

Habitat expansion of a tropical chironomid by seasonal alternation in use of littoral and profundal zones

Javier Alcocer,^{1*} William M. Lewis Jr.,^{2,3} María del Carmen Hernández,⁴ Luis A. Oseguera,¹ Vania J.J. Pérez,⁵ Narcís Prat⁶

¹Grupo de Investigación en Limnología Tropical, Facultad de Estudios Superiores Iztacala, Universidad Nacional Autónoma de México, Tlalnepantla, Estado de México, México; ²Center for Limnology, Cooperative Institute for Research in Environmental Sciences, 216 UCB, University of Colorado, Boulder, CO, USA; ³Department of Ecology and Evolutionary Biology, 334 UCB, University of Colorado, Boulder, CO, USA; ⁴Programa de Posgrado en Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México, Ciudad de México, Mexico; ⁵Laboratorio de Paleontología y Ciencias de la Tierra, Facultad de Estudios Superiores Iztacala, Universidad Nacional Autónoma de México, Tlalnepantla, Estado de México, México; ⁶Grupo de Investigación FEHM (Freshwater Ecology Hydrology and Management), Departamento de Biología, Evolutiva, Ecología y Ciencias Ambientales, Facultad de Biología, Universidad de Barcelona, Spain

ABSTRACT

The consistent warming of tropical lakes at all depths causes rapid development and long persistence of seasonal anoxia in the hypolimnion, which greatly reduces the biodiversity of hypolimnetic benthic invertebrates. Full mixing of the water column in a typically annual cool-season creates a benthic habitat suitable for invertebrates but offers little time for colonization before the return of anoxia. In Lake Alchichica, Mexico, the endemic midge *Chironomus alchichica* has evolved a life cycle consisting of reproduction in waters of the littoral zone, which is suboptimal for development, followed by colonization of the hypolimnetic benthic zone during its oxic phase. As shown by the sampling of both littoral and benthic habitats over an annual cycle, the development of *Ch. alchichica* in the profundal zone is favoured by minimal competition (only one other invertebrate species present) and no significant predation. The rapid maturation of the midge leads to a high density of pupation before the seasonal anoxia.

INTRODUCTION

Deep tropical lakes would be warm monomictic, displaying a single predictable annual period of deep mixing or complete overturn, circulating in association with the hemispheric winter (Lewis, 1983). The mixing season in the tropics may be as short as a month or six weeks

(Lewis, 1996), implying an extended stratification period. 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 (i.e., the hypolimnia of temperate lakes become anoxic only when eutrophic while remaining oxygenated in oligotrophic). During stratification, when oxygen cannot be renewed either by photosynthesis or by mixing, the biochemical oxygen demand of the hypolimnion leads to oxygen depletion and even anoxia (Lewis, 1987). Soon after the onset of the stratification, the hypolimnion became anoxic and remained so as long as the lake's stratification persisted.

Benthic communities have an important 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 anoxia frequently is long-lasting. On the contrary, complete overturn of the water column brings back favourable conditions to the deep benthos opening a habitat 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. Chirono-

Corresponding author: : jalcocer@unam.mx

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mids are well suited to colonize and exploit this new habitat among these organisms.

Chironomus midges are globally known for inhabiting fine and soft sediments of aquatic ecosystems from the tropical to arctic latitudes (Pinder and Reiss, 1983; Merritt *et al.*, 2018). These up to 15 mm long chironomid larvae are commonly known as bloodworms, as the bright-red colour originates from the high haemoglobin (Hb) concentration (Moreno-Rulz *et al.*, 2000). This feature allows chironomids to inhabit –and even dominate– in hypoxic and anoxic environments (Strayer, 2009). Recently, *Chironomus* species' ability to respond to anoxic situations to produce more Hb protein has been studied and is considered a key factor for its resistance to anoxia (Manfrin *et al.*, 2018).

Some species of *Chironomus* are recognized as indicator organisms of highly productive and organically polluted aquatic bodies, where *Chironomus* could thrive under anoxic conditions, even for extended periods (Trivinho-Strixino, 2011; Pérez *et al.* 2013). Moreover, just a few *Chironomus* species can tolerate the presence of the toxic H₂S (1 mg·L⁻¹) that is frequently associated with anoxic environments (Neumann *et al.*, 1994). Nonetheless, *Chironomus* species differ in their capacity to acquire anaerobic metabolism and in their ability to endure under anoxic conditions (Nagell and Landahl, 1978; Lindegaard, 1992, 1995).

Even though *Chironomus* is commonly known as a typical deep benthic component of lakes, particularly those with low dissolved oxygen concentrations, fine sediments, rich in organic matter, and predominantly phytoplankton – diatoms detritus (Prat *et al.*, 1992; Dinsmore *et al.*, 1999), it is also commonly found in the littoral and sub-littoral zones (Real *et al.*, 2000). Previous studies of the benthos (Alcocer *et al.*, 1993, 1998, 2016) have shown that the endemic chironomid *Chironomus alchichica* Acosta & Prat 2017 (Diptera, Chironomidae), from here on abbreviated as *Ch. alchichica*, inhabits the littoral and deep benthos of Lake Alchichica (Acosta *et al.*, 2017). These studies show that the midge populations are not very dense in the littoral zone. Hernández *et al.* (2014) found that *Ch. alchichica*, identified as *Chironomus cf. austini*, produces large emergence of adults, which suggests that the deep benthic habitat is the main source of emerging adults. The latter is unexpected because the lake's profundal area is anoxic during the extended stratification period. In this work, our primary goal was to understand how *Chironomus alchichica* expands its habitat from the littoral down to the deep benthic habitat to complete its life cycle.

For this purpose, we addressed the following research questions: i) How is *Ch. alchichica* population dynamics in the littoral and the deep benthos? ii) How is the benthic community dynamics in the littoral and the deep benthos?

iii) What are the circumstances promoting the migration of *Ch. alchichica* down to the deep benthos? Our central hypothesis was that the deep benthic zone of the warm monomictic Lake Alchichica, while oxygenated, plenty of food, and free or almost free of competition and predation, provides valuable habitat to *Ch. alchichica*, which is able to migrate and fast develop before stratification transformed it into a harsh habitat (anoxic, H₂S).

Specifically, we expected the higher competition for space and food, and predation in the littoral, while low or inexistent competition and predation in the deep zone: i) lower density of *Ch. alchichica* in the littoral compared with the deep zone; ii) lower biomass of *Ch. alchichica* in the littoral compared with the deep zone; iii) fast colonization and development in the deep zone while oxygenated; and iv) a massive emergence of *Ch. alchichica* from the deep zone at the onset of the stratification and further hypolimnetic anoxia. To answer the research questions and test the proposed hypothesis, our approach was to evaluate the temporal changes in the: a) *Ch. alchichica* density and biomass in the littoral and deep benthic zone; b) benthic macroinvertebrates community density and biomass in the littoral and deep benthic zone; c) water and sediments main characteristics in the littoral and deep benthic zone.

Study area

Alchichica is a maar lake at a high elevation (2,300 m asl) in Puebla State on the Mexican Plateau (Fig. 1). Lake Alchichica has a maximum depth of 62 m and an average depth of 48.4 m (Filonov *et al.*, 2006), is warm monomictic (Alcocer *et al.*, 2000), and oligotrophic (Ramírez-Olvera *et al.*, 2009). It is circular (diameter ~1.7 km) and has a surface area of 2.4 km² and 5.8 km of coastline. The lake is cylindrical with a narrow littoral area and a discontinuous ring of stromatolites (microbialites) extending from the surface to 30-40 m.

The littoral zone (<5 m) is sharply separated from the deep benthic zone (40-60 m) by a steep slope from the littoral to the deep zone. A plateau with a gentle slope range at 50 to 60 m depth occupies most of the lake's bottom (Hernández *et al.*, 2014). The lake is saline (TDS = 8.5±0.52 g L⁻¹, K₂₅ = 13±0.5 mS cm⁻¹) and alkaline (pH: 8.7-9.2); chloride, bicarbonate, sodium, and magnesium are dominant ions (Alcocer *et al.*, 2000; Armienta *et al.*, 2008). Lake Alchichica mixes fully during the cold, dry season, from the end of December or the beginning of January to the end of March or April. The lake remains stratified throughout the warm rainy season (April or May to December), and the hypolimnion is anoxic during stratification (Alcocer *et al.*, 2000). No water pollution has been identified. The endemic atherinid fish *Poblana alchichica* de Buen, 1945 inhabits the lake in low density; its vertical distribution is limited by anoxia (Arce *et al.*,

2011). Although largely benthivores, *P. alchichica* feeds mostly close to the littoral zone (Alcocer *et al.*, 2010).

METHODS

Sampling of benthic invertebrates was monthly from September 2009 to August 2010 at nine sites: five in the littoral zone (<1 m) and four in the deep plateau between 50 and 61 m (Fig. 1). Water temperature, dissolved oxygen concentration (DO), pH, and specific conductance (K_{25}) were recorded with a Hydrolab DS4 multiparameter sonde at each sampling date. Water samples were filtered (Whatman 0.7 μm GF/F) for chlorophyll *a* (Chl-*a*) analysis. Pigments were extracted from the filters with 90%

acetone at 4°C overnight. Samples were then analyzed with a fluorometer (EPA 445.0) (Arar and Collins, 1997).

Sediment texture was determined with a dry sieving technique for large particles (gravel and sand) and pipetting of wet samples for fine particles (silt and clay) (Folk, 1980). Particle size was characterized following the classification scale of Wentworth (Welch, 1948). The percentages of organic matter and carbonate in the sediment were calculated by the loss on ignition (LOI) technique at 550°C and 950°C, respectively (Weber, 1973). Sediment Chl-*a* was extracted from 1 cm³ over 12 hours with 90% acetone at 4°C. Samples were then analyzed following the same method as for water. In the littoral zone, aquatic macrophytes from a measured area were dried and weighed as a means of estimating their abundance.

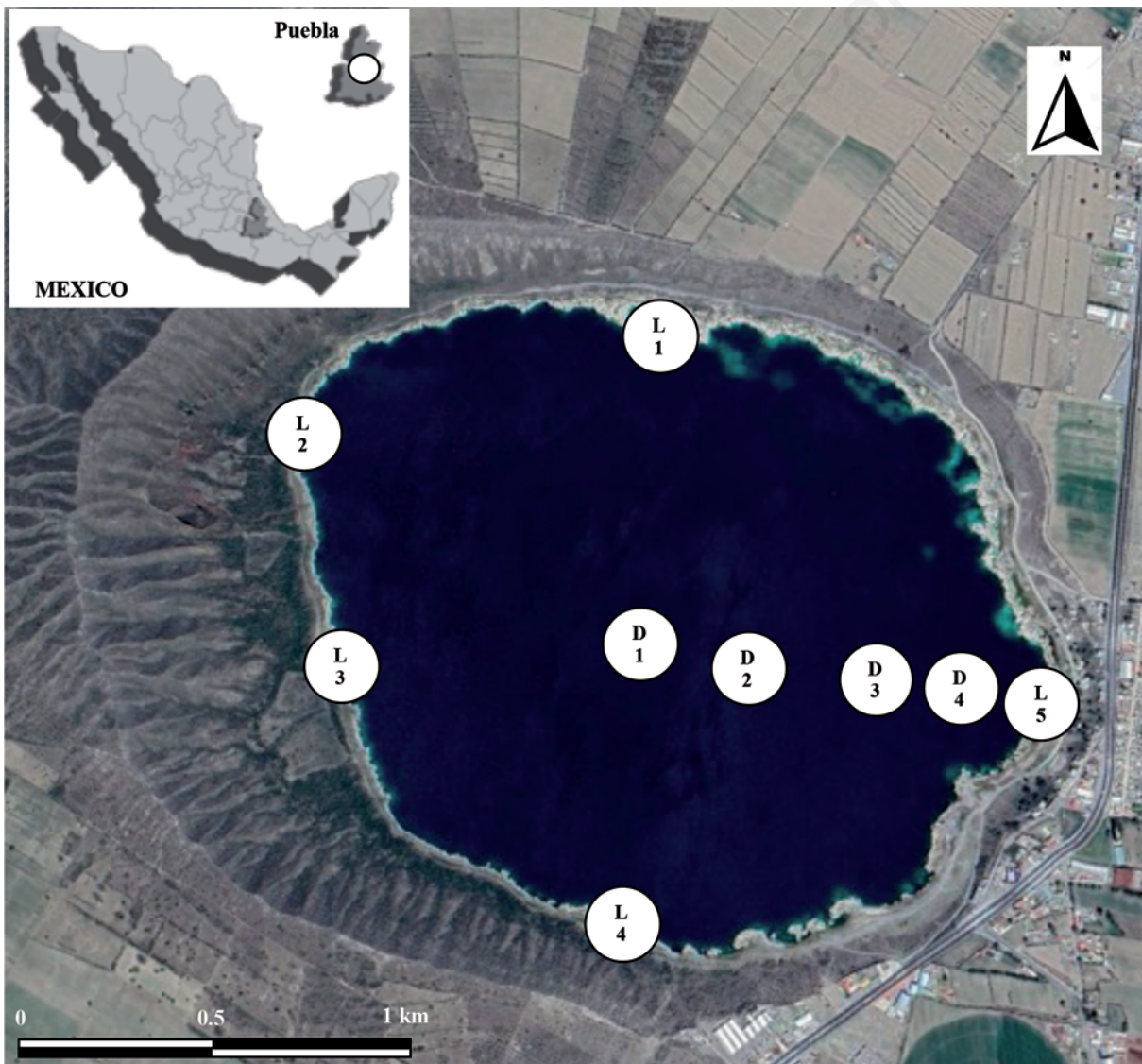


Fig. 1. Lake Alchichica, Mexico. White circles, sampling stations; L, littoral; D, profundal.

The benthic zone was sampled in triplicate at each site with an Ekman grab sampler (0.0225 m²). The top 10 cm of sediment was analyzed (Tudorancea *et al.*, 1979). Each sediment sample was sieved for macroinvertebrates with a 0.59 mm mesh (Gray, 1981; Wetzel, 1981). Samples were preserved in 96% ethanol (APHA *et al.*, 1999). Sampling the slope was impossible using the same method because the stromatolites covering the slope are solid mounds or cylinders of carbonate that retain minimal sediment. Hernández *et al.* (2010) found a few invertebrate species at low abundance by diving along the slope but did not find *Ch. alchichica*. Screening through 0.59 mm mesh excluded meiobenthos, including *Ch. alchichica* smallest instars. Ramos-Hernández *et al.* (2015) found a few *Ch. alchichica* as part of the littoral meiobenthos. Moreover, *Chironomus* instar I is planktonic and not benthic (Takagi *et al.*, 2005). Differently, *Ch. alchichica* first instars were absent while instars III and IV were present in the profundal sediments as revealed by careful examination of unscreened deep sediment samples.

Chironomids were separated manually from other invertebrates, identified, and expressed as individuals m⁻². Biomass (mg C m⁻²) was estimated based on body length and width. Biovolume (nl) was transformed to wet weight, dry weight, and carbon following Gerlach (1971), Feller and Warwick (1988), and Giere (2009).

For *Ch. alchichica* in the profundal benthos, larval instars were measured for total body length, head capsule length, and width (Sæther, 1980; Prat *et al.*, 1992; Prat and Rieradevall, 1995; Yan *et al.*, 1999). The abundance of each instar was calculated. The density of *Ch. alchichica* in the littoral zone was insufficient to support estimates of instar abundance.

A cluster analysis (CA) was performed with Ward's method according to Euclidean distances for each zone (five littoral and four profundal) to determine the environmental differences between the sampling locations. Principal component analysis (PCA) was used to determine which environmental variables were the most important in differentiating the sampling locations. The environmental data for the CA and PCA were transformed with "Z" so that high values did not excessively bias the results. The Spearman non-parametric correlation coefficient was used to correlate environmental variables (water and sediment) with biological variables (density and biomass of *Ch. alchichica* and macroinvertebrate community) for littoral and profundal zones. All data were transformed to log₁₀(n+1).

Since assumptions of normality and homogeneity were not fully resolved with log₁₀(n + 1) transformed data, Friedman two-way non-parametric analysis of variance was carried out for each zone as a means of identifying differences in density and biomass (total

invertebrates and *Ch. alchichica*) between the stations in the littoral and the deep zones. Additional Friedman tests identified temporal differences in density and biomass for all invertebrates at the two sampling areas. A Holm method (Holm, 1979) was also used to identify differences between pairs of means. All statistical analyses are based on SPSS Version 18.0.

RESULTS

Habitat features

In the littoral zone at depths below 1 m, the temperature averaged 18.3°C, and the annual fluctuation range (11.9°C) was similar to the mean diel range (10.4°C). The water was well-oxygenated, alkaline, saline, and oligotrophic. Sediments consisted of silty sands with abundant carbon, low sedimentary Chl-a concentrations, and macrophyte (*Ruppia maritima* Linnaeus, 1753) cover or, in some places, naked sediment (Tab. 1).

A cluster analysis (Supplementary Material Fig. 1A) showed that littoral stations (L1, L2, and L3 were not statistically different; L4 was similar to the L1-L2-L3 cluster, and L5 differed from the other sampling stations. The PCA explained the separation of L4 and L5 from the rest of the sampling stations based on their low presence (L5) or absence (L4) of aquatic vegetation and amounts of organic matter. L5 differed from L4 in that the sediment was gravel rather than sand.

The deep zone was colder than the littoral, and its DO concentration ranged from 80% saturation to anoxia (<2 mg L⁻¹). The sediments were clayed silt with higher organic matter concentrations but lower Chl-a content than the littoral zone (Tab. 1). The DO concentrations (Fig. 2) were high from February to June and low or absent the rest of the year. A previous study has shown that when the deep benthic zone is anoxic, hydrogen sulfide accumulates to concentrations as high as 3.08 mg L⁻¹ (Hernández *et al.*, 2014).

A cluster analysis (Supplementary Material Fig. 1B) for profundal stations showed progressive linkage from station D1 to D4, with the most significant difference between D1 and D4. According to the PCA, differences are associated with DO concentration and elemental carbon content; D4 had the lowest DO concentration and the highest percentage of elemental carbon.

Composition of the macrobenthic community

Twenty-eight taxa composed the macroinvertebrate community in the littoral zone (Supplementary Material Tab. 1). However, only two taxa (*Ch. alchichica* III and IV, and *Candona alchichica* Cohuo, Hernández, Pérez & Alcocer, 2017, an ostracod) occurred in the deep benthic zone.

Ch. alchichica contributed 0.5% numerically and

0.03% of the biomass in the littoral invertebrate community. The oligochaete *Limnodrilus hoffmeisteri* Charpède, 1862 and the amphipod *Hyaella azteca* Saussure, 1858 dominated the littoral community. *Ch. alchichica* accounted for 2% of individuals in the deep benthic zone and 29% of the biomass. The ostracod *C. alchichica* accounted for the rest of the individuals and biomass in the deep benthic zone (Supplementary Material Fig. 2).

Density and biomass

The density of *Ch. alchichica* in the littoral zone averaged 37 ± 30 individuals m^{-2} ; maximum densities occurred in May, and minimum densities occurred in October (Fig. 3). *Ch. alchichica* density was significantly higher ($p < 0.05$) at station L1 than at other stations (Fig.

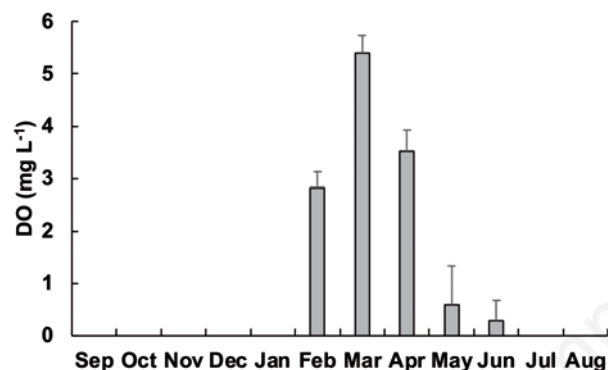


Fig. 2. Dissolved oxygen concentration in the deep zone of Lake Alchichica.

4). In the deep zone, *Ch. alchichica* was present only from February to June, while the profundal zone remained oxygenated over these months; the mean density was 67 ± 82 individuals m^{-2} . Maximum densities occurred in April (185 ± 315 individuals m^{-2}) and minimum densities in February (7 ± 26 individuals m^{-2}) and June (7 ± 17 individuals m^{-2} ; Fig. 3). *Ch. alchichica* density at D4 was significantly higher ($p < 0.05$) than at the other three stations (Fig. 4).

Invertebrate densities in the littoral zone averaged $14,519 \pm 5,390$ individuals m^{-2} ; densities were maximum in May and minimum in August (Fig. 3). Densities in August were not significantly different from those of July ($p > 0.05$) but were significantly lower ($p < 0.05$) than in the other months. Densities at the littoral zone stations L3 and L5 were significantly lower ($p < 0.05$) than at stations L1, L2, and L4 (Fig. 4). In the deep zone, densities averaged $1,764 \pm 2,233$ individuals m^{-2} ; maximum densities occurred in November ($4,304 \pm 4,472$ individuals m^{-2}), and minimum densities occurred in June (596 ± 540 individuals m^{-2}) (Fig. 3). No significant differences were found among the sampling months. Spatially, D1 and D2 showed significantly smaller densities ($p < 0.05$) than D4 but not D3. Densities at stations D3 and D4 were not significantly different ($p > 0.05$) (Fig. 4). Biomass of *Ch. alchichica* in the littoral zone averaged 0.5 ± 0.4 mg C m^{-2} ; maximum values occurred in May (1.52 ± 3.2 mg C m^{-2}), and the minimum occurred in October (0.08 ± 0.3 mg C m^{-2}) (Fig. 3). The biomass of *Ch. alchichica* at L1 was significantly higher ($p < 0.05$) than at other stations (Fig. 4). In the deep zone, the mean biomass of *Ch. alchichica* was 15.7 ± 23.4 mg C m^{-2} ; biomass reached a maximum in May (16.26 ± 26.55 mg C m^{-2}) and a minimum in Feb-

Tab. 1. Averages and ranges for water and sediment supporting *Chironomus alchichica* in Lake Alchichica.

Variable	x±SD	Littoral		x±SD	Profundal	
		min	max		min	max
Water						
T (°C)	18.3±3.0	16.73	20.04	14.5 ±3.0	14.41	14.52
DO (mg L ⁻¹)	8.0±1.8	6.88	11.38	2.02±1.97	0.00	5.91
DO%sat (%)	119±32	96.2	174.9	35.4±27.8	0.7	80.4
pH	8.8±0.6	8.69	9.11	9.2±0.1	8.79	9.57
K ₂₅ (mS cm ⁻¹)	13.6 ±0.8	3.06	14.61	13.0±0.5	12.43	14.74
Chl-a (µg L ⁻¹)						
	0.55±0.35	0.05	1.64	3.19±2.02	2.03	9.34
Sediment						
Gravel (%)	7±6	2	16	0	0	0
Sand (%)	80±16	65	95	3±5	0	15
Silt (%)	11±13	3	28	58±38	0	100
Clay (%)	1±1	0.3	2	19±24	0	94
OM (%)	6±3	1	8	35±4	29	42
CO ₃ (%)	47±7	32	68	13±4	6	25
Chl-a (µg cm ⁻²)	18±11	8	28	3±2	1	9
AM (gDW m ⁻²)	93±53	0	164	0	0	0

x, average; min, minimum; max, maximum; T, temperature; DO, dissolved oxygen; DO%sat, DO saturation percentage; K₂₅, electric conductivity at 25°C; Chl-a, chlorophyll "a" concentration; OM, organic matter; CO₃, carbonates; AM, aquatic macrophytes—*Ruppia maritima*.

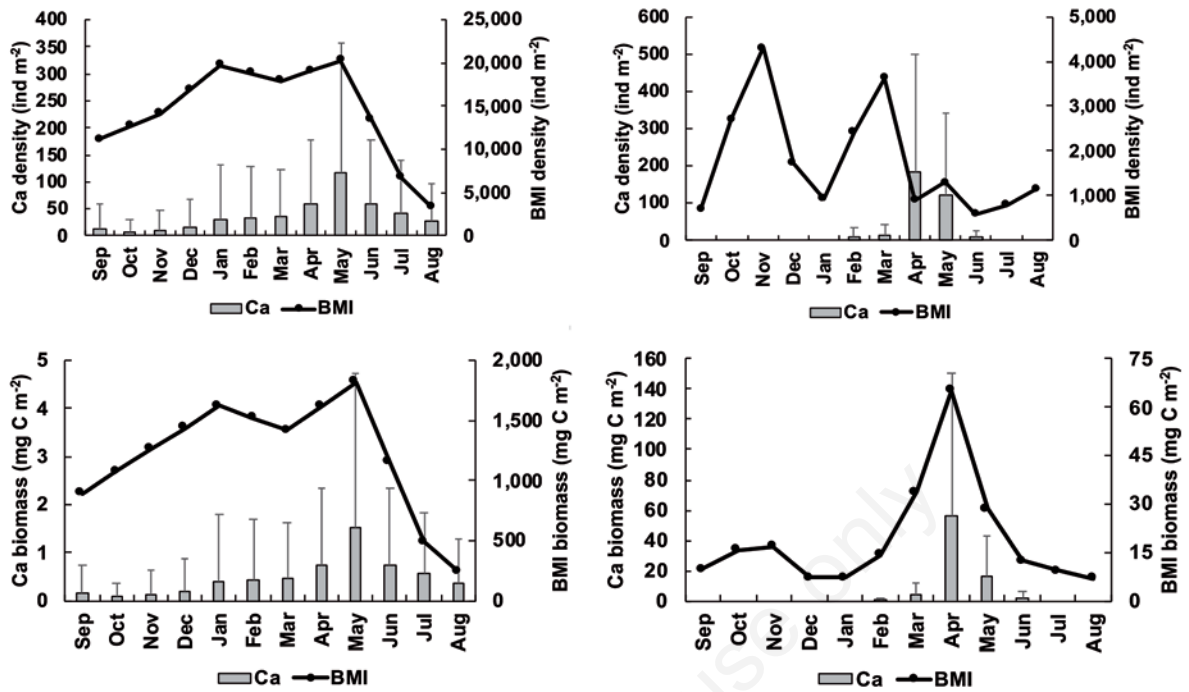


Fig. 3. Temporal variation of density and biomass for *Chironomus alchichica* (Ca) and the benthic macroinvertebrate community (BMI) (average±SD) in the littoral (left) and profundal (right) zones, from September 2009 to August 2010. Only *Chironomus alchichica* instars III and IV; in the deep zone, months shown blank are 0.

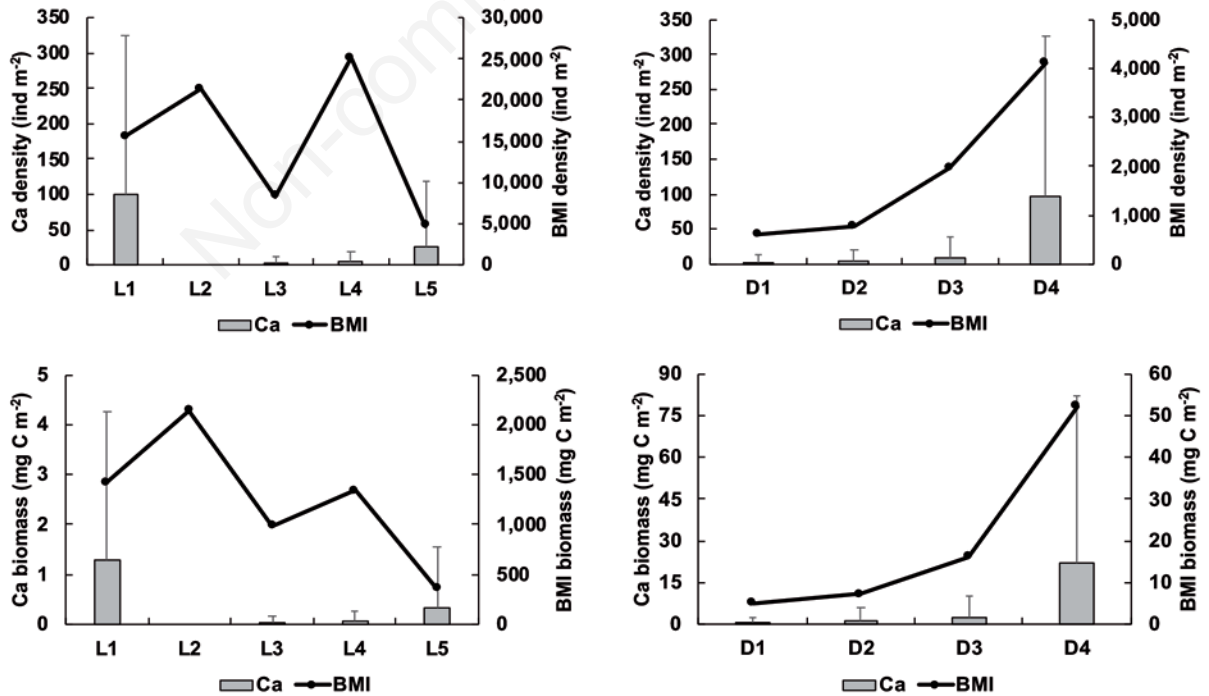


Fig. 4. Spatial variation of density and biomass for *Chironomus alchichica* (Ca) and the benthic macroinvertebrate community (BMI) (average±SD) in the littoral (left) and profundal (right) zones, from September 2009 to August 2010 (only *Chironomus alchichica* instars III and IV).

ruary ($0.31 \pm 1.09 \text{ mg C m}^{-2}$) (Fig. 3). Biomass was higher at station D4 ($p < 0.05$) than at the other three stations (Fig. 4). Invertebrate biomass in the littoral zone averaged $1,213.2 \pm 473.5 \text{ mg C m}^{-2}$; it was maximum in May ($1,818.3 \pm 1,709.0 \text{ mg C m}^{-2}$) and minimum in August ($245.2 \pm 259.5 \text{ mg C m}^{-2}$) (Fig. 3). Biomass at L5 was significantly lower ($p < 0.05$) than at the other stations (Fig. 4). In the deep zone, biomass averaged $19.0 \pm 16.8 \text{ mg C m}^{-2}$; it was maximum in April ($65.2 \pm 95.9 \text{ mg C m}^{-2}$) and minimum in August ($7.1 \pm 6.1 \text{ mg C m}^{-2}$) (Fig. 3). Invertebrate biomass at D4 was significantly higher ($p < 0.05$) than at the other three stations (Fig. 4). High standard deviations for all density and biomass measures are accounted for by high spatial variance on all dates.

For the littoral zone, positive significant ($p < 0.05$) correlations were found for BMI density with silt and elemental carbon, and negative significant ($p < 0.05$) correlation with temperature. *Ch. alchichica* density was positively correlated ($p < 0.05$) with aquatic macrophytes. BMI biomass had a positive significant ($p < 0.05$) correlation with chlorophyll “a” concentration, organic matter, and silt, while *Ch. alchichica* biomass did not correlate with any variable. The profundal zone density and biomass of MIB were positively ($p < 0.05$) correlated with chlorophyll “a” concentration. MIB biomass and *Ch. alchichica* had a significant positive correlation ($p < 0.05$) with dissolved oxygen.

Development of *Chironomus alchichica*

Ch. alchichica instars were distinguished based on head capsule width (Tab. 2) (Prat and Rieradevall, 1995). The larval length ranged from 4.21 to 14.67 mm in the deep zone; larvae attained a similar length in the littoral. While instars I to IV inhabit the littoral (I and II as meiobenthos, while III and IV as macrobenthos), only instars III and IV reside in the deep zone.

Tab. 2. Mean (first row) and range (second row) head capsule (length and width in mm) of *Chironomus alchichica* in the profundal zone.

Instars	Larvae		Head capsule		n
	L	W	L	W	
III	4.86 ± 0.28	0.26 ± 0.06	0.47 ± 0.07	0.27 ± 0.04	15
	4.21-5.19	0.19-0.31	0.29-0.55	0.24-0.40	
IV	9.98 ± 2.45	0.64 ± 0.21	0.47 ± 0.09	0.48 ± 0.04	82
	5.22-14.67	0.33-1.14	0.27-0.62	0.40-0.60	

Tab. 3. Relative abundance (%) of instars III and IV for *Chironomus alchichica* in the profundal zone.

Instars	Feb	Mar	Apr	May	Jun
III	0	0	8	31	0
IV	100	100	92	69	100

DISCUSSION

Distribution of *Chironomus alchichica* in Lake Alchichica

Hernández *et al.* (2010) did not find *Ch. alchichica* in the stromatolite-covered slopes. The food supply along the side profile of the lake probably is low because the deposition of particulate matter per unit area is inversely related to slope, which causes organic matter and diatoms, the food of *Ch. alchichica* (Prat *et al.*, 1992), to be scarce on the slope.

The highest *Ch. alchichica* densities and biomasses in the littoral zone were found at L1 and L5, not showing high similarity in habitat. Unmeasured variables such as competition and predation may control the abundance of *Ch. alchichica* in the littoral zone.

Because *Ch. alchichica* is present in the profundal benthic zone only when the water column is oxygenated during seasonal circulation, *Ch. alchichica* appears to be intolerant of low DO concentrations and the presence of H_2S . Given that all deep benthic stations were environmentally similar, the higher densities of *Ch. alchichica* at D3 and D4 near the lateral margin of the deep zone may reflect their migration route (Hernández *et al.*, 2014).

Dynamics of the *Chironomus alchichica* population

Only instars III and IV were found in the deep zone (Tab. 3). Instar III had peak abundance in May. The larvae became scarce in June, suggesting the rapid development of larvae in April-June.

The data indicate that eggs are laid on the littoral zone where they hatch as instar I, which becomes instar II. Migration to the lake bottom occurs as instars III or IV. It seems instar IV is better suited to make it to the deep benthos and establish prompter than instar III (February and March). While instar IV is already at the deep benthos, in-

star III arrives (April and May) and moults to instar IV. By June, all individuals had reached instar IV or already pupated and migrated back to the surface. As anoxia approaches, pupation and emergence at the surface take place.

The emergence of *Ch. alchichica* produces large swarms of midges that gather around the lake's littoral zone in April and May. Abundant pupal exuviae float in the littoral area when emergence occurs. This period coincides with the increase of daylength and water temperature, the end of the lake's full mixing period, the end of the annual diatom bloom, and the onset of a sharp decline in the DO concentration in the profundal zone when stratification begins, as in other lakes (Jónasson, 1972). In Lake Alchichica, the winter diatom bloom consists mainly of the large (>50 µm) and fast sinking diatom *Cyclotella alchichicana* Oliva, Lugo, Alcocer & Cantoral-Uriza 2006 (Ardiles *et al.*, 2012; Alcocer *et al.*, 2014), which provides food for the deep benthos (Hernández *et al.*, 2014). Some *Chironomus* species thrive in the profundal zone despite anoxia using extracellular haemoglobin (Nath, 2018). High amounts of sulfide during anoxia can cause the disappearance of chironomid species from the profundal area of the lakes even when the species can tolerate oxygen depletion (Prat *et al.*, 1992). In Lake Alchichica, a different survival strategy, diapause, allows the ostracod *C. alchichica*, which lives in the deep benthos zone, to survive the anoxic period (Hernández *et al.*, 2014). In the profundal zone, the only potential competitor of *Ch. alchichica* is *C. alchichica* (Hernández *et al.*, 2014). The only potential predator of *Ch. alchichica* in the profundal zone is the silverside fish *Poblana alchichica*, but *P. alchichica* feeds most often in the stromatolites close to the shoreline, and in the limnetic zone consumes primarily copepods (Arce *et al.*, 2011).

In the littoral zone, competition for habitat and predation pressure probably is high because *Ch. alchichica* shares the habitat with many other invertebrate taxa (Hernández *et al.*, 2014) (Supplementary Material Tab. 1). Predation could be an important factor in explaining the lower densities of *Ch. alchichica* in the littoral compared with the deep zone where there is little fish predation.

CONCLUSIONS

As do many tropical lakes, Alchichica has a warm monomictic thermal regime, develops an anoxic hypolimnion during the long stratification period, and shows high oxygen concentration along the full water column during mixing in the cool season. Although the deep benthic zones of tropical lakes are harsh anoxic environments most of the year, the complete mixing of the water column creates an advantageous environment that can be colonized seasonally by *Ch. alchichica*, which has specific adaptations that compensate for the annual return of conditions that prevent growth and maturation. This habitat shifting strat-

egy from the littoral to the deep zone allows *Ch. alchichica* to complete its life cycle successfully and persist by seasonally taking advantage of a low competition and low predation benthic zone rich in food resources moving out from a high competition and high predation littoral zone. In this way, *Ch. alchichica* can re-stock its littoral population.

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