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ORIGINAL ARTICLE

Physicochemistry and zooplankton of two karstic sinkholes in the Yucatan Peninsula, Mexico

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ABSTRACT

*The planktonic communities composed of rotifers and crustaceans of two tropical karstic lakes in the Yucatan Peninsula, Mexico, with similar origin but different trophic state were analyzed. Both systems, the meso-eutrophic (El Padre) and oligotrophic (Minicenote) were considered as monomictic lakes. The abundance, temporal distribution of species, richness and diversity were measured and discussed in relation to the influence of abiotic factors and the presence of a natural predator. These analyses indicated that these tropical systems were not homogenous for several of these measures at both spatial scales and during the annual cycle analyzed, despite their reduced temperature variation compared to temperate lakes. The results indicated that the dynamics in the zooplankton community were related to the environmental factors, the opportunistic species (with maximum densities related to resource maxima), and the exploitative competition between the dominant herbivorous species. Independently of the trophic condition, the abundance, richness, and diversity were lower during the mixing period. During the annual cycle studied in the meso-eutrophic system, the key environmental parameters related to plankton abundance were pH and temperature whereas in the oligotrophic system, oxygen concentration was important. In both lakes, richness and diversity were related to conductivity, although in the oligotrophic lake the relation was negative whereas in the meso-eutrophic lake it was positive. No relationship was found between the abundance of the studied predator (*Chaoborus *sp.) and the changes in the abundance, diversity and richness of zooplankton in the systems.*

*Key words: Sinkholes, chlorophyll-*a*, zooplankton, tropical, abundance.*

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INTRODUCTION

Some measures of diversity of the freshwater zooplankton communities, *e.g.*, their abundance, richness, diversity, and vertical distribution, has been explained by abiotic and biotic factors such as nutrient limitation, temperature, ultraviolet radiation, food availability, and predation avoidance, in temperate and tropical aquatic systems (Williamson *et al.*, 1996; Plath and Boersma 2001; Winder *et al.,* 2004). In tropical systems, physical and chemical variables are quite similar in different seasons; additionally, the notion that low variability of water temperature in tropical regions favors environmental stability in freshwater systems is widely accepted (Lewis, 1996). However, the processes related to zooplankton abundances and its possible natural variability in tropical (Lugo, 2000) and subtropical systems (Mazumder and Havens, 1998) are not well understood.

The variation in abundance, biomass (Torres-Orozco and Zanatta, 1998), communities (Deevey *et al.,* 1980; Haberyan *et al.,* 1995), and vertical distribution (Cervantes-Martínez *et al.,* 2005) of zooplankton in tropical systems during annual cycles has been described. However, the causes of these changes remain vague (Crisman and Streever, 1996). Similarly the zooplankton communities in small, tropical lakes (such as the sinkholes of the Yucatan Peninsula) and the factors related to their dynamics, have received limited attention (Lewis, 1990; Crisman and Streever, 1996).

Based on samples collected in two distinct sinkholes, we described the influence of abiotic and biotic variables on the abundance, richness, and diversity of limnetic zooplankton in one oligotrophic and one mesotrophic karstic lake (sinkholes). We considered one annual cycle and spatial scales (related to different depth layers in the sinkholes) to test the hypothesis that seasonal changes in environmental factors and predator abundance influence succession of zooplankton species in these tropical systems.

METHODS

Study site

Physical, chemical, and biological samples were taken at monthly intervals from June 2003 to May 2004 from the limnetic zone of two natural karstic lakes: El Padre (EP) and Minicenote (MC), in the Yucatan Peninsula, Mexico (19° 36’ 23” N; 87° 59’ 18” W). The surveyed sinkholes originated due to dissolution of the carbonate rock [*i.e.*, dissolution lakes *sensu* Hutchinson (1957), Roldán-Pérez and Ramírez-Restrepo (2008)] in the karstic platform of Quintana Roo. Quintana Roo is considered a young karst region without superficial currents, probably developed during the Eocene tectonic events in the Caribbean (Perry *et al.,* 2002). The elevation of the Yucatan Peninsula is about ten meters above sea level on average, and it has a mean precipitation of 172,158 x 10^6 m^3 per year (Schmitter-Soto *et al.,* 2002).

The main morphometric features of EP and MC are described in Tab. 1. Thermal stratification was recorded in both systems, and, based on the three tropical climatic seasons, three periods were defined: June to October=rainy, November to February=winter storm; and March to May=dry season (Schmitter-Soto *et al.,* 2002).

Sampling

In EP samples were analysed from strata at 0.5, 2.5, 5, 10, and 15 m, whereas in MC the strata were 0.5, 5, 10, 15, 20, and 30 m. Duplicates were collected for all samples (n_{EP}=120; n_{MC}=144). Sampling was performed at night, during the new moon phase of the lunar cycle to reduce the effect of visual predation by fish on the zooplankton distribution (Lampert and Sommer, 2007), and limiting the primary carnivore level almost entirely to the phantom midge larvae *Chaoborus* sp.

Environmental samples

In a profile of the water column, water temperature, dissolved oxygen, conductivity and pH were measured *in situ* with a multiparametric probe Horiba-U10. Chlorophyll-*a* was measured by spectrophotometry (APHA, 1996) and is an indicator of the trophic state (OCDE, 1982) and algal biomass (Lewis, 1990).

Zooplankton samples

Duplicate 5 L water samples taken with a van Dorn bottle from each layer were filtered through a 50 µm net. Abundance of adults of each zooplankton species and each developmental instar of *Chaoborus* sp. (organism L^{-1}; org. L^{-1}) was estimated based on total counts (Lewis, 1979) performed with an Eclipse E-400 compound microscope. Diversity was calculated monthly at each layer of both lakes, using the Shannon Index (Shannon and Weaver, 1949):

$$H'=-\Sigma pi \ln pi$$

The monthly averages of environmental factors, abundance, richness, and zooplankton diversity were analyzed. *Chaoborus* sp. was excluded in the richness and Shannon calculations.

Tab. 1. Main morphometric features of El Padre and Minicenote (Cervantes-Martínez *et al.*, 2002).

	El Padre	Minicenote
Maximum depth (m)	15	47
Mean depth (m)	8.7	16.7
Maximum length (m)	111.5	18.5
Maximum width (m)	108.4	15.6
Shoreline (m)	339.8	54.8
Volume (m^3)	79,856.3	4419.8
Area (m^2)	9100	264

Data analysis

Two-way ANOVA was performed to investigate the effect of season, strata, and their interaction on environmental factors, and on zooplankton abundance, richness, and diversity, followed by a Tukey *post hoc* multiple comparison test. Statgraphics v. 10.0 was used for the analysis. The transformation y'_i=log (y_i+1.1) was satisfactory to normalize the data.

The relationship between *Chaoborus* sp., the environmental parameters and the zooplankton richness, diversity and abundance; were examined with a canonical correspondence analysis CCA. A Principal Coordinate Analysis (PCoA) was applied to analyze community composition, considering the abundance of each species during the annual cycle in both systems (number of observations in EP=60 and MC=72). The CCA and PCoA were performed with the Statistical Package MVSP 3.21.

RESULTS

During the annual cycle a total of 23 and 19 zooplankton species were identified in EP and in MC, respectively (Supplementary Tab. 1). *Anuraeopsis fissa* (Gosse, 1851), *Dipleuchlanis propatula* (Gosse, 1886), *Macrochaetus collinsi* (Gosse, 1867), *Colurella uncinata* cf. *bicuspidata* (Ehrenberg, 1832), *Lepadella heterostyla* (Murria, 1913), *Lecane aculeata* (Jakubski, 1912) and *L. signifera* (Jennings, 1896) were recorded only in EP; whereas *L. patella* (O.F. Müller, 1773), *Dissotrocha aculeata* (Ehrenberg, 1832), and *Latonopsis australis* (Sars, 1888) were recorded only in MC.

Spatial and temporal dynamics

Physical and chemical variables: two-way ANOVA showed that water temperature and dissolved oxygen were statistically different between the surveyed seasons and layers in EP and MC (Supplementary Tab. 2). During stratification, the difference in water temperature along the water column exceeded 1°C; therefore, both EP and MC were considered monomictic lakes, with one annual mixing during the winter storm season (Fig. 1 A,D) when the water column temperature is approximately at 24°C in EP and 25°C in MC.

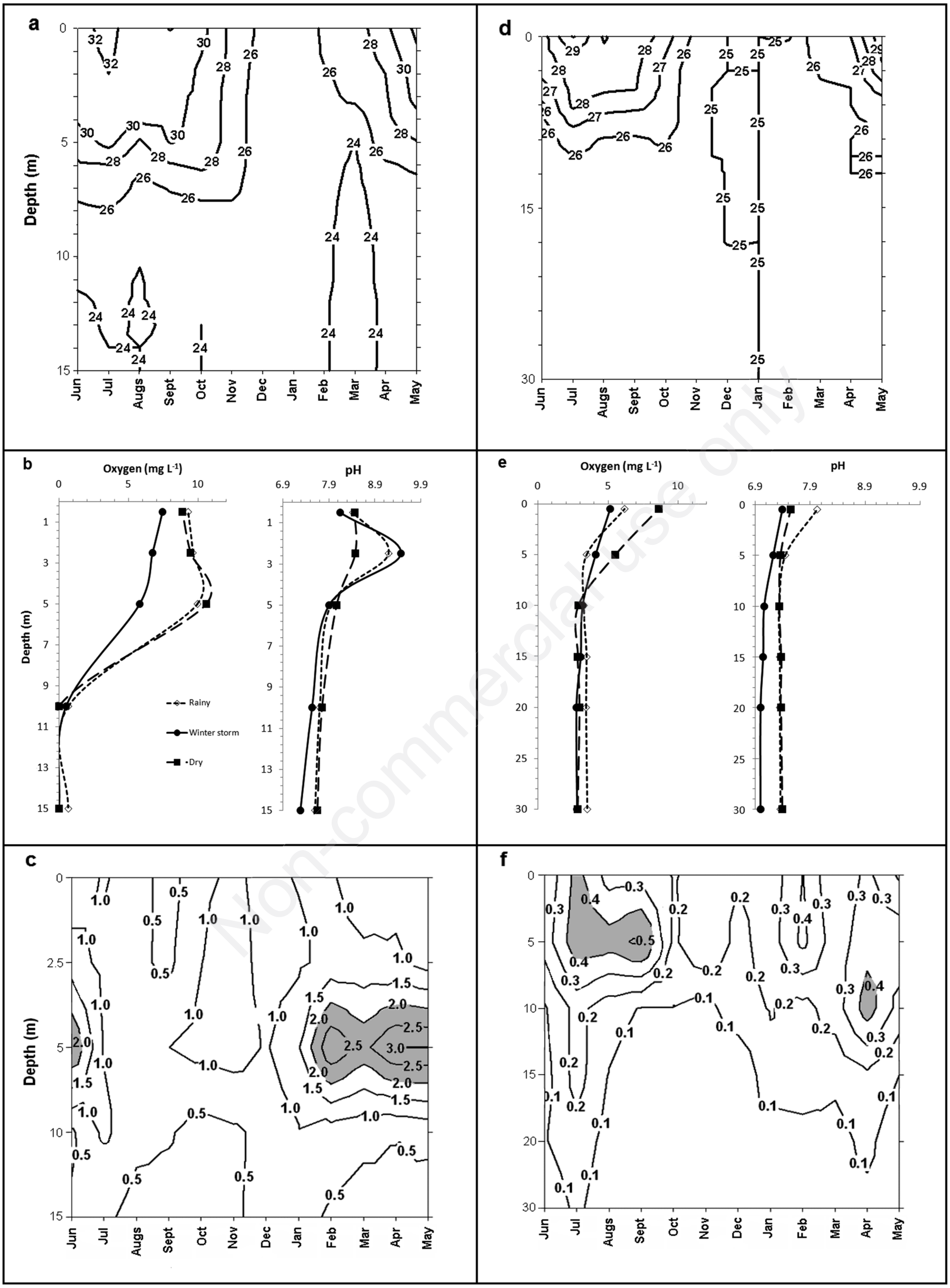

Fig. 1. Change in environmental variables in different layers; panels a-c refer to El Padre, panels d-f refer to Minicenote. a,d) Contour plots of water temperature. b,e) Vertical profiles of dissolved oxygen and pH as a function of climatic seasons. c,f) Contour plots of chlorophyll-a concentration; in (c) the chlorophyll-*a* concentration ≥2 mg m^{-3} is shaded; in (f) concentration over 0.4 mg m^{-3} is shaded.

In EP, the average oxygen concentration ranged from 5.8 to 10.6 mg L^{-1} in the 0.5 to 5 m layers, whereas at depths of 10 and 15 m the concentration ranged from 0 to 0.7 mg L^{-1} (Fig. 1B). In EP the oxygen concentration in the upper layers was statistically different from the deeper layers, and the oxygen concentration in the winter storm season was statistically different from the rainy and dry seasons (Supplementary Tab. 2). In the upper layers of MC, the oxygen concentration ranged from 2.9 to 8.6 mg L^{-1} on average in both the dry and rainy seasons (Fig. 1E), but at depths of 15 to 30 m this concentration ranged from 2.8 to 3.5 mg L^{-1}, on average (Fig. 1E). The oxygen concentration during the dry season was different to the winter and rainy seasons in MC, and the oxygen concentration recorded in the 0.5 m layer was different from that in other layers (Supplementary Tab. 2). Neutral and acidic values in pH were recorded at shallow depths in the winter storm season, as well as in deeper layers in both sinkholes. The lakes showed neutral or basic values during both rainy and dry seasons at 0.5 to 5 m (Fig. 1B,E). This variability was statistically different between seasons and layers (Supplementary Tab. 2).

The chlorophyll-*a* concentration was higher in EP than in MC (Fig. 1 C,F). In EP the chlorophyll-*a* concentration reached its maximum in the dry season (Fig. 1C), but was only statistically different to the rainy season (Supplementary Tab. 2). In MC the chlorophyll-*a* concentration in the upper layers was statistically different from the deeper layers, and the chlorophyll-*a* concentration in the dry season was statistically different from the rainy and winter storm seasons (Supplementary Tab. 2). When both lakes were thermally stratified, the chlorophyll-*a* concentration was higher in the metalimnion than in the hypolimnion (Fig. 1 C,F). In both lakes, a higher concentration of chlorophyll-*a* was found in the period from March to May (1.14±0.092 mg m^{-3} in EP; and 0.20±014 mg m^{-3} in MC) than in other months. Conductivity was similar between seasons in both systems (Fig. 2 A,D) but statistically different (lower) at the upper layers (Supplementary Tab. 2).

Biological variables

A high variability of zooplankton abundance, diversity, and richness was observed in both lakes. In EP the rotifers had the highest abundance (Fig. 3A), but in MC copepods were the most abundant zooplankton (Fig. 3 H,I). The abundance of *Chaoborus* sp. in EP (Fig. 3E) was five times higher than in MC (Fig. 3J).

The change of the abundance of Cyclopoida in MC between seasons was statistically significant (Supplementary Tab. 2), the highest abundance was found in the rainy season at the 0.5-5 m layers (Fig. 3H). In both lakes, higher abundances of rotifers, cladocerans, cyclopoids, and calanoids were found in the upper layers (0.5-5 m) (Fig. 3). In both systems significant differences were found in the abundance of the dominant zooplankton fraction (*i.e.,* rotifers in EP and calanoids in MC), diversity, and richness between seasons. In MC no differences were found in the Shannon index between strata (Supplementary Tab. 2).

The highest diversity index was recorded during the rainy season in EP (H'_{range}=0.12-0.78; $H'_{average}$=0.48), and the lowest during the winter storm and dry seasons (H'_{range}=0.09-0.65; $H'_{average}$=0.35) (Fig. 2B). In MC the H' ranged from 0 to 0.76 during the annual cycle in the surveyed strata (Fig. 2E). In both lakes the richness was significantly lower in the winter storm season ($S_{average}$=7.7±2.1 species in EP; and $S_{average=}$6.1±1.7 species in MC) than in the rainy and dry seasons (Supplementary Tab. 2); in all seasons, the surface layers showed the highest richness in the surveyed systems (Fig. 2 C,F).

Zooplankton community dynamics

In the PCoA biplot the species were grouped along a gradient from low to high abundance in the analyzed annual cycle. Axis 1+2 explained 55.6% of variability in EP (Fig. 4A), and up to 52.7% in MC (Fig. 4B). Five groups were found in each case. In EP groups 1 and 2 (Fig. 4A) are comprised of species that were spatially restricted to intermediate layers during the annual cycle [*i.e. C. uncinata* cf. *bicuspidata*, *Keratella lenzi* (Hauer, 1953), *L. lunaris* (Ehrenberg, 1836), and *Mastigodiaptomus nesus* Bowman, 1986] or species restricted to the dry season, for example *Trichocerca weberi* (Jennings, 1903), or to the rainy season, for example *Brachionus falcatus* Zacharias, 1898, with a maximum abundance of around 5 org. L^{-1}. Group 3 encompasses species that were recorded only in one or two layers of the water column during the dry season as *L. aculeata*, *L. bulla* (Gosse, 1851), *P. patulus* (O.F. Müller), *L. hornemanni* (Ehrenberg, 1832), and *A. fissa*; during the rainy season as *L. heterostyla* and *L. leontina* (Turner, 1892) and during winter storms as *L. signifera* or *L. halyclista* Harring & Myers, 1926 with abundance lower than 1.5 org. L^{-1}. Species in the fourth group showed low abundance during the rainy season and maximum abundance in the dry season [*Tropocyclops prasinus* cf. *aztequei* Lindberg, 1955, and *Hexarthra intermedia* f. *braziliensis* (Hauer, 1953)] or maximum abundance in the winter storm season as *Bosmina hagmanni* Stingelin, 1904, with abundance ranging from 2.4 to 88.8 org. L^{-1}. The most abundant and frequent species recorded in EP (group 5 in Fig. 4A) occurred in the entire water column and in all water samples during the annual cycle, with abundance ranging from 21.3 org. L^{-1} for *T. inversus* Kiefer, 1936 to 1082.8 org L^{-1} for *K. americana* Garlin, 1943.

The gradient in abundance (showing species with low, intermediate, and high abundance) described before in EP was similar in MC, but the community composition was different. In MC the species with low abundance were *L. halyclista*, *T. prasinus* cf. *aztequei*, *K. lenzi*, *L. lunaris*, *P. patulus*, *T. weberi*, and *B. falcatus*, ranging from 0.3 to 27.8 org. L^{-1} (groups 1 and 2 in Fig. 4B).

The species of group 3 (Fig. 4B) were incidental species with abundance ranging from 0.1 to 1.7 org. L^{-1} as *L. leontina*, *L. patella*, *L. autralis*, *L. bulla*, *L. hornemanni*, and *D. aculeata*. Species of group 4 (Fig. 4B) including *K. americana* and *Brachionus havanaensis* Rousselet, 1911 showed maximum abundance during one or two seasons: the maximum abundance of *K. americana* was recorded in the dry season (17.75 org. L^{-1}), and it was

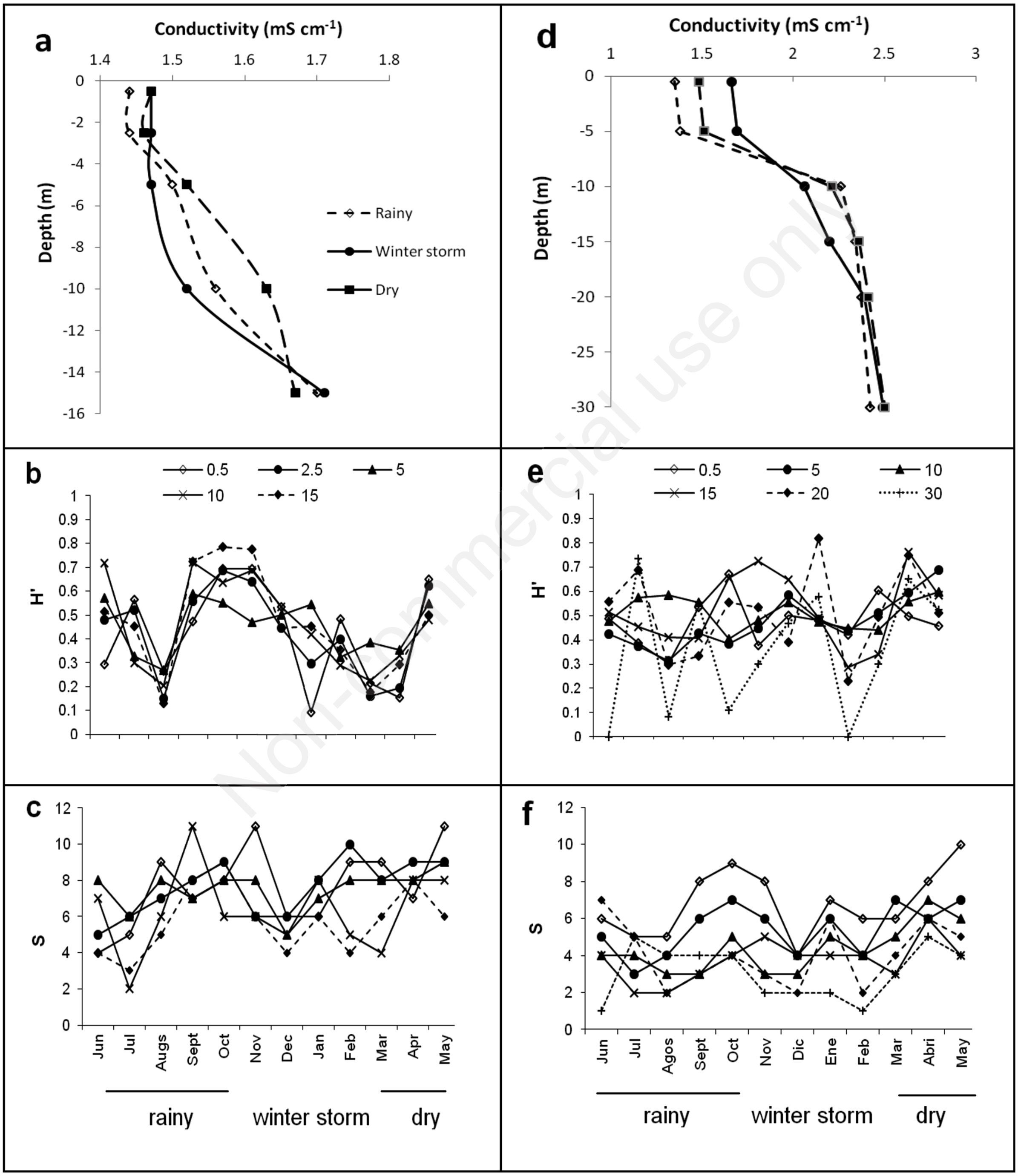

Fig. 2. Seasonal change in physical and biological variables; panels a-c refer to El Padre, panels d-f refer to Minicenote a,d) Vertical profiles of conductivity as a function of climatic seasons. b,e) Monthly changes in zooplankton diversity (H') as a function of depth. c,f) Monthly changes in zooplankton richness (S) as a function of depth. Arabic numbers represent the sampled depths in b, c, e, and f.

absent in the rainy season; *B. havanaensis* showed a maximum abundance of 14.2 org. L^{-1}, and this species was restricted to the rainy and dry seasons.

Group 5 encompasses the most abundant species in MC, recorded almost throughout the entire water column and in all of the samples. These were *Thermocyclops inversus* and *M. nesus*, with abundance ranging from 90 to 95.62 org. L^{-1} (Fig. 4B). Only *T. inversus* was one of the most abundant species in both lakes.

Biological, physical, and chemical relationships in CCA

In CCA of the zooplankton abundance and indicators of biodiversity of EP, the first and second canonical axes accounted for 58.6 and 31.6% of variability, respectively (Tab. 2, Fig. 5A). The first axes discriminated the zooplankton abundances of rotifers, cladocerans and copepods; the variables that best correlated with axis 1 were pH and water temperature (Tab. 2). The second axis discriminated the richness and diversity; this second axis was best correlated to conductivity and oxygen concentration (Tab. 2).

In MC the first canonical axis explained 73.1% of the cumulative variance, and the second 21.5% (Tab. 2, Fig. 5B). The first axis discriminated indicators of biodiversity, the variables that best correlated with the CCA axis 1 were: conductivity, chlorophyll-*a*, and water temperature (Tab. 2). The zooplankton abundances of each group were discriminated in the second axis, the variable that best correlated with the CCA axis 2 was oxygen concentration (Tab. 2).

DISCUSSION

Spatial and temporal dynamics

Our results support the hypothesis that tropical, freshwater, aquatic systems are not homogeneous spatially during the annual cycle despite the low water temperature oscillations of these systems. Changes are related to the mixing and stratification periods: during circulation the water column is unstable, leading to a lack of nutrient intake in the euphotic zone in tropical meso-eutrophic, monomictic lakes (Lewis, 1990). Eventually, these phenomena can be linked to lower chlorophyll-*a* concentration during mixing, when the lower water temperature and strong north winds occur in the humid tropics (Lewis, 1979; Schmitter-Soto *et al.,* 2002). In the study region, other shallow, low surface lakes have also been recorded as monomictic (Alcocer *et al.,* 2000).

High values of algal biomass have been related to the increase of oxygen concentration in tropical systems (Flores-Nava, 1994; Lugo, 2000; González *et al.,* 2004). During this survey high chlorophyll-*a* and high oxygen concentration occurred during the dry and rainy seasons when the lakes were thermally stratified. This indicates that the onset of the photosynthetic activity occurred during the dry season because of favourable growth conditions linked to water temperature and nutrient availability. A higher photosynthetic rate during stratification was indicated by the local change from neutral or acidic to alkaline pH and/or by the alkaline conditions in the strata with higher chlorophyll-*a* concentration. El Padre was anoxic below the 10 m strata, with a positive heterograde profile during stratification or clinograde profile during mixing. The positive heterograde profile (Fig. 1B) is usually the result of elevated algal photosynthesis in the metalimnion (Kalff, 2002). Minicenote was well oxygenated throughout the water column. The oxygen concentration was found to be highest in the upper layer and was almost constant at depths of 10 to 30 m throughout the year. Differences in the pH between both systems (slightly more acidic in MC than in EP) can be related to the trophic

Tab. 2. Summary statistics for canonical correspondence analysis between environmental variables (abundance of *Chaoborus* sp. and environmental parameters) and site scores (zooplankton richness, diversity and abundance of rotifers, cladocerans, cyclopoids, and calanoids).

	El Padre		Minicenote	
	Axis 1	Axis 2	Axis 1	Axis 2
Eigenvalue	0.06	0.03	0.08	0.02
Site scores-environmental variables correlations	0.74	0.74	0.85	0.50
Cumulative percentage variation explained by site scores-environmental variables	58.63	90.22	73.18	94.74
Intersect correlations between environmental variables and site scores				
Chlorophyll-a	0.05	-0.34	0.68	0.12
Water temperature	0.24	-0.50	0.51	-0.09
Oxygen concentration	0.07	-0.65	-0.41	-0.38
pH	0.52	-0.47	0.36	-0.01
Conductivity	0.18	0.66	-0.79	0.11
Abundance of *Chaoborus* sp.	0.04	-0.39	0.17	0.09

Significance set at $P<0.05$.

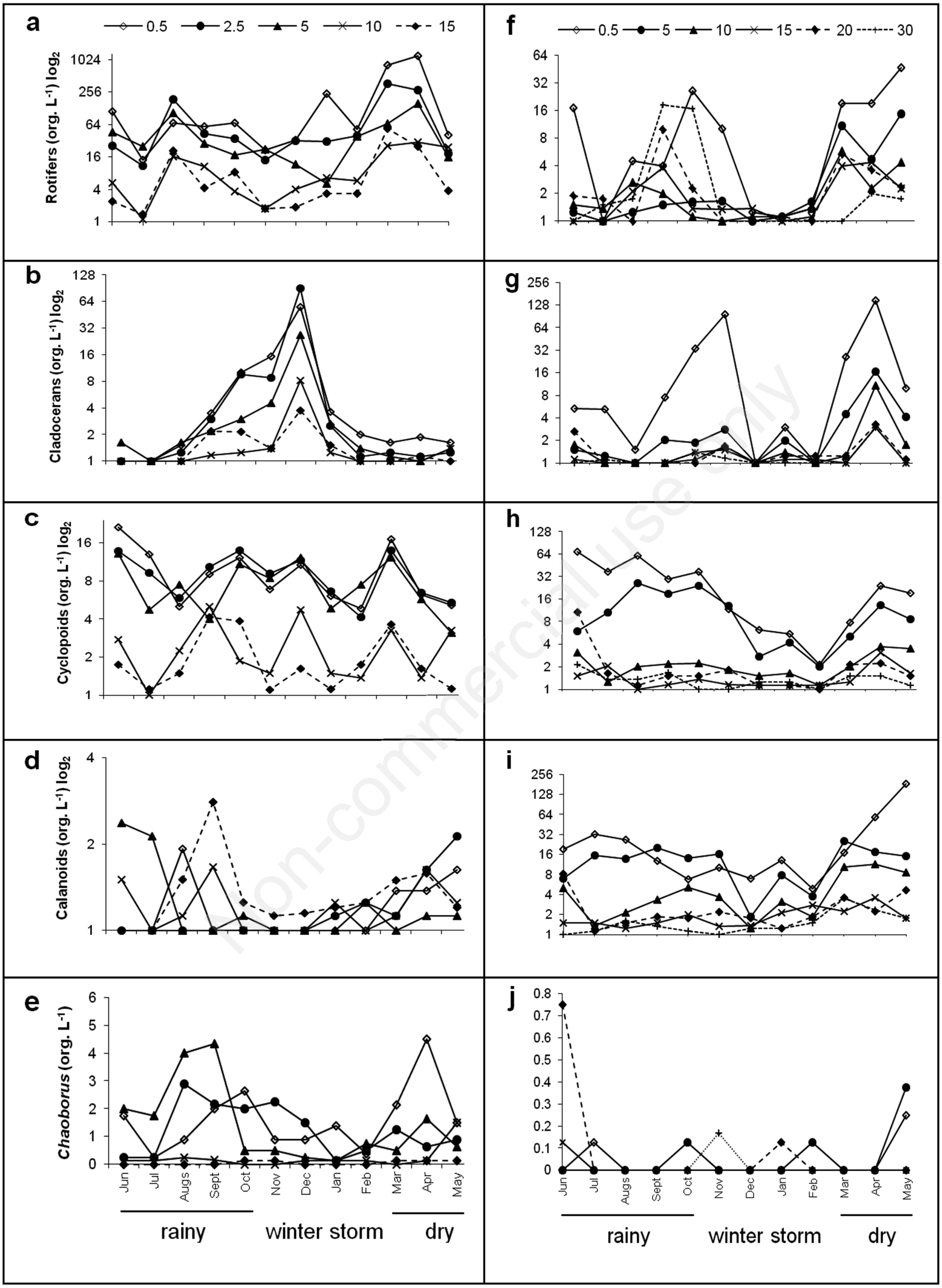

Fig. 3. Monthly changes in zooplankton abundances as a function of depth in El Padre (a-e) and Minicenote (f-j). Note the different scaling of the *y*-axis in the rows, and the $\log_2$ scale for the abundance of rotifers, cladocerans, cyclopoids, and calanoids (only adults). Last row represents the abundance of the midge larvae *Chaoborus* sp. Sampled depths in Arabic numbers.

state: freshwater mature systems are more alkaline than the younger systems (Schmitter-Soto *et al.,* 2002). Therefore, based on the chlorophyll-*a* concentration (Margalef, 1983), differences in pH and oxygen concentration EP can be considered a meso-eutrophic system whereas MC is an oligotrophic system. In tropical systems the zooplankton abundance, biomass, and richness are adversely affected by the onset of seasonal circulation (Lewis, 1979), when these measures decline (Lewis, 1990; López-López and Serna-Hernández, 1999). In EP the low richness during the seasonal circulation leads to the significant diminishing in the diversity index; whereas in MC the circulation

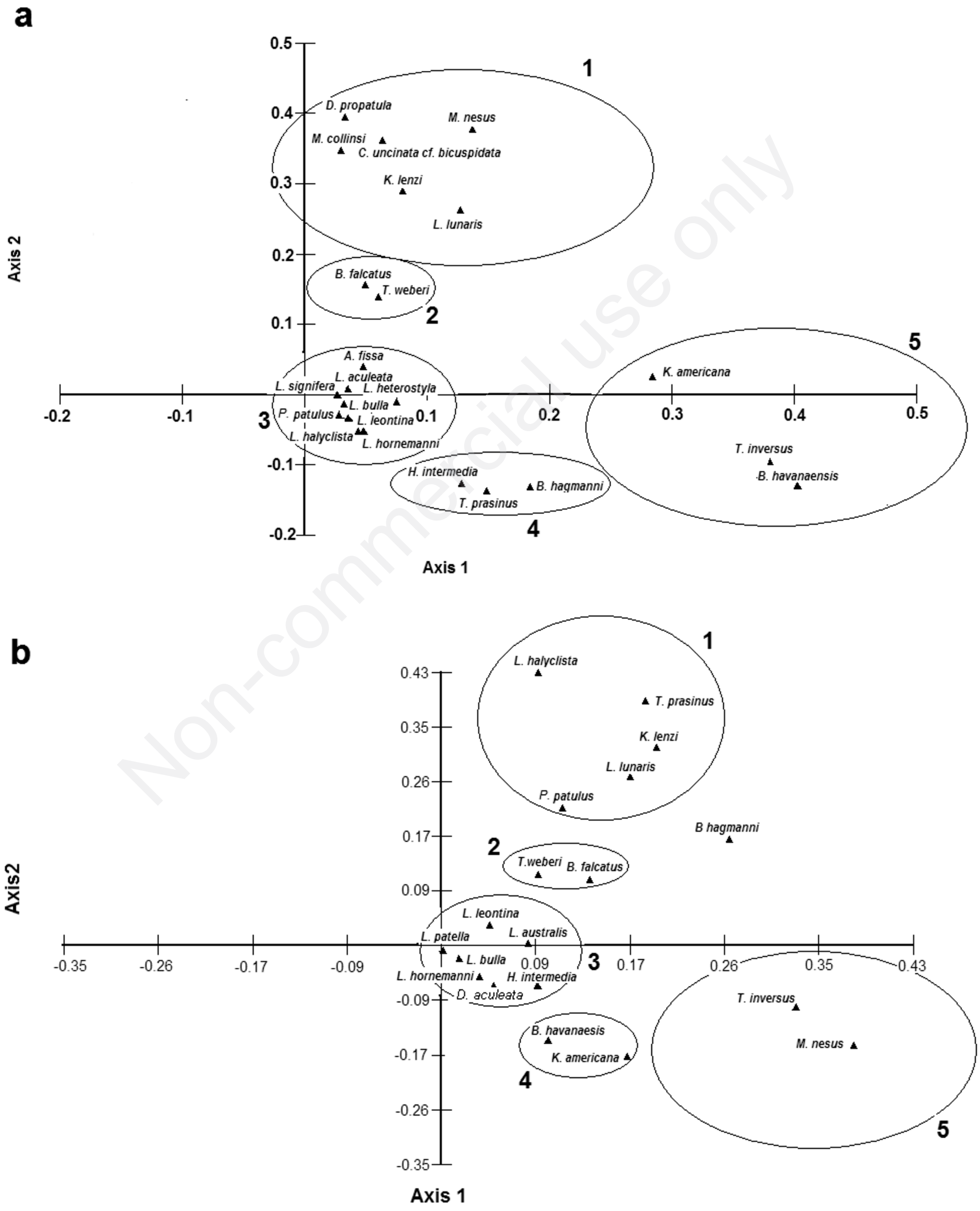

Fig. 4. PCoA biplot of the zooplankton community in El Padre (a) and Minicenote (b). The numbers indicate the grouping of species (see results).

does not affect the diversity index even with both the lower abundances and richness recorded.

Previous research has shown a temporal concordance between the decrease in the water temperature in tropical systems during either the mixing period (Lewis, 1979; López-López and Serna-Hernández, 1999) or the recycling of nutrients in the same season (Lewis, 1990) and the lower abundance of rotifers, cyclopoids and calanoids.

Zooplankton community dynamics

The limnetic richness recorded here was similar to records of other karstic lakes from different latitudes (Armengol and Miracle, 1999; Lemma, 2009). The zooplankton species in the surveyed lakes appear to occupy separate niches in the spatial and temporal scales analysed. In EP *T. inversus*, *B. havanensis*, and *K. americana* showed stable population densities, whereas the spatially and temporally stable species in MC were *M. nesus*, and *T. inversus*. Therefore, in the meso-eutrophic system (EP) the micro-zooplankton was more abundant, whereas in the oligotrophic system (MC) the macro-zooplankton showed higher abundance. This is consistent with records made in subtropical and temperate lakes where small-size species are dominant in mesotrophic lakes (Bays and Crisman, 1983; Mazunder and Havens, 1998), while calanoid copepods have high densities in oligotrophic lakes (Tavernini *et al.,* 2003). *Thermocyclops inversus* is considered one of the most common and widely distributed cyclopoid species in southeastern Mexico and the Neotropics (Suárez-Morales *et al.,* 2004), and in this study it was the only species found abundantly in both lakes. Therefore, this pelagic species is able to inhabit and dominate with high abundances of fluctuating environmental conditions, including the oligotrophic, and meso-eutrophic conditions surveyed here.Species which were spatially or temporally restricted were mainly rotifers (groups 1-4 in Fig. 4A, and 1-3 in Fig. 4B); their higher abundances were independent of the trophic state in *K. lenzi*, *L. lunaris*, *T. weberi*, *B. falcatus*, *P. patulus, H. intermedia* and the copepod *T. prasinus,* indicating that these species have maximum densities which correlate with resource maxima (and that they are an opportunistic species), which is consistent with Peacock and Smyly (1983), who classified *T. prasinus* as opportunistic in the wild, taking food from any source available.

Explaining the changes in the zooplankton community based on functional traits; *i.e.* by changes in feeding strategy as a function of temporality (Obertegger *et al.,* 2011) was not so clear for the surveyed systems, because practically the whole zooplankton community was herbivorous. Except for the raptorial *T. weberi* (Smith, 2001), the omnivorous *L. australis* (Chaparro-Herrera *et al.,* 2012), or the opportunistic species mentioned before, the zooplankton community in EP and MC consisted of microbivorous rotifers of the genus *Anuraeopsis*, *Brachionus*, *Plationus*, *Dipleuchlanis*, *Lepadella*, or *Hexarthra* (Smith, 2001) or herbivorous crustaceans including *B. hagmanni* and *M. nesus* (de Bernardi and Giussani, 1990; Cervantes-Martínez *et al.,* 2005). In both lakes the raptorial *T. weberi* was present only during the dry season, when the onset of photosynthetic activity and the highest richness occurred. Probably these conditions could benefit the presence of *T. weberi*; but the abundance of this organism was never higher than 5 org. L^{-1} in the systems.

Even though no experimental evidence supported the presence of exploitative competition in the zooplankton community analysed here, the change in the abundance of some species could indicate certain relationships. For instance during the mixing process, the higher abundance of *B. hagmanni* was coincident with the decrease of *K. americana* in EP, and with the decrease of rotifers and cyclopoids in MC. In addition the highest level of Cladocera abundance was recorded in April, just before the highest (and dominant) levels of *M. nesus* or rotifers occurred in MC. The cladoceran dominance during the mixing period is consistent with records made in tropical lakes (Torres-Orozco and Zanatta, 1998; Gómez-Márquez *et al.,* 2003), and probably this could be related to avoidance of inter-species competition during stratification, as observed in temperate lakes (Lampert, 1997). With the onset of increased primary productivity during the early thermal stratification period (March to May) the dominance of rotifers in EP was absolute, with species such as *K. americana*, *B. havanaensis*, *H. intermedia*, and *K. lenzi*; but in MC the community was dominated by the Calanoida *M. nesus* or the Rotifera *K. americana*, *K. lenzi*, *P. patulus*, *B. havanaensis*, and *B. falcatus*. During early thermal stratification, a bloom of unicellular or filamentous cyanobacteria has been recorded in tropical, oligotrophic, monomictic lakes (Alcocer *et al.,* 2000, Hernández-Morales *et al.,* 2011). The bloom of the cyanobacteria could be the cause of the predominance of rotifers and calanoids in MC during the early thermal stratification.

By contrast, it was observed that the presence of some species appears to be related with the trophic condition of the lakes: *Anuraeopsis fissa*, *L. heterostyla*, *D. propatula*, *M. collinsi*, and *C. uncinata* were recorded exclusively in EP, because these species are able to inhabit eutrophic, alkaline conditions (Sharma and Sharma 1987). Species including *L. patella*, *D. aculeata*, and *L. australis* are typically able to inhabit environments with low food availability (Chaparro-Herrera *et al.,* 2012), therefore they were only recorded in MC in this study. Some species of the genus *Lecane* were recorded as exclusives for each system (groups 1 and 3 in EP or group 3 in MC in Fig. 4), however, since the genus *Lecane* is considered as littoral (Segers, 1995) but capable of inhabiting the entire water column (Fernando, 2002), we hypothesize that the presence of these species was incidental at the limnetic zone of each system.

Biological, physical, and chemical relationships in CCA

Even though empirical evidence has shown that *Chaoborus* feed on *Keratella* and other limnetic microzooplankton species in tropical systems (Lewis, 1979), there was no recognizable or significant relationship between the abundance of *Chaoborus* sp. and the abundance of rotifers, cladocerans, cyclopoids, and calanoids. This indicates either that phantom larvae do not cause a detectable variation in the zooplankton, or, alternatively, that this predator is not the primary carnivore in these systems. Additionally, the results indicated that in the meso-eu-

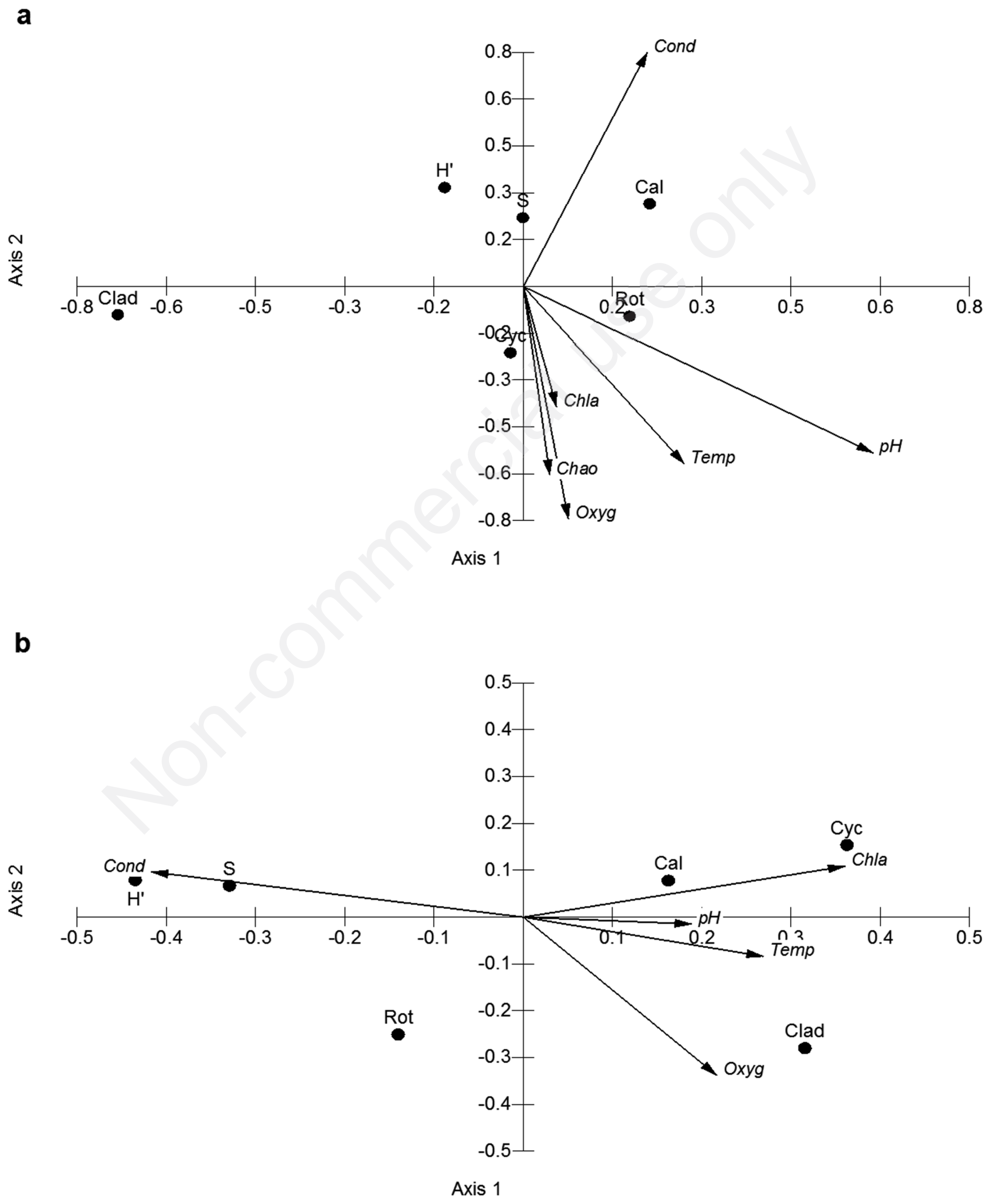

Fig. 5. Canonical Correspondence Analysis of zooplankton structure from El Padre (a), and Minicenote (b). Dots labeled as Rot, Clad, Cyc, and Cal represent abundance of Rotifera, Cladocera, Cyclopoida, and Calanoida, respectively. Dots labeled as H' and S represent diversity index and richness, respectively. Arrows are the environmental variables (Chl a, chlorophyll-*a* concentration; Temp, water temperature; Oxyg, oxygen concentration; Cond, conductivity).

trophic system, the mechanisms related to plankton abundance included the pH and temperature; whereas, in the oligotrophic system, the plankton abundance was best correlated with the oxygen concentration.

Considering the results, the significant changes in zooplankton diversity, abundances, and richness were recorded at the epilimnion in both lakes (0.5 to 5 m) between seasons. Therefore, the anoxic or acidic conditions in EP, and the low algal biomass availability in MC, generated homogeneity in these measures at the hypolimnion in the systems. The higher temperatures at superficial layers have been shown to benefit zooplankton growth and reproductive maturity (Lampert and Sommer, 2007); this factor and the basic values in pH seem to favour the abundance of dominant rotifers in the meso-eutrophic lake and the indicators of biodiversity (specially richness) in the oligotrophic lake. Additionally, higher concentration of chlorophyll-*a* favours the growth and survival rates of zooplankton (Pilati and Wurtsbaugh, 2003) and generates lower ionic content (Kalff, 2002): these factors seem to be related to the greater richness and diversity in the oligotrophic lake.

Finally, the abundance and distribution of the zooplankton that inhabit the oligotrophic lake and the indicators of biodiversity in the meso-eutrophic lake were correlated to the oxygen concentration because this factor influences the metabolic processes of zooplankton including respiration, reproduction and growth (De Meester and Vyverman, 1997).

CONCLUSIONS

Resources and environmental conditions can vary both spatially and during the annual cycle in tropical freshwater systems. Environmental changes were noticeable between seasons and layers, but the changes in the abundance, diversity, and richness of zooplankton were evident only between seasons at the epilimnion of the surveyed lakes (0.5 and 5 m in MC, 0.5, 2.5, and 5 m in EP). Dynamics in the zooplankton community were related to i) the physicochemical variables: the abundance of the dominant species in the oligotrophic lake was best correlated to oxygen concentration; whereas the pH and temperature were both important to explain the abundance of zooplankton in the meso-eutrophic lake; ii) opportunistic feeding: the rotifers *K. lenzi*, *L. lunaris*, *T. weberi*, *B. falcatus*, *P. patulus* or *H. intermedia*, and the cyclopoid copepod *T. prasinus* are proposed as opportunistic species, spatially or temporally restricted but inhabiting oligotrophic or meso-eutrophic conditions with maximum densities related to resource maxima; and iii) the exploitative competition: the abundance of *B. hagmanni* increased during the stratification in the oligotrophic and meso-eutrophic lakes, avoiding inter-species competition with another herbivores. The factors influencing indicators of biodiversity were primarily environmental factors; there was no recognizable or significant relationship between the abundance of the predator (*Chaoborus* sp.) and these measures in the systems.

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