Profundal benthic invertebrates in an oligotrophic tropical lake: different strategies for coping with anoxia

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ABSTRACT

The deep benthic communities of tropical lakes are poorly understood with respect to their composition, abundance, biomass and regulatory factors. Whereas the hypolimnia of temperate oligotrophic lakes remain oxygenated, the higher temperatures in tropical lakes frequently lead to the rapid development of hypolimnetic anoxia independent of trophic status. The deep benthic communities of tropical lakes must therefore develop strategies to respond to anoxic conditions. The dynamics of the deep benthic community of Lake Alchichica were studied over 15 months. We hypothesized that the sedimentation of the winter diatom bloom constitutes an input of high-quality food that contributes to the establishment and development of the deep benthic community. However, the remineralization of this organic matter leads to the prompt development of hypolimnetic anoxia, thus limiting the establishment and/or persistence of the deep benthic community. In contrast with the diverse littoral benthic community (50 taxa) in Lake Alchichica, only two species constitute its deep benthic community, the ostracod Candona cf. patzcuaro *and the chironomid* Chironomus cf. austini, *which combined exhibit a low density (1197±1976 ind m⁻²) and biomass (16.13±30.81 mg C m⁻²).* C. patzcuaro *is dominant and is present throughout the year, whereas* Ch. austini *is recorded only when the bottom water of the lake is oxygenated. A comparison with the analogous but temperate Lake Mergozzo in Italy illustrates the role that anoxia plays in tropical lakes by diminishing not only taxonomic richness (13* vs *2 spp. in temperate versus tropical lakes, respectively) but also abundance (1145* vs *287 ind m⁻², respectively).* C. patzcuaro *is found throughout the annual cycle of the lake's profundal zone, entering into diapause during the anoxic period and recovering as soon as the profundal zone reoxygenates.* Ch. austini *has adjusted its life cycle to use the habitat and available resources while the bottom of the lake is oxygenated and emerges en masse at the onset of anoxia. The presence of oxygen and abundant fresh food favors the development of the deep benthic community and yields increases in density and biomass. However, the anoxia that rapidly occurs during the stratification period and the presence of hydrogen sulfide are the key factors that limit deep benthic community colonization and/or permanence in the profundal zone of the tropical Lake Alchichica.*

Key words: Deep benthos, density, biomass, anoxia, tropical lake.

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INTRODUCTION

The bottom of a deep lake is a homogeneous habitat with fine sediments and no vegetation (Wetzel, 2001), which results in the reduced local diversity of deep benthic species (Margalef, 1983; Wetzel, 1981; Jónasson, 2004). This community includes groups of invertebrates that have developed metabolic adaptations to respond to the environmental challenges involved in colonizing these habitats (Hamburguer *et al.*, 2000). The decreased diversity is compensated by the increased abundance of the tolerant species (Newrkla and Wijegoonawardana, 1987).

The distribution patterns and abundance of benthic populations are controlled by diverse environmental factors (Peeters *et al.*, 2004). The distribution pattern of profundal benthic fauna with lake depth is particularly dependent on factors such as the bathymetric gradient of

the lake (Goldman and Horne, 1983) and the type of sediment (Newrkla and Wijegoonawardana, 1987). However, the quantity and quality of the organic matter that settles to the lake bottom (Valdovinos and Figueroa, 2000) and the level of hypolimnetic dissolved oxygen (DO) are the key factors in the regulation of these communities (Jyväsjärvi *et al.*, 2009). Massive phytoplankton sedimentation events, particularly of diatom blooms, generate seasonal variation in the community structure and growth patterns of benthic invertebrates (Jónasson, 1972). Invertebrates respond rapidly to these inputs of fresh organic matter, and the assimilation of these nutrients affects the population dynamics of each species in a manner closely associated with the species' feeding habits and trophic levels (Peeters *et al.*, 2004). The use of this influx of organic matter is not necessarily expressed in population numbers,

as the organic matter may also be used as energy for somatic growth or sexual maturation (Goedkoop and Johnson, 1996). The sedimentation of organic matter benefits certain groups by providing an abundant food supply in the sediment while simultaneously hindering sensitive species to change in food supply, or in physical or chemical conditions in the benthic environment, depending on the feeding habits and the particular needs of each taxonomic group (Nalepa *et al.*, 1998). Thus, feeding conditions improve as the amount of organic matter increases, but decomposition processes also increase, decreasing the concentration of oxygen in the sediment (Jørgensen and Revsbech, 1985). This phenomenon limits the occurrence of benthic aerobic fauna and affects the distribution of species along the bathymetric gradient (Johnson, 1974; Newrkla and Gunatilaka, 1982). Bentho-pelagic coupling directly determines the dynamics of deep benthic communities (Valiela, 1984). However, these dynamics have been poorly studied in lentic environments, and their structural variation and temporal and spatial patterns are practically unknown (Michiels and Traunspurger, 2004). Most recent studies have focused on temperate lakes and dealt mainly with littoral macrofauna. In contrast, the benthos (particularly the meiobenthos *i.e.*, <0.59 to >0.062 mm length) of deep areas is practically unexplored (Moore, 1981; Gaedke, 1993; Rasmussen, 1993; Specziár and Bíró, 1998).

Among the few relevant previous studies (Marshall, 1978; Lindegaar, 1992; Cohen, 1995; Nalepa *et al.*, 1998; Jyväsjärvi *et al.*, 2009), only a few mention the importance of hypolimnetic anoxia and the tolerance of deep benthic species to these conditions (Johnson and Wiederholm, 1989). Knowledge of this dynamic is particularly lacking with respect to the profundal fauna of tropical lakes and their community ecology (Sibaja-Cordero and Umaña-Villalobos, 2008). The hypolimnia of temperate eutrophic lakes are known to easily become anoxic, whereas those of temperate oligotrophic lakes remain oxygenated. In contrast with temperate lakes, the higher temperatures in tropical lakes frequently result in the rapid development of hypolimnetic anoxia independent of trophic status. The oxygen uptake capacity of the water, and therefore the oxygen reserve in the hypolimnion, are reduced under high hypolimnetic temperatures. In addition, the speed of oxygen depletion in warmer tropical lakes is increased by the higher metabolic rates of their bacteria and benthic fauna (*e.g.*, $Q_{10} \cong 2$). Thus, tropical lakes become anoxic during the stratification period more quickly than do temperate lakes due to their lower DO concentrations, higher biochemical oxygen demands, longer stratification seasons and generally greater productivity and the fact that tropical lakes achieve DO saturation less readily during the mixing season (Lewis, 1987).

To address the knowledge gap on this important dynamic, the present study was established to describe the composition and structure of the zoobenthos (macro- and meiobenthos) and the environmental factors involved in the temporal and spatial dynamics of the deep sediment community of Lake Alchichica, Mexico. As Alchichica is an oligotrophic lake that experiences a winter diatom bloom, the role that the sedimentation of this bloom plays in the dynamics of the deep benthic community was also studied. The sedimentation of the diatom bloom was hypothesized to constitute a valuable food resource, in terms of both quantity and quality, for the benthos and to substantially contribute to the establishment and development of deep benthic invertebrates. However, the remineralization of the abundant organic matter provided by the diatom bloom was hypothesized to cause an elevated consumption of DO, eventually leading to hypoxic and anoxic conditions that represent a limiting factor for the establishment and/or persistence of the deep benthic community. We also hypothesized that deep regions closer to the lake's edge were more likely to be colonized by the littoral zone biota. Therefore, we expected that even within a similar water depth range (50-62 m), the deep area closer to the littoral zone would show a different species composition and a higher species richness, density and biomass compared to the deep central zone.

Study area

Lake Alchichica (19°24.7' N, 97°24.0' W) is a volcanic maar lake located in the Oriental drainage basin (4982 km²) on the southeastern region of the Mexican high central plateau between the states of Puebla, Veracruz and Tlaxcala (Alcocer *et al.*, 2000; Filonov *et al.*, 2006). The lake is almost circular (area 2.3 km²), with a circumference of 5.1 km and a diameter of approximately 1.7 km (Fig. 1). The lake's greatest depth is 62 m, and its average depth is 40.9 m (Filonov *et al.*, 2006). Alchichica has steep slopes and a deep benthic region (≥50 m) that constitutes a large percentage (45%) of the lake's bottom area. As such, Alchichica possesses the typical morphometry of a maar lake (Hutchinson, 1975). The climate in the region is semiarid, with an average temperature of 12.9°C, an annual evapotranspiration rate of 1,690 mm and less than 500 mm of rainfall (Adame *et al.*, 2008; Alcocer *et al.*, 2000). Alchichica is an endorheic lake with no surface influent or effluent; the volcanic rim surrounding the lake constitutes its watershed, resulting a very small drainage basin. The lake is mostly fed by groundwater. The saline (salinity 8.5±0.52 g L⁻¹, conductivity 13±0.5 mS cm⁻¹) and alkaline (pH 8.7-9.2) water is dominated by bicarbonate, chloride and sodium and magnesium ions (Vilaclara *et al.*, 1993; Alcocer *et al.*, 2000). Alchichica is a warm, monomictic lake with a mixing period during the cold, dry season (late December/early January to late March/early April) and a stratification period that lasts

throughout the warm, rainy season (Alcocer *et al.*, 2000). This warm monomixis pattern is commonly found in deep tropical lakes (Lewis, 1996); thus, Alchichica is a representative example of these lakes.

Previous studies on the benthic fauna of the lake have focused on its littoral area (Alcocer *et al.*, 1993a, 1993b; Alcocer, 1995; Alcocer *et al.*, 1998; Alcocer *et al.*, 2002; Hernández, 2001; Peralta *et al.*, 2002). To date, 50 littoral taxa have been identified (Tab. 1), among which nematodes, trichopterans, coleopterans and dipterans contribute most to the lake's taxonomic richness.

METHODS

Sampling took place over 15 months (October 2009-December 2010) in the deep part of the lake (≥50 m), where four stations (E1=62 m, E2=61 m, E3=60 m,

Tab. 1. Taxonomic groups present in the littoral fringe of Lake Alchichica (from Alcocer *et al.,* 1998).

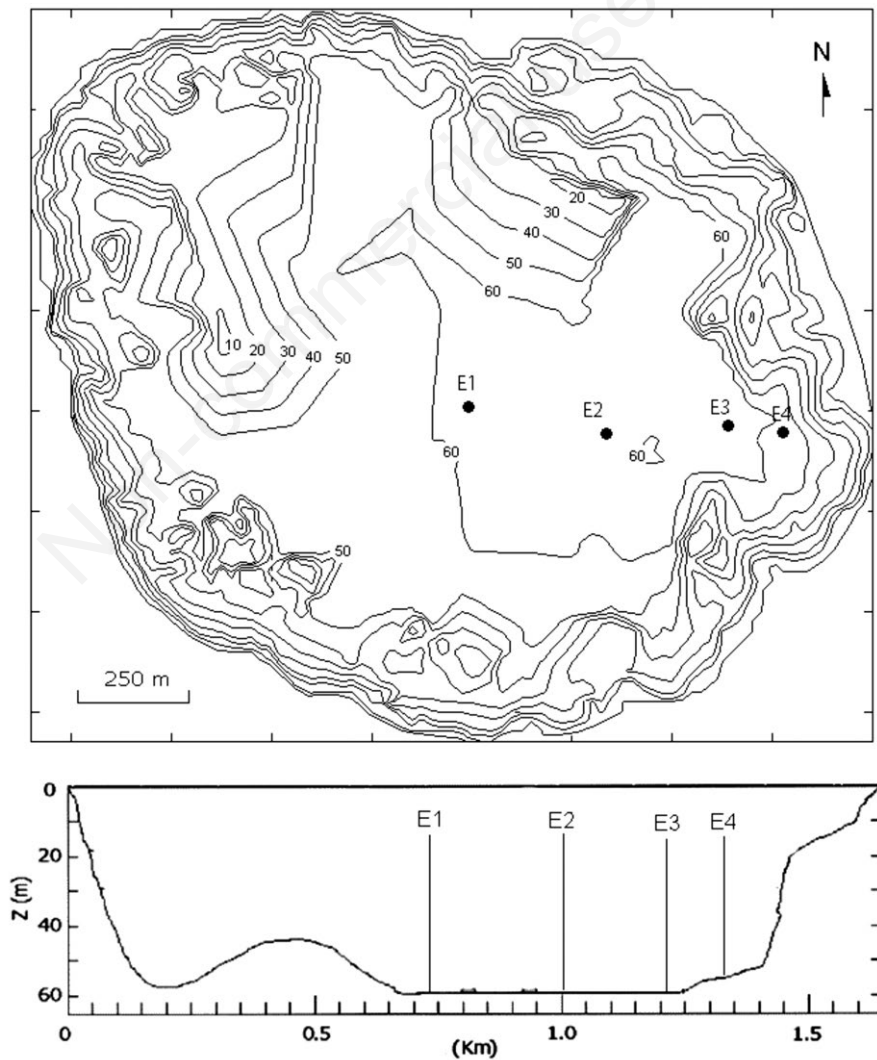| Group	No. of taxa
Turbellaria	1
Nematoda*	8
Oligochaeta	2
Hirudinea	2
Ostracoda	2
Amphipoda	1
Ephemeroptera	1
Odonata	2
Hemiptera	3
Trichoptera	4
Coleoptera	6
Diptera	17
Gastropoda	1
TOTAL	50

Hernández, unpublished data.

Fig. 1. Bathymetric chart of Lake Alchichica showing the locations of the four sampling stations in the deep areas.

E4=50 m) were established to represent an offshore-bathymetric gradient (Fig. 1). The station nearest to shore (E4) was located approximately 175 m from the shore, and the station farthest from shore (E1), at the center of the lake, was located at a distance of approximately 900 m. *In situ* temperature and DO vertical profiles (surface to bottom) were recorded at each sampling date with a DS4 Hydrolab (Hach Hydromet, Loveland, CO, USA) water quality-monitoring multiprobe, which was coupled to a SVR4 Hydrolab logging system for data collection and storage. Sediment texture was determined following the dry sieving technique for large particles (sand) and by pipetting wet samples for fine particles (silt and clay) (Folk, 1969). Particle size was characterized following the classification scale of Wentworth (Folk, 1969; Welch, 1948). The contents (%) of organic matter and carbonate in the sediment were calculated based on the loss on ignition (LOI) technique at 550°C and 950°C, respectively (Hammer *et al.*, 1990; Weber, 1973). Sediment trap stations (KC Denmark, Silkeborg, Denmark) were placed and collected monthly (deploy time approx. 30 days) to evaluate the flux of chlorophyll a (Chl-a), which represents the source of the pelagic potential food supply (phytoplankton cells) that reaches the benthos. Our sediment trap' sampling scheme was similar to those reported elsewhere (Callieri, 1997; Veronesi *et al.,* 2002). A sample was taken from each trap and evaluated using fluorometry following the technique of Arar and Collins (1997). A 5 mL aliquot of each sample was filtered through a Whatman GF/F fiberglass filter (0.7 µm nominal pore size). The filters were disintegrated in a macerator with a Teflon tip, and 10 mL of 90% acetone was added to each sample to extract the Chl-a over 20 hours in darkness at 4°C. The samples were then centrifuged, and the fluorescence of the supernatants was read in a 10-AU fluorometer (Turner Designs, Sunnyvale, CA, USA).

Three replicate samples (top 10 cm only) of benthic fauna were collected with an Ekman-type grab sampler (0.0225 m² area, 15×15×15 cm) at each sampling station. Each sediment sample was sieved *in situ* through a 0.59 mm mesh pore size to retain macrofauna and then through 0.062 mm mesh pore size to retain meiofauna (Gray, 1981; Wetzel, 1981). The samples were preserved in 96% alcohol+Bengal Rose as a vital dye (APHA *et al.*, 1985).

The specimens were identified to the lowest possible taxonomical hierarchical level following the general (Edmonson, 1959; Pennak, 1978) and specialized (Epler, 2001; Meisch, 2000) taxonomic keys for each group. The specimens of each species were quantified to determine their density (ind·m⁻²). The biomass was calculated following the biovolume method (Warwick and Price, 1979; Higgins and Thiel, 1988). The biovolume (nL) was transformed into preserved wet weight, dry weight and carbon using the conversion factors proposed by Gerlach (1971),

Feller and Warwick (1988) and Giere (1993), respectively.

A $\log_{10}$ (n+1) data transformation was used to reduce the variables variance to satisfy the required normality assumptions. We used one-way analyses of variance (ANOVA) to test whether the means of the environmental variables differed spatial and temporarily. We used Tukey *post-hoc* tests to identify differences among the means after ANOVA. Since the biological variables were not normally distributed we used a Friedman test, which is a non-parametric two-way variance analysis, to compare the biological variables (density and biomass) in time and space. A Holm (1979) test was applied in those cases where significant differences were found in order to perform multiple comparisons and to identify differences among pairs of averages. SPSS (ver. 18.0) was used for the analysis.

RESULTS

We found no significant environmental differences (P>0.05) among the four sampling stations (E1-E4). For this reason, we treated the four sampling stations as environmental replicates throughout the remainder of the analysis. In general, the deep benthic area of Lake Alchichica presented fine sediments dominated by clayed silts (sand 4%, silt 72%, clay 24%) and high contents of organic matter (34.7±3.5%) and carbonate (13.6±3.7%). The temperature remained almost constant throughout the year, with an average of 14.5±0.1°C. Similarly, the pH remained stable at 9.17±0.14. These environmental parameters showed no significant differences (P>0.05) over the study period.

In contrast, both DO and Chl-a flux showed significant temporal differences. Regarding DO, the lake bottom was oxygenated for four months (February-May), reaching the highest DO values in March (5.40±0.34 mg L⁻¹) and the lowest in May (0.28±0.4 mg L⁻¹). The DO values from February to April were significantly different from those during the rest of the year (P<0.05). The Chl-a flux values were also significantly different (P<0.05) during February to May as compared to those during the rest of the sampling period. The highest Chl-a flux was recorded in March 2010 (8.23±0.71 mg m⁻² d⁻¹).

The benthic invertebrate assemblage of the deep area of Lake Alchichica was restricted to two taxa: the ostracod *Candona cf. patzcuaro* Tressler (1954) and the chironomid *Chironomus cf. austini* Beck and Beck (1970). Both species were found as meio- (juvenile stages: mostly A3-A4 *C. patzcuaro* larvae and 2nd *Ch. austini* instar) and macrofauna (mostly *C. patzcuaro* adults and late *Ch. austini* instars). Considering the frequency (92%) and abundance (98%) of *C. patzcuaro*, the species was dominant across the four stations, and the ostracod was collected throughout the sampling period. *Ch. austini* was also present across all four stations, but at a much lower abundance

(2%) and frequency (12%), and the species was only collected from February to May, the same period when the bottom water remained oxygenated (Tab. 2).

The average total density (±standard deviation) of the benthic invertebrates was 1197±1976 ind m^{-2}; the density of *C. patzcuaro* was 1169±1970 ind m^{-2}, and that of *Ch. austini* was 28±146 ind m^{-2}. The maximum total density (3629±3564 ind m^{-2}) was recorded in March 2010, and the minimum (274±154 ind m^{-2}) was recorded in October 2010 (Fig. 2). Meiobenthos made up 76% of the density (75% *C. patzcuaro*, 1% *Ch. austini*), whereas macrobenthos comprised only 24% (20% *C. patzcuaro*, 4% *Ch. austini*). Considering the density, the four stations exhibited significant differences (X^2_r=47,441.33, P<0.05) in the temporal and spatial scales. Station E1 (the central and deepest station, 62 m) had the lowest average density (452±782 ind m^{-2}). The density then increased gradually toward the shore (E4), where the greatest average density (2485±3026 ind m^{-2}) was found. Densities were significantly higher in March than in the other months.

The average biomass (±standard deviation) of the benthic invertebrate assemblage was 16.13±30.81 mg C m^{-2}. *C. patzcuaro* contributed the most to total biomass, with an average of 11.12±12.94 mg C m^{-2} (71%), whereas *Ch. austini* had an average value of 4.92±27.33 mg C·m^{-2} (29%). On the temporal scale, the greatest biomass value (65.22±95.85 mg C·m^{-2}) was recorded in April 2010, and the lowest (5.9±3.39 ind m^{-2}) was observed in October 2010 (Fig. 3). Macrobenthos made up 76% (47% *C. patzcuaro*, 29% *Ch. austini*) of the biomass, whereas meiobenthos comprised only 24% (23.9% *C. patzcuaro*, 0.1% *Ch. austini*).

Significant differences in biomass were also observed in space and time (X^2_r=47,707.14, P<0.05), with the value increasing toward the shore, with the lowest values at E1 (4.09±4.07 mg C m^{-2}) and the highest at E4 (40.93±52.76 mg C m^{-2}). Significantly higher biomass was observed in March than in the other months.

DISCUSSION

Species richness and density

The low taxonomic richness of benthic invertebrates recorded in the deep area of Lake Alchichica is in line with similar results obtained in other studies of tropical lakes that develop stratification and anoxic hypolimnia (Tudorancea and Harrison, 1988; Jiménez and Springer, 1996; Sibaja-Cordero and Umaña-Villalobos, 2008). The low taxonomic richness of the profundal zone of Alchichica is markedly different from the numerous and diverse assemblage of the lake's littoral benthic invertebrates, which is represented by 50 different taxa (Tab. 1), some of which are highly capable of migrating to the deep area.

The reduction of benthic taxa with increasing depth is a common pattern, particularly in lakes that stratify (eutrophic temperate and tropical lakes), and is associated with both habitat homogeneity (Newrkla and Wijegoonawardana, 1987; Cleto-Filho and Arcifa, 2006) and the thermal stratification that induces hypolimnetic oxygen deficits in the deeper parts of these lakes during the warmer months (McLachlan and McLachlan, 1971; Tudorancea and Harrison, 1988; Jiménez and Springer, 1996). This phenomenon is attributed to the rapid consumption of oxygen, which impedes species diversifica-

Tab. 2. Spatial distribution of benthic invertebrate taxa in the deep areas of Lake Alchichica.

mm/dd/yyyy	E1 (62 m)		E2 (61 m)		E3 (60 m)		E4 (50 m)	
	C. patzcuaro	*Ch. austini*	*C. patzcuaro*	*Ch. austini*	*C. patzcuaro*	*Ch. austini*	*C. patzcuaro*	*Ch. austini*
10/19/2009	X	-	X	-	X	-	X	-
11/16/2009	X	-	X	-	X	-	X	-
12/07/2009	X	-	X	-	X	-	X	-
01/05/2010	X	-	X	-	X	-	X	-
01/02/2010	X	-	X	-	X	-	X	X
03/01/2010	X	-	X	X	X	X	X	X
04/06/2010	X	X	X	-	X	X	X	X
05/04/2010	X	X	X	-	X	X	X	X
05/24/2010	X	-	X	X	X	-	X	X
06/29/2010	X	-	X	-	X	-	X	-
07/27/2010	X	-	X	-	X	-	X	-
08/24/2010	X	-	X	-	X	-	X	-
09/21/2010	X	-	X	-	X	-	X	-
10/19/2010	X	-	X	-	X	-	X	-
11/16/2010	X	-	X	-	X	-	X	-
12/13/2010	X	-	X	-	X	-	X	-

X, present; -, absent.

tion (Payne, 1986; Lewis, 1996). Thus, the small number of benthic taxa is attributed to the anoxia of the profundal zone (Jónasson, 1992; Kajak, 1977; Moore, 1981; Ohtaka *et al.*, 2006). Overcoming anoxia is difficult for most metazoans (Babler *et al.*, 2008), with the exception of a few species that are capable of tolerating anoxic conditions (Brodersen *et al.*, 2004; Hamburger *et al.*, 2000; Cleto-Filho and Arcifa, 2006).

The taxonomic groups that comprised the benthic invertebrate assemblage of the deep area of Lake Alchichica, namely, ostracods and chironomids, are frequently present in tropical lakes (Tudorancea and Harrison, 1988; Jiménez and Springer, 1996; Sibaja-Cordero and Umaña-Villalobos, 2008). In the case of the ostracods,

two taxa have been reported in the littoral area of Alchichica, of which only *C. patzcuaro* has been able to inhabit the deep area. Regarding chironomids, out of the 17 taxa present in the littoral zone, only *Ch. austini* (previously identified as *Ch. stigmaterus* by Alcocer *et al.*, 1993b, 1998) has been able to colonize the deep area of Alchichica during the oxygenated phase. Only a few species of chironomids, tubificid oligochaetes, ostracods, nematodes and copepods are found in the anoxic sediments of deep lakes (Strayer, 2009). Some authors (Ohtaka *et al.*, 2006) have attributed the disappearance of certain taxa that are considered *typical* for the deep areas of lakes to the prolonged hypolimnetic anoxia generated during the stratification period.
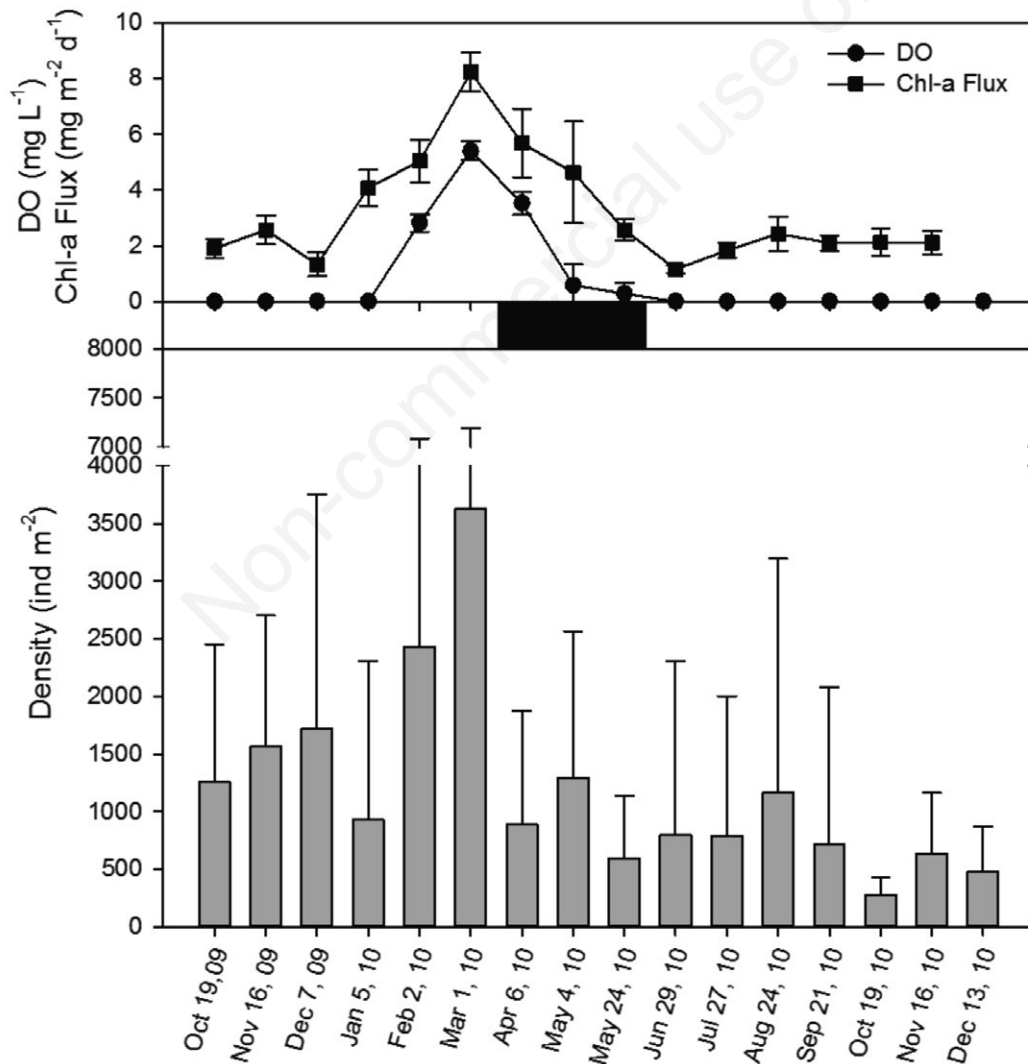

Fig. 2. Monthly average density±standard deviation of the benthic invertebrate assemblage and the variation of dissolved oxygen (DO) and chlorophyll *a* (Chl-a) fluxes in the deep areas of Lake Alchichica. The black bar in the DO graph indicates the massive emergence period of *Ch. austini*.

The lack of studies of the deep benthos of tropical lakes precludes general comparisons of the composition, density and biomass of benthic invertebrates. Only a few studies of this type have been conducted, most of them descriptive (Timms, 1979; McLachlan and McLachlan, 1971, Sibaja-Cordero and Umaña-Villalobos, 2008) while others considering only the shallow, littoral areas of deep lakes (Tudorancea and Harrison, 1988). However, the few studies conducted in deep tropical lakes show low densities of zoobenthos; this seems to be a common phenomenon of deep tropical lakes, a characteristic that is in sharp contrast to the high densities recorded in the northern deep temperate lakes (Atobatele and Ugwumba, 2010). For example, the average density (1504 ± 2522 ind m^{-2}) and bio-

mass (16.84 ± 30.95 mg C m^{-2}) of profundal benthic invertebrates in Lake Alchichica were low compared to the results of a similar study of the temperate and sub-arctic lakes Esrom, Mývatn and Thingvallavatn: the density and biomass in these lakes reached 200,000 ind·m^{-2} and 5.3 g C m^{-2}, respectively (Jónasson *et al.*, 1990). Moreover, the density (874,829 ind m^{-2}) and biomass (1745.6 mg C m^{-2}) of the zoobenthos of Alchichica's littoral area are 731 and 108 times higher, respectively, than the same variables in the deep zone of the lake (Alcocer, 1995; Hernández, 2001).

Density and biomass, but not species richness (which remained constant), exhibited a gradual decrease from the deep areas nearest the shore to the central and deepest area
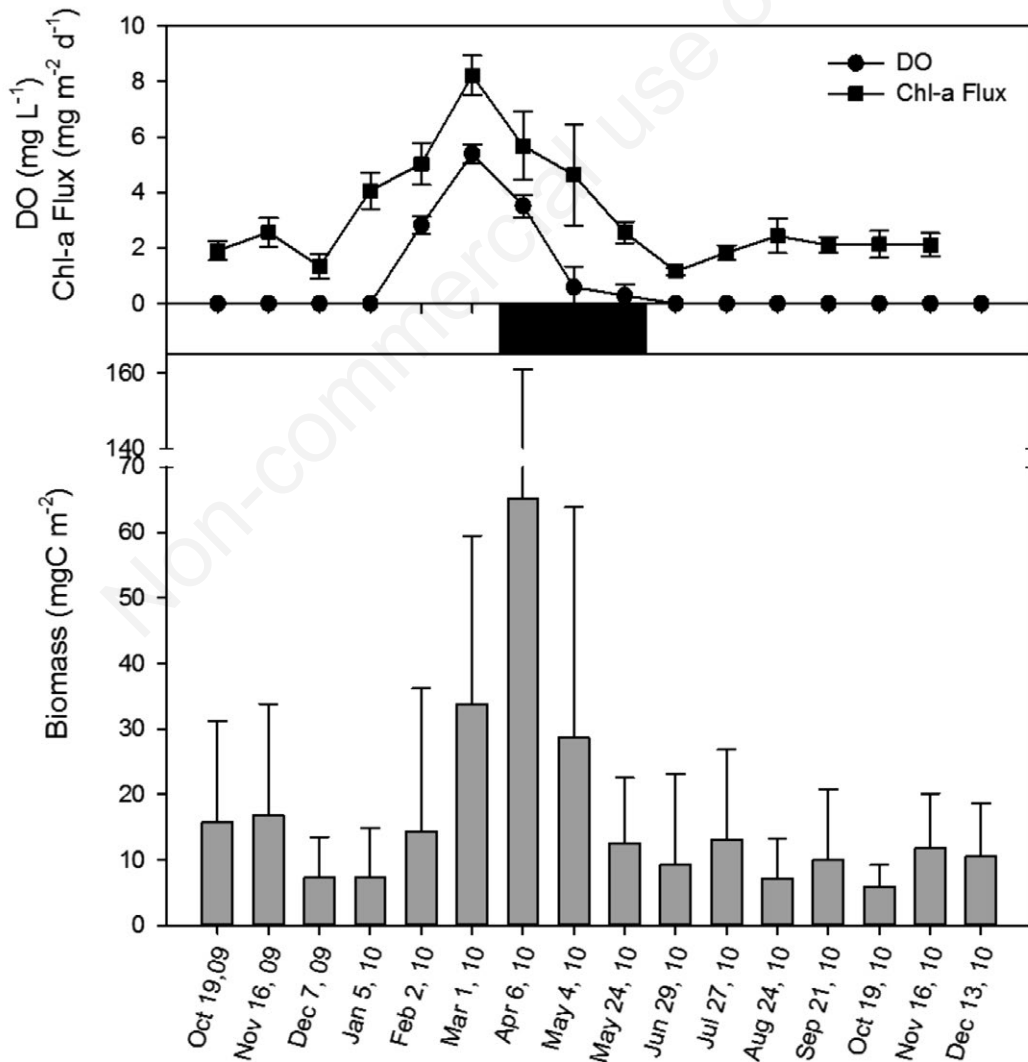

Fig. 3. Monthly average biomass±standard deviation of the benthic invertebrate assemblage and the variation of dissolved oxygen (DO) and chlorophyll *a* (Chl-a) fluxes in the deep areas of Lake Alchichica. The black bar in the DO graph indicates the massive emergence period of *Ch. austini*.

of the lake. This pattern most likely result from differing proximity to the littoral fringe, an area from which organisms can migrate. A similar pattern has been observed in several African tropical lakes (McLachlan and McLachlan, 1971), where the distribution of deep benthic fauna is strongly influenced by proximity to the coastline.

Role of food availability

Diatom blooms provide the main food source for the deep benthic communities of oligotrophic lakes (Jyväsjärvi *et al.*, 2013), in which the majority of the benthic fauna are detritus feeders (Pennak 1978). For example, *Chironomus* (Lathrop, 1992) is commonly abundant in areas of *high-quality* detritus (Jiménez and Springer, 1996). The largest diatom flux (304×10^6 cells m^{-2} day^{-1}) in Lake Alchichica occurs in February, soon after the onset of the diatom bloom (Ardiles *et al.*, 2012).

Unpublished data for Lake Alchichica (Alcocer *et al.*) show that higher Chl-a fluxes occur closer to the shore and diminish toward the center of the lake (*e.g.*, March: E4=6 mg Chl-a m^{-2} d^{-1}; E1=5 mg Chl-a m^{-2} d^{-1}). This evidence indicates that more high-quality food is available in the deep areas closer to the shore. Greater food availability helps to explain the higher zoobenthos densities and biomasses found closer to Alchichica's edge, particularly after the winter diatom bloom, when the highest zoobenthos numbers and biomasses were recorded.

Role of hydrogen sulfide

The low number of invertebrates in the central and deepest parts of Alchichica may be due not only to their intolerance to prolonged anoxic conditions but also to the presence of high concentrations of hydrogen sulfide (Alchichica 50 m=2.66 mg· H_2S L^{-1}, Alchichica 60 m=3.08 mg· H_2S L^{-1}); this gas is toxic or lethal to most invertebrates (Lathrop, 1992). The combination of anoxia and the presence of H_2S may limit the development and survival of the profundal benthos (Corbari *et al.*, 2005). Rieradevall and Prat (1991) reported anoxia and high concentrations of H_2S as responsible for the reduced presence of profundal benthos in Lake Banyoles, Spain. Strayer (2009) reported that the combination of these factors may well constitute the main reason for the distribution of benthic organisms along a depth gradient.

Adaptation to profundal life in Alchichica

To take advantage of Alchichica's deep benthic area, a nearly uninhabited habitat with a large amount of fresh food and virtually no competitors and predators, organisms must cope with the hostile environment (the hypolimnion) that develops as soon as the lake stratifies by becoming anoxic and rich in H_2S. The two species observed in this study have adopted different ecological approaches to respond to anoxia.

The ostracods are a poorly studied group, and little is known of their ecology and distribution in lakes (Cohen, 1995). Ostracods have been reported to colonize a variety of habitats (Nagorskaya and Keyser, 2005), including deep-lake areas (Griffiths *et al.*, 1993), and can tolerate low levels of DO (De Dekker, 2002). *C. patzcuaro* prefers sediments rich in organic matter and has a high capacity to adapt, and it exhibits broad tolerance to the adverse conditions present by deep-lake areas (Decrouy, 2009). Despite being a cosmopolitan species that is highly adaptable to a wide range of environmental conditions (Külköylüoğlu and Sari, 2012), this ostracod is considered highly sensitive to the presence of H_2S (toxic concentration=0.20 mg·L^{-1}) in epicontinental systems (Gamenick and Theede, 1996). *C. patzcuaro* has been able to survive in Alchichica by developing adaptive dormancy strategies (*e.g.*, entering diapause, forming resistant eggs, shortening its life cycle) that allow it to inhabit deep areas (Meisch, 2000) in response to environmental (mainly DO) changes. As a result, *C. patzcuaro* is found throughout the entire cycle of the lake's deep portion, entering into diapause during the anoxic period and recovering as soon as the lake's bottom reoxygenates to reproduce. Although *Chironomus* is a cosmopolitan genus, few *Chironomus* species have been reported to inhabit the deep areas of lakes (Lindegaard, 1995); instead, they show a preference for colonizing shallower depths, for example from 26 to 30 m in Lake Ikeda, Japan (Ohtaka *et al.*, 2006). However, each chironomid taxon presents markedly different responses to hypolimnetic oxygen conditions (Little and Smol, 2001). Several species of *Chironomus* have developed an anaerobic metabolism (Jónasson, 2004) and are capable of resisting low DO concentrations and tolerating high H_2S concentrations (Neumann *et al.*, 1994), whereas others simply *escape* the hypoxic or anoxic bottom conditions by emerging at opportune times. The latter response seems to be the case for the *Ch. austini* in Lake Alchichica, a species that is found only during the period when the lake bottom remains oxygenated and shows a massive emergence period at the onset of stratification (April-May) (Figs. 2 and 3). Other tropical lakes show a similar complete absence of chironomids in their deep areas in response to anoxia during the warm season of stratification (McLachlan and McLachlan, 1971; Tudorancea and Harrison, 1988).

The great mobility of chironomids enables them to recolonize sites suitable for larval development and to rebuild their numbers quickly (Atobatele and Ugwumba, 2010). The juvenile chironomids move to the deep zone in search of food when there is DO available, which occurs during the circulation period (Cleto-Filho and Arcifa, 2006). When the oxygen deficit occurs, the larvae move from the deep sediment to the shallows in preparation for

emergence (Añon, 1991). Thus, the distribution of benthic invertebrates in the profundal zone of Alchichica seems to be primarily limited by the presence of DO; however, food availability also plays an important role. The highest numbers and biomasses of the benthic invertebrate community coincide with the peak of the Chl-a flux, which represents an abundance of high-quality, fresh food resources (*i.e.*, diatoms) for these organisms. *C. patzcuaro* and *Ch. austini* colonize the deep benthic area of Alchichica using different ecological strategies. *Ch. austini* has adjusted its life cycle to use the habitat and resources available during the mixing (well-oxygenated) period of the lake. In contrast, *C. patzcuaro* remains throughout the year in the deep sediments of the lake by entering diapause in the juvenile stage. Ecologically, deep benthic organisms are capable of settling throughout a

wide variety of aquatic habitats (Külköylüoğlu and Sari, 2012), exhibiting low extinction rates (Cohen and Johnston, 1987) and increasing persistence over time.

Comparative limnology

The tropical Lake Alchichica can be compared with the temperate Lake Mergozzo, as the two are very similar in a number of respects (morphology, oligotrophy and a warm monomictic pattern) (Bonacina *et al.*, 1992; Marziali *et al.*, 2008 Rossaro *et al.*, 2006; Bonomi and Ruggiu, 1966 and Nocentini, 1966; both in Ruggiu and Saraceni, 1972). However, Alchichica is tropical, with a summer period of anoxia, whereas the hypolimnion of Mergozzo remains oxygenated during stratification (Tab. 3). Data from Ruggiu and Saraceni (1972) indicate that at similar depths as those stud-

Tab. 3. Comparative data from the tropical Lake Alchichica (2009-2010) and the temperate Lake Mergozzo (1963-64).

	Alchichica (Mexico)	Mergozzo (Italy)
Latitude	19º 24' N	45º 57' N
Longitude	97º 24' W	8º 28' E
Mean altitude (m asl)	2350	194
Maximum length (km)	1.8	1.8
Maximum width (km)	1.5	1.1
Surface area (km²)	2.3	1.81
Maximum depth (m)	62	73
Mean depth (m)	40.9	45.4
Water volume (m³)	94.2 x 10⁶	82.9 x 10⁶
Shore length (km)	5.1	6.2
Mixing type	Warm-monomictic Holomictic	Warm-monomictic Holomictic
Deep zone (≥50 m) characteristics		
Depth range (m)	50-62	50-73
Bottom temperature (ºC)	14.2-14.5	3.7-4.6
Bottom minimum DO (% saturation)	0	24
Anoxic period span (months)	8	0
Macrobenthic species richness	2	13
Average density (ind m⁻²)	287*	1145
Biodiversity:		
Oligochaeta	---	*Potamothrix hammoniensis* *Tubifex tubifex* *Peloscolex ferox* *Stylodrilus lemani* *S. heringianus* *Bichaeta sanguinea*
Chironomids	*Chironomus austini*	*Chironomus gr. anthracinus* *Tanytarsus gr. inermipes-gregarius* *Prodiamesa olivacea* Pentaneurinae
Bivalves	---	*Pisidium personatum* *P. conventus* *P. casertanum*
Ostracods	*Candona patzcuaro*	---

*Only the macrobenthos were considered for comparative purposes; see the text for further explanation. Lake Mergozzo data from Bonacina et al., 1992; Marziali et al., 2008; Rossaro et al., 2006; Bonomi and Ruggiu, 1966; and Nocentini, 1966; the latter two studies appeared in Ruggiu and Saraceni, 1972).

ied in Lake Alchichica (≥50 m), Lake Mergozzo was inhabited by 13 species, two of them (*Stylodrilus heringianus* and a member of the Pentaneurinae) at their lower depth limit of distribution; in contrast, Alchichica supports only two species. The density of macrobenthos in Alchichica (287 ind m^{-2}) resulted roughly one fourth that of Mergozzo (1,145 ind m^{-2}). As noted above, the macrobenthos abundance in Lake Alchichica constitutes only 24% of the total, whereas the meiobenthos constitute the remaining 76%. The dominant groups in Mergozzo were the Oligochaeta, the Chironomidae and the bivalve *Pisidium*; in Alchichica, the Ostracoda were dominant. The tropical maar Lakes Barrine and Eacham in northern Australia (Timms, 1979) are also similar to Lake Alchichica but are smaller in size (1.035 and 0.503 km^2, respectively). Both lakes display roughly 20 benthic species overall, but just one (*Chaoborus* sp.) is found in their profundal zones (>35 m), and this species is found at low densities (Barrine 11 ind m^{-2}, Eacham 89-189 ind m^{-2}) and biomasses (Barrine 0.02 g m^{-2}, Eacham 0.11-0.27 g m^{-2}). Although Timms (1979) provides no explanation for the rather low species diversity, density and biomass in the profundal zones of Lakes Barrine and Eacham, the low food availability (*i.e.*, both lakes are oligotrophic) and the hypolimnetic anoxia developed during the long stratification period are likely causes.

From the above discussion, it seems reasonable that our findings can be extrapolated to the numerous tropical deep maar lakes with steep bathymetry that are found in tropical volcanic regions, such as Lake Monoun in Cameroon (http://mhalb.pagesperso-orange.fr/nyos/2006/06bathymetry_monoun.html), Lake Guatavita in Colombia (Rivera Rondón *et al.*, 2010), Caliente Lake in Costa Rica (Tassi *et al.*, 2009) and Lake Loreto in Equatorial Guinea (Schabetsberger *et al.*, 2004), as well as those lakes along the Trans-Mexican Volcanic Belt in Mexico [Lake Santa María del Oro in Nayarit (Serrano *et al.*, 2002); Lakes Atexcac, Quechulac, La Preciosa and Aljojuca in Puebla (Arredondo-Figueroa *et al.*, 1983); and Lakes Majahual, Chalchopan and Manantiales in Veracruz (Vázquez *et al.*, 2004)].

CONCLUSIONS

The deep benthic fauna of Alchichica is favored during the lake's mixing period, when the deep area presents favorable conditions (the presence of DO and fresh, abundant food). However, the community is severely affected by the rapid onset of a lengthy period of anoxia and the presence of high H$_2$S concentrations, both of which are generated as soon as the lake stratifies as a result of the remineralization of the settled organic matter (*i.e.*, mostly the winter diatom bloom). These characteristics result in a highly simplified community structure consisting of two species (the ostracod *Candona patzcuaro* and the chironomid *Chironomus austini*) at low density (1197±1976 ind m^{-2}) and biomass (16.13±30.81 mg C m^{-2}). Areas closer to the shoreline have higher deep benthos density and biomass but not species richness. The chironomid adjusts its life cycle to be condensed into the well-oxygenated period (February-May) and emerges as soon as anoxia begins; the ostracod survives throughout the year by entering diapause in its larval stage and reproducing during the lake's oxygenated period.

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