP was taxonomically related to phyla Alpha- and Beta-proteobacteria and Bacteroidetes, and Flavobacteriales. Beta-propeller phytases found in this alkaline lake were similar to phytases found in forest soils, glaciers, lake sediments, and fish gut microbiota (Huang et al. 2009).

Alkaline phosphatase *phoX* was the marker among DOP utilization enzymes that showed the highest ratio of unique sequences/total sequences (Valdespino-Castillo et al. 2014). Gene dynamics showed that the lake's hydrologic cycles (summer stratification-winter circulation) could impact the lake's DOP utilization potential. The highest DOP utilization diversity in microbialites together with this result may account for the resilience of microbialites. The bacterioplankton, instead, exhibited a faster response to environmental change and less diversity (Valdespino-Castillo et al. 2014, 2017). Together, these results outline divergent biogeochemical strategies between microbialites and bacterioplankton to face environmental change, which should be further studied, particularly to understand microbialite formation and history.

22.7.3 Sulfur Cycling

The circulation-stratification hydrological cycle leads to different sulfur (S) redox environments related to the season and the lake compartments. Nevertheless, the microbial mats of microbialite surface most likely offer millimetric redox gradients relevant for sulfur transformations. Torres-Huesca (2018) studied some of the genetic markers related to the sulfur cycle in littoral microbialites and at different depths, taking samples up to hypolimnion from the stratified water column with anoxic conditions and reducing redox conditions. The author focused on the characterization of sulfate-reducing bacteria through 16S rRNA analysis using Next-generation sequencing (NGS) and the diversity of the functional gene *dsrA*. A low abundance of potential sulfate-reducing bacteria (~ 1%) was found relative to the total prokaryotic community, probably because the microbial mat samples in the Alchichica microbialites were thin (0.5-1 mm from the surface) and not optimal for anaerobic metabolisms (Muyzer and Stams 2008).

Similarly to these results, deltaproteobacteria's contribution as sulfate reducers accounted for less than 0.01% of the relative abundance in the littoral microbialite samples (Valdespino-Castillo et al. 2018). In the metagenomics study of Alchichica's microbialites, conducted by Saghaï et al. (2015), sulfate reduction gene signals exhibited very low abundance. In his study, Torres-Huesca (2018) showed genetic diversity of *dsrA* genes was affiliated mainly with Deltaproteobacteria within the *Syntrophaceae*, *Desulfobacteraceae*, *Desulfobulbaceae*, and *Desulfovibrionaceae* families, these are characteristic groups in saline-alkaline microbial mats and other microbialites (Foti et al. 2007; Sorokin et al. 2011; Casaburi et al. 2016). Ongoing analyses show that sulfur oxidation's potential might be related to gammaproteobacteria Chromatiales in Lake Alchichica (Torres-Huesca 2018), their exploration has been expanded to lake's different compartments: sediments, water column, and microbialites. Previous work by Santillan-Manjarrez (2018) and by Torres-Huesca (2018) explored the potential of sulfate reduction and sulfur oxidation in these microbialites.

22.7.4 Trace Metal-Microbe Interactions

Mineral matrices of living microbialites accumulate organic matter and trace metals from the surrounding environments. This enrichment has been attributed to the binding of cations to extracellular polymeric substances (EPS) in the surface of microbial mats and the redistribution into sulfide-rich laminae upon degradation of EPS during early diagenesis (see Bruggmann et al. 2020). A cross-comparison of microbialites from different locations, including those from lake Alchichica revealed specific relationships of microbes and trace metals (Valdespino-Castillo et al. 2018). The microbialites studied showed higher concentrations of trace elements than other microbial carbonates (see Kamber and Webb 2007). The results reported in Valdespino-Castillo et al. (2018) revealed a strong correlation pattern of microbial taxa with transition elements such as cadmium, cobalt, chromium, and copper. Chromium and copper, known to be toxic for many microorganisms, showed positive correlations with some bacterial groups. In detail, Alphaproteobacterial families Sphingomonadacea and Rhodobacteraceae (e.g., *Rubellimicrobium*) were strongly and positively correlated to Cr concentration in the mineral matrix. Specific homeostasis proteins were linked to bacterial strategies to deal with trace metals. For example, Proteobacteria harbored more than half of the proteins annotated for copper homeostasis (NCBI Protein database, Jan 2018), and more than 80% of the proteins were associated with copper resistance. Copper homeostasis genes (e.g., protein *cutC* and copper transporter *cupA*) have been identified in Lake Pavilion's freshwater microbialites (White et al. 2015). Alphaproteobacteria also harbor 10.7 and 40% (respectively) of the total annotated bacterial *cutC* and *cupA* genes (NCBI Protein database, Jan 2018). In contrast, cadmium and cobalt were significantly but inversely related (lower microbial abundance correlates with higher metal content) to the distribution of dominant microbialite organisms, overall supporting their toxic effect. Specific microbe-trace metal correlations showed the highest scores for Cyanobacteria (Oscillatoriales and Synechococcales), Bacteroidetes (Cytophagales and Flavobacteriales), Alphaproteobacteria (Rhodobacterales, Rhizobiales, and Sphingomonadales), Gammaproteobacteria (Pasteurellales, Aeromonadales, and Enterobacteriales), Firmicutes (Lactobacillales and Clostridiales).

22.8 Biodiversity Conservation Challenges

Microbialites represent ancient ecosystems of high microbial diversity and constitute excellent models to understand microbial evolution and elemental cycling in the biosphere. Our research of Alchichica microbialites has just started. Their unique microbial composition, their vast metabolic potential, and the formation of microhabitats favoring other species settlement such as the endemic amphibian *Ambystoma taylori*, lead to the broad recognition of microbialites as biodiversity hotspots. These biodiversity hotspots are of utmost importance to setting conservation priorities and implementing strategies to preserve biodiversity.

The high biological diversity found in microbialites might be a key factor to their adaptive success through millions of years. The research of these microbialite structures can provide valuable insights to the fields of Astrobiology, Geosciences, Ecology, and Biogeochemistry. However, these microbialite structures are threatened by the increasing regional water use associated with large-scale agricultural practices. Puebla and Veracruz's local governments hold a major responsibility in the conservation of this diversity hotspot. Even a micromolar increase in the nutrient content, regional temperature and rainfall changes can pose drastic impacts. We have started to increase the societal awareness about these concerns; for example, during the First National Day of Stromatolites in Mexico (July 5th, https://youtu.be/ac5aev2XMVs) science-outreach and community activities took place around the importance of the diversity and conservation for these ecosystems. Also, science-related publications for a broader audience are available (Valdespino-Castillo et al. 2015; Valdespino-Castillo et al. 2019; Falcón et al. 2020; Yanez-Montalvo et al. 2020), besides informal talks. The conservation of Lake Alchichica and the Axalapascos offers a challenging panorama involving climate change and increasing water use. Scientists, local government, and society must work together in the conservation of Alchichica biodiversity. By overcoming the challenges at this biodiversity hotspot, we can set up a model system for sustainability and conservation throughout the Central Mexican Highlands.

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Chapter 23
The Lake Alchichica from an Astrobiological Perspective

Karina Elizabeth Cervantes-de la Cruz, Elizabeth Chacón-Baca, and Lilia Montoya

23.1 Introduction

Astrobiology is the transdisciplinary science behind the study of life potential across the Universe, in order to know whether life's principles and theories are equally universal for example, in physics and chemistry (Blumberg 2011); thus, with knowledge resulted from deductive or inductive reasoning; their performances come from the development of self and unique concepts, methods, and subjects such as habitability, biosignature, life detection, habitable zone, and environmental analogue. These concepts apply the understanding of interdisciplinary processes such as biogeochemical cycling, fossilization, minimal cell, chemical evolution, life definition, origin of planetary systems and intelligence implying the crossover between multiple sciences, e.g., geology, chemistry, oceanography, astrophysics, informatics, and biology (Czyżewska 2011). Therefore, astrobiology is surprisingly developing in an age of science reductionism despite being multi- and trans disciplinary.

K. E. Cervantes-de la Cruz
Departamento de Física, Facultad de Ciencias, Universidad Nacional Autónoma de México.
Universidad Nacional Autónoma de México, Ciudad de México, Mexico
e-mail: cervantes@ciencias.unam.mx

E. Chacón-Baca
Facultad de Ciencias de la Tierra, Universidad Autónoma de Nuevo León,
Linares, Nuevo León, Mexico
e-mail: elizabeth.chaconbc@uanl.edu.mx

L. Montoya (✉)
Facultad de Ciencias de la Tierra, Universidad Autónoma de Nuevo León,
Cuernavaca, Morelos, Mexico
e-mail: lilia.montoya@uaem.mx

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23.2 The Search for Life in the Solar System Begins on Earth

23.2.1 Extreme Environments and Habitability

Assessing the universality of life implies being aware of life distribution here on Earth and inventorying the places where organisms may and may not be possible as well as analyzing organism adequacy under experimental conditions, among other approaches. Habitability can be defined as the potential of an environment (past or present) to support active life (Cockell 2014; Airo et al. 2014). The concepts of "habitat" and "niche" from ecology have nurtured "habitability" in astrobiology, however, the ecological view of habitat has been focused on or dominated by multicellular organisms (Cockell et al. 2016). Consequently, there has been a progressive feedback between microbial ecology, geomicrobiology, environmental microbiology and astrobiology since the early finding of life in extreme environments to define the processes that determine the distribution of microorganisms and the habitability principles. The boundaries of life are at the expense of two kinds of parameters: biological (i.e., evolutionary, and ecological) and environmental; examples of the latter are temperature, water activity, pH, pressure, nutrients, radiation, and electron donors and acceptors (Jones et al. 2018). In this sense, it has been understood that environmental processes are more relevant in determining the limits of life than the historical ones, at least in small scales and extreme environments. This can be argued since foreseen recovery of microbes with specific dissimilatory metabolisms, and adaptive strategies in specific environmental conditions until certain extent given the unpredictability in the identities of microbial taxa (Morris 2011; Macalady et al. 2013). An example of a weak or inconsistent biogeographical regionalization for extremophiles comes from halophiles (Clark et al. 2017); in this study, authors analyzed the clustering of 17 halite-associated archaeal communities, and found that three species are abundant and widespread in all samples.

It is an oversimplification to rewrite the search for life in the Universe as the search for ecological niches on planets and satellites, because "habitable" does not imply "inhabited." This distinction is carefully made by astrobiologist to take into consideration relevant uncertainties, such as the physicochemical conditions that promote the origin of life, the continuum between activity, maintenance, survival and dead states in microorganisms, potential for panspermia, local environmental constraints in other planetary bodies and the influence of life itself on the environment (Hoehler and Jørgensen 2013; Cockell et al. 2016). Though this relationship between life and environment is complex, all knowledge obtained about the distribution of life in extreme habitats and extremophilic organisms is contributing to predict the potentially habitats on other planetary bodies because, though remarkably diverse regions on Earth are habitable, others are not after almost 3.8 billion years of evolution (Lineweaver and Chopra 2012; Cockell 2014). Besides, under certain conditions, some metabolisms are at their optimum while others are not as a result bioenergetic differences, ruled by universal laws, instead of differences in their evolutionary history (Oren 2011; Montoya et al. 2011). Therefore, extreme environments are still notoriously useful to contribute to study habitability and the preservation of past life.

23.2.2 Extreme Environments as Analog Environments

Specific locations on Earth have been used as field facilities or reference sites for exploration, because of its resemblance with extraterrestrial regions and are known as “analogue sites” or “analogue environments”. Usually, terrestrial analogs are extreme environments (Preston and Dartnell 2014; Gómez 2011). The resemblance may include a broad set of conditions or only one. Analogue sites are applied in astrobiology by several purposes (Table 23.1).

(i) Analogues: provide broadly clues to evaluate habitability in Solar System bodies and as a guide to early evolution of life on Earth (Léveillé 2010). Analogue environments provide insights on open inquiries in astrobiology, e.g., (a) at what extent energy limitation in dissimilatory/assimilatory metabolism is a determinant of optimal and tolerance conditions within single extreme conditions (pressure, pH, temperature, salinity, radiation, water activity), (b) the predictability of habitability under a combination of extreme conditions (i.e., poly or pluriextreme environments) (Harrison et al. 2015) and an ion-specific effect on habitability (Stevens and Cockell 2020; Avendaño et al. 2015). Moreover, there are few studies that confront the effect of trophic interactions on optimal/tolerant limits, e.g., parasitism, competition, symbiosis, and syntrophism (Seto and Iwasa 2019).

(ii) Analogue missions: simulation of human and/or robotic planetary operations for field training and testing (https://www.nasa.gov/analogs). Commonly multidisciplinary, necessarily *in situ,* and mission oriented. These campaigns are focused on obtaining experiences to validate and interpret information, including aspects such as human factors, human-robot interaction, and workflow or sequence of measurements and procedures (Groemer and Ozdemir 2020; Léveillé 2009; Martins et al. 2017) to reduce costs and risks associated with eventual missions (Léveillé 2010), and to obtain results, not only feasible and reliable but also independent on context. Collected samples are not necessarily extant, also extinct or fossilized and molecules that reveal their state (biosignatures-extant and biomarkers-extinct) are also studied. The process of preservation is of astrobiological interest because extreme conditions may slow or accelerate degradation processes of biomolecules or biogenic structures (Baucon et al. 2017).

Table 23.1 Classification of the research activities performed in environmental analogs based on Martins et al. (2017) and Gómez (2011)

Analogue	Example
Analogues	
Life tolerance limits	The Dallol geothermal dome, Danakil Depression Ethiopia: The combination acid-saline (pH 0; salt 35%) sets limit to microorganisms regardless of temperature (Belilla et al. 2019).
Biomarker preservation in evaporites	The hypersaline lake Tirez, Spain: A Mid-IR and Near-IR spectroscopic examination of evaporites was performed to identify amides, carboxylic acids, and chlorophylls. These biomarkers are well preserved in the Na and Mg-sulfate evaporites, a chemical salt composition useful for being analogous to Mars and Europa (Preston et al. 2020).
Spectroscopy of chemical analogues	Anoxic springs associated with evaporite diapirs, Axel Heiberg Island, Canada: Subzero (<0 °C) and hypersaline springs (>10 wt. %) that precipitate hydrated Na-sulfates and NaCl salts were characterized spectroscopically by their vis-NIR spectral properties because of their relevance as chemical analogs of Europa (Fox-Powell et al. 2019).
Analogue mission	
Sample analyzing equipment	Rio Tinto Basin, Spain: NASA Mars Astrobiology Research and Technology Experiment (MARTE) simulated a drilling mission and obtained cores and subsamples to further analyses (Cannon et al. 2007).
Organics in soils	Dry Valleys, Antarctica; Atacama Desert, Chile, and Peru; Libyan Desert, Egypt; Rio Tinto, Spain and the Panoche Valley and Mojave Desert, U.S. as Mars analog soils were analyzed to compare the detection of organics by a TV-GC-MS used as a standard method for organic detection on Mars as in the European Space Agency ExoMars mission and compare them with the Viking TV-GC-MS results (Navarro-González et al. 2006).
Geological interpretations	Atacama Desert, Chile: A comparison of the performance of five scientists participating in the 2005 season of the Life in the Atacama (LITA) Mission project considering personal bias (individuality) in certainty, accuracy, and consistency of geological interpretations of rover data and orbital image analysis (Thomas et al. 2007).
Planetary protection protocols	Lake Bonney, McMurdo Dry Valleys, Antarctica: ENDURANCE (Environmentally Non-Disturbing Under-ice Robotic Antarctic Explorer) is an autonomous underwater vehicle capable of creating 3D maps of underwater environments and designed to fulfill the strict Antarctic environmental protocols (Doran et al. 2010)

23.3 Biomarkers: Direct and Indirect Indicators of Life

23.3.1 Chemical Signals of Ancient Activity

Biomarkers are chemical compounds indicative of either environmental factors acting upon specific organisms over time, or species-specific chemical indicators. The search for biomarkers is a fruitful tool in paleontology and astrobiology, among them highlight the hopanoids, which are lipidic compounds consisting of pentacyclic triterpenoids that are widely distributed in prokaryotic microorganisms, especially cyanobacteria (Rohmer et al. 1984). Other aromatic molecules may function as biomarkers too but lack the high preservation potential and stability of hopanoids.

Hopanoids are essential metabolites that act as membrane stabilizers (Ourisson et al. 1987), and reserve pools for cell signaling and metabolism. Usually, the biosynthesis of hopanoids follows the Bloch-Lynen pathway in Eukarya (Nes and McKean 1977) and Archaea (Langworthy et al. 1976). However, their biosynthesis in some Bacteria takes a different path (Rohmer 2010). In recent and fossil sediments, bacterial hopanoids are reliable biomarkers, therefore, are frequently used as molecular biosignatures (Ourisson et al. 1982; Ourisson et al. 1987). The search for biomarkers includes the extraction of organic matter from a specific sediment or a rock. Pioneer studies on bacterial biomarkers have been conducted by researchers from the University of Strasbourg (Summons 1988; Ourisson et al. 1982; Rohmer 2010). Another research group dedicated to recent and ancient biomarkers has been developed by Roger E. Summons in Canberra, Australia, and the Massachusetts Institute of Technology (https://summons.mit.edu/).

The oil industry has also developed biomarker extraction techniques, such techniques have been applied to paleontology and astrobiology. Extraction techniques with polar solvents depend on the host rock and diagenetic alteration (Summons 1988; Summons and Jahnke 1992). The organic matter is extracted with polar solvents and concentrated in different organic fractions that are analyzed by CG-MS; accordingly, this analysis includes their fragmentation patterns, distribution, and abundance of major ions, where the biomarkers identification is based on the distribution and abundance of peaks, and comparison with standards. Usually, the biomarker analysis has been known as molecular paleontology since it reveals key information of organisms and their response to specific environmental factors (Summons 1988; Briggs et al. 2000). Contamination may be a serious weakness in some especial cases, but in general, this tool has been successfully explored in many Precambrian sediments (Summons et al. 1994; Summons 1988; Briggs and Summons 2014; Brocks and Summons 2013; Summons and Jahnke 1992), and it is a reliable technique to be applied in extraterrestrial samples (Liu et al. 2016; McMahon et al. 2018; Broz 2020).

The co-occurrence of mineral biomarkers and organic or molecular signatures are complementary evidence; therefore, the formation of lipid biomarkers in modern terrestrial carbonates provide good models to identify ancient and novel, and extraterrestrial biomarkers and palaeoecological reconstructions (Dong et al. 2019).

23.3.2 Geological and Morphological Imprints

Since microbialites formed by benthic microbial communities may bind, trap and precipitate sediments (Burne and Moore 1987), the genesis of biomarkers as they grow and mineralize also increases; especially those biomarkers synthetized in response to environmental factors. Furthermore, microbialites may show specific mineral structures and microfabrics that reflect the environmental conditions of diverse sedimentary environments, such as tidal flats, hypersaline lakes, hydrothermal sources, and caves, among others.

The occurrence in microbialites in modern environments not only allows the reconstruction of ancient environments, but also analogues for astrobiology. For example, to solve sedimentary features at the ancient playa lake environment in the Gillespie Lake Member, Mars (<3.7 Ga) controversially interpreted as microbialites (Noffke 2014). Alkaline carbonates are particularly important to study mineral-microbial interactions that may be preserved as microbialites; for this reason, a wide variety of experimental approaches documents the richness of microbial mats as rich source of signatures (Chacón 2010), among them, biomarkers (Fig. 23.1). The origin of microbialites depends on microbial communities but also on the cation availability for the carbonate system, including any other mineral precipitation, and their preservation. In fact, the mineralization of benthic microbial mats within a loci of calcium carbonate involves simultaneous geobiological, sedimentological, geochemical, microbial, molecular, and mineral processes. Microbial mats and microbialites are significant sources of hopanoids and a rich source of molecular biomarkers in general; the high diversity of metabolisms involved inside microbialites are associated to carbonate precipitation. Therefore, for being survivable, reasonable detectable, and widely distributed hopanoids are among the central molecules in life detection (Neveu et al. 2018).

In addition to hopanoids, spring carbonates are rich repositories of microbial lipid biomarkers, i.e., branched alkanes, which are related to their depositional environments, if preservation is good and without substantial diagenetic alterations, which may vary among diverse environmental settings (Martinez-Frias et al. 2007; Hays et al. 2017).

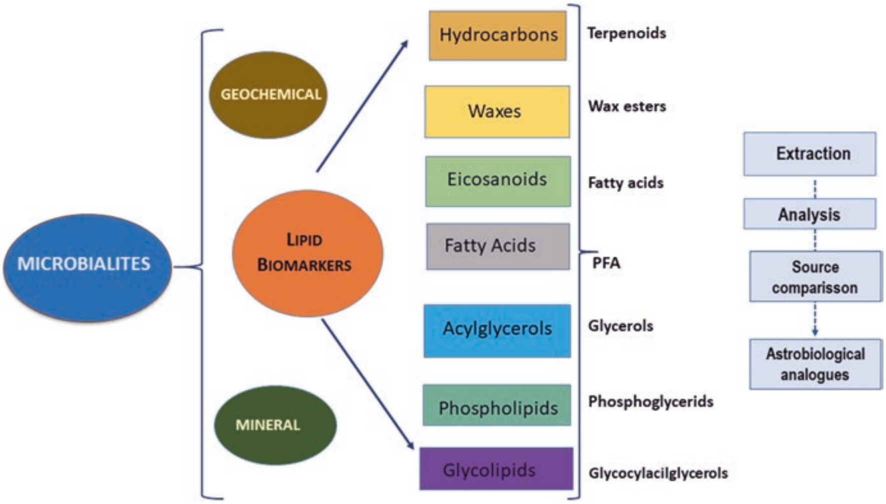

Fig. 23.1 General techniques for lipid biomarkers. Modified from Kumar et al. (2015)

Therefore, the search of biomarkers in fossil and modern microbialites encompasses multiple analyses under a sedimentological, biogeochemical, microbiological, and mineralogical perspective that may be interpreted within a given geological context. The study for lipid biomarkers in Lake Alchichica would not only be useful to infer ancient microbial processes, but the biomarkers distribution coupled with a geological, sedimentary, and biogeochemical characterization may be necessary in order to accomplish a multidisciplinary approach for the interpretation of microbial biomarkers (Briggs and Summons 2014).

23.4 The Lake Alchichica Seen as a Planetary Feature

23.4.1 General Features

According to Carrasco-Núñez et al. (2014), Lake Alchichica is a semicircular lake of 1.8 km of diameter and 60 m deep (se Chaps. 2, geological evolution, and 6, meteorological regime). The endorheic Serdán Oriental Basin (SOB) is located at Transmexican Volcanic Belt near the Folds and Faults Belt province. Stratovolcanoes have N-S trending, while monogenetic basaltic volcanoes have a preferential E-W o ENE-WSW trending (Carrasco-Núñez et al. 2014). Serdán Oriental is an example of subduction change style and differential stress along the subduction zone (Castellanos et al. 2018). Rotational trending contrasts with the homogeneous distribution of vulcanism in an isotropic stress regimen (Marliyani et al. 2020), such as in Tharsis Montes and Olympus Mons on Mars (Platz et al. 2015).

At SOB there are Tepeyahualco and Totolcingo two intermittent lakes at 2300 MSL, and eleven maars, such as Lake Alchichica (Caballero et al. 2003). Also, it is one of the most prominent tephra rings in Mexico (Carrasco-Núñez et al. 2014; Chako-Tchamabé et al. 2020a, b), its basin has an asymmetric clastic ring of dark greenish gray material, and dull yellow-orange sediments surround the ring. The west sector has the highest elevation (Fig. 23.2a).

The tuff-ring of Lake Alchichica has the next volcanic sequences (Carrasco-Núñez et al. 2014; Chako-Tchamabé et al. 2020a; Chako-Tchamabé et al. 2020b). The pre-maar member has four stratigraphic units: from the base to the top, the first unit shows aa-type lava of andesitic-basaltic composition. The next is a phreatomagmatic-derived basaltic pyroclastic density current cover by fall rhyolitic pumice from near region volcanoes, in the top is a paleosoil; this sequence is at N-NW sector. The second pre-maar unit is a dark reddish-brown scoria deposit from a small strombolian-type volcano cone (Carrasco-Núñez et al. 2014) of basaltic composition (Fig. 23.2b); this unit and the feeder dikes are in the western sector of the volcano (Chako-Tchamabé et al. 2020b).

The lower sequence has consolidated massive pyroclastic density currents of course-grain sequences (heterolytic tuff-breccia) intercalated with lapilli-tuffs, lithic-rich; the deposit corresponds to the beginning of the maar formation. The top

Fig. 23.2 Lake Alchichica geological features. (**a**) The top part of the photograph shows the northwest side of the tuff-ring covering the previous scoria-cone (red line). At the inferior-left portion, there is an uncovered terrace of sediments of the lake and microbialites; (**b**) photograph's central part shows a feeder-dyke surrounded by the pre-maar unit's scoria fall deposits (with lines); (**c**) photograph of an outcrop of the upper maar unit showing intercalations of fine lapilli rich layers with cross-laminated pyroclastic density currents deposits with some impact sags of basement lithics (red lines)

is the upper sequence and has the juvenile-rich lithic proportion of basaltic composition formed by accretionary lapilli-rich layers of pyroclastic density currents in well-stratified periodic layers with notable impact sags (Fig. 23.2c); the deposits correspond to phreatomagmatic eruptions (Chako-Tchamabé et al. 2020a; Chako-Tchamabé et al. 2020b). For more details, consult Chap. 2 (Geological evolution).

At the NW sector of the external ring, the drainage is a radial centrifuge, and the drainage at the inner ring is radial centripetal (Fig. 23.2a), e.g., Chako-Tchamabé et al. (2020b).

According to Chako-Tchamabé et al. (2020b), the maar sequences are compounded by different basaltic compositions of juvenile fragments (Chako-Tchamabé et al. 2020a), recycled juvenile fragments, and accidental lithics. Component analysis of the fine lapilli fraction shows vesicular juvenile glass.

Furthermore, Lake Alchichica diameter is covered by lake sediments. Caballero et al. (2003) reported four wide-ranging units from the drill study: At the bottom of the lake sequence, they report a microbialite formation. This unit is overlapped by a silt deposit that represents a lacustrine episode-like current conditions. Above, rest a coarse-sand and gravel-rich horizon with calcareous concretions and roots fragments; this deposit represents a dry period with low water level and high evaporation. The top horizon shows carbonate-rich levels, overlapped by silt layers, and finally, a carbonate-rich formation with roots is over of all sequence; the actual conditions of the shore lake show a low water level that exposes the spongy microbialites that protrude until 2 MSL (Fig. 23.2a).

The lowest driest episode may correlate with events reported in Lake Aljojuca (Caballero et al. 2019), where Bhattacharya et al. (2015) report a drought period between 600 to 1100 CE Lake Aljojuca is a basaltic-andesitic maar 30 km to SW from Lake Alchichica (De León-Barragán et al. 2020).

23.4.2 Geologic Origin and Evolution of Lake Alchichica

According to Carrasco-Núñez (2019) the formation of Lake Alchichica is just as Lorenz (1986), where the phreatomagmatic explosions occurred by the Molten Fuel Coolant Interaction (MFCI) between magma (molten fuel) and water (coolant) interaction (see Chap. 2, Geological Evolution of the Alchichica Crater). According to the Valentine and White (2012) model, when the magma rises through a fault and interacts with water causes MFCI explosions at depths less than 2 km; these explosions lead to crater widening. Part of juvenile and accidental lithics return to the central basin and form a filled structure called diatreme, the other part of material forms the tuff-ring deposits around the central crater.

The interaction of water and magma causes consolidation of the pyroclastic sequences because pyroclastic material is hydrated. Another result of the magma and water explosive eruptions is the formation of accretionary lapilli, a wet center material surrounded by fine-like ash (Carrasco-Núñez 2019). The weathering of glass has an essential role in ions' leaching to escape from the water lake and supply ions to the lake organism, such as microbialites.

23.4.3 Hydration of Volcanic Glass

Sideromelane formation happens when basaltic magma is quenching to high temperatures in a wet environment. If the sideromelane glass is in contact with aquatic fluids, a phenomenon called palagonitization occurs. The palagonite is the hydrated basaltic glass formed under variable chemical and physical conditions, such as temperature, pH, eH, etcetera (Stroncik and Schmincke 2002). For example, pH <3 produces incongruent glass dissolution, while pH >9 conduces to congruent glass dissolution (Stroncik and Schmincke 2002). Palagonite is the first stable mafic glass product compound for different clay minerals such as the smectite group (montmorillonite, nontronite, saponite), carbonates, and zeolites. The Al and Si leached from the glass to fluids, while the Fe and Ti accumulated passively. The glass alteration might be a mechanism for supplying elements to the solutions of hydrothermal systems such as REE, Zn, Cu, Ni, Cr, Hf, Sc, Co, and major elements except for Fe and Ti, then Ti concentrations in glasses compared with palagonite can be used to constrain the elements lost during glass alteration (Staudigel and Hart 1983; Carracedo-Sánchez et al. 2016). The alteration of volcanic glass significantly influenced natural waters' chemistry (Stroncik and Schmincke 2002; Maynard 1976). For example, the lower content of titanium from Lake Aljojuca sediments has correlated with the severely dry conditions during 600–1100 CE (Bhattacharya et al. 2015; Caballero et al. 2019).

It is essential to mention that microorganisms may influence the palagonitization process (Stroncik and Schmincke 2002). Microorganism may modify the pH and accelerate the palagonitization. Furnes et al. (2008) summarize two main types of bioalteration texture of volcanic glass: granular and tubular. Microorganism etches fresh glass and causes tubes or granular aggregates around fractures increasing ramified alteration front between fresh-altered barriers on the glass. Bioaleteration, including palagonitization, is of interest as well-preserved 3.5 Ga glassy rocks on Earth have bioaltered textures (Furnes et al. 2008), therefore, these structures are excellent ichnofossils to look for evidence of early life. At Lake Alchichica, some studies reported the relationship between microorganisms and minerals, e.g. Valdespino-Castillo et al. (2019) and reference therein.

23.4.4 Morphometry of Lake Alchichica

Graettinger (2018a, 2018b) generated a database of Quaternary crater maars to approach the normal size and shape of features in order to compare them with maars on the other planetary bodies in the Solar System. If a maar crater is the top structure of a larger diatreme produced by phreatomagmatic explosions, thus the size and shape of the craters reflect the growth history of the structure during the eruption. The morphometric parameters (see Chap. 6. Meteorological Regime, Local Climate, and Hydrodynamics of Lake Alchichica) indicated that maar craters are typically not circular, and the shapes resemble overlapping circles because phreatomagmatic explosion locations migrate (Table 23.2).

Aspect ratio is a measure between the major and minor axis: The maar craters have an average of 0.81 and a range between 0.8 and 0.95; Lake Alchichica has an AR of 0.81 (Table 23.2). Elongation compares the maar area to the one of one circle with the diameter of the major axis; average maars crater has 0.8 and a range between 0.88 and 0.84; Lake Alchichica shows an elongation of 0.87. Isoperimetric

Table 23.2 Morphometric parameters of Lake Alchichica from Graettinger (2018a)

Structure	**Major axis (m)**	**Minor axis (m)**	**Average Diameter (m)**	**Aspect Ratio [AR]**	**Area (km^2) [A]**	**Perimeter (km) [p]**
	D_{maj}	**D_{min}**	**–**	**$D_{min/}$ D_{maj}**	**–**	**–**
Alchichica	2290	1860	2075	0.81	3.56	6.88
Earth maars	6100	4300	1122 (69–5000)	0.81 (0.8–0.95)	1.5	0.2–16
Structure	**Elongation [EL]**	**Isoperimetric circularity [IC]**	**Elevation (m)**	**Depth (m)**	**Depth/ diameter**	
	$A/[\pi*(D_{majr}/2)^2]$	**$4\pi A/p^2$**	**–**	**–**	**–**	
Alchichica	0.87	0.95	240	160, lake = 64.6	0.09	
Earth maars	0.8 (0.84–0.88)	0.9 (0.9–1)	–	5–400	0.10	

circularity measure is the curvature variation with values between 0–1, with 1 being a circle. Database craters show an average of 0.9 and a range of 0.9–1; Lake Alchichica has an isoperimetric circularity of 0.95.

Graettinger (2018b) explains that host rock influences the availability of aqueous fluids. This water could be as ice in permafrost or liquid; this is important to understand because it could explain how maars could be formed in a glacial environment when comparing with possible maars on Mars or another planet with similar conditions.

23.5 The Analogies of Lake Alchichica with Terrestrial and Icy Worlds in the Solar System

23.5.1 Maar Systems in Mars and Titan

At present, Earth is the only planet where water coexists in liquid, gas, and ice form on the surface, but in other planetary bodies such as Mars, water is as ice in the cryosphere and possibly existed in liquid form in the Hesperian, around 3–3.7 Ga ago (Smellie and Edwards 2016). Glaciovolcanism occurs when fluid in a solid-state interacts with magma Smellie and Edwards (2016) propose some volcanic fields on Mars. They observed the morphology and the geology context to propose the hydrovolcanic origin of structures that resemble the terrestrial tuff cones, tuff rings, lava domes, and possible maars, such as pitted cones of Nephentes/Amenthes region at SE of Utopia Planitia, and another field at the north of Isidis Planitia in Arena Colles region.

In contrast, in the ancient Titan, a Saturn's satellite, when the hydrosphere was dominated by nitrogen instead of methane, the near-surface aquifers filled with liquid nitrogen and little quantity of methane could undergo temperature changes producing an energetic phase transition of nitrogen from liquid to gas and formed maar-like structures; in the present, this satellite has a lake of methane-ethane (Mitri et al. 2019; Tuttle Keane 2019). Cassini spacecraft image shows the possible composite maar-like cryovolcanic structures in the Winnipeg Lacus area in the northern hemisphere (78° N, 155° W). Lake Alchichica is an excellent morphologic analog to understand the complex volcanic evolution.

23.5.2 The Lake Alchichica as an Analogous Environment of Enceladus Ocean

The geochemistry and physicochemical of Lake Alchichica are already detailed in Chaps. 5 (Hydrogeology and Hydrochemistry of the Serdán-Oriental Basin and the Lake Alchichica) and 7 (Physicochemical Characteristics) in present book, however, an astrobiological approach is obtained after a comparison of Lake Alchichica with the most similar site within the Solar System: Enceladus. Orbital observations of the Saturn satellite Enceladus performed by Cassini revealed that beneath an ice crust of water, there is a global ocean (about −0.15 °C) interacting with a deformable rocky core at high temperature (>90 °C) and emanating from the south pole and to space extensive plumes of water vapor and grains with nanometer sized SiO_2 (silica) particles (Hsu et al. 2015). Enceladus internal activity has been explained its interaction with Saturn and the moons Thetys and Dione which results in high levels of tidal dissipation. Subsequently, mechanical energy is converted to heat at enough levels to preserve a water ocean over tens of millions to billions of years and driving hydrothermal circulation and chemical reactions because of water-rock interactions (Choblet et al. 2017). Hydrothermal reactions are suggested by several lines of evidence including the nanometer-sized silica particles and the plume content chemicals detected by the Cassini's Cosmic Dust Analyzer (CDA) and the Ion Neutral Mass Spectrometer (INMS) which described macromolecular organic compounds, and low molecular weight molecules hydrogen (H_2), carbon dioxide (CO_2), methane (CH_4) and ammonia (NH_3) (Waite et al. 2017). Hydrocarbons, carboxylic acids, methane, and hydrogen have been explained by serpentinization, i.e., high temperature chemical interactions at the water- rock interface (carbonate upper layer, serpentinized interior), this suggestion enhances the interest of this satellite for astrobiology, because of its potential to sustain chemoautotrophic life (Sekine et al. 2015) living at the expense of the same kind of redox reactions that methanogenic archaea harvest on Earth. Cassini observations also implied that the water reservoir exhibits an alkali salt content it contains 0.5–2% sodium and potassium salts by mass, mainly NaCl, $NaHCO_3$ and/or Na_2CO_3 (Postberg et al. 2018; Waite et al. 2017). The resemblance of Lake Alchichica with Enceladus water composition can

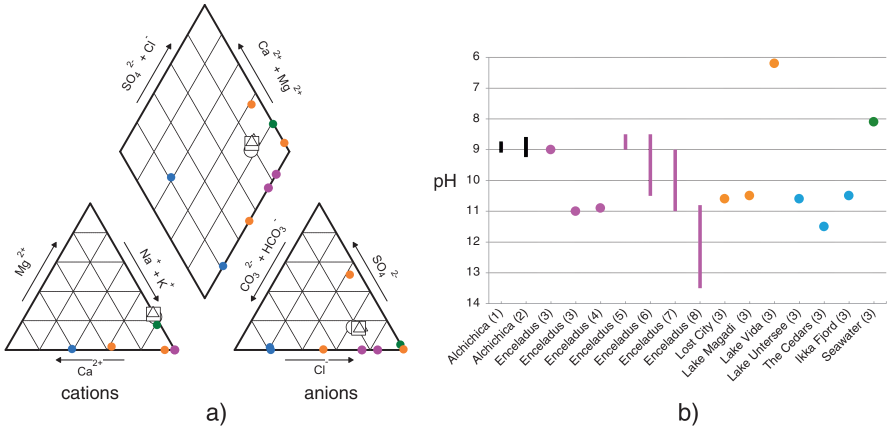

Fig. 23.3 A physical chemical comparison of Lake Alchichica with Enceladus and other analog sites. (**a**) Piper diagram of the major cations and anions. (**b**) pH values. The Lake Alchichica (black), Enceladus (pink), geochemical analogs of Enceladus (orange), temperature analogues of Enceladus (blue), and seawater as a reference (green). Piper diagram was computed using software GW_Chart MODFLOW, v.4 (Winston 2000). Data were obtained from (1) Santillán-Manjarrez (2018), (2) Alcocer and Bernal-Brooks (2010), (3) Glein et al. (2018), (4) Zolotov (2007), (5) Postberg et al. (2018), (6) Hsu et al. (2015), (7) Waite et al. (2017), and (8) Glein et al. (2015)

be recognized with a Piper diagram depicting the major cations and anions (Fig. 23.3), and emphasizes the chemical analogy of Lake Alchichica to Enceladus ocean (Glein et al. 2018). These two sites can be classified as alkaline water, mainly chloride. Also, in the Piper diagram are included other sites already recognized as physicochemical and temperature analogous of Enceladus ocean. The pH represents another analogy between Lake Alchichica and Enceladus ocean (Table 23.3): according to several theoretical models of chemical equilibrium which contemplates water and chondritic rock and consistent with H_2O/CO_2 ratio in the plume, Enceladus harbors an alkaline ocean with a pH between 8.5 and 13.5.

23.6 Geobiological Processes in Lake Alchichica: Implications for Life in the Precambrian

The high diversity of geochemical processes in the early Earth can be inferred by evidence of mineral assemblages and microstructures preserved in the oldest rocks, but also in the chemical fossils derived from microbialites, particularly molecular biomarkers. Microbialites, such stromatolites, are the most ancient evidence of Archean life and niches (Nisbet and Fowler 1999). Morphologically, lamination and clotted microbialites produced by microbial communities may preserve sedimentary, mineralogical, and chemical clues about ancient biosedimentary processes at different scales during Precambrian times. The reader is referred to the Chap. 22

Table 23.3 Most important analog geological features and processes in Lake Alchichica, Mexico. Parameters proposed according to Hipkin et al. (2013)

Rank category of feature or process	Applicability
Mineralogy/petrology	Basalts; palagonitization of volcanic glass; Mg or Ca-carbonate microbialites
Chemistry	Calc-alkali rock suites, basalts
Sedimentology	Silt to blocks derived of volcanic products
Stratigraphy	Pre-eruptive limestone and volcanic sequences, phreatomagmatic basaltic eruptive sequence, lake sequence (silts, sand and microbialites)
Geomorphology	Maar with overlapping circles shape; spongy microbialites
Hydrology	Alkaline lake, pH around 8.9
Biology	Haloalkaliphilic archaea and cyanobacteria
Ecology	Microbialites formed through the mineralization of benthic microbial mats by precipitation of carbonate
Geological setting	Maar volcano, phreatomagmatic
Environmental setting	Volcanic lake
Gradients, fluxes, and transport	Oxygenated surface layer mix with a deep anoxic water once a year
Metabolism	Carbonate precipitation in microbialites results from a combination of metabolic processes such as photosynthesis, heterotrophy, anaerobic sulfur and sulfide oxidation and sulfate reduction

(Microbialites: diversity hotspots in the Mexican Plateau) for a detailed description of microbialites.

It has been estimated that 3800 My ago, the sedimentary deposition in carbonate platforms included tsunamis, currents, turbidites and violent geological processes (Wright and Altermann 2000). By then, microbial life had already proliferated in most extreme environments (Falkowski et al. 2008). Some protected environments are represented by carbonates and mineral interphases and therefore, the utility of carbonate systems is ideal as geosedimentary models. For instance, lacustrine carbonates are important astrobiological targets to search biomarkers since they probably contain embedded organic molecules in the mineral matrix, with similar processes that can be found in terrestrial carbonates; for instance, at the alkaline lake Van, in Turkey, carbonates (Benzerara et al. 2006; Gérard et al. 2013).

There is a general belief that extraterrestrial environments might be similar in energy sources and chemistry to Earth's subsurface habitats (Jones et al. 2018). Also, some modern environments may still retain some relict biochemical pathways that reflect ancient processes on the early Earth. Therefore, Precambrian analogues are useful models for the understanding and monitoring of preservation mechanisms, and to gain a better insight into the interpretation of the fossil record.

Regarding microbialite studies, it has been shown that a particular mineralogical structure and microfabric is associated with organics that may be used as biomarkers (Benzerara et al. 2006; Dupraz et al. 2009). For a detailed discussion see Sect. 23.4.

Since microbialites are common in the fossil record, they provide microbial files of past geological processes on the Earth's surface and subsurface, as well as their biogeochemical evolution; they are a rich source of microbial fossil and recent signatures (Chacón 2010).

The significance of lacustrine carbonates in astrobiology is also directly linked to the occurrence of the marginal "White Rock" at the Sabaea Terra crater in Mars (Russell et al. 1999), and, more recently, to localities at the Noachian Jezero crater (Horgan et al. 2020). This geological structure has been interpreted as an evaporating crater lake where magnesian carbonates are present. Therefore, modern settings with continental carbonates, such as Lake Alchichica and other lakes such Salda Golu, Turkey (Russell et al. 1999), can be considered as terrestrial analogues to ancient alkaline environments.

Geochemically, most of the microbialites in Lake Alchichica are composed with hydromagnesite; instead, aragonite is distributed very locally (Kaźmierczak et al. 2011). In Lake Alchichica, an oxygenated surface layer mix with deep anoxic waters once a year; these chemical gradients in turn, promote dynamic microbial ecosystems with specific nutrient requirements. Alkaline lakes are also characterized by a high productivity, where extreme microbial communities can grow not only at very high pH and salinity conditions, but also in the presence of elevated concentrations of toxic elements (e.g., As, Se, Te) (Pecoraino et al. 2015). The common presence of the ions Ca^{2+}, Mg^{2+}, Zn^{2+} (Valdespino-Castillo et al. 2018), as well as CO_3^{2-} and PO_3^{3-} provide a richer pool of nutrients for microorganisms. When these microbial communities mineralize, they have greater chances to be preserved in the fossil record.

The Lake Alchichica exhibits geological, sedimentary, and biological features that are considered of astrobiological relevance (Fig. 23.4). As an alkaline crater, Lake Alchichica contains special geochemical conditions that prevent most stenohaline species to compete under harsh conditions, which promote the colonization of organisms with more exotic metabolisms, for example, euryhaline organisms, that includes chemolithotrophs and other microbial metabolisms. Such microbial communities can withstand extreme parameters and therefore, represents probable astrobiological targets in the long term. In the short-term Lake Alchichica represents a sedimentary environment that may have been common during the evolution of the early biosphere, particularly, during the anoxygenic-oxygenic atmospheric transition and provides an excellent analogue of one of several Precambrian environments that probably were abundant for millions of years, with specific chemical requirements as carbon, nitrogen, phosphorus, and ionic salts. Perhaps, the most attractive astrobiological feature in Lake Alchichica is its sedimentary context and geochemistry favorable enough to form carbonate microbialites. As organosedimentary deposits, the microbialites from Lake Alchichica are a result of the mineralization of calcium carbonate by benthic microbial mats (Kaźmierczak et al. 2011; Couradeau et al. 2011). The precipitation of travertine is usually associated with hot springs and therefore, with volcanic settings. Furthermore, at the microstructural level, travertine crusts are precipitated around EPS as main nucleation sites (Greer et al. 2017). The microbialites from Lake Alchichica are formed in a high-altitude

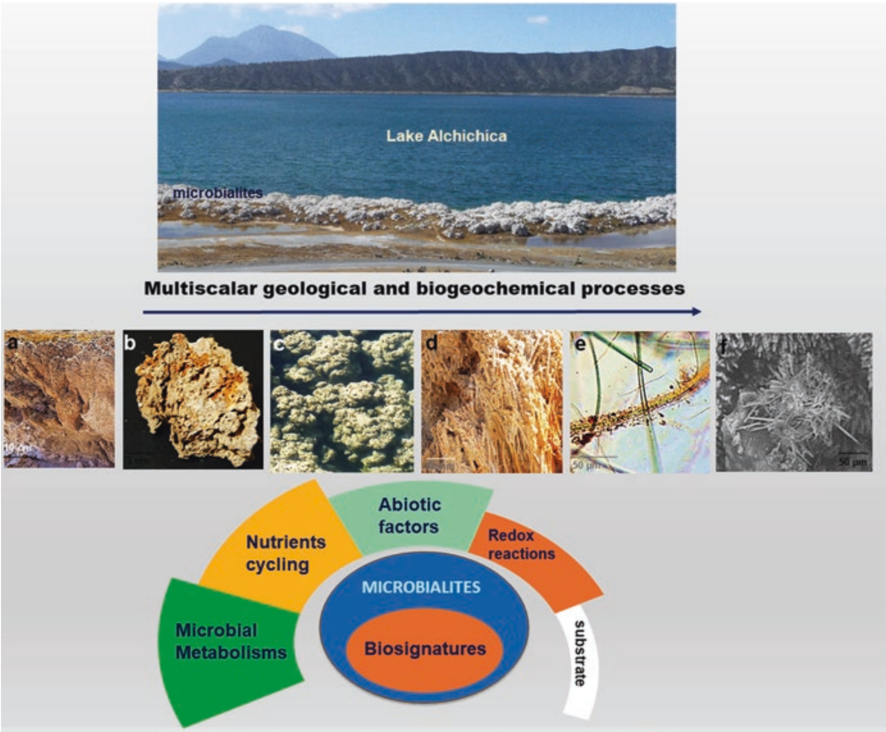

Fig. 23.4 Multiple scalar interaction between microbialites and geological and biogeochemical processes in Lake Alchichica. (**a**) Macrostructure of a brown travertine, (**b**) microbialite fragments with aragonite mineralized patches (darker areas), (**c**) a fragment of submerged microbialite (8 m depth), (**d**) mesoscale of fibrous structures, (**e**) cyanobacterial filaments with bound sedimentary particles, and (**f**) radial aragonite inside microbialites

alkaline lake, with a pH around 8.9 along a 64 m vertical profile; not only mineral encrustations of specific cyanobacteria are common inside microbialites (Couradeau et al. 2011), but also cyanobacteria with intracellular carbonate precipitation. Through diverse techniques, these microbialites have been characterized by their microfabric, molecular diversity, organic content, and associated mineralogy; all these studies suggest that the organic matrix is used as nucleation centers.

Since mineralization may preserve relevant microbial biosignatures and biomarkers, the microbialites from Lake Alchichica are of great geobiological relevance, where biotic and abiotic factors play a defining role in their formation and accretion that exhibit different types of microbial fabrics according to depth and variation of microenvironmental conditions (Kaźmierczak et al. 2011; Benzerara et al. 2006; Couradeau et al. 2013). A few studies conducted in this locality have revealed unique biomineralization processes involved in the formation of microbialites (Couradeau et al. 2011). These studies also have shown that carbonate precipitation in Lake Alchichica results from a combination of metabolic processes such as photosynthesis, heterotrophy, sulfide oxidation, and sulphate-reduction, among others (Couradeau et al. 2011). A detailed analysis of submerged microbialites also revealed unique mineralogical signatures. Cyanobacterial EPS plays an important role in mineralization; sometimes inducing calcium carbonate precipitations, and others, precluding their precipitation.

The microbialites in Lake Alchichica occur in a special geosedimentary context: a highly alkaline pH, and this condition may exclude the majority of euryhaline species. The carbonate system in Lake Alchichica is especially suitable to be an analog of Archean environments during the atmosphere oxygenation. Therefore, the use of microbialites from Lake Alchichica as a proxy to understand and monitor biogeochemical processes among bacteria, mineral surfaces and organic matter are of significant astrobiological interest.

23.7 Conclusions

The Lake Alchichica is a high-altitude volcanic lake that offers the potential to carry on analog missions or other multidisciplinary studies (Table 23.3). The highlights are enlisted. Analog conditions: a) extreme alkaliphilic archaea in Lake Alchichica offer the opportunity to understand the life tolerance limits, because they develop their metabolism in extreme halophyte conditions, b) Cyanobacteria and mats build microbialites of different carbonate composition that propositions excellent molecular and fossil biomarkers. These biomarkers aim to interpret ancient climatic change and c) palagonitization is a process of alteration of glass, and this usually is abiotic, but when it is biotic it could generate a specific biomarker to be considered in Lake Alchichica. Analog mission: (a) the geological phreatomagmatic setting of Lake Alchichica could be like those that occur on Mars and Titan. Its complex overlapping circles' shape morphology, basement deposits, and lacustrine sequence offer a good place to probe future missions and (b) the limnological environment may be like Enceladus water.

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Chapter 24
Lake Alchichica Traditions, Myths, and Legends: Interviews with Local Residents

Verónica A. Arellano Peralta, Ángel Arellano Peralta, and Javier Alcocer

24.1 Introduction

The next chapter deals with the legends, myths, and traditions that exist around Lake Alchichica. These stories were told by two residents, Doña Martha and Don Licho, whose lives have been linked to the lake since childhood.

24.2 A Lake with Blue and Green Hues

In a place near the border of Puebla and Veracruz's states, federal highway 140 hides a surprise. The arid landscape of hills with little vegetation, "magueyes," and truck body garages changes abruptly at kilometer 76. As one goes along the road, little by little, a lake with blue and green hues can be seen, adorned with a cluster of white rocks (stromatolites) that the locals call "texcales" and that make up, near the shore, a discontinuous ring that surrounds the lake.

You can see the lake entirely from the roadside, located in the gas station oriel on the volcanic crater's edge, within which the lake lies. People living and working near the lake are so used to it that they seem to ignore it. Regularly, no one is on the shore of the lake, and it seems that nobody is aware of its beauty either. The reality

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V. A. Arellano Peralta (✉)
Independent Consultant on Environmental Issues, Ciudad de México, Mexico

Á. Arellano Peralta
El Heraldo Media Group. Radio producer, Ciudad de México, Mexico

J. Alcocer
Tropical Limnology Research Group, FES Iztacala, Universidad Nacional Autónoma de México, Tlalnepantla, Estado de México, Mexico
e-mail: jalcocer@unam.mx

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is different. First, people who live there and those from nearby towns do not call it a “lake,” but a “lagoon,” the Alchichica lagoon.

Between May and September, people who live in Itzoteno, Techachalco, or San José, come to fish “charales” (silversides) of Alchichica, a species of fish that only lives there. Villagers use bed sheets as nets to catch them. Traditionally, two women tie two ends of a bedsheet to their ankles, and two other people hold the other two ends with their hands as they drag the net onto the bottom of the lake. One or two more persons walk in front of the group, moving two sticks with rags tied at their end to scare the fish and pen them into the net, where they are trapped.

When they have enough, they eviscerate them with their fingers and wash them. Then, they put some on a corn husk to make a “tamal”; add minced “epazote,” salt, green chili, or tree chili and put them to roast on the hotplate. These are the locally famous and highly appreciated “tamales de charal”.

Some locals often carry their shotguns to the Alchichica lagoon if they see a duck or a rabbit. Others take one for safety reasons because times have changed. In the past, a person could walk safely without any other concern than avoiding being bitten by a rattlesnake or hurting their feet with a “tencholote” (a spherical cactus covered with dangerous thorns that abound on the hillside of the lagoon).

24.3 A Glimpse of the Past

Seventy-five years ago, back in the early 1940s, life was like this. There were not many cars around. The gas station probably did not even exist. People arrived at the Alchichica lagoon by bicycle or “carretón,” a transport made of wooden boards placed as if it were a raft but mounted on a car axle. Although donkeys pulled it, the “carretón” ride was reasonably smooth because it had car tires.

On Wednesday, March 6th, 1940, Mr. Reynaldo Osorio Alanís went to Itzoteno for the first time. He struggled with some paper sheets that the wind folded while he was trying to write on them on his lap. It was the official stationery of the Department of National Economy. In those headed, squared sheets, one could read “General Statistics Office.” He had been hired 1 month before to collect information for the 1940 census. He was commissioned along with other colleagues to walk down the towns and ranches of the municipality of Tepeyahualco, Puebla. Driving a car, their boss dropped them off in various locations in the morning, and he would be back to pick them up later. It was three in the afternoon. Reynaldo had reached the last house in Itzoteno and fought against the wind to write down the final figures. Itzoteno was inhabited by 561 persons: 293 men and 268 women.

Reynaldo looked at a nearby hill. He wanted to know its name and asked a boy who had not stopped looking at him since he wrote the final number. “It is Cerro Pinto,” said the boy, “and what is your name, boy?” –added Reynaldo– The boy looked at the hill as well and said: - “My name is Licho.”

Reynaldo regretted not carrying a notebook to lean against when he was writing, but it no longer mattered. He also blamed himself for not having asked what time they were going to pick him up. However, it was not helpful to keep thinking about it, either. The only thing he could not stop thinking about was that he had not carried a warmer jacket with him because he was freezing. He had been overconfident because usually, March was not too cold, but he had never been to Itzoteno. He heard a horn and turned his head. They had come to pick him up.

Licho watched as the vehicle drove away in the middle of a cloud of dust while thinking about two things. A car was something that did not come to his town every day and that he did not have many things to do to entertain himself there in Itzoteno, a small town with dusty streets. Alchichica lagoon was six kilometers away from Itzoteno. He was once there with his dad, but it had not been as much fun as, he supposed, going with his friends. Licho was going to be 5 years old on May 24th, in a few days. He thought it would be good to turn five because he would be old enough to go with his friends to the lagoon.

Eliseo Ventura was his name, but he had always been named Licho. Some of the things that he longed for were to be old enough to drive by himself a cart ("carretón"), to have a shotgun to go hunting at Cerro Pinto, and to go with other boys to play in the lagoon. That is why he devised a plan when he knew that several of his friends would go with his older brothers to the lagoon next Saturday. They went all together to ask permission to be allowed to go to the Alchichica lagoon. His dad accepted, and that was how he fulfilled one of his wishes.

A few years later, Licho drove a "carretón"; he also became a good hunter, although always with borrowed shotguns, and he became fond of visiting the Alchichica lagoon. As a child, he also liked sitting on one of the corn bags in the shop to listen to the stories related by the men who used one of the only two shops in Itzoteno as a tavern. It was the only option because around nine at night, the other store in town was already closed. Although the store-tavern was far from Licho's house, he was always lucky that one of those men who went to drink beer and tell stories was often a relative. So, he always arrived on time mounted on the bicycle that one of his relatives was riding.

24.4 The Silver-Haired Mermaid and the Goblins ("Duendes")

People in the town say that a mermaid comes out of the lagoon.

– From Alchichica?
– Yes, from Alchichica. Don't you know that the lagoon is connected to the sea? That's why the water is salty.

Licho had heard that story several times. It was a silver-haired mermaid that appeared on the surface of the water mirror. Her singing made the men fall in love with her. The mermaid made men go mad after her, walking towards the lagoon even without reacting when they were sinking in the water. She would get farther and farther away, and those unfortunates who heard the song ended up drowning in the waters of the deep lagoon. Licho knew the story well. Nevertheless, he was dying to tell them what happened to him (Fig. 24.1).

It was Holy Week. Licho was playing on the shores of the lagoon with some boys. Since he was the youngest, he was sent to buy cigarettes at a small store located on the crater's edge. To get there, he had to go around the lagoon, so in a few minutes, the voices of his friends were lost, and he could only hear his footsteps burying in the sand and the wind slapping against his face. He bought the cigarettes, and when he was on his way back, the wind was no longer blowing so much; he could clearly hear the little footsteps that followed him. Turning his head, he saw several little men. They looked like children, but it could not be because Licho was himself a little boy, and they were much smaller than him. They were naked and had huge bellies. They must be "duendes" (goblins), Licho thought. He was afraid but also curious. So, he let them come up to him. It was daytime, and the sunlight was intense, so he could see their faces sharply.

They had mischievous faces and offered him a large cone of ice cream. He hesitated for a moment, and fear overcame curiosity. He felt himself breathing harder, and soon his nose was not enough. He started to pull air through his mouth. He turned around and escaped awkwardly. If someone has tried to run on dry sand, they know that fatigue is too much and progress is too little. Licho cried and shouted, but

Fig. 24.1 A silver-haired mermaid that appeared on the surface of the water mirror. (Original drawing by Edgar M. Caro Borrero)

he was too far from his friends or from the woman of the store to hear him. The goblins chased him and threw rocks at him until he managed to leave them behind or until they decided to leave him alone. He arrived where his friends were but said nothing to them (Fig. 24.2).

That night, while he was sitting on the sack of corn and staring at the dim light bulb that lit the store, he did not tell the men either, who were telling stories and drinking beer. When the store was closed, his relative walked away with the other men. They had bought three beers each and went to finish them at one of their houses. Licho had to ride the bicycle. He kept thinking how much he would have liked those men to know about the goblins he had seen. That is what he thought all the way home and for all the years that followed until the day he died when he was 84 years old.

As Licho grew up, opportunities to tell what he had seen became more frequent, not only in the lagoon but also in his hometown, Itzoteno, which after all turned out to be a not-so-boring place. In the mornings, before going to school, he had to scrape the "magueyes." Scraping is a procedure for making pulque and involves scrubbing the inner walls of the heart of the maguey with a knife to obtain mead, a sweet liquid that, when fermented, is transformed into pulque. In the afternoon, Licho took the goats to graze in the fields. There he met other boys who also carried

Fig. 24.2 The goblins that scared Licho. (Original drawing by Edgar M. Caro Borrero)

their herd. It was the place where he exchanged stories. He told them what happened with the goblins in the lagoon, and in exchange, he knew what “the charms” were.

24.5 The Charms

On the night of June 23rd, many people go to the lagoon. They want to verify what some people say: “if you listen carefully, you can hear the music of great beauty from the Alchichica lagoon and its surroundings.” Most people, however, are motivated by ambition. Rumor has it that on that very night, on June 23rd, a glow (or several lights) appears from the ground, an indication that there, exactly at that point, there is money buried inside the soil, perhaps gold coins. Once the light is found, people must wait until midnight because that is when the floor opens. It is said that at this moment, “the charm opens,” and people “get spellbound.” The story of a man who was literally swallowed by his ambition was famous. Although his name is not known, he was from Techachalco, a nearby town.

One night in June, on the 23rd, he went to the lagoon. A little skeptical, he settled in a place away from the other people who came that night. After a while, and as people had told him, he perceived a light emanating from the ground. Patiently, he waited until it was midnight. Right at midnight, he heard a noise that he assumed was the ground opening, but he could not see anything. He was about to leave when it occurred to him to see into the scrubs, and that was when he discovered a hollow from where a dim glow was barely distinguishable in the dark. He knew then what it was to “be spellbound,” and without much thought, he went into the bowels of the earth. It is said that the man found many treasures, but he entertained himself so much trying to fill his pockets that he did not see the charm began to close. He was left in absolute darkness, panicked and regretting being carried away by his ambition without realizing that the passage was closing. One day passed. Unexpectedly, the entrance opened again. He did not want to make the same mistake, so soon as he noticed that the earth was opening, he quickly left, leaving all the treasure he had found inside. It was night, which confirmed that he must have spent an entire day trapped.

He was looking forward to returning home to tell the adventure he had had. He imagined that his family would be overly concerned about his absence. He was running at first, but he felt he had to slow down because he was starving and weak. If he did not measure his strength, he might not be able to get there before he passed out. On the way, he cut some prickly pears. He ate them and sat down to rest a little. He began to doze off, but the cold woke him up. Much more comforted, he resumed his walk home.

He arrived at his house at around three in the morning. He saw that someone had lit a fire. He surrounded a fence that marked his yard, made of rusted sheets, sticks, piled stones, and bushes. He reached the entrance, and when he unhooked the wire that held the leaf door, the creak woke up a dog that began to bark. The bark, in turn, woke up his family. His wife came out. Then, he thought that she would scold him or complain about his absence, but instead, she started crying. The man was surprised because one of his brothers and other relatives (who lived in Veracruz) immediately came out of their house. He realized that they were surprised to see him. Even more, one of them could not hide a gesture of terror. After a few minutes, they told him that they had gathered to hold the first anniversary prayers, that is, the mourning ceremonies performed in honor of a person to remember a year of his death. He understood that he had been presumed dead and that he had not spent a day underground as he thought, but a whole year (Fig. 24.3).

That is the story of the man from Techachalco who entered the bowels of the earth. However, many things are said about the Alchichica lagoon; for example, there is an old graveyard on the hillside that nobody visits. The deceased who rest there would be those who died of leprosy. At least that is what Licho had been told; he says that he confirmed these tombs' existence as a young man, but today they are hardly visible. At 84, he no longer ventured out to look for them.

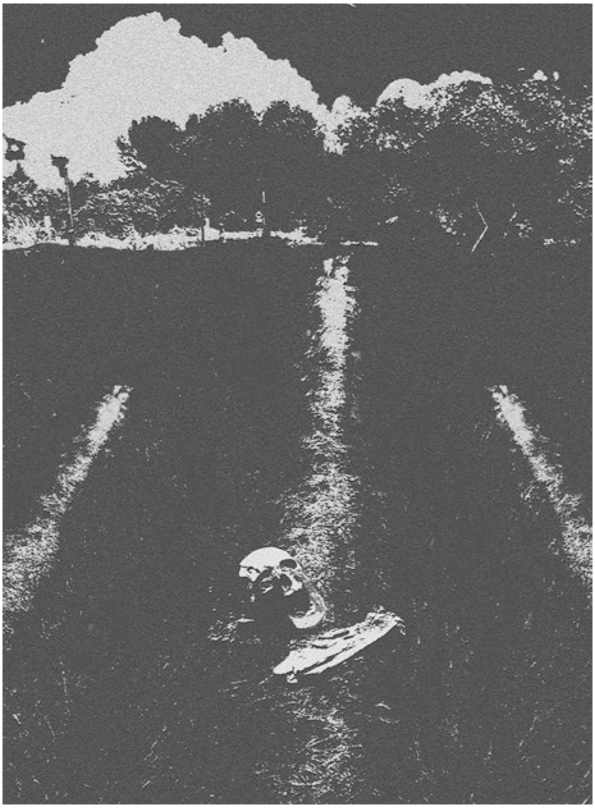

Fig. 24.3 The charms of the Laguna de Alchichica. (Original drawing by Edgar M. Caro Borrero)

24.6 Lake Alchichica, a UFO Base

Another thing is that the lagoon maintains communication with other nearby lagoons: La Preciosa, Quechulac, and Atexcac. When the water level rises or decreases in one, it happens the same way in the others. It is also rumored that those who drown in the Alchichica lagoon's waters and whose bodies are never found frequently appear in Altotonga, Veracruz; in a place called Pancho Poza, 48 kilometers away from there.

Some say that at the bottom of the Alchichica lagoon, there is a ceremonial center of ancient pre-Hispanic cultures. Others affirm that the lagoon has no bottom since NASA personnel tried to measure the depth using a sounding line (a rope over 120 meters long) and never reached the bottom. Some locals claim that at the depths of the lagoon, there is a cavern where mysterious spheres of glowing multicolored light go in and out; that there is an alien base established at the bottom of the crater, where an alien mother ship lies. Another story says that a shaman saved the life of a seriously ill girl there and that this was possible with aliens' help.

An excursionist relates that he once saw a UFO flying over the lagoon and heard a loud buzz before the ship dove into the water without a trace. Other stories talk about beings with long reddish hair descending from UFOs, with slanted, green, and shiny eyes. These stories do not just come from the locals. A digital magazine called The Journal of Hispanic Ufology, where a publication links the Alchichica lagoon with UFOs. This publication, whose author is a man named Arturo del Moral, dates from January 12th, 1998. He relates that he, along with other explorers, camped next to the Alchichica lagoon, recording various strange events. One of them was the impossibility of their devices picking up radio waves. Another phenomenon that happened was that the batteries in their recorders discharged without explanation. According to his hypothesis, these phenomena are due to an electromagnetic cone like that of the Zone of Silence located in Durango.

Del Moral says he interviewed a man named Roberto Sánchez from the town of El Seco. This man told him that 2 years earlier, on a night in March 1996, he was waiting for a bus to return home after visiting a friend who lives on the shores of the Laguna de Alchichica. From where he was, he could see an intense yellow glow coming out of the waters. He approached the cliff, out of curiosity, when suddenly, "a luminous object of considerable size, white in color, emerged from the lagoon, floating for a few seconds, a few meters above its surface, before flying off." (Fig. 24.4)

24.7 The Infestation of Tiger Salamanders

That is what they say. God knows what reality is- clarifies Licho when he tells things that did not happen to him or things that he has not seen, such as UFOs. -What I did see was when axolotls "flooded" the town. It was the rainy season. A

Fig. 24.4 A UFO base in the Alchichica lagoon. (Original drawing by Edgar M. Caro Borrero)

storm inundated streets and houses in Itzoteno. Even the extensive plain on the slopes of Cerro Pinto became a temporary lake due to the downpour. In this regard, he relates as follows.

It was on September 29th. I remember the date very well because it was the feast day of San Miguel. I remember because there were plenty of people and because in those days, they put up many food stalls. “I got caught in the rain in the plateau,” -says Licho. - He was pasturing the goats. When the rain stopped, I gathered the animals and went home. But when I went through a little puddle, I saw that something started to move strongly in the water. It even splashed me on the arm. I saw an “ajolotito” coming out, it wanted to swim, but it couldn’t because it got stuck in the sand. I thought that the little animal had been trapped in the puddle and that it didn’t have time to hide because it had been caught in the water. But there were other puddles a little further ahead, and there were more little axolotls, but in large numbers. That day I was with my cousin Moy, and I told him, look, there is a bunch of axolotls here too. Then Moy and I got scared. He was younger than me, and he said we’d better go because by then, the axolotls began to move in the whole plateau, and it seemed like when they take the fish out of the sea, and they move in the net. This way, the animals were on all the plateau, making a lot of noise from the splashing. We rather left. When we got to town, there were also a lot of axolotls there. A man told us that they were not axolotls but salamanders. People had already caught some. They were huge, black with yellow spots, and they were everywhere: on the floor, on the walls, on the ceilings. Some had already climbed on the cables and the bulb lights of the houses. Some young guys who once came from Mexico said they were named “tiger salamander.” The people who went to sell to the festivity just had to resign themselves.

I think the animals were hungry because they climbed on the food stalls. First, people removed them, but they were so many that people gave up. The salamanders were even on the food by the hundreds, and the stallholders could no longer sell it. People tried to dodge them, but at night, they hardly saw them. When people walked, they felt the ground squishy. It was impossible not to step on them. When you squashed them, they were like smoothie banana mush. By that time, many locals were drunk, so that was a mess. Many of those men slept right there. The little animals walked all over them, but they are harmless; they did nothing wrong to them. The 8 o’clock mass wasn’t even celebrated because people couldn’t stand anywhere because of those many salamanders. The same also happened in other places. In Tetipanapa, Pizarro, and Tepeyahualco, they were also infested. They were like this for 3 years, and little by little, the salamanders were gone. Sometimes they came out of the ground when we walked with the plow. They appeared suddenly. We killed some salamanders, but it was unintentional; it’s just that we didn’t see them. Maybe they were looking for humidity. Since the time they infested the town, we are not sure because they didn’t come out in the same amount, even though it was raining heavily. Who knows why? (Fig. 24.5).

24.8 Water Snake and Rain of Silversides (“Charales”)

On another occasion, it rained “charales.” Licho recognizes that many people do not believe him, at least at first. Then the people whom I talk to don’t believe me - he says - but I saw it. They tell me: How does it rain charales? It is because over here, some tornadoes get into the Alchichica lagoon or into the other lagoons that are around here, and they trap water; they suck it; that is why they name them the “water snake.”

Some say, but how if it is quite dry here, what do you mean “water snake”? But it is not an animal like the rattlesnake, but a piece of water that goes from the ground to the cloud. Then, if you walk where the water snake passes, you can clearly see the path that it leaves in the sand. Sometimes it gets into the grass, and if it goes through the houses, it rips the roofs off. Well, once, out there in a town called La Gloria, there was a strong tornado. It started first over there in Las Minas, and I don’t know if you know it. It is also called La Preciosa lagoon. From Alchichica, it is like 10 min away. There, the tornado sucked water from that lagoon, the one in Las Minas, and it sucked many “charalitos” and threw them wherever it went by. One could see how they writhed poor little animals because they were on the sand or the scrubs. The “charales” from there are larger and bonier than the ones from here in

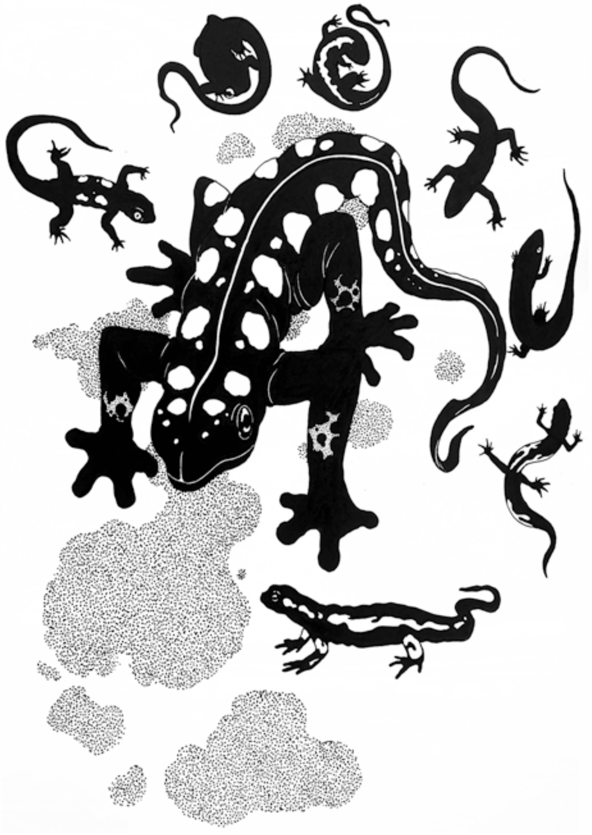

Fig. 24.5 The infestation of salamanders. (Original drawing by Edgar M. Caro Borrero)

Alchichica. When you eat them and pass through the throat, the skeleton feels slightly stiff, but the one from here doesn't. The one from here is small and soft, and you don't even feel it. It feels like pure meat (Fig. 24.6).

24.9 Living Next to the Crater

María Martha Ignacia Hernández López, better known as Doña Martha, also knows how to distinguish at first glance, which is the "charal" from Alchichica and which is not. She knows the Alchichica lagoon like no one else. She was born on July 21st, 1955, in Zalayeta, a town in the municipality of Perote, Veracruz, located a few meters from the lagoon. She was about 28 years old and, together with her husband Pedro Espinosa Lorenzo, decided to live close to the lagoon, inside the crater. Sometime later, perhaps a couple of years, her brother Rubén moved and established close to Doña and became her neighbor. Then, more people came, and a small colony formed on the hillside. Doña Martha claims to be the first to have come to

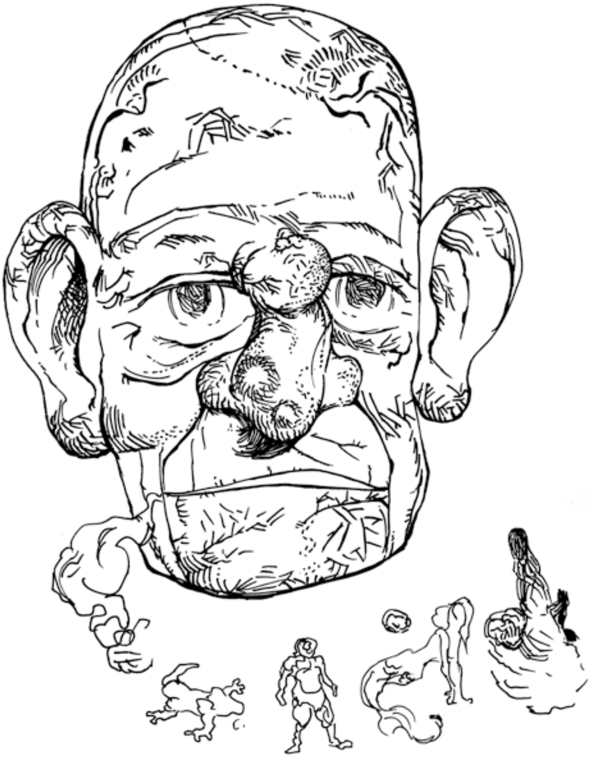

Fig. 24.6 The stories of the Alchichica lagoon. (Original drawing by Edgar M. Caro Borrero)

live in the lagoon. She has four children: Verónica, Alberto, María del Carmen, and Norma Angélica. The territorial division indicates that the Alchichica lagoon is in the territory of Puebla. However, Doña Martha indicates her address: José María Morelos number two, Zalayeta, Perote, Veracruz. For some reason, she says that the lagoon (or at least her home) belongs to the state of Veracruz.

For more than three decades, Doña Martha has witnessed what has happened in the lagoon. She says that years ago, people used to go down the lagoon to wash their clothes. Before that, there was a nearby freshwater well. However, about 25 years ago, the government installed potable water and drainage services. That is why almost no one goes down to wash or draw water anymore. She remembers that before, there was more water in the lagoon. Perhaps the groundwater level feeding the well has been reduced due to a lack of rain. However, it is also due to groundwater exploitation for agricultural irrigation since the lagoon is fed by water from the water table. Doña Martha says, time ago, we did not see those white rocks called "texcales," they were underwater, but today they are seen, standing out of the water, a clear sign that the lagoon has been drying up. She also says that each year, between the first and the 5th of May, the lagoon "gets sick": "it covers with a dark green or grey, oily layer, but after a few days it disappears. When it is windy, the water turns

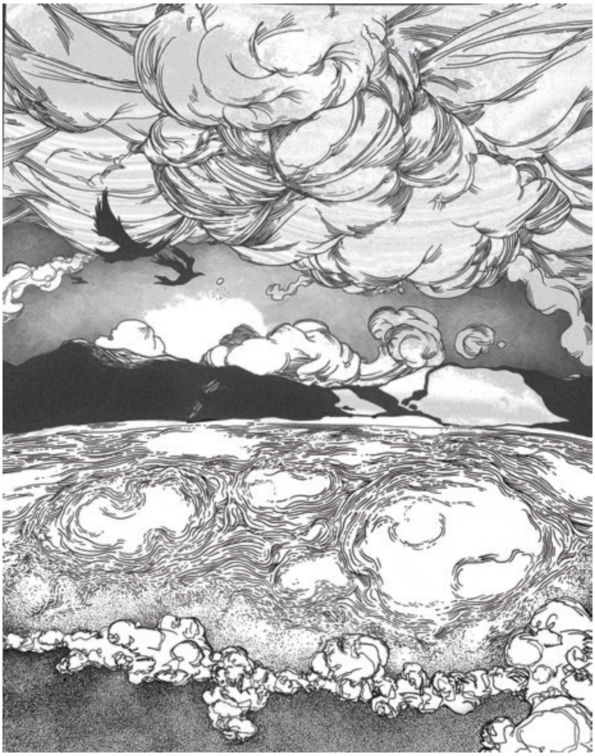

Fig. 24.7 The Alchichica lagoon "gets sick." (Original drawing by Edgar M. Caro Borrero)

blue again, and it looks clear, but when the wind isn't blowing or stops, the water turns gray again" (Fig. 24.7).

Doña Martha says that it was rumored the owners of "Africam Safari Zoo", a private wildlife conservation park in Puebla, had bought the lagoon and no longer let people enter that they went fishing for axolotls at night. Perhaps it refers to the fact that back in 2015, a conservation project was launched - which today is a program - to preserve the species known as the axolotl of Alchichica or Taylor's salamander, endemic (unique) to that body of water.

For a long time -continues Doña Martha-, people made a living from fishing charales in Alchichica. They sold them prepared in tamales or fish "chilposito", a popular dish in Veracruz that, in addition to "charales", contains "nopales" and "epazote". The "chilposito" usually is served hot because it usually is freezing in those lands. Since the lagoon's water level descended, the shallow littoral area where people fish has almost disappeared along with the fishery. It is currently rare to see someone fishing, but few people still participate in this activity. There are a few "charales" now, so some people decided that it was better to work offering boat rides to tourists (Fig. 24.8).

Fig. 24.8 Charales fishing in the Alchichica lagoon. (Original drawing by Edgar M. Caro Borrero)

Sometimes, some visitors do not listen to the warnings and enter the lagoon's treacherous and cold waters to swim. A little skeptical, Doña Martha repeats the well-known story that the drowned in Alchichica, whose bodies are not located, appear in a pond, Pancho Pozas, in Altotonga, Veracruz, almost 50 kilometers away. Her mother told her that once a boat sank and the drowned person appeared in Altotonga. -They also say that once they threw a bale of grass, and then it emerged in Pancho Pozas, "but who knows"- she says with a loud laugh.

Despite 35 years of watching the lagoon every day, Doña Martha has not had a UFO experience like those reported by occasional visitors. She admits that she has never seen lights or heard anything unusual, except what is said. On the day of the strong earthquake, she was not near the lagoon, but she suggests asking her daughter, Norma Angélica Espinosa Hernández. Norma lives with Doña Martha and witnessed the intense agitation and wobble of the waters of Alchichica on September 19th, 2017, with the 7.1-magnitude earthquake that was registered in the central zone of Mexico. Unlike her mother, Norma said she did see a UFO. She remembers that some days before the quake, she perceived a large red light flying slowly above that area and suddenly disappeared like a shooting star.

24.10 The Giant Axolotl of Alchichica

Clerks at the Alchichica gas station often tell customers that a huge axolotl comes out of the lagoon from time to time to sunbathe on the beach. That in that place, this giant animal rests and can be seen with its huge dark brown body with black spots, like the many smaller axolotls that inhabit the lagoon, but giant. Doña Martha says that, according to the gasoline service station employees, the axolotl is very shy. When people get close, it gets scared and quickly throws itself into the lagoon. Someone even thought that if the famous monster that supposedly lives in Loch Ness, in Scotland, is called “Nessi,” the giant axolotl of Alchichica could be named “Alchi.” (Fig. 24.9).

24.11 La Llorona

Moreover, since the stories are popping up, Doña Martha reaches back into her memory and finally brings herself to say what she experienced a few years ago. Before, there was no electric light in the town. They used to light up candles. That is why it was not appropriate to walk at dusk by the lagoon. It was better to do everything when the sun was still shining. However, sometimes it was inevitable that the night would surprise someone outside the home.

That happened to Doña Martha and her brothers, once, when she was a young girl. They were not far from their home when the sunset gave way to the darkness of the night. Fortunately, she and her brothers knew the route well. In any case, it was essential to be careful where one stepped to avoid slipping down. When they reached the edge of the Laguna crater, they knew that they should go along it because it was the path they knew well and the shortest to get home. Martha stopped staring at the

Fig. 24.9 The axolotl of Alchichica (Taylor’s salamander). (Original drawing by Edgar M. Caro Borrero)

road for a moment and shifted her gaze towards the lagoon. Despite the darkness, she could clearly see, near the water, a woman wearing a white nightgown and a veil covering her face. Doña Martha stopped and touched the arm of one of her brothers. She did not need to point to the lagoon. He was also looking at that woman whose white dress and veil fluttered with the wind. Immediately, they both moved their eyes to the road to stop looking at that disturbing apparition, and they continued their way until they reached home. Although the woman in white walked in complete silence, they, Martha, and her brother knew it: they had just seen "La Llorona" (The Weeping woman).

The legend of "La Llorona" is well known throughout Mexico. It first appeared in Mexico City, 230 kilometers away from Alchichica. Although this entity is also known in Spanish-speaking countries, it has other names and origins. With her characteristic white dress, the Mexican La Llorona appeared in stories told in Mexico City's streets. One of these stories reveals that she would be the goddess "Cihuacóatl," a gatherer of souls, also considered the protector of women who died giving birth. Other versions indicate it is the specter of La Malinche, Marina, Malinalli, Malinali, or Malintzin, that woman close to the Spanish conqueror Hernán Cortés. The first reference that La Malinche is La Llorona and that she appears in Mexico City can be found in the book "Las calles de México, Leyendas y sucedidos," from 1922, by the chronicler Luis González y Obregón.

24.12 The Ancient City of Cantona

The Cantona Archaeological Zone is 62 kilometers away from the Laguna de Alchichica. There is a site museum exhibiting a collection of objects and relics of this pre-Hispanic city. It also provides information on obsidian exploitation in the region and the culture's understanding of the cosmovision. However, there is also a parallel collection. It was collected by a man named Juventino Limón and by his family. Many years before, the National Institute of Anthropology and History (INAH) carried out excavations. They took the findings into the custody of Mr. Limón, which already had many archaeological objects, some of which were placed for exhibition in a museum inside his own house, empirically classified and, apparently, without official records. The INAH decided not to recover the collection that the Limón family has. So much information and secrets from that place were lost, at least partially.

There is a story that Mr. Limón used to talk about the birth of the first Mexican, or the first mestizo, son of La Malinche (Doña Marina) and Hernán Cortés. According to the story, on the way to Tenochtitlán from Veracruz, Hernán Cortés and Doña Marina passed through Alchichica. She had a very advanced pregnancy. The story tells that the woman was strongly attracted by the lagoon's bright blue color and wanted to drink the water from there. She did that, but the water tasted bitter to her (now we know that this bitterness is a product of high concentrations of sulfates and magnesium); after this, childbirth happened. It was then that La

Malinche gave birth to the first mestizo, supposedly in Alchichica; his name was Martín, the first son of Cortés and Doña Marina. The ethnologist Luis Barjau researched for 10 years on that legendary woman, La Malinche. The book The Conquest of La Malinche is a product of that work. On page 169, he writes:

> *… Marina had two children, a boy, Martín, with Hernán Cortés and a girl, María, with her legitimate husband, Juan Jaramillo. Martín is the first mestizo of a vast population that would inhabit a new nation. (…) Martín Cortés, the son of La Malinche and the Marquis, was born in Coyoacán towards the end of 1522 (three years and a few months after the beginning of the relationship between Doña Marina and Cortés in Veracruz on July 26th, 1519) (…) He received the name of his paternal grandfather in the Spanish way.*

These data discredit the birth of Martín in the Laguna de Alchichica. There are many stories. Perhaps Martín was not born in Alchichica, and it is false that there is an extraterrestrial base at the bottom of the lagoon or that one can find goblins ("duendes") or the giant axolotl "Alchi" sunbathing. However, Licho and Martha are real people, even though Licho recently died. They do not know each other, but their amazing gazes stared 1 day at the lagoon. Licho wanted to stop being a child and play in that singular body of water. At 84, he no longer wanted to play or climb the hill. However, he recounted what he saw and what he heard, what he lived. Doña Martha fell in love with the lagoon so much that she wanted to live near it forever. Live by it. Whoever wants to meet them must travel on the federal highway 140 and reach a point near Puebla and Veracruz's border. Reaching the lagoon, one must go down to the hillside houses and ask for Doña Martha. Licho died on July 4th, 2019, and his family still lives in Itzoteno. The detour is a little before kilometer 76. The exit sign towards the town is there.

If one comes from Mexico City, it should be considered that access to the town is on the left side. It is important to be careful when crossing the highway because cars often come at high speed. Once having passed the access to the town, you must follow a dirt road. After arriving at the populated area, one must look for West Street 9 (in Spanish, Calle 9 Poniente), go to the last house on the street (and the last one in town), and ask for Don Licho's family. He was called Eliseo Ventura, and he was a good man. One day, as a child, he dreamed of being a grown-up. Furthermore, he made it to be a great man.

Acknowledgments We thank Mrs. María Martha Ignacia Hernández López (Doña Martha), Norma Angélica Espinosa Hernández, and Mr. Eliseo Ventura López (Don Licho, RIP), for allowing the interviewed and sharing the wonderful experiences described in this chapter. To Mr. Sixto Ventura Martínez and, in general, to the Ventura Martínez family, for their hospitality provided during the visit to Itzoteno and the Laguna de Alchichica. To Ph.D. Gloria Vilaclara Fatjó and to M. in Sc. Daniela Cortés Guzmán for conducting the additional interviews. To Eric Fugarolas for reviewing the text in English.

"Don Licho" and her niece, Verónica Arellano, at Don Licho's house in Itzoteno. (Original photograph by Elva Escobar)

Doña Martha cleaning "charales" to prepare tamales at her house in Alchichica. (Original photograph by Javier Alcocer)