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Ecology

Zooplankton biodiversity in tropical karst lakes of southeast Mexico, Chiapas

Biodiversidad de zooplankton en lagos tropicales kársticos del sureste de México, Chiapas

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Abstract

This study describes the biodiversity of the limnetic zooplankton communities of 18 tropical karst lakes of the Lagunas de Montebello National Park, Chiapas. Sampling was carried out in 2 contrasting climatic periods. A total of 59 zooplankton species were identified (25 Copepoda, 13 Cladocera and 21 Rotifera). Montebello's global biodiversity is relatively high (~11%) with reference to what is reported for the entire country. However, the species richness per lake varies from 4 to 24 species with an average of 10.2 ± 6.0. The most frequent species are the copepods *Mastigodiaptomus maya* and *M. nesus*, the cladocerans *Diaphanosoma* cf. *birgei*, *Ceriodaphnia dubia* and *Eubosmina tubicen*, and the rotiferan *Keratella americana*. Eutrophic lakes showed higher species richness and share more species in common than oligotrophic lakes; the species richness of the deep lakes is lower than that of the shallow, and that of the plateau doubles those of the mountain lakes. *M. maya* is the only species inhabiting all lake types. The high singularity of the zooplankton of each lake demonstrates the fragility of these ecosystems so pollution and/or eutrophication threaten the high regional zooplankton biodiversity.

Keywords: Species richness; Copepoda, Cladocera; Rotifera; Lagunas de Montebello National Park

Resumen

Este estudio presenta la biodiversidad de las comunidades limnéticas de zooplancton de 18 lagos kársticos tropicales del Parque Nacional Lagunas de Montebello, Chiapas. Los muestreos se llevaron a cabo en 2 períodos climáticos contrastantes. Se identificaron un total de 59 especies de zooplankton (25 Copepoda, 13 Cladocera y 21 Rotifera). La biodiversidad global de Montebello es relativamente alta (~11%) con referencia a lo reportado para todo el país. Sin embargo, la riqueza específica por lago varía de 4 a 24 especies con un promedio de 10.2 ± 6.0 especies. Las especies que se registraron en un mayor número de lagos fueron: los copépodos *Mastigodiaptomus maya* y *M. nesus*, los cladóceros *Diaphanosoma* cf *birgei*, *Ceriodaphnia dubia* y *Eubosmina tubicen*, y el rotífero *Keratella*

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americana. Los lagos eutróficos mostraron una mayor riqueza específica y comparten más especies en común que los lagos oligotróficos; la riqueza específica de los lagos profundos es menor a la de los someros y la de los lagos de planicie duplica a los de montaña. La elevada singularidad del zooplankton de cada lago evidencia la fragilidad de estos ecosistemas por lo que su contaminación y/o eutroficación amenaza la elevada biodiversidad regional de zooplankton.

Palabras clave: Riqueza específica; Copepoda, Cladocera; Rotifera; Parque Nacional Lagunas de Montebello

Introduction

Previous taxonomic studies dealing with zooplankton allow recognizing the great biodiversity of Mexican inland waters. Up to date, 300 rotifer species have been recorded in Mexico, this is, ≈14% of the total rotifer species reported worldwide (García-Morales & Elías-Gutiérrez, 2013; Sarma & Elías-Gutiérrez, 1999). In addition, Elías-Gutiérrez et al. (2008) and Mercado-Salas and Suárez-Morales (2011) enumerated 150 species of cladocerans and 90 species of copepods in Mexico. Currently, a total of 540 zooplankton species have been reported from Mexican inland waters.

Taxonomic lists are not only useful in recording the biodiversity but also in recognizing zoogeographic patterns, and even relating species to water quality (Sládeček, 1983). Based on the presence or absence, frequency and density, and water quality, diverse indexes have been developed to use zooplankton species as bioindicators of trophic state, water pollution and other water characteristics from epicontinental aquatic ecosystems (Lougheed & Chow-Fraser, 2002).

The heterogeneous orographic conformation of the Mexican territory shaped an ample diversity of inland (lotic and lentic) waters (Alcocer & Bernal-Brooks, 2010). Nonetheless, large lake-districts could be recognized in Mexico; of particular interest are those lakes originated by dissolution on the ample karst landscapes of the eastern and southeastern Mexican territories. Well-known examples in this area are the "cenotes" (sinkholes) of the Yucatán Peninsula and the Lagunas de Montebello National Park (LMNP) in Chiapas.

The LMNP includes more than 60 lakes with a broad array of bathymetric and morphometric characteristics (Alcocer et al., 2016, 2018). The lake diversity provides a unique opportunity to uncover the largely unknown inland aquatic biodiversity of Chiapas and Mexico. A previous study on the LMNP benthic invertebrate's biodiversity (Cortés-Guzmán et al., 2019) showed a high regional biodiversity but at the same time a large singularity of the benthic invertebrate fauna from each lake, so we expect similar results for the zooplankton. The aim of the present study is to provide accurate data on the largely unknown biodiversity of the zooplankton communities of the LMNP lakes, Chiapas, Mexico. It should be noted that there are only 2 previous published studies concerning zooplankton of this area both describing new species: *Eucyclops tziscao* from lake Tziscao (Gutiérrez-Aguirre & Cervantes-Martínez, 2013) and *Mastigodiaptomus suarezmorelesi* from lake Montebello (Gutiérrez-Aguirre et al., 2013).

Materials and methods

The LMNP is in the southeastern region of Chiapas State, at the border with the Guatemala Republic (Fig. 1). Extreme coordinates of the LMNP are 16°04'40" - 16°10'2" N, 91°37'40" - 91°47'40" W (Conanp, 2007), with an altitude between 1,200 and 1,800 m asl (Durán-Calderón et al., 2014). It covers an area of 6,022 h and includes part of 2 municipalities, La Independencia and La Trinitaria, the latter encompassing 95% of the LMNP.

Climate in the LMNP is mostly C(fm) type (humid temperate with rains all year round), while in the extreme NW is A(cm) type (warm humid with abundant rains in summer and with absence of frosts in the coldest months) (Conanp, 2009). The average monthly temperature is 23.6°C with an annual rainfall of 1,862 mm (García, 2004).

The LMNP belongs to the Hydrological Region No. 30 Grijalva-Usumacinta (Conanp, 2007). The main watercourse is the Río Grande. Mesozoic to Lower Cretaceous series composes the limestone-type sedimentary class lithology. The lake district is karst landscape (solution lakes) with dolines, uvalas and poljes (Alcocer et al., 2016). There are more than 60 lakes (just in Mexico) along a NW-SE oriented fault system. Durán-Calderon et al. (2014) classified the lakes in 2 large groups: mountain lakes, mostly groundwater fed, and plateau lakes, largely fed by surface runoff (Río Grande).

We selected 18 water bodies along the fault system covering the entire lake district. The lakes included shallow and deep, oligotrophic and eutrophic, and mountain and plateau lakes (Table 1). Further geographical, bathymetric and morphometric information is provided elsewhere (Alcocer et al., 2016).

Two field campaigns were carried out in 2014, the first one in the cold and dry season (February) and the second in the warm and rainy season (October). Water samples were obtained with an UWITEC water sampler bottle at 2

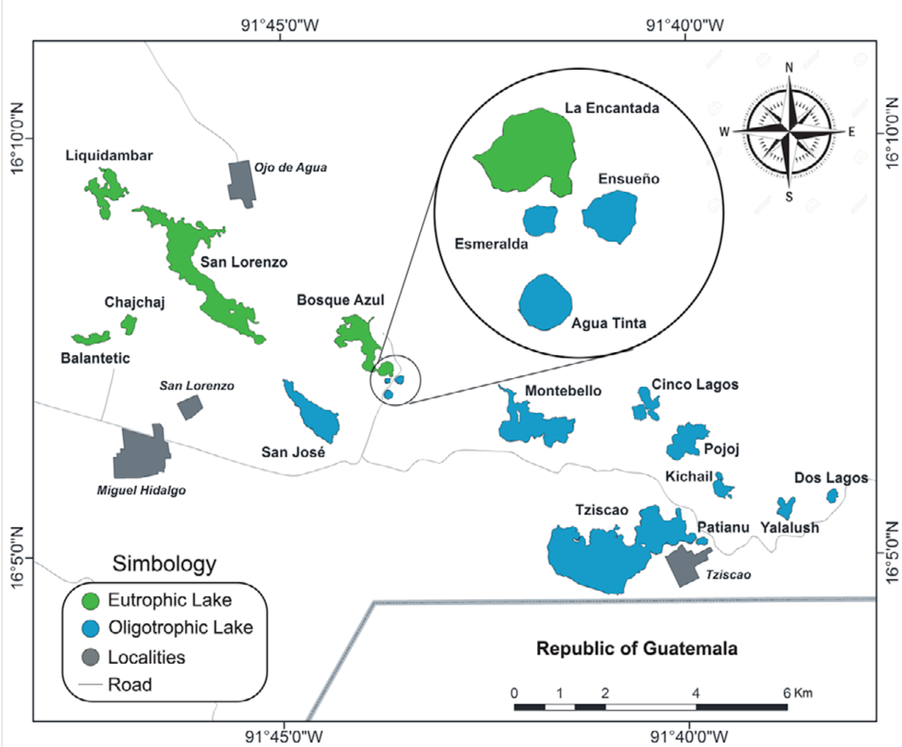

Figure 1. Location of the lakes in the LMNP (modified from Alcocer et al., 2016).

(shallow lakes) or 5 (deep lakes) water depths, along the water column. Water samples were filtered *in situ* through a 54µm aperture mesh; retained organisms were fixed with 4% formaldehyde. We used specialized taxonomic keys to identify the rotifers (Koste, 1978, Sarma & Nandini, 2017), and cladocerans and copepods (Benzie, 2005; Elías-Gutiérrez et al. 2008; Korovchinsky, 1992, 2002; Mercado-Salas et al., 2012).

To verify the similarity of the taxonomic composition between lakes, a dendrogram was made based on the species presence-absence by means of the Jaccard index and the linkage between groups with SPSS v21.

Results

We identified 59 zooplankton taxa, 90% identified to species and 10% at genus level; from here on, all taxa are referred to as "species" (Table 2). Out of the 59, 47 species are new records for Chiapas, and 2 (*Daphnia gessneri* and *D. hyalina*) are new records for Mexico. In addition, we found 4 species of copepods (*Arctodiaptomus dorsalis*, *Mesocyclops aspericornis*, *M. thermocyclopoides* and *Thermocyclops crassus*) usually reported as exotic or invasive species (Elías-Gutiérrez et al., 2008; Suárez-Morales et al., 2011).

There are 25 copepods (42.4%), 13 cladoceran (22.0%) and 21 rotifer (35.6%) species. Among copepods, 7 are Calanoidea (Diaptomindae) and 18 Cyclopoida (Cyclopidae). There are 13 Cladocera species represented by 4 families, Sididae (1), Daphniidae (8), Moinidae (2) and Bosminidae (2). Finally, 21 species belong to Rotifera, subclass Monogononta, with 8 families.

Table 3 shows the distribution of the zooplankton species in the 18 lakes; out of the 59 species, 44% were restricted to a single lake, and 27% of the species were found in 2-3 lakes. Regarding Calanoidea, 2 species (*Mastigodiaptomus maya* and *M. nessus*) are present in most of the lakes, and the remaining 5 species were restricted to a single lake. 10 species of the Cyclopoidea are restricted to a single lake while 8 species were distributed in 2 to 6 lakes; *Microcyclops ceibaensis* was the most distributed species found in 6 lakes. Three cladocerans (*Diaphanosma birgei*, *Ceriodaphnia dubia* and *Eubosmina tubicen*) were observed in more than 9 lakes, 4 species were distributed between 2 to 5 lakes, and 46% of cladocerans (6 species) were restricted to only 1 lake. Only *Keratella americana* out of the 21 rotifer species was observed in 9 lakes, 3 rotifer species were present in 4 to 6 lakes, and the remaining 15 species were distributed in 1-3 lakes.

Table 1

List of lakes of the PNLM included in this study and their classification in the main categories. Depth and thermal type according to Alcocer et al. (2016, 2018), trophic state according to Vera-Franco et al. (2015), and geographic site type according to Durán-Calderon et al. (2014).

Lake	Abr.	Depth	Thermal type	Trophic state	Site type
Balantetic	BL	Shallow	Warm polymictic	Eutrophic	Plateau
Chajchaj	CH	Shallow	Warm polymictic	Eutrophic	Plateau
Liquidámbar	LI	Deep	Warm monomictic	Eutrophic	Plateau
San Lorenzo	SL	Deep	Warm monomictic	Eutrophic	Plateau
Bosque Azul	BA	Deep	Warm monomictic	Eutrophic	Plateau
La Encantada	EC	Deep	Warm monomictic	Eutrophic	Plateau
Esmeralda	ES	Shallow	Warm polymictic	Oligotrophic	Mountain
Ensueño	EN	Deep	Warm monomictic	Oligotrophic	Mountain
Agua Tinta	AT	Deep	Warm monomictic	Oligotrophic	Mountain
San José	SJ	Deep	Warm monomictic	Oligotrophic	Plateau
Montebello	MB	Deep	Warm monomictic	Oligotrophic	Mountain
Cinco Lagos	CL	Deep	Warm monomictic	Oligotrophic	Mountain
Pojoj	PO	Deep	Warm monomictic	Oligotrophic	Mountain
Kichail	KI	Deep	Warm monomictic	Oligotrophic	Mountain
Tziscao	TZ	Deep	Warm monomictic	Oligotrophic	Mountain
Patianú	PA	Deep	Warm monomictic	Oligotrophic	Mountain
Yalalush	YA	Shallow	Warm polymictic	Oligotrophic	Mountain
Dos Lagos	DL	Deep	Warm monomictic	Oligotrophic	Mountain

Zooplankton species richness (S_{ZOO}) ranged from 4 (6.8%) to 24 (40.7%) species with an average of 10.2 ± 6.0 species per lake. Six lakes (San Lorenzo, Chajchaj, Balantetic, Bosque Azul, La Encantada and Tziscao) out of 18 displayed high S_{ZOO} (12-24 species). On the contrary, 4 lakes (Esmeralda, Pojoj, Ensueño and Montebello) displayed the lowest S_{ZOO} values (< 7 species) (Fig. 2).

Copepods were found in the 18 lakes. The copepod species richness (S_{COP}) averaged 3.9 ± 2.5 species (1-9 species). The highest S_{COP} was found in Bosque Azul (9 species), and San Lorenzo and Tziscao (8 species each). The cladocerans species richness (S_{CLAD}) averaged 2.8 ± 1.7 species (0-5 species). The highest S_{CLAD} was found in Bosque Azul, La Encantada and Tziscao (5 species), and the lowest (0, absence) in Liquidambar and Chajchaj. Finally, the average rotifer species richness (S_{ROT}) was 3.5 ± 4.1 species (0-12 species). The highest rotifer species richness (S_{ROT}) was found in San Lorenzo (12 species), Chajchaj (11 species) and Balantetic (10 species), and the lowest (0, absence) in Ensueño, San José, Pojoj, Pataniu and Yalalush (Fig. 2)

The $S_{COP}/S_{CLAD}/S_{ROT}$ ratio of the Montebello lakes averages 1.4/1.0/1.2. The ratio was different in eutrophic lakes (1.6/1.0/3.3) where S_{ROT} augmented while S_{COP} diminished. In the oligotrophic lakes (1.2/1.0/0.4) the ratio inverted with S_{ROT} diminishing while S_{COP} augmenting. The ratio in plateau (1.3/1.0/2.1) and mountain lakes (1.2/1.0/0.4) was similar to the eutrophic and oligotrophic lakes, respectively.

There is a large singularity of zooplankton species in each lake. Although a single species could be found between 1 and up to 16 lakes (not a single species was found inhabiting the 18 or even 17 lakes), most species (76%) were found inhabiting between 1 and 3 lakes (Fig. 3). One species (*Mastigodiaptomus maya*) was found in 16 lakes, 2 species (*M. nesus*, *Diaphanosoma* cf. *birgei*) were found in 11 lakes, 1 species (*Ceriodaphnia dubia*) was found in 10 lakes, and 2 species (*Eubosmina tubicen, Keratella americana*) were found in 9 lakes. The other 53 species (≈ 90%) were found in less than 50% (< 9) of the lakes.

S_{ZOO} was higher (× 2.3 times) in eutrophic lakes with 16.3 ± 6.3 species (7-24 species) than in oligotrophic lakes

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Table 2

Taxonomic list of the zooplankton species (Copepoda, Cladocera, Rotifera) recorded in the 18 lakes of the Lagunas de Montebello National Park, Chiapas.

Order Calanoida Sars, 1903
Family Diaptomidae Sars, 1903
Subfamily Diaptominae Kiefer, 1932
1. *Arctodiaptomus dorsalis* (Marsh, 1907)
2. *Leptodiaptomus cuauhtemoci* (Osorio-Tafall, 1941)
3. *L. mexicanus* (Marsh, 1929)
4. *Mastigodiaptomus maya* Suárez-Morales y Elías-Gutierrez, 2000
5. *M. nesus* Bowman, 1986
6. *M. suarezmoralesi* Gutiérrez-Aguirre y Cervantes-Martínez, 2013
7. *Mastigodiaptomus* sp. 2 Light, 1939

Order Cyclopoida Burmeister, 1834
Family Cyclopidae Dana, 1846
Subfamily Cyclopinae Kiefer, 1927
8. *Apocyclops panamensis* (Marsh, 1913)
9. *Diacyclops puuc* Fiers y Reid, 1996
10. *Mesocyclops aspericornis* (Daday, 1906)
11. *M. brasilianus* Kiefer, 1933
12. *M. edax* (Forbes, 1981)
13. *M. longisetus* (Thiébaud, 1912)
14. *M. pescei* Petkovski, 1986
15. *M. thermocyclopoides* Harada, 1931
16. *Microcyclops ceibaensis* (Marsh, 1919)
17. *M. dubitabilis* (Kiefer, 1934)
18. *Thermocyclops tenuis* (Marsh, 1910)
19. *T. inversus* Kiefer, 1936
20. *T. crasssus* (Fischer, 1853)
Subfamily Eucyclopinae Kiefer, 1927
21. *Ectocyclops* sp. Brady, 1904
22. *Eucyclops tziscao* Mercado-Salas, 2013
23. *Macrocyclops albidus* (Jurine, 1820)
24. *M. fuscus* (Jurine, 1820)
25.*Tropocyclops prasinus prasinus* (Fischers, 1995)

Order Cladocera Milne-Edwards, 1840
Family Sididae Baird, 1850 (emend. Sars, 1865)
26. *Diaphanosoma* cf *birgei* Korineck, 1981
Family Daphniidae Straus, 1820
Subgenus *Daphnia* O.F. Müller, 1785
27. *Daphnia ambigua* Scourfield, 1947
28. *D. cheraphila* Hebert & Finston, 1996
29. *D.* cf *galeata* Sars, 1864
30. *D. gessneri* Herbst, 1967
31. *D.* cf *hyalina* Leydig, 1860
32. *D. obtusa* Kurz, 1875
33. *Ceriodaphnia dubia* Richard, 1894
34. *C. lacustris* Birge, 1893
Family Moinidae Goulden, 1968
35. *Moina micrura* Kurz, 1874
36. *Moinodaphnia* sp. Herrick, 1887
Family Bosminidae Baird, 1845 (emend. Sars, 1865)
37. *Eubosmina tubicen* Brehm, 1953
38. *Bosmina* sp. Baird, 1845

Phylum Rotifera Cuvier, 1798
Subclase Monogononta Plate, 1889
Order Flosculariaceae Harring, 1913
Family Hexarthridae Bartos, 1959
39. *Hexarthra intermedia* (Wisniewski, 1929)
Family Testudinellidae Harring, 1913
40. *Testudinella patina* (Hermann, 1783)
41. *Ptygura* sp. Ehrenberg, 1832
Family Trochosphaeridae Harring, 1913
42. *Filinia longiseta* (Ehrenberg, 1834)
43. *F. terminalis* (Plate, 1886)

Order Ploima (Hudson & Gosse, 1886)
Family Asplanchnidae Eckstein, 1883
44. *Asplanchna girodi* de Guerne, 1888
Family Brachionidae Ehrenberg, 1838
45.*Brachionus angularis* Gosse, 1851
46. *B. bidentatus* Anderson, 1889
47. *B. calyciflorus* Pallas, 1766
48. *B. havanaensis* Rousselet, 1911
49. *B. rubens* Ehrenberg, 1838
50. *Keratella americana* Carlin (1943)
51. *K. cochlearis* (Gosse, 1851)
52. *K. tropica* (Apstein, 1907)
53. *Plationus patulus* (Müller, 1786)
54. *Platyas quadricornis* (Ehrenberg, 1832)
Family Lecanidae Remane, 1933
55. *Lecane bulla* (Gosse, 1851)
56. *L. papuana* (Murray, 1913)
Family Synchaetidae Hudson & Gosse, 1886
57. *Polyarthra vulgaris* Carlin, 1943
58. *Synchaeta oblonga* Ehrenberg, 1831
Family Trichotriidae Harring, 1913
59. *Macrochaetus* sp. Perty, 1850

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with 7.2 ± 2.7 taxa (4-14 species). Similar figures (× 2.1 times) were found for S_{ZOO} in plateau lakes with 15.0 ± 6.8 species (7-24 species) comparing to mountain lakes with 7.2 ± 2.8 (4-14 species). Differently, S_{ZOO} in deep lakes with 9.9 ± 6.1 species (4-24 species) was similar to shallow lakes with 11.3 ± 6.4 species (4-18 species). S_{ZOO} in deep eutrophic lakes with 16.3 ± 8.1 species (7-24 species) was similar to shallow eutrophic lakes with 16.5 ± 2.1 species (15-18 species). Finally, S_{ZOO} in deep oligotrophic lakes with 7.4 ± 2.7 taxa (4-14 species) was slightly higher than shallow oligotrophic lakes with 6.0 ± 2.8 species (4-8 species).

Table 3

Distribution of the zooplankton species in the 18 lakes of the Lagunas de Montebello National Park, Chiapas. (* = first record in Chiapas, ** = first record in Chiapas and reported as exotic/invasive, X = previously reported in Chiapas, *X = first record in Mexico).

Copepoda	BL	CH	LI	SL	BA	EC	ES	EN	AT	SJ	MB	CL	PO	KI	TZ	PA	YA	DL
Arctodiaptomus dorsalis																	**	
Leptodiaptomus cuauhtemoci																	*	
L. mexicanus																	*	
Mastigodiaptomus maya		X		X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
M. nesus	*					*		*	*	*	*		*	*	*	*	*	
M. suarezmoralesi										X								
Mastigodiaptomus sp. 2															*			
Apocyclops panamensis		*		*	*		*											*
Diacyclops puuc				*	*													
Mesocyclops aspericornis					**													
M. brasilianus		X																
M. edax	*													*	*			
M. longisetus				X														
M. pescei		X																
M. thermocyclopoides				**														
Microcyclops ceibaensis		*		*	*			*				*			*			
M. dubitabilis															*	*		
Thermocyclops tenuis					*													
T. inversus		*		*	*				*								*	
T. crasssus					**													
Ectocyclops sp.				*	*													
Eucyclops tziscao		X				X									X			
Macrocyclops albidus																	*	
M. fuscus								*										
Tropocyclops prasinus			*															
Subtotal	2	7	1	8	9	3	2	4	3	3	2	2	2	3	7	3	7	2
Cladocera																		
Diaphanosoma cf birgei		*			*	*			*	*	*	*	*		*	*	*	
Daphnia ambigua															*			*
D. cheraphila											*							
D. cf galeata										*					*			*
D. gessneri										*X			*X	*X		*X	*X	*X
D. cf hyalina														*X				
D. obtusa						*												
Ceriodaphnia dubia		*		*	*	*		*	*	*				*	*	*		
C. lacustris		*			*	*								*				
Moina micrura				*														
Moinodaphnia sp.				*														
Eubosmina tubicen		*			*	*	*		*			*			*	*		*
Bosmina sp.					*													
Subtotal	0	4	0	3	6	5	1	1	3	4	2	2	2	4	5	4	2	4

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Table 3
Continued

Copepoda	BL	CH	LI	SL	BA	EC	ES	EN	AT	SJ	MB	CL	PO	KI	TZ	PA	YA	DL
Rotifera																		
Hexarthra intermedia	X	X			X	X												
Testudinella patina			*	*										*				
Ptygura sp.									*		*	*						
Filinia longiseta	*	*	*	*	*	*												
F. terminalis		*	*		*													
Asplanchna girodi		*	*	*														
Brachionus angularis	*	*		*														
B. bidentatus				*														
B. calyciflorus	*		*	*														
B. havanaensis	X	X	X		X	X						X						
B. rubens				*					*									
Keratella americana	*	*	*		*	*						*		*	*			*
K. cochlearis		*	*		*													
K. tropica		*	*		*													
Plationus patulus		*	*	*														
Platyas quadricornis					*													
Lecane bulla		*		*														
L. papuana		X	X															
Polyarthra vulgaris				*														
Synchaeta oblonga							*											
Macrochaetus sp.											*							
Subtotal	6	12	11	10	8	4	1	0	2	0	2	3	0	2	1	0	0	1
Total	7	24	18	15	23	12	4	5	8	7	6	7	4	9	13	7	9	7

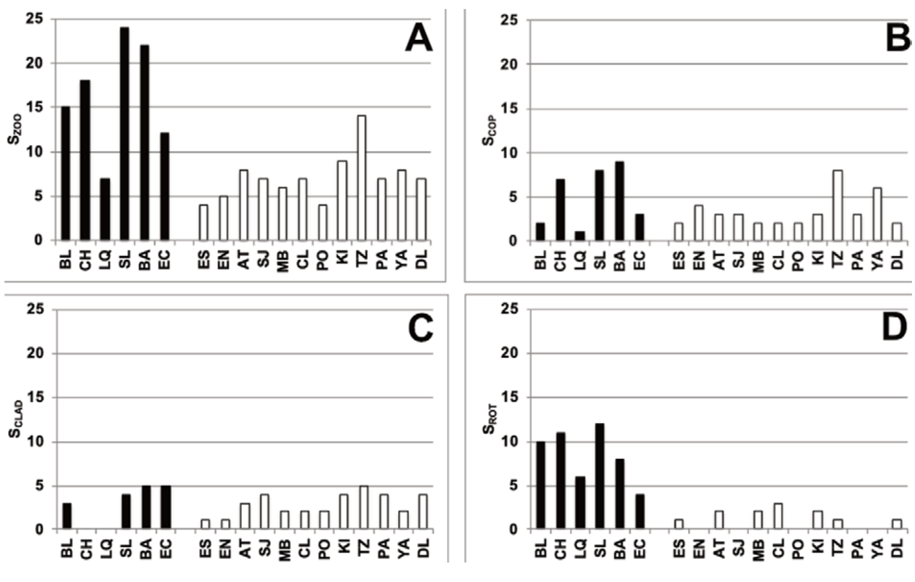

Figure 2. A: Zooplankton species richness (S_{ZOO}), B: copepod species richness (S_{COP}), C: cladoceran species richness (S_{CLAD}), and D: rotifer species richness (S_{ROT}) found in the Montebello lakes. Lake abbreviations follow Table 1. Black bars indicate eutrophic lakes; white bars indicate oligotrophic lakes.

Figure 4 shows the groups of lakes formed by the cluster analysis based on species presence/absence of the Montebello lakes. The most similar lakes are: eutrophic San Lorenzo and Bosque Azul, and oligotrophic Pojoj, Patianú, and San José; the rest of the lakes turn out to be taxonomically different. Nonetheless and with a lower level of similarity, the eutrophic lakes clustered together, and the oligotrophic lakes formed another cluster. As previously explained, most species are restricted to a single or a few lakes instead of showing an ample distribution; this explains the low degree of similarity between the lakes.

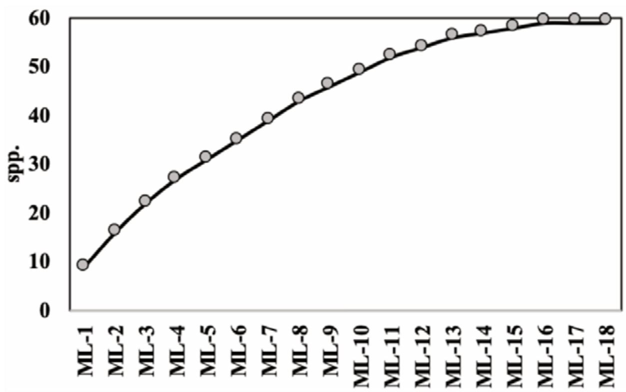

Figure 3. Accumulation curve of species recorded in 18 Montebello lakes, Chiapas.

Out of the 59 species registered for the Montebello lakes, 8 (2 copepods, 2 cladocerans and 4 rotifers) characterized (present in ≥ 65% of each lake type) the different lake types (Table 4). Six species characterized eutrophic lakes (1 copepod, 1 cladoceran, and 4 rotifers), while 3 species characterized oligotrophic lakes (2 copepods and 1 cladoceran); the only species in common for eutrophic and oligotrophic lakes was the copepod *Mastigodiaptomus maya.*

Seven species characterized plateau lakes (1 copepod, 2 cladocerans, and 4 rotifers), while 2 characterized mountain lakes (2 copepods); the only species in common for plateau and mountain lakes was, once again, the copepod *Mastigodiaptomus maya.* Finally, 2 species characterized deep lakes (1 copepod, and 1 cladoceran), while 1 species characterized shallow lakes (1 copepod); the only species in common in deep and shallow lakes was, one more, the copepod *Mastigodiaptomus maya*. In this way, the copepod *Mastigodiaptomus maya* was the only species common to all lake types. Not a single species of cladoceran or rotifer were common to all lake types.

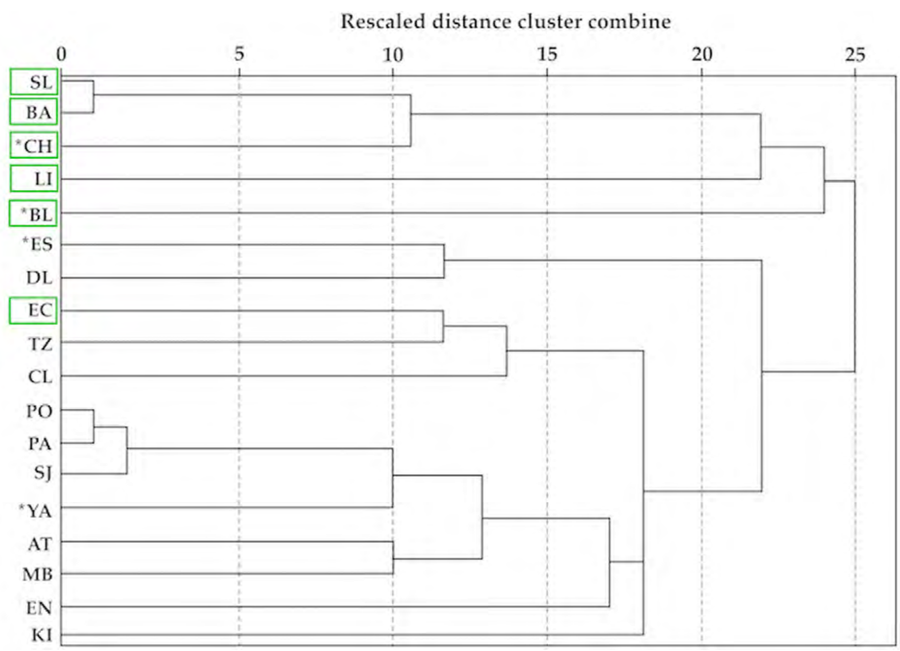

Figure 4. Dendrogram based on the zooplankton taxa presence-absence in the Montebello lakes. Jaccard index, between-group linkage. Green box = eutrophic lakes; * = shallow lakes.

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Table 4

Characteristic (most frequently found ≥ 65% of lakes) zooplankton species cataloged by lake type in the 18 lakes of the Lagunas de Montebello National Park, Chiapas. E = Eutrophic lakes, O = oligotrophic lakes, P = plateau lakes, M = mountain lakes, D = deep lakes, S = shallow lakes.

Species	E	O	P	M	D	S
Copepoda						
Mastigodiaptomus maya	X	X	X	X	X	X
Mastigodiaptomus nesus	-	X	-	X	-	-
Subtotal	1	2	1	2	1	1
Cladocera						
Diaphanosoma cf birgei	-	X	X	-	X	-
Ceriodaphnia dubia	X	-	X	-	-	-
Subtotal	1	1	2	0	1	0
Rotifera						
Filinia longiseta	X	-	X	-	-	-
Brachionus havanaensis	X	-	-	-	-	-
Keratella americana	X	-	X	-	-	-
Hexarthra intermedia	X	-	X	-	-	-
Subtotal	4	0	4	0	0	0
Total	6	3	7	2	2	1

Discussion

The zooplankton species richness in the limnetic (pelagic) zone of the Montebello lakes is comparatively high (~11% of the total S_{ZOO} reported from Mexico), including 27.7% copepods, 8.7% cladocerans, and 7.0% rotifers those numbers reported for Mexico (90 copepods, 150 cladocerans, and 300 rotifers). However, these figures will surely increase by incorporating the species inhabiting in the littoral zone that are generally more numerous than those dwelling in the limnetic zone.

It is generally accepted that oligotrophic lakes shelter a larger number of species compared with the eutrophic ones (e.g., Pinto-Coelho et al., 2005). This is in contrast with what we found in the Montebello lakes where S_{ZOO} was 43 species in eutrophic and 31 species in oligotrophic lakes, this is, approximately 1.4 times higher in eutrophic than in oligotrophic lakes. This is also opposite to Cortés-Guzmán et al. (2019), who found deep benthic macroinvertebrates of the Montebello lakes to be more diverse in oligotrophic than in eutrophic lakes.

Montebello eutrophic lakes share a higher number of species in common (60.5% of taxa in ≥ 2 lakes) than the oligotrophic lakes (48.4% of taxa in ≥ 2 lakes). Since eutrophic lakes are: *1)* located at the plateau area, *2)* fed largely by surface run-off and the Río Grande, and *3)* artificially interconnected through channels, the zooplankton from one lake could easily disperse to others nearby. Also, the flooding events during the rainy season, characteristics of the tropical karst regions, interconnect the lakes otherwise separated on the surface, and then zooplankton could also be spread among adjacent lakes. Differently, mountain lakes are isolated and fed mostly by groundwater that limits zooplankton dispersal.

The zooplankton of eutrophic lakes comprises mainly cosmopolitan species, mostly rotifers (Beaver & Crisman, 1990; Jeppensen et al., 2011; Lougheed & Chow-Fraser, 2002; Sládeček, 1983). Differently, the zooplankton of oligotrophic lakes is composed mostly by copepods and cladocerans (~ 80%). Some taxa of the oligotrophic lakes indicate oligotrophic conditions such as the cladoceran *Daphnia gessneri* and the calanoid copepods (Branco et al., 2002; Cervantes-Martínez & Gutiérrez-Aguirre, 2015).

There are differences between the zooplankton of the Montebello lakes and that reported from other temperate and tropical lakes. Copepods showed the largest number of taxa (25) followed by rotifers (21) and cladocerans (13), while other studies (Dodson & Silva-Briano, 1996; Guevara et al., 2009; Papa & Zafaralla, 2011; Pinto-Coelho et al., 2005) report rotifers and cladocerans as the dominant groups. *Diaphanosoma*, *Ceriodaphnia*, *Macrothix* and *Moina* are frequently reported as dominant in tropical and subtropical lakes (Dodson & Frey, 1991; Sarma et al., 2005), while in Montebello the dominant gender is *Daphnia* with 6 species out of 13 cladocerans (46%).

Elías-Gutiérrez et al. (2008) and Suárez-Morales et al. (2011) reported the presence of 5 invasive or exotic copepods in Mexican inland waters, 4 of them were found in the Montebello lakes: *Arctodiaptomus dorsalis* (Yalalush), *Mesocyclops aspericornis* (Bosque Azul), *M. thermoscyclopoides* (San Lorenzo), and *Thermocyclops crassus* (Bosque Azul). Three exotic copepods are distributed in eutrophic lakes located in the plateau, and 1, *A. dorsalis*, was found in an oligotrophic, mountain lake.

Summarizing, the zooplankton species richness of the Montebello lakes with 59 species comprises 27.7%, 8.7%, and 7.0% of those species of copepods, cladocerans, and rotifers, respectively, reported for Mexico. Forty-eight out of the 59 species are new records for Chiapas, 2 species (*Daphnia gessneri* and *D. hyalina*) are new records for Mexico, and 4 species (*Arctodiaptomus dorsalis*, *Mesocyclops aspericornis*, *M. thermocyclopoides* and *Thermocyclops crassus*) are reported as exotic or invasive species.

Slightly less than half the species (26 out of 59, 44%) were found in a single lake, which stresses the singularity of the zooplankton community from each lake, making evident the fragility of these ecosystems.

The disappearance of the fauna from a single lake means a high probability of its disappearance from the entire region. Not a single species was found in the 18 lakes; the copepod *Mastigodiaptomus maya* (but not other copepod, cladocerans, or rotifer) was found inhabiting eutrophic and oligotrophic, plateau and mountain, and deep and shallow lakes. Eutrophic lakes showed higher taxonomic richness compared to the oligotrophic lakes and share more species in common (60.5%), than the oligotrophic lakes (48.4%).

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