



# Article Regional Pelagic Rotifer Biodiversity in a Tropical Karst Lake District

# Rocío Fernández<sup>D</sup>, Javier Alcocer \*<sup>D</sup> and Luis A. Oseguera<sup>D</sup>

Grupo de Investigación en Limnología Tropical, FES Iztacala, Universidad Nacional Autónoma de México, Av. de los Barrios 1, Los Reyes Iztacala, Tlalnepantla, Estado de México, C.P. 54090, Mexico;

biol.fernandez@gmail.com (R.F.); loseguera@unam.mx (L.A.O.)

\* Correspondence: jalcocer@unam.mx

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**Abstract:** The species richness, composition, abundance, and biomass of pelagic rotifers were determined in 17 karst lakes of the "Lagunas de Montebello" National Park, Chiapas, Mexico. The species richness of the region (21 species) and single lakes (1–12 species) was smaller than that of other Mexican, tropical, and temperate lakes. It is worth noting the high dissimilarity in species composition—about half (52%) of the species were observed in only 1–3 lakes. A total of eight rotifer families, all from the Monogononta subclass, were recorded. *Keratella americana* was the species with the highest occurrence (13 lakes), followed by *Ptygura* sp. (8 lakes). The abundance (0 to 536 ind L<sup>-1</sup>) and biomass (0 to 21  $\mu$ g L<sup>-1</sup>) of rotifers were low. The highest values of species richness, abundance, and biomass were found in eutrophic lakes, and the lowest in oligotrophic lakes. The low values of rotifer biodiversity, abundance, and biomass in the Montebello lakes are probably the product of the interaction of different factors—such as environmental homogeneity (all water bodies are karst lakes), the low availability of "good-quality" food, and predation by cyclopoid copepods in the eutrophic lakes, and the low availability of food, and competitive interference by calanoid copepods and cladocerans in the oligotrophic lakes.

**Keywords:** species richness; abundance; biomass; trophic status; zooplankton; Montebello; Chiapas; Mexico

## 1. Introduction

Species diversity of terrestrial ecosystems increases in the tropics, which results in high biodiversity in tropical rainforests [1]. Mexico is one of the 12 top megadiverse countries holding 70% of the vertebrate (amphibians, reptiles, birds, and mammals) and vascular plant diversity worldwide [2]; however, the studies of aquatic invertebrates in Mexican freshwaters is scant, and to date [3], it is undetermined whether these inland aquatic ecosystems display the same tendency of high biodiversity that terrestrial communities show [4,5].

Approximately 300 species of rotifers have been recorded in the epicontinental waters of Mexico [6]. Most inventories have been conducted in one or a few aquatic bodies (e.g., References [7,8]), with species richness ranging from 2 to 125 species per aquatic system [9–11] and densities ranging from 1 to more than 1000 ind  $L^{-1}$  (e.g., Reference [12]). Although regional rotifer studies in Mexico are rare, Walsh et al. [13] and Rios-Arana et al. [14] found 57 and 64 rotifer species in 47 and seven water bodies, respectively (e.g., saline ponds, desert springs, playa lakes), disseminated in the arid, northern territories of Mexico, while Arroyo-Castro et al. [15] reported 36 species from 17 karstic water bodies of the Cozumel Island. The three studies found that the water bodies within the same geographic region (i.e., lake district) share few rotifer species in common [13–15].

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It is well known that both biotic (e.g., predation, competition [16,17]) and abiotic (e.g., rainfall, dissolved oxygen, temperature, turbidity [18–21]) factors influence the biodiversity of aquatic organisms. In temperate aquatic systems, biodiversity has been positively related to primary productivity [22,23] and the morphometry of lakes [24]. In recent decades, numerous aquatic ecosystems have been anthropogenically impacted, especially by agro-industrial practices [25], which have caused changes in the biodiversity of aquatic ecosystems [26] by extinguishing sensitive species or reducing beta diversity or functional diversity through habitat homogenization [27–29].

Located in the state of Chiapas, southern Mexico, the "Lagunas de Montebello" was designated National Park (1959), UNESCO-MAB Biosphere Reserve, Important Bird Area, and Wetland of International Importance Ramsar Site 1325 (2003). The "Lagunas de Montebello" National Park (PNLM) takes its name from the lake district, and consists of more than 60 karst lakes, which vary widely in size and depth [28]. Besides recognized as one of the most beautiful and pristine natural landscapes in the country, the basin has been included in the Water Reserve Program of CONAGUA/WWF as a National Water Reserve for the future (50 years). Despite the name of this National Park and Ramsar site (i.e., Lagunas de Montebello), the limnology of the lakes is essentially unknown [30].

As most Mexican epicontinental aquatic ecosystems, these lakes have not escaped anthropogenic impacts. Starting in 2003, changes in the coloration and transparency of the waters began to be reported in some of the lakes in the northwestern zone of the PNLM, evidencing a local eutrophication process [30,31].

The PNLM lakes constitute a natural laboratory in which to explore and recognize patterns of regional aquatic biodiversity—pelagic rotifers in this case—through a comparison between the numerous natural aquatic bodies that comprise the lake district. Furthermore, the eutrophication of some of these lakes makes it possible to recognize the effects of eutrophication on aquatic biodiversity by comparing the species richness and composition of planktonic rotifers in both pristine (oligotrophic) and impacted (eutrophic) systems.

Therefore, the aim of the present work was to study the biodiversity of pelagic rotifers in a set of PNLM lakes with different morphometric characteristics and trophic statuses. Likewise, we sought to reveal the biodiversity patterns of rotifers, as well as which of the evaluated characteristics (i.e., surface area, maximum and average depth, chlorophyll a concentration, total abundance of copepods, total abundance of cladocerans), have greater relevance in explaining the composition, species richness, abundance, and biomass of the different assemblages of pelagic rotifers of the PNLM lakes.

## 2. Study Site

The PNLM is in the southwestern portion of the state of Chiapas, bordering Guatemala. Its extreme coordinates are 16°04′40″–16°10′2″ N and 91°37′40″–91°47′40″ W (Figure 1); it extends over an area of 64.2 km<sup>2</sup> in the municipalities of La Independencia and La Trinitaria [32]. The climate of the area is temperate, wet, with long summers, the mean annual temperature of 17.3 °C, and precipitation of 1800 mm, and a warm-rainy season lasting from May to December [33].

The area is covered by Lower Cretaceous limestone and is associated with the formation of a karst lake complex composed of dolines, uvalas, and poljes [34] distributed along an elevation gradient of 1200–1800 m a.s.l. [30]. The basin is endorheic and is part of hydrological region number 30, Grijalva–Usumacinta, fed superficially by the Grande de Comitán River; however, due to its karst nature, the main water supply is underground [32].

A total of 17 lakes were chosen (Figure 1) following an NW–SE orientation along the fracture zone [34], which best represent the morphometric and trophic status (according to chlorophyll "a" concentration, Vera-Franco et al. [35]) diversity present in the area (Table 1). Geomorphologically the water bodies could be classified [36] in a) plateau lakes (at the NW, surface water fed, eutrophic) and b) mountain lakes (at the SE, groundwater fed, oligotrophic). Water depth and surface area-among other



variables-determine the lake's thermal type. By incorporating both morphometric characteristics, the lakes turned out to be warm polymictic when shallow, while warm monomictic when deep.

Figure 1. Location of the studied lakes of the "Lagunas de Montebello" National Park, Chiapas, Mexico.

**Table 1.** Morphometry (A = surface area,  $D_{MAX}$  = maximum depth, and  $D_{MEAN}$  = mean depth), thermal type, and trophic status of the studied lakes of the "Lagunas de Montebello" National Park (PNLM), Chiapas, Mexico. Surface, depth, and thermal type are according to Alcocer et al. [28,33], while trophic status, according to Vera-Franco et al. [35]. (Abr. = lakes' names abbreviation).

| Lake         | Abr. | A<br>(ha) | D <sub>MAX</sub><br>(m) | D <sub>MEAN</sub><br>(m) | D <sub>MEAN</sub><br>(m) | Trophic<br>Status |  |  |
|--------------|------|-----------|-------------------------|--------------------------|--------------------------|-------------------|--|--|
| Balantetic   | BL   | 13.6      | 3                       | 1.7                      | Warm polymictic          | Eutrophic         |  |  |
| Chajchaj     | СН   | 9.2       | 12                      | 5.3                      | Warm polymictic          | Eutrophic         |  |  |
| San Lorenzo  | SL   | 181.3     | 67                      | 11.8                     | Warm monomictic          | Eutrophic         |  |  |
| Bosque Azul  | BA   | 52.5      | 58                      | 7.1                      | Warm monomictic          | Eutrophic         |  |  |
| La Encantada | EC   | 8.2       | 89                      | 27.5                     | Warm monomictic          | Eutrophic         |  |  |
| Esmeralda    | ES   | 1.1       | 7                       | 3.6                      | Warm polymictic          | Oligotrophic      |  |  |
| Ensueño      | EN   | 2.7       | 35                      | 21.6                     | Warm monomictic          | Oligotrophic      |  |  |
| Agua Tinta   | AT   | 3.0       | 24                      | 14.7                     | Warm monomictic          | Oligotrophic      |  |  |
| San José     | SJ   | 60.6      | 30                      | 10.3                     | Warm monomictic          | Oligotrophic      |  |  |
| Montebello   | MB   | 96.2      | 45                      | 12.3                     | Warm monomictic          | Oligotrophic      |  |  |
| Cinco Lagos  | CL   | 23.7      | 162                     | 42.5                     | Warm monomictic          | Oligotrophic      |  |  |
| Pojoj        | РО   | 43.7      | 198                     | 35.2                     | Warm monomictic          | Oligotrophic      |  |  |
| Kichail      | KI   | 12.5      | 22                      | 9.5                      | Warm monomictic          | Oligotrophic      |  |  |
| Tziscao      | ΤZ   | 306.6     | 86                      | 28.9                     | Warm monomictic          | Oligotrophic      |  |  |
| Patianú      | PA   | 3.4       | 26                      | 10.8                     | Warm monomictic          | Oligotrophic      |  |  |
| Yalalush     | YA   | 11.5      | 23                      | 9.9                      | Warm polymictic          | Oligotrophic      |  |  |
| Dos Lagos    | DL   | 5.2       | 42                      | 25.2                     | Warm monomictic          | Oligotrophic      |  |  |

#### 3. Methods

Two sampling campaigns were carried out in 2015, corresponding to the two hydrologically contrasting seasons in which the largest differences were expected to occur. The first sampling campaign was in the cold and dry season (C, February), which represents the circulation season of the lakes, and the second campaign took place during the warm and rainy season (W, October), when the lakes are anticipated to be well stratified.

All lakes were sampled in the same way, following the same procedures, and all samples were analyzed equally. The water samples were obtained with a 5-L Uwitec water-sampling bottle in the pelagic zone corresponding to the central and deepest areas of the lakes. A 30-L water-column integrated sample was taken from each lake. The complete 30-L water sample was filtered in situ through a 54 µm mesh size net, and all the retained organisms were concentrated in vials of 50 mL and fixed with 4% formaldehyde for further analysis. We analyzed (identified and counted) all individual concentrated in the 50-mL vials of each one of the 17 lakes for a total of 34 samples (17 from the cold and dry season, and 17 from the warm and rainy season). We counted the entire 50 mL samples; no sub-sampling (i.e., aliquot) method was used.

We first quantified the total zooplankton abundance using a Sedgwick Rafter chamber under an optical microscope. Rotifers were further separated from the rest of the zooplankton and identified using specialized taxonomic keys [6,37]. All rotifer names were confirmed with the World Rotifer Catalog (Jersabek and Leitner [38]) and the List of Available names (LAN) part Rotifera; International Commission of Zoological Nomenclature: http://iczn.org/lan/rotifer. The total zooplankton biomass was evaluated, according to Bonecker et al. [39]. The rotifer biomass was measured as biovolume calculated based on the geometric formulas proposed by Ruttner-Kolisko [40]. The wet weight was estimated from the biovolume of each individual [41]. The dry weight corresponds to 10% of the wet weight [42].

## 4. Data Analysis

A species accumulation curve was calculated, according to Ugland et al. [43] to estimate the number of species in the region (i.e., lake district) and indicate the adequacy of the rotifer survey in representing their biodiversity of Montebello lakes. We calculated alpha (species richness per lake) diversity. To identify the dissimilarity between the lakes, we used the Bray Curtis index. To compare the abundance and biomass of the rotifer communities of the lakes between both seasons (cold/dry and warm/rainy), a paired samples Student's *t*-test was used, and the data was ln-transformed [ln(x + 1)] to reduce skew distributions. To compare the rotifer communities (abundance and biomass) between eutrophic and oligotrophic lakes and between shallow and deep lakes, Student's *t*-tests for independent samples were used, since the "n" of the lake groups are different and are not paired (eutrophic = 5; oligotrophic = 12; shallow = 4; deep = 13). We first verified that normality (Kolmogorov-Smirnov test) and homogeneity (Levene test) of variance assumptions were met for all Student's *t*-test.

To describe the faunistic dissimilarity between lakes, the lakes were classified considering abundance values of the rotifer species  $[\ln(x + 1)]$  with a cluster analysis (UPGMA) based on the Bray Curtis dissimilarity index. A similarity percentage analysis (SIMPER) was performed on the rotifer species abundance data to identify the species most responsible for the formation of lake groups.

To explore the variables that better explained the lakes' similarity regarding rotifer species abundance, a canonical correspondence analysis (CCA) was carried out, including maximum and average depth, trophic status (as chlorophyll a concentration), surface area, total abundance of copepods, and total abundance of cladocerans as independent variables; while the rotifer species abundance was used as the dependent variable. Another equivalent CCA was carried out but now considering biomass of copepods, cladocerans, and rotifers instead of abundance. The statistical significance of the CCA analysis was tested using a Monte Carlo permutation test, and the variance inflation factors (VIF) of the variables were calculated to determine the possible linear dependencies. Student's *t*-tests and

cluster were performed using IBM SPSS Statistics V25.0 and Bray Curtis index, SIMPER, and CCA with R Core Team [44].

#### 5. Results

#### 5.1. Species Richness and Composition

A total of 21 rotifer species belonging to the Monogononta subclass, represented by eight families, were identified in the pelagic zone of the lakes (Table 2). The regional species accumulation curve (Supplemental Materials Figure S1) suggests that this value is close to the actual species richness present in the PNLM. The species richness was 19 species ( $\approx$ 91% of total identified rotifers) for the cold/dry season and 16 species ( $\approx$ 76% of total identified rotifers) for the warm/rainy season. The species richness per lake ranged from 1 (5%) to 12 (57%) species, with an average ± standard deviation of 5.2 ± 3.2. A total of six lakes (Balantetic, Chajchaj, San Lorenzo, Bosque Azul, La Encantada, and Kichail) showed the highest species richness, with 7 to 12 species. The other 11 lakes had species richness values lower than 7.

Out of the 21 species, 14 species (67%) were found in both seasons; while five species (24%) were found only in the cold/dry season and two species (10%) were found only in the warm/rainy season. The species found only in the warm/rainy season were *Lecane papuana* and *Macrochaetus* sp., while those found only in the cold/dry season were *Testudinella patina*, *Brachionus bidentatus*, *B. rubens*, *Platyias quadricornis*, and *Synchaeta oblonga*.

A total of 18 (86%) species were found in the eutrophic lakes, while 15 (71%) were found in the oligotrophic lakes; six species (29%, *Filinia terminalis, Asplanchna girodi, Brachionus bidentatus, Plationus patulus, Platyias quadricornis,* and *Polyarthra vulgaris*) were restricted to the eutrophic lakes, while three species ( $\approx$ 14%, *Ptygura* sp., *Synchaeta oblonga,* and *Macrochaetus* sp.) were restricted to the oligotrophic lakes. (Table 2). Most of the species, 12 (57%), were found in both eutrophic and oligotrophic lakes.

Regarding the species richness, no significant differences were found between the seasons (Student's *t*-tests, n = 34, t = 2.087, p = 0.053) and morphometry (Student's *t*-tests, n = 17, t = 0.393, p = 0.700); while a significant difference was found (Student's *t*-tests, n = 34, t = 6.714, p = 0.000) for trophic status with higher species richness in the eutrophic lakes with  $10 \pm 2$  species compared to the oligotrophic lakes with only  $4 \pm 2$  species.

Independent of the lake category, we found a high dissimilarity in species composition between lakes. *Keratella americana* was the species that occurred in most of the studied lakes (13 lakes,  $\approx$ 77% of all investigated lakes), followed by *Ptygura* sp. (8 lakes,  $\approx$ 47%) and *Filinia longiseta* (7 lakes,  $\approx$ 41%). On the contrary, in total, around half (52%) of the species were observed in only 1–3 lakes.

**Table 2.** Taxonomic list of the planktonic rotifer assemblages of the lakes of the PNLM, Chiapas, Mexico, in both seasons (C = cold/dry; W = warm/rainy, S = species richness, Nr. = number of lakes where each species was recorded). (Abbreviations of lakes' names as in Table 1.).

| Phylum Rotifera Cuvier 1798                     | Eutrophic |     |     |     |     |    | Oligotrophic |     |     |    |     |     |     |     |    |    | Nr  |      |
|---|-----------|-----|-----|-----|-----|----|--------------|-----|-----|----|-----|-----|-----|-----|----|----|-----|------|
|   | BL        | СН  | SL  | BA  | EC  | ES | EN           | AT  | SJ  | MB | CL  | РО  | KI  | ΤZ  | PA | YA | DL  | 141. |
| Subclass Monogononta Plate, 1889                |           |     |     |     |     |    |              |     |     |    |     |     |     |     |    |    |     |      |
| Order Flosculariaceae Harring, 1913             |           |     |     |     |     |    |              |     |     |    |     |     |     |     |    |    |     |      |
| Family Hexarthridae Bartos, 1959                |           |     |     |     |     |    |              |     |     |    |     |     |     |     |    |    |     |      |
| 1. Hexarthra intermedia (Wisniewski, 1929)      |           |     | C/W | C/W | W   |    | С            |     |     |    |     |     | С   | С   |    |    |     | 6    |
| Family Testudinellidae Harring, 1913            |           |     |     |     |     |    |              |     |     |    |     |     |     |     |    |    |     |      |
| 2. Testudinella patina (Hermann, 1783)          | С         | С   |     |     |     |    |              |     |     |    |     |     | С   |     |    |    |     | 3    |
| 3. <i>Ptygura</i> sp.                           |           |     |     |     |     |    | C/W          | C/W |     | С  | С   | С   | С   | С   | С  |    |     | 8    |
| Family Trochosphaeridae Harring, 1913           |           |     |     |     |     |    |              |     |     |    |     |     |     |     |    |    |     |      |
| 4. Filinia longiseta (Ehrenberg, 1834)          | C/W       | C/W | C/W | С   | C/W |    |              |     | W   |    |     |     |     |     | С  |    |     | 7    |
| 5. F. terminalis (Plate, 1886)                  |           | W   | C/W | С   |     |    |              |     |     |    |     |     |     |     |    |    |     | 3    |
| Order Ploima (Hudson and Gosse, 1886)           |           |     |     |     |     |    |              |     |     |    |     |     |     |     |    |    |     |      |
| Family Asplanchnidae Eckstein, 1883             |           |     |     |     |     |    |              |     |     |    |     |     |     |     |    |    |     |      |
| 6. Asplanchna girodi de Guerne, 1888            | W         | W   |     |     | С   |    |              |     |     |    |     |     |     |     |    |    |     | 3    |
| Family Brachionidae Ehrenberg, 1838             |           |     |     |     |     |    |              |     |     |    |     |     |     |     |    |    |     |      |
| 7. Brachionus angularis Gosse, 1851             | C/W       | C/W |     |     | С   |    | С            |     |     |    |     |     |     | С   |    | W  |     | 6    |
| 8. B. bidentatus Anderson, 1889                 | С         |     |     |     |     |    |              |     |     |    |     |     |     |     |    |    |     | 1    |
| 9. B. calyciflorus species complex Pallas, 1766 | C/W       | C/W |     | W   |     |    |              |     |     |    |     |     |     |     | С  | W  | W   | 6    |
| 10. B. havanaensis Rousselet, 1911              |           | C/W | C/W | С   | С   |    |              |     |     |    | С   |     |     |     | С  |    |     | 6    |
| 11. <i>B. rubens</i> Ehrenberg, 1838            |           |     |     | С   |     |    |              | С   |     |    |     |     |     |     |    |    |     | 2    |
| 12. Keratella americana Carlin 1943             |           | C/W | C/W | C/W | C/W |    | C/W          |     | C/W | С  | C/W | C/W | C/W | C/W | С  |    | C/W | 13   |
| 13. K. cochlearis (Gosse, 1851)                 |           | C/W | C/W |     | C/W |    |              |     |     |    |     |     | С   |     |    |    |     | 4    |
| 14. K. tropica (Apstein, 1907)                  |           | C/W | C/W | C/W |     |    |              |     |     |    |     |     | С   |     |    |    | C/W | 5    |
| 15. Plationus patulus (Müller, 1786)            | C/W       | W   | W   |     |     |    |              |     |     |    |     |     |     |     |    |    |     | 3    |

Table 2. Cont.

| Phylum Rotifera Cuvier 1798                 |   | Eutrophic |     |    |    |    |    | Oligotrophic |    |    |    |    |    |    |    |    | Nr |   |
|---|---|-----------|-----|----|----|----|----|--------------|----|----|----|----|----|----|----|----|----|---|
|   |   | СН        | SL  | BA | EC | ES | EN | AT           | SJ | MB | CL | РО | KI | ΤZ | PA | YA | DL |   |
| 16. Platyias quadricornis (Ehrenberg, 1832) |   |           |     | С  |    |    |    |              |    |    |    |    |    |    |    |    |    | 1 |
| Family Lecanidae Remane, 1933               |   |           |     |    |    |    |    |              |    |    |    |    |    |    |    |    |    |   |
| 17. Lecane bulla (Gosse, 1851)              | W |           | C/W |    | С  |    |    |              |    |    |    |    | W  | С  |    |    | С  | 6 |
| 18. <i>L. papuana</i> (Murray, 1913)        |   |           | W   |    |    |    |    |              | W  |    |    |    |    |    |    |    |    | 2 |
| Family Synchaetidae Hudson and Gosse, 1886  |   |           |     |    |    |    |    |              |    |    |    |    |    |    |    |    |    |   |
| 19. Polyarthra vulgaris Carlin, 1943        |   | C/W       |     |    |    |    |    |              |    |    |    |    |    |    |    |    |    | 1 |
| 20. Synchaeta oblonga Ehrenberg, 1831       |   |           |     |    |    | С  |    |              |    |    |    |    |    |    |    |    |    | 1 |
| Family Trichotriidae Harring, 1913          |   |           |     |    |    |    |    |              |    |    |    |    |    |    |    |    |    |   |
| 21. Macrochaetus sp.                        |   |           |     |    |    |    |    |              |    | W  |    |    |    |    |    |    |    | 1 |
| S Subtotal C                                | 6 | 9         | 8   | 8  | 7  | 1  | 4  | 2            | 1  | 2  | 3  | 2  | 6  | 5  | 5  | 0  | 3  |   |
| S Subtotal W                                | 6 | 11        | 10  | 4  | 4  | 0  | 2  | 1            | 3  | 1  | 1  | 1  | 2  | 1  | 0  | 2  | 3  |   |
| S Grand Total                               | 8 | 12        | 10  | 9  | 8  | 1  | 4  | 2            | 3  | 3  | 3  | 2  | 7  | 5  | 5  | 2  | 4  |   |

#### 5.2. Abundance and Biomass

The rotifer abundance ranged from 0 to 538 ind L<sup>-1</sup> ( $42 \pm 131$  ind L<sup>-1</sup>) in the cold/dry season and from 0 to 227 ind L<sup>-1</sup> ( $20 \pm 55$  ind L<sup>-1</sup>) in the warm/rainy seasons. No significant difference (Student's *t*-tests, n = 34, t = 1.155, p = 0.265) was found between seasons. The highest abundance was recorded in the shallow and eutrophic lakes Balantetic (C = 120, W = 17 ind L<sup>-1</sup>) and Chajchaj (C = 538, W = 227 ind L<sup>-1</sup>), followed by the deep eutrophic lakes San Lorenzo (C = 17, W = 60 ind L<sup>-1</sup>), Bosque Azul (C = 20, W = 26 ind L<sup>-1</sup>), and La Encantada (C = 23, W = 3 ind L<sup>-1</sup>). No significant difference (Student's *t*-tests, n = 10, t = -2.239, p = 0.056) was found between the shallow and deep eutrophic lakes. All the oligotrophic lakes, regardless of their water depth, had a very low abundance of less than 2 ind L<sup>-1</sup> (Table 3). No significant difference (Student's *t*-tests, n = 24, t = -1.245, p = 0.235) was found between the shallow and deep oligotrophic lakes. However, we did find a significant difference (Student's *t*-tests, n = 34, t = 3.133, p = 0.004) between the eutrophic lakes (with higher abundance) and the oligotrophic lakes (with lower abundance) (Figure 2).



**Figure 2.** Pelagic rotifer abundance (**A**) and dry biomass (**B**) boxplots of the eutrophic (n = 5), oligotrophic (n = 12), shallow (n = 4) and deep (n = 13) lakes of the PNLM, Chiapas, Mexico.

The rotifer biomass ranged (minimum to maximum) from 0 to 20.82 µg L<sup>-1</sup> (2.20 ± 5.40 µg L<sup>-1</sup>) for the cold/dry season and from 0 to 1.95 µg L<sup>-1</sup> (0.2 ± 0.5 µg L<sup>-1</sup>) for the warm/rainy season. No significant difference (Student's *t*-tests, n = 34, t = 2.78, p = 0.797) was found between the seasons. The biomass followed a pattern similar to that of abundance: The shallow eutrophic lakes had the highest values (8.1 ± 9.3, 0.3 to 2.10 µg L<sup>-1</sup>) followed by the deep eutrophic lakes (0.26 ± 0.19, 0.07 to 0.57 µg L<sup>-1</sup>), while all the oligotrophic lakes had biomass values less than 0.04 µg L<sup>-1</sup> (Table 3). Similar to abundance, no significant differences were found between the shallow and deep eutrophic (Student's *t*-tests, n = 10, t = -1.602, p = 0.148) or shallow and deep oligotrophic (Student's *t*-tests, n = 34, t = 2.514, p = 0.017) was found between the eutrophic lakes (which had higher biomass values) and the oligotrophic lakes (which had lower biomass values) (Figure 2).

The highest densities (>100 ind L<sup>-1</sup>) were observed for only three species (14% of all identified rotifer taxa)—*K. americana* (Nmax 260 ind L<sup>-1</sup> in Chajchaj), *K. tropica* (Nmax 140 ind L<sup>-1</sup> in Chajchaj), and *T. patina* (Nmax 102 ind L<sup>-1</sup> in Balantetic)—during the cold/dry season, and only one species (5% of the total identified rotifer taxa)—*K. americana* (Nmax 100 ind L<sup>-1</sup> in Chajchaj)—during the warm/rainy season.

For the cold/dry season, the biomass of 86% of the species was less than 1 µg L<sup>-1</sup>, the highest biomasses (>1 µg L<sup>-1</sup>) were observed again only in three species, *T. patina* (Bmax 18.7 µg L<sup>-1</sup> in Balantetic), *K. americana* (Bmax 1.3 µg L<sup>-1</sup> in Chajchaj), and *A. girodi* (Bmax 1.16 µg L<sup>-1</sup> in Chajchaj). In the warm/rainy season, the biomass of 95% of the species was less than 0.2 µg L<sup>-1</sup>, only *K. americana* contributed the most to the biomass with 0.5 µg L<sup>-1</sup> in Lake Chajchaj.

|              | Laka         |   | Cold/Dr           | y                       | Warm/Rainy |                          |                         |  |  |  |
|--------------|--------------|---|-------------------|-------------------------|------------|--------------------------|-------------------------|--|--|--|
|              | Lake         | S | N (ind $L^{-1}$ ) | B (μg L <sup>-1</sup> ) | S          | N (ind L <sup>-1</sup> ) | B (μg L <sup>-1</sup> ) |  |  |  |
|              | Balantetic   | 6 | 120               | 20.82                   | 6          | 17                       | 0.31                    |  |  |  |
|              | Chajchaj     | 9 | 538               | 9.23                    | 11         | 227                      | 1.95                    |  |  |  |
| Eutrophic    | San Lorenzo  | 8 | 17                | 0.23                    | 10         | 60                       | 0.57                    |  |  |  |
|              | Bosque Azul  | 8 | 20                | 0.12                    | 4          | 26                       | 0.43                    |  |  |  |
|              | La Encantada | 7 | 23                | 0.16                    | 4          | 3                        | 0.07                    |  |  |  |
| -            | Esmeralda    | 1 | <0.1              | < 0.01                  | 0          | 0.0                      | 0.00                    |  |  |  |
|              | Ensueño      | 4 | 0.2               | < 0.01                  | 2          | 1.9                      | 0.02                    |  |  |  |
|              | Agua Tinta   | 2 | 0.2               | < 0.01                  | 1          | 0.3                      | 0.01                    |  |  |  |
|              | San Jose     | 1 | 1.4               | 0.04                    | 3          | 1.3                      | 0.01                    |  |  |  |
|              | Montebello   | 2 | 0.1               | < 0.01                  | 1          | 0.6                      | 0.01                    |  |  |  |
| Oligotrophic | Cinco Lagos  | 3 | 0.1               | < 0.01                  | 1          | 0.5                      | 0.01                    |  |  |  |
|              | Pojoj        | 2 | 0.7               | 0.01                    | 1          | 0.2                      | < 0.01                  |  |  |  |
|              | Kitchail     | 6 | 0.7               | 0.04                    | 2          | 1.8                      | 0.03                    |  |  |  |
|              | Tziscao      | 5 | 1.1               | 0.02                    | 1          | 0.1                      | < 0.01                  |  |  |  |
|              | Pataniu      | 5 | 1.1               | 0.02                    | 0          | 0.0                      | 0.00                    |  |  |  |
|              | Yalalush     | 0 | 0.0               | 0.00                    | 2          | 0.3                      | < 0.01                  |  |  |  |
|              | Dos Lagos    | 3 | 0.3               | < 0.01                  | 3          | 0.3                      | 0.02                    |  |  |  |

**Table 3.** Species richness (S), abundance (N), and dry biomass (B) of the planktonic rotifer assemblages of the lakes of the PNLM, Chiapas, Mexico. (Abr- = lakes' names abbreviation as in Table 1.).

#### 5.3. Multivariate Analysis

The cluster analysis (Bray Curtis index) showed two main groups and one lake (cut at a dissimilarity distance of 0.97) (Figure 3). The first group was comprised of 11 lakes, all of them oligotrophic (10 deep and 1 shallow). All these lakes shared a lower rotifer abundance values compared with the other group. The second group incorporated the five eutrophic lakes (three deep and two shallow). The five lakes of the second group showed higher rotifer abundance. Lake Esmeralda, that was not placed in either of these two groups, is the lake-oligotrophic with the lowest rotifer abundance of all.

The SIMPER analysis showed *Keratella americana* explained the maximum dissimilarity between oligotrophic and eutrophic lakes (~52%), as well as between shallow and deep lakes (~38%); the other rotifer species contributed with <20% of the total dissimilarity (Supplemental Materials Table S1).

For the two CCAs, a p < 0.05 (Monte Carlo permutation test) was observed for the first two axes, as well as VIF values for both CCAs were less than 6, so it was not necessary to eliminate any of the variables. Both canonical correspondence analyses (abundance-based and biomass-based) showed similar results (Figure 4). The lakes were separated into two groups on the first component according to their trophic status, and the abundance and biomass of Copepoda and Cladocera. With the highest densities and biomasses of Copepoda and Cladocera, the eutrophic lakes are located on the right side of the diagrams, while the oligotrophic lakes with lowest densities and biomasses placed on the left side.

In the second component, the water depth (shallow = warm polymictic, deep = warm monomictic), separated the lakes. The shallow and warm polymictic lakes were on the upper part of the diagrams, while the deep and warm monomictic lakes were on the lower part. The species were grouped together with the lakes in which they were present in higher densities and biomasses; the higher densities and biomass clustered towards the right side of the diagrams, while the lower densities and biomass clustered towards the left side (Figure 4).



**Figure 3.** Dendrogram based on abundance values of the rotifer species (Bray Curtis dissimilarity index) lakes of the PNLM, Chiapas, Mexico. (Abbreviations of the lakes' names as in Table 1. S = Functionally shallow lakes; D = deep lakes; O = oligotrophic lakes; E = eutrophic lakes).



**Figure 4.** Canonical correspondence analysis (CCA) triplots of the pelagic rotifers of the PNLM, Chiapas, Mexico (**A**) based on rotifer abundance, and (**B**) based on rotifer biomass. Lakes are indicated by red circles (the abbreviations of the lakes' names as in Table 1). Rotifer species are indicated by blue asterisks (the numbers are the species' names as in Table 2). The arrows represent the environmental constraints (A = surface area,  $D_{MAX}$  = maximum depth,  $D_{MED}$  = mean depth, TS = trophic status (chlorophyll "a" concentration),  $N_{Cop}$  = total abundance of Copepoda,  $N_{Clad}$  = total abundance of Cladocera,  $B_{Cop}$  = total biomass of Copepoda, and  $B_{Clad}$  = total biomass of Cladocera).

#### 6. Discussion

The ample climatic (convergence of temperate and tropical zones) and orographic heterogeneity in Mexico results in an enormous diversity of aquatic ecosystems (Nearctic and Neotropical biogeographic regions conjunction) that has played a very important role in the development of diverse inland water communities [3]. Rotifer inventories of Mexican inland waters report species richness values of 10–125 in rivers [9,11], 7–60 in reservoirs [7–9], 10–65 in oligotrophic [10,45], and 35–80 in eutrophic lakes [9,12]; however, our 21 pelagic rotifer species richness for the PNLM lakes is on the lower limit of those ranges. It is noteworthy that the low biodiversity recorded in the pelagic rotifer assemblage from the lakes of the PNLM matches the low biodiversity reports for other biological assemblages (e.g., benthic macroinvertebrates [46]) of these same lakes.

At a regional scale, the study of Arroyo-Castro et al. [15] in 17 sinkholes from the Cozumel Island, Quintana Roo, showed 36 rotifer species richness, ranging from 0 to 19 species per water body. Although the number of the studied water bodies is equal to our study, the regional (36) species richness of Arroyo-Castro et al. [15] is higher than ours in the PNLM (21). It must be noted that 17 (47%) of the species found in the Cozumel Island were registered only in 1–3 water bodies, which is a similar case to the lakes of the PNLM with 11 species (52%) in 1–3 lakes.

In the Chihuahan desert, the northern Mexican arid zone, Walsh et al. [13] reported 59 rotifer species from 47 saline water bodies, ranging from 1 to 15 species per water body. Once again, 50% of the reported species were found in just a few water bodies. Rios-Arana et al. [14] found a similar singularity (50% of the species present in a single water body) in seven desert springs of the Chihuahan desert, with a species richness of 57 ranging from 1 to 28 species per water body.

All the 21 rotifer species found in the PNLM lakes during the present study have already been reported from water bodies in easter/southeastern Mexico [47,48]; most of the species herein recorded are considered cosmopolitan. *Keratella americana* is commonly found in the Americas, *Brachionus havanaensis* and *Hexarthra intermedia* are neotropical, while *Lecane papuana* is tropicopolitan [48]. Other species found in the PMLM lakes (e.g., *Lecane bulla, Brachionus calyciflorus*, and *Platyias quadricornis*) show large genetic variability [47], indicating that they constitute cryptic species complexes.

Environmentally, based on the studied parameters the lakes of the PNLM differed just in their trophic status (chlorophyll-a concentrations) but in no other environmental characteristics (e.g., temperature, dissolved oxygen, pH) (Alcocer et al. [31]). It is well known that eutrophic lakes have higher concentrations of nutrients, chlorophyll-a, seston, and particulate organic carbon compared to the oligotrophic lakes. Accordingly, although the rotifer abundance of the lakes of the PNLM varied widely between species and lakes (from 0 to 538 ind  $L^{-1}$ ), the largest differences were between the eutrophic lakes (average of  $105 \pm 167$  ind  $L^{-1}$ ) and the oligotrophic lakes ( $0.6 \pm 0.6$  ind  $L^{-1}$ ). It should be noted that in the eutrophic lakes, only three species contributed 80% of the total abundance, which is also recorded in other studies from other eutrophic Mexican lakes (e.g., References [12,49,50]) with abundance values between 500 and 5000 ind  $L^{-1}$ , with three to six species making up more than 70% of the total abundance.

Cervantes-Martínez and Gutiérrez-Aguirre [51] report an average abundance of most rotifers' species ranging from 0 to 20 ind  $L^{-1}$ , where *K. americana* is the most abundant species; these figures and the dominant species are similar to our study. Although biomass of rotifers is not often reported, in tropical lakes, biomass varies from 5 to 10% of the total zooplankton biomass [35,52,53]. The rotifer biomass of the PNLM lakes contributed a similar percentage (5%) to the total zooplankton [54]

Several authors [19,22,55] mention that the species richness and abundance of zooplankton have a positive relationship with the primary productivity of lakes because, when there is more food available in an aquatic system, there is the potential to support more species and in higher densities. Accordingly, it would be expected to have higher values of rotifer species richness and abundance in the eutrophic lakes, while lower in the oligotrophic [55], which was the case in PNLM lakes where eutrophication influenced the rotifer assemblages by augmenting species richness, abundance, and biomass.

Our findings showed a simple rotifer assemblage of the PNLM lakes, for the lower limit of reported species richness ranges in the Mexican area. There is not a simple explanation that could be provided on this; however, some arguments could be considered. First, it must be noted that our regional study involved water bodies of the same type (all karstic lakes), while other regional studies report the biodiversity from various water body types present in the region (e.g., temporal, perennial, lakes, ponds, spring, rivers, streams), which most likely results in higher biodiversity. Second, even though the regional species accumulation curve suggests that the regional species richness value (21) is close to the actual species richness present in the lakes of the PNLM, two methodological concerns must be mentioned. a) Most rotifer studies use nets with smaller mesh size ( $35-\mu$ m or  $25-\mu$ m, References [56-58]) than our ( $54-\mu$ m). b) Rotifer biodiversity studies usually report species from both the littoral and the pelagic zones (e.g., References [7-9,12]), while ours included just the pelagic zone. Lower diversity in the pelagic zone is usually associated with its homogeneity compared with the littoral zone [59].

Alcocer et al. [31] found the PNLM lakes are environmentally similar (e.g., morphometry, water chemistry) to other karstic lakes worldwide. So, if environmental variables apparently are not playing a major role in explaining the comparative simplicity of the rotifer assemblage of the Montebello lakes, it could be assumed that biological variables are important in defining the rotifer biodiversity in the lakes of the PNLM. Although trophic relations are the way the food web functions in oligotrophic and eutrophic lakes worldwide, the specific combination of factors could result in different final scenarios. We herein discuss two factors (food availability—quantity and quality—and competition/predation) are interplaying differently in oligo and eutrophic lakes, so rotifers could be controlled by starvation plus predation in eutrophic lakes, and by starvation plus competition in oligotrophic lakes.

Food availability (phytoplankton type and quantity) is probably influencing rotifers differently in oligo and eutrophic lakes of the PNLM. In the oligotrophic lakes, phytoplankton is represented by small centric diatoms (*Cyclotella*) [31], a "high-quality" food but in rather limited amount ( $<2 \ \mu g \ L^{-1}$ , Vera-Franco et al. [35]). On the other hand, in eutrophic lakes of the PNLM, phytoplankton is dominated (95%) by large filamentous –40 to >100  $\mu$ m-cyanobacteria (e.g., *Limnothrix, Planktothrix* and *Cylindrospermopsis* [54]), a "low quality" food (e.g., hard to manage, low nutritional value with insufficient essential components, production of cyanotoxins [60–63], but rather abundant (>14  $\mu g \ L^{-1}$ , Vera-Franco et al. [35]). In both cases, rotifers could be limited by competition for better-quality food [64,65], which often leads to lower rotifer fitness as observed in other studies [66].

In addition to the low "high quality" food availability, the zooplankton community of the eutrophic lakes of the PNLM includes numerous species of cyclopoid copepods [67], which are natural predators of rotifers. *Microcyclops ceibaensis* and *Thermocyclops inversus* are characteristic examples of cyclopoid copepods inhabiting the eutrophic lakes of the PNLM [67]. Cyclopoid copepods composed  $40 \pm 15\%$  of the total zooplankton biomass of the eutrophic lakes of the PNLM [54]. Therefore, copepods predation [68,69] could also be limiting rotifers in the eutrophic lakes of the PNLM.

On the other hand, in the oligotrophic lakes of the PNLM, the competitive interference with more efficient macrofiltering zooplankton (e.g., Reference [70]) could be another factor playing against the rotifers. The macrofiltering zooplankton of the oligotrophic lakes of the PNLM is represented by calanoid copepods (*Mastigodiaptomus maya, M. nesus,* and *Aglodiaptomus clavipes*) and cladocerans (*Daphnia gessneri* and *D. galeata*) [39]. Calanoid copepods and cladocerans composed 71 ± 13% and  $15 \pm 10\%$ , respectively, of the total zooplankton biomass of the oligotrophic lakes of the PNLM (Fernández, unpublished data). Therefore, competitive interference [57] by filter-feeding copepods and cladocerans could be probably limiting rotifers in the oligotrophic lakes of the PNLM. Of course, we acknowledge mentioned that there might other factors not examined here involved in explaining the comparative simplicity of the rotifer assemblage of the Montebello lakes.

In summary: (a) The regional and individual biodiversity (per lake) of planktonic rotifers of the PNLM is low (regional diversity = 21, per lake diversity = 1 to 12) compared to that reported for other Mexican epicontinental aquatic bodies and other tropical and temperate lakes. (b) The trophic status

was the variable that had the greatest influence on classifying lakes into two groups: Eutrophic lakes (which had higher species richness, abundance, and biomass of planktonic rotifers), and oligotrophic lakes (which had lower species richness, abundance, and biomass of planktonic rotifers). (c) The general low "high-quality" food—phytoplankton—availability coupled with predation pressure (cyclopoid copepods) and cyanotoxins presence in eutrophic lakes, and competitive interference (calanoid copepods) in oligotrophic lakes, most likely explain the simplicity of the rotifer community in the lakes of the PNLM. (d) The lakes of the PNLM showed high distinctiveness (singularity) in species composition, with most species inhabiting just one to three aquatic bodies of the lake districts.

**Supplementary Materials:** The following are available online at http://www.mdpi.com/1424-2818/12/12/454/s1, Figure S1: Accumulation curve of species of pelagic rotifers in 17 lakes of the PNLM, Chiapas, Mexico, Table S1: SIMPER analysis showing the contribution of each specie according to average Bray Curtis dissimilarity between group of depth and trophic status of lakes of the PNLM, Chiapas, Mexico. (Av. Abund. = average abundance, Av. Diss. = average dissimilarity, Contrib. % = percentage contribution, Cum. % = cumulative contribution percentage, Av. Dissimilarity = average dissimilarity).

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