

Chapter 14

Metazooplankton: The Joys and Challenges of Living in a Saline, Oligotrophic, Warm Monomictic Lake



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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.

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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 $\mu\text{S}/\text{cm}$) 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 $211.5 \pm 21.2 \mu\text{m} \times 143.7 \pm 15.5 \mu\text{m}$ (mean length including spines \times width, \pm 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. jenkinsae*

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. jenkinsae* (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. jenkinsae*, so the identity of these clades could not be settled. The clade present in lakes Alchichica, Atexcac, and Aljojuca was labeled as *Hexarthra cf. jenkinsae* 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 *Leptodiptomus garciai*

In 1942, Osorio-Tafall described the calanoid copepod *Diptomus 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

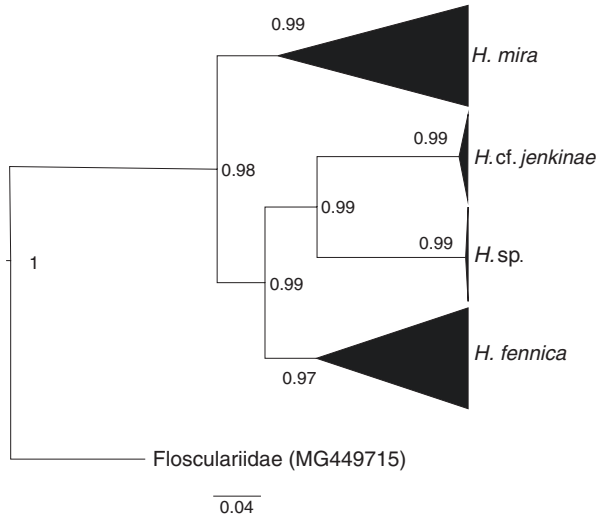


Fig. 14.1 Bayesian phylogenetic tree (chain length = 10,000,000; HKY + G substitution model) for all available COI sequences of the *Hexarthra* genus, including *H. cf. jenkiniae* (present in lakes Alchichica, Atexcac and Aljojuca) and *H. sp.* (Lake Tecuitlapa). The posterior probability for each clade 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 revindicate 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 \pm standard deviation; female: $960 \pm 179 \mu\text{m}$; male: $910 \pm 179 \mu\text{m}$; $n = 20$; 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 *Leptodiptomus* 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. jenkinsae*), *Brachionus* (*B. sp. 'Mexico'*) and *Leptodiptomus* (*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

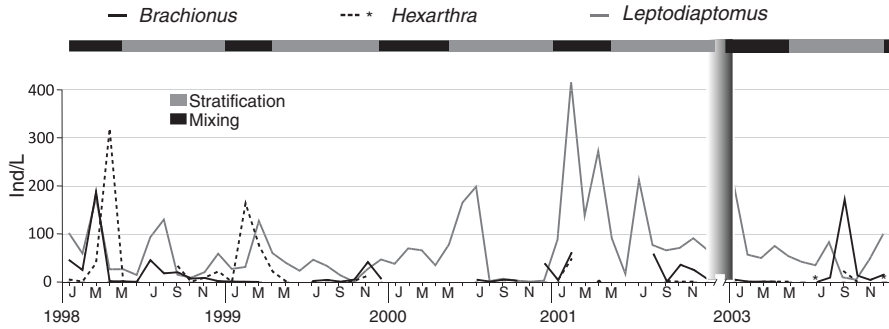


Fig. 14.2 Temporal variation of the monthly average of the metazooplankton abundance in Lake Alchichica (*Brachionus* sp. ‘Mexico’, *Hexarthra* cf. *jenkiniae* and *Leptodiptomus garciai*), for 1998–2001 and 2003. From 1998 to 2001 the sampling was performed at 2, 5, 10, 20 and 50 m, at daytime (10–16 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 for *Leptodiptomus* (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 *Leptodiptomus* 105 ind/L) also was higher than during the stratification (*Brachionus* 14; *Hexarthra* 11 and *Leptodiptomus* 56 ind/L), although a U-Mann Whitney analysis indicated that this difference was statistically significant only for *Leptodiptomus* ($U = 201.5$, $p = 0.0007$).

On the other side, the main difference between the three species is that while the *Leptodiptomus* 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

| Year | <i>B. sp. 'Mexico'</i> | | <i>H. cf. jenkinsae</i> | | <i>L. garciai</i> | |
|------|------------------------|------------------|-------------------------|------------------|-------------------|--------------|
| | 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 (\pm 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, *Leptodiptomus* 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 ($86 \pm 11\%$) and from November onwards ($60 \pm 30\%$). The rest of the year (April to September), when light penetration was deeper, the biomass diminished due to the contraction of the *Leptodiptomus* population. It was mainly allocated between 18–28 m ($26 \pm 27\%$) and 30–40 m ($45 \pm 26\%$). As we discuss here below, the seasonal deepening of the distribution of metazooplankton biomass in this period is explained by

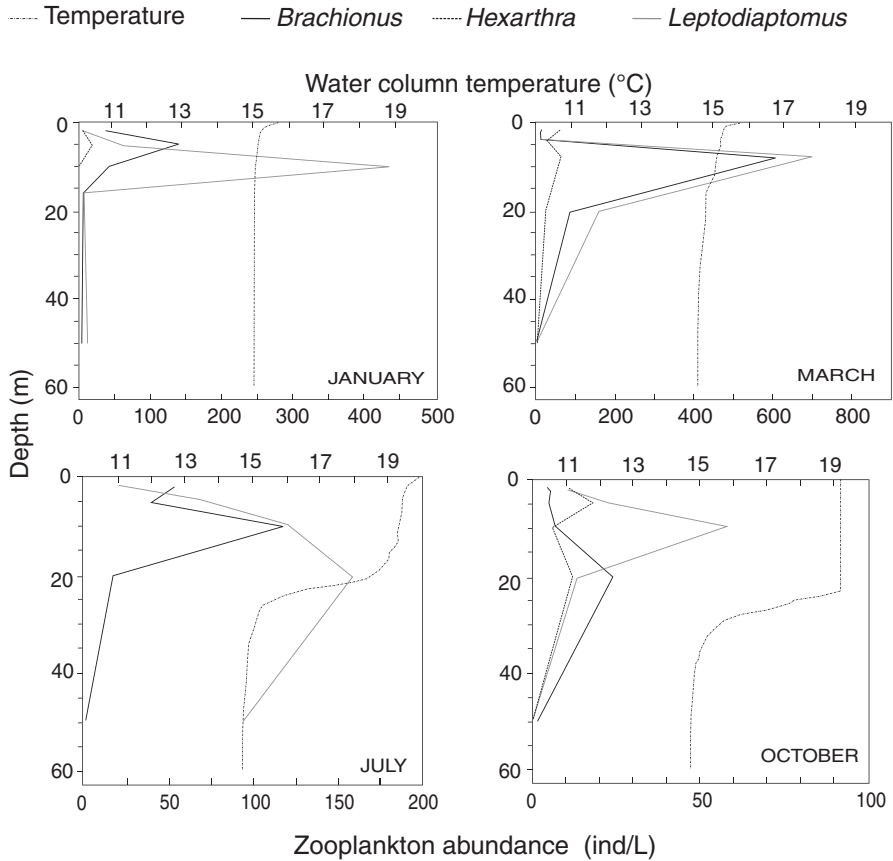


Fig. 14.3 Vertical distribution of the three zooplankton species (*Brachionus* sp. 'Mexico', *Hexarthra* cf. *jenkinae* and *Leptodiaptomus garciai*) and temperature profiles for four dates during 1998. January corresponds to the mixing of the water column, March is at the beginning of the stratification 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

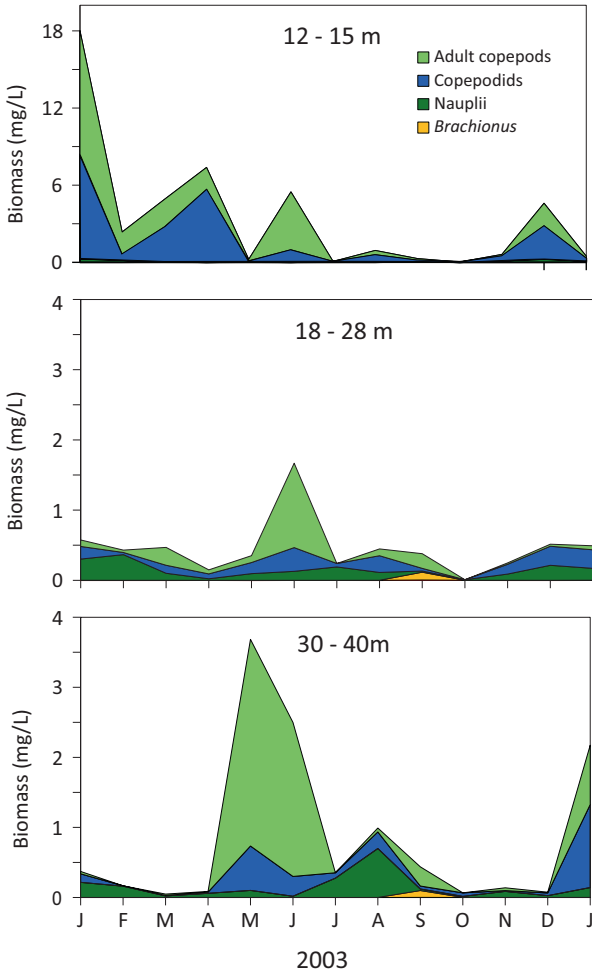


Fig. 14.4 The contribution of *Brachionus* sp. 'Mexico' and *Leptodiatomus garciai* (nauplii, copepodids and adults) to the metazooplankton biomass (wet weight) from January 2003 to January 2004 at three different strata of the water column. The contribution of *Hexarthra* cf. *jenkiniae* is unnoticeable. 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. jenkiniae* 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 *Leptodiptomus* 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* ($73 \pm 26\%$ 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 $45.0 \pm 6.5 \mu\text{m}$ (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 $\leq 20 \mu\text{m}$) constituted the $27 \pm 26\%$ 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

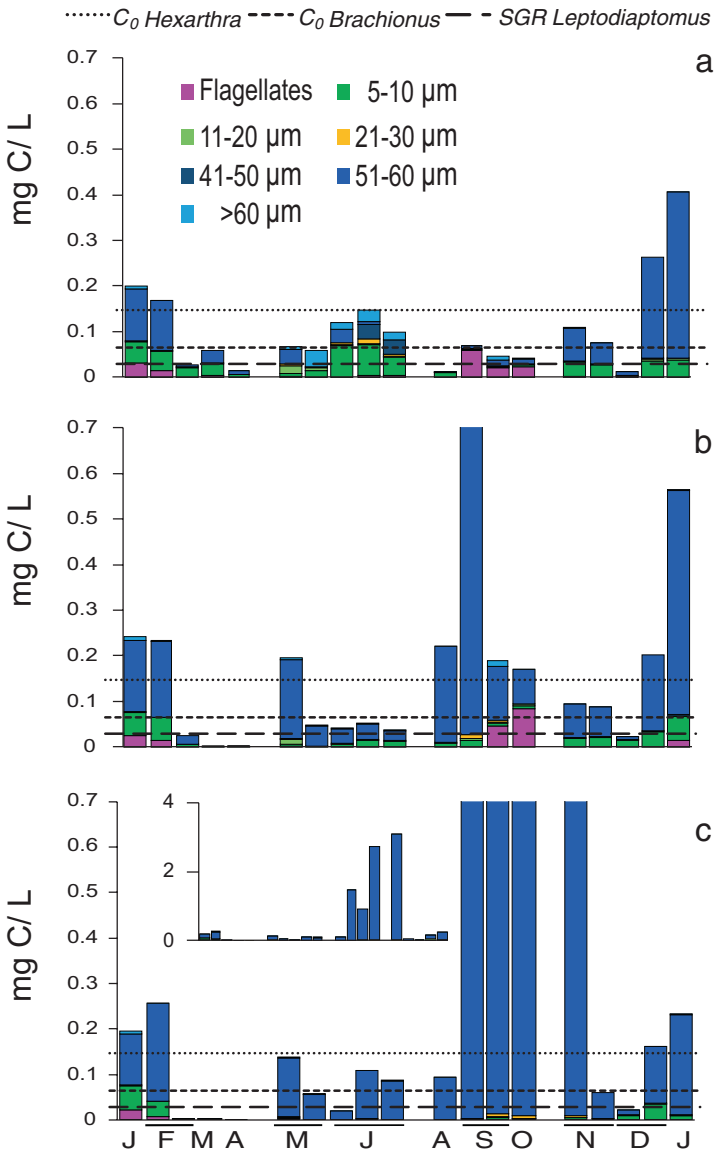


Fig. 14.5 Seasonal abundance of phytoplankton and small heterotrophic flagellates (<10 μm) biomass at three depths in Lake Alchichica from January 2003 to January 2004. (a) 12–15 m; (b) 18–28 m, and (c) 30–40 m. The contribution of different size categories (according to their greatest axial linear dimension) 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. *jenkiniae* or food concentration at which the specific growth rate (SGR) for *Leptodiatomus 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 (≥ 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

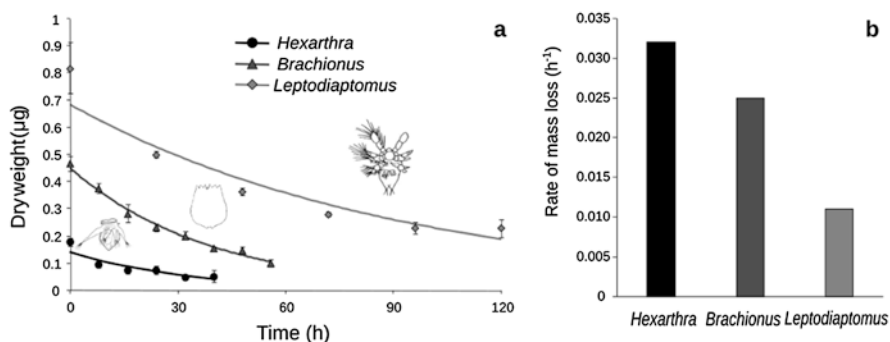


Fig. 14.6 (a) Individual body mass of *Brachionus* sp. ‘Mexico’, *Hexarthra* cf. *jenkiniae* and *Leptodiaptomus garciai* vs. starvation time; symbols are average \pm SE. (b) Rate of mass loss, calculated as the slope of the linear regression of \ln (body mass) vs. starvation time

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 *Leptodiatomus: 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 *Leptodiatomus* 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; Ciroso-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 (Ciroso-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 $\approx 22.7 \pm 2.1$ m). *Brachionus* performed upward movements not associated with DVM, avoiding UVA and UVB, but not the euphotic zone (MPD $\approx 15.0 \pm 1.8$ m). During the well-established stratification, both rotifer species were confined within the epilimnion, exposed to visible light and UVA (MPD $\approx 22.9 \pm 1.2$ m for *Brachionus*; $\approx 16.5 \pm 1.0$ 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 *Leptodiatomus*, 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 *Leptodiatomus* 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/cm²), 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 ≤ 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 *Leptodiatomus: 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 *Leptodiatomus* 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) | <i>Range</i> | 762–1176 | <i>Minimum</i> | 821 \pm 18 (Aug) |
| | <i>Avg. \pm SD</i> | 933 \pm 83 | <i>Maximum</i> | 1026 \pm 51 (Dec) |
| | <i>n</i> | 601 | <i>PPI (%)</i> | 20 |
| Female biomass (μg) | <i>Range</i> | 41–113 | <i>Minimum</i> | 49 \pm 3 (Aug) |
| | <i>Avg. \pm SD</i> | 67 \pm 14 | <i>Maximum</i> | 82 \pm 9 (Dec) |
| | <i>n</i> | 601 | <i>PPI (%)</i> | 41 |
| Egg diameter (μm) | <i>Range</i> | 75–150 | <i>Minimum</i> | 89 \pm 42 (Sep) |
| | <i>Avg. \pm SD</i> | 106 \pm 16 | <i>Maximum</i> | 131 \pm 81 (Mar) |
| | <i>n</i> | 1218 | <i>PPI (%)</i> | 32 |
| Egg biomass (μg) | <i>Range</i> | 0.2–1.8 | <i>Minimum</i> | 0.37 \pm 0.04 (Sep) |
| | <i>Avg. \pm SD</i> | 0.7 \pm 0.3 | <i>Maximum</i> | 1.17 \pm 0.28 (Mar) |
| | <i>n</i> | 1218 | <i>PPI (%)</i> | 68 |
| Clutch size (eggs/ind) | <i>Range</i> | 1–16 | <i>Minimum</i> | 2.1 \pm 0.6 (May) |
| | <i>Avg. \pm SD</i> | 4.8 \pm 2.4 | <i>Maximum</i> | 9.3 \pm 2.0 (Nov) |
| | <i>n</i> | 1258 | <i>PPI (%)</i> | 77 |
| Hatching success (%) | <i>Range</i> | 0–100 | <i>Minimum</i> | 65 \pm 41 (Mar) |
| | <i>Avg. \pm SD</i> | 92 \pm 9 | <i>Maximum</i> | 98 \pm 6 (Sep) |
| | <i>n</i> | 649 | <i>PPI (%)</i> | n.s. |
| Nauplii per female | <i>Range</i> | 1–13 | <i>Minimum</i> | 1.7 \pm 0.7 (Apr) |
| | <i>Avg. \pm SD</i> | 4.2 \pm 2.4 | <i>Maximum</i> | 8.7 \pm 2.5 (Nov) |
| | <i>n</i> | 643 | <i>PPI (%)</i> | 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 *Mastigodiatomus* cf. *albuquerqueensis* and *Leptodiatomus* 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 *Leptodiptomus* 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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