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Rotifers (Rotifera: Monogononta) Associated with Littoral Macrophyte Habitats in Flooded Neotropical Ponds: A Qualitative Study

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Abstract: Rotifers represent an important component of freshwater zooplankton. The high richness of taxa, particularly in littoral macrophyte zones of water bodies in tropical and subtropical flood-prone areas, is a repeatedly reported fact. However, studies on the composition of periphytic rotifers in the Neotropics are reduced and almost non-existent in some regions. A qualitative study on rotifers (Monogononta) associated with littoral aquatic vegetation and their seasonal variation was carried out in three flood-prone ponds in the "Esteros de Camaguán Fauna Reserve" in the Venezuelan plains. For the selection of the collection sites, the two-stage stratified method with proportional affixation was used. Samples of macrophytes and the water associated with them were taken in littoral zones. The percentages of occurrence and numerical frequency were calculated for each rotifer taxa. The faunal similarities and correlations within and between ponds in the same and different climatic seasons were estimated using the Jaccard and Spearman coefficients (α = 0.05), respectively. In total, 102 rotifer taxa associated with 11 species of aquatic macrophytes were identified. The genus *Taphrocampa* with two taxa plus ten other taxa, are new records for Venezuela and one of them for South America. The taxocenosis and the geographic distribution of the reported taxa reflect a typical composition of the littoral zones of tropical regions. The total richness of both planktonic associated with aquatic vegetation and periphytic assemblages were similar. The highest richness of rotifer taxa coincided with the rainy season and the lowest with the early rainy season. The rotifer fauna presented low similarity values within and between ponds according to seasonality and, with some exceptions, between planktonic and periphytic environments. The importance of sampling periphytic rotifers and the influence of the flood cycle, and the degree of macrophyte development in the structuring of periphytic rotifer communities, were confirmed.

Keywords: biodiversity; species composition; rotifer assemblages; epiphyton; Venezuela

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1. Introduction

The phylum Rotifera represents a relatively small group (about 2000 species) of aquatic and semiaquatic organisms whose particular characteristics make them one of the main components of continental zooplankton communities [1]. Rotifers transfer energy from the first links in the food chain to the higher ones [2]; they have extensive feeding habits that include microalgae, bacteria, and detritus due to highly adaptive trophic apparatus [3] while being a food source for both fish and invertebrates. Rotifers are minute metazoans (size range between 50 and 2000 µm) [4] with a short life cycle (the shortest among planktonic metazoans) and high population renewal rates, making them opportunistic and highly adaptable [3]. In addition, characteristics such as parthenogenetic reproduction with the production of resting eggs (in monogononts) or anhydrobiosis (in bdelloids) in situations of environmental stress favor their dispersal and make them, in theory, excellent colonizers [5,6]. Among rotifers, the subclass Monogononta which is characterized by having one ovary, is the richest, with 1570 recognized taxa in more than 100 genera [7]. Most prefer fresh waters and littoral or benthic habitats, with only 200 to 250 being true planktonic species [3].

Lakes and other lentic ecosystems contain numerous habitats, such as the relatively homogeneous pelagial habitats [8] and many different sub-habitats in the littoral zone [9]. In inland water bodies' littoral zones, aquatic macrophytes represent one of the most important habitats, hosting a great diversity of plant and animal groups [10]. It has been shown that rotifers develop diverse and abundant assemblages on aquatic macrophytes and other substrates, with a great majority of the species richness of this group being found on macrophytes [9,11,12].

Aquatic macrophytes offer a set of potential advantages such as microhabitat diversity [6,11,13,14]; a variety of food resources (algae, bacteria, and detritus) [13–15]; refuge against predators [11,14,15]; and reproductive sites [16]. Particular characteristics of plants such as life form (floating, rooted, or submerged), morphological complexity and spatial structure, arrangement and orientation of leaves, stems, and roots [15,17], as well as age, density, and diversity of macrophytes [17,18], among others, create a heterogeneity of habitats and variable conditions that can influence the composition, richness, and density of the rotifers associated with them [15,17].

Many studies have registered complex and diverse associations of rotifers to structurally more complex macrophytes [15,17,18]. Studies carried out in ponds of flooded areas also have shown a higher diversity of rotifer taxa in the littoral zones compared to the pelagic zone [11,16,19–21]

Surprisingly, despite the high diversity of rotifers in littoral macrophyte habitats, there is still relatively little knowledge about the periphytic or planktonic rotifers associated with macrophyte patches. Therefore, the biodiversity of rotifers in these habitats must be considered important and must be used in the monitoring of aquatic ecosystems [12,22] and conservation/management plans [10].

In Venezuela, few studies have included samplings of the littoral macrophyte zones in inland water bodies [19,23–31] but none have included periphytic rotifers.

Hortal et al. [32] suggested that the issue of within-lake habitat diversity can be easily resolved by conducting research separately in each habitat or by including habitat diversity explicitly in the analyses. Therefore, generalizations on zooplankton species distribution across different water bodies, within a single lake, or between the pelagic and littoral zones cannot be made easily without considering this diversity of habitats [10].

The main objective of this study was to contribute to the knowledge of the diversity of planktonic and periphytic rotifer Monogonta fauna associated with littoral aquatic vegetation and its spatial and temporal variations in three shallow ponds in a floodplain region of the Venezuelan plains. Additionally, we studied the similarities and differences between periphytic rotifers assemblages of macrophyte species and structures such as roots, leaves, and stems. We expected to verify the importance of taxonomic surveys that involve aquatic vegetation as substrate-habitats for rotifers in short- and long-term studies and protocols for biomonitoring in neotropical regions.

2. Methods

2.1. Sampling Sites

The Esteros de Camaguán are located in the southwest of Guárico State, Venezuela, and are geographically located between 7°46′00″ and 8°8′30″ north latitude and between

67°15′00″ and 67°37′00″ west longitude, at an altitude of 56 m above sea level (Figure 1). They cover an approximate area of 19,300 ha and are flooded during the rainy season, as a result of the overflow of the Portuguesa River, to the north of its mouth in the Apure River. The region presents a bi-seasonal annual hydrological regime characteristic of the Venezuelan plains, with a dry period from December to April and one rainy period from May to November. The annual average precipitation is 1620 mm, with maximum values between June and August. The average annual temperature is 27 °C, with small variations during the year. The maximum and minimum temperature peaks occur between March and April, during maximum evaporation and July, respectively (Meteorology Service, Venezuelan Ministry of Defense, average data for 1990–1999).

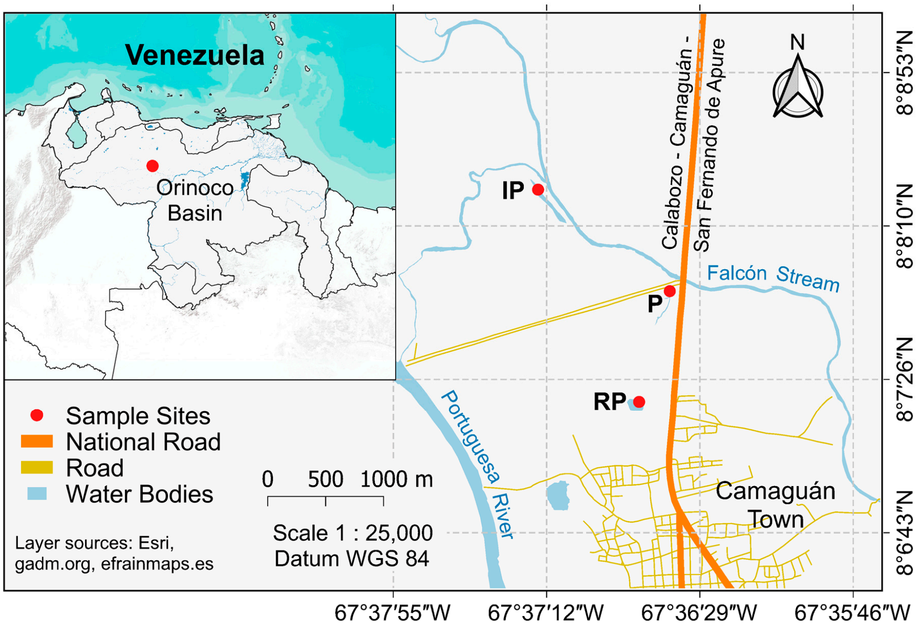

Figure 1. Map of the study area. P: Préstamo, IP: Intermittent Pond, RP: Redonda Pond.

In this research, three ponds near Camaguán town were chosen and called Préstamo (P), Intermittent Pond (IP), and Redonda Pond (RP) (Figure 2). According to Pardo and Zoppi de Roa [33], these ponds show the following general characteristics:

P: It is a rectangular, permanent artificial pond, with an approximate constant area of 12,500 m^2. It has a well-defined littoral zone with a marked slope, surrounded by abundant aquatic macrophytes. At all times, the littoral zone is 100% covered by dense patches of aquatic macrophytes; most of the time, some species are intermixed with others, forming dense communities. Depth: 1.5–4 m; transparency: 12–60 cm; temperature: 28.5–34 °C; conductivity: 70–160 µmhos/cm; dissolved oxygen: 2–6.6 mg/L; pH: 6–7.5.

IP: This temporary natural pond is the smallest of the three studied, with an approximate maximum area of 2710 m^2 and a minimum of 590 m^2. The maximum depth reached is 1.93 m in the rainy season, becoming completely dry in the months of maximum drought. The marginal region presents a very slight slope, with scarce aquatic vegetation distributed heterogeneously around the pond during the study. Perhaps due to its shallowness, the pond almost always presents a low richness and abundance of macrophytes. Depth: 0.06–2 m; transparency: 6–14 cm; temperature: 27.5–42 °C; conductivity: 60–160 µmhos/cm; dissolved oxygen: 6.6–7 mg/L; pH: 6.5–7.2.

RP: It is the largest and deepest of the ponds studied, with an approximate area of 27,445 m^2. The characteristics of the littoral zone are very similar to those of the IP with a slight slope and vegetal heterogeneity both in distribution around the pond and in coverage. Depth: 1.45–5 m; transparency: 11–90 cm; temperature: 31–34 °C; conductivity: 74–99 µmhos/cm; dissolved oxygen: 2.3–7 mg/L; pH: 6.3–7.3.

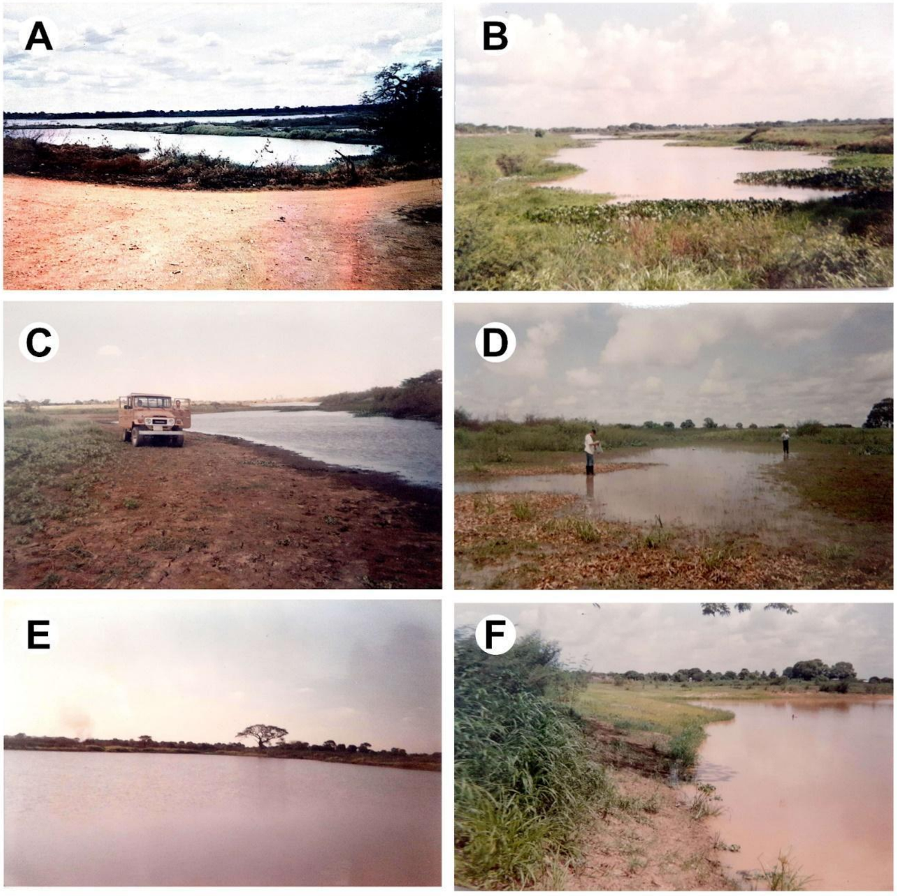

Figure 2. General view of water bodies in contrasting seasons. Préstamo: (**A**) beginning of the drought, (**B**) beginning of the rain. Intermittent Pond: (**C**) beginning of the drought, (**D**) beginning of the rain. Redonda Pond: (**E**) beginning of the drought, (**F**) beginning of the rain.

2.2. Field Samplings

The ponds were sampled on four different dates: the beginning of the drought, the beginning of the rains, the full rains (full flood) in 1996, and the end of the drought in 1997.

The choice of the sampling points in each pond and the climatic season was made using the Two-Stage Stratified method with Proportional Allocation [34,35]. In this design, each pond presented a well-defined littoral zone with different areas of macrophyte species around it. The first step in choosing the sampling points was to discriminate the different areas in which the littoral was constituted based on the presence of macrophyte species and their coverage. That is, the littoral zone of each pond was stratified, thus establishing the primary strata. Therefore, each primary stratum consisted of a specific plant species composition, whose number remained fixed throughout the study. When more than one area with the same macrophyte species composition was present around the pond, the same number was assigned to each.

Once established, each primary stratum was divided into sampling points by numbered imaginary lines. The sampling points were selected by stratum through a table of random numbers. Each macrophytes species within each primary stratum corresponds to the secondary stratum in that primary stratum, and all species were sampled. The number of sampling points and the number of samples of each plant species (secondary stratum) depended on the coverage of the stratum and the abundance of the macrophyte species.

Once the primary and secondary strata were selected, the following procedure was followed in each pond and climatic season:

1. For the qualitative study of the periphytic rotifers, 2–30 plants were taken from the submerged part of the rooted macrophytes and complete plants of the floating aquatic

macrophytes. The number of macrophyte units collected varied depending on the density of each macrophyte species in the ponds on each sampling date. Macrophytes were stored completely and individually in plastic bags, labeled, and preserved in a 5% formalin solution.

2. To study littoral planktonic rotifers, water samples were taken in the same primary strata identified in each pond and climatic season. When the littoral zone was deep enough, the samples were taken with a pump and a 2-L Van Dorn bottle and filtered with a 45 µm hand mesh. In times of maximum drought and early rain, when the littoral zones were very shallow, a 45 µm mesh size hand net was used to avoid reaching the bottom so as not to resuspend the sediments. The water samples were also preserved in a 5% formalin solution.

2.3. Laboratory Analysis

For the littoral planktonic rotifers, the filtered water samples were entirely analyzed. To analyze periphytic rotifers, a combination of two methods was used: (1) For macrophyte species with large stems and leaves, their surfaces were scraped with a small spatula and repeatedly washed with tap water. (2) In plant species with very small leaves, the samples were washed and shaken several times under clean running water to ensure no adhering organisms remained. In both cases, the water samples obtained were passed through several sieves until they were finally filtered with a 45 µm mesh to eliminate plant remains and other large particles as much as possible. The resulting samples were preserved in 5% formalin solution and analyzed entirely, or subsamples were analyzed repeatedly until no new species were found. The rotifer specimens were observed in Bogorov chambers and identified under a microscope in temporary mounts with glycerin and Hoyer's medium on slides. This method makes it possible to gradually lighten the specimen without breaking it up or disintegrating it, so internal characters such as trophies or external ones such as plates, folds, extensions of the lorica, and other characters can be more easily visualized. This semi-permanent mounting technique allows the identification of some species with thin lorica or those in which the preservation medium produces artifacts.

For the taxonomic identification of rotifers, the following works were consulted: [27,36–46] among others. The information on the current valid species names was confirmed using the "Rotifer World Catalog" [47].

2.4. Data Analysis

The percentage frequency of occurrence (% F.A.) and the numerical frequency (% F.N.) of each species within and between ponds in each climatic season were calculated to estimate the relative importance of each rotifer species by habitat and according to seasonality. To estimate the similarity in the composition of species between the different strata of each pond and between ponds concerning seasonality, the Jaccard Community Coefficient (taken from Shiel et al. [48]) was used:

$CC = c/(a + b - c)$ where:

a is the number of taxa in sample 1;

b is the number of taxa in sample 2;

c is the number of taxa common to both samples.

Likewise, the statistical method of Spearman's Rank Correlation Coefficient [49] with a 5% significance level was used.

3. Results

3.1. Composition of Littoral Macrophytes

The primary and secondary strata resulting from the sampling by pond and according to seasonality are shown in Figure 3. A total of 22 primary strata were obtained, and 11 secondary strata (species of macrophytes) were identified throughout the study period. Differences regarding the number of strata were obtained, not only between the ponds on the same sampling date but also between different sampling dates. The primary strata, characterized by a species or a community of species of macrophytes, were, with rare exceptions, very different from one another and showed variations in both diversity and coverage on the littoral margin of the three ponds. While P maintained a littoral zone bordered by abundant and diverse macrophytes throughout the study, the other two ponds presented littoral zones free of aquatic vegetation or with a low coverage, especially at the sampling times corresponding to the beginning of the rains (two ponds) and at the end of drought (RP). At the end of the drought, IP was completely dry. The most frequent and abundant aquatic macrophyte species in P were *Pontederia crassipes* Mart. (floating), *Hymenachne amplexicaulis* (Rudge) Nees (rooted, emergent), *Salvinia auriculata* Aubl. (floating), and *Marsilea polycarpa* Hook & Grew (floating), which occurred in isolated patches or formed part of a stratum. IP showed the least diversity, with *Hymenachne amplexicaulis* being the dominant species at the beginning of the rain (only incipient coverage) and in full rain (practically covering the entire pond). RP presented a scarce development of macrophyte coverage that was almost always less abundant. *Pontederia crassipes* and *Marsilea polycarpa* were the most frequent species, never alone and associated with other pre-existing or new species such as *Ludwigia helminthorrhiza* (Mart.) Hara (rooted, emergent), *Aeschynomene* sp. (rooted, emergent), and *Paspalum repens* Berg and *Echinochloa crus-galli* (L.) P. Beauv. (rooted, emergent). *Cyperus blepharoleptos* Steud (rooted, emergent), only present at the beginning of the drought, was the most abundant aquatic plant in the three ponds. Other low abundant species that were recorded were *Cyperus* sp. (only in P) and *Pontederia cordata* L. (in P and in RP).

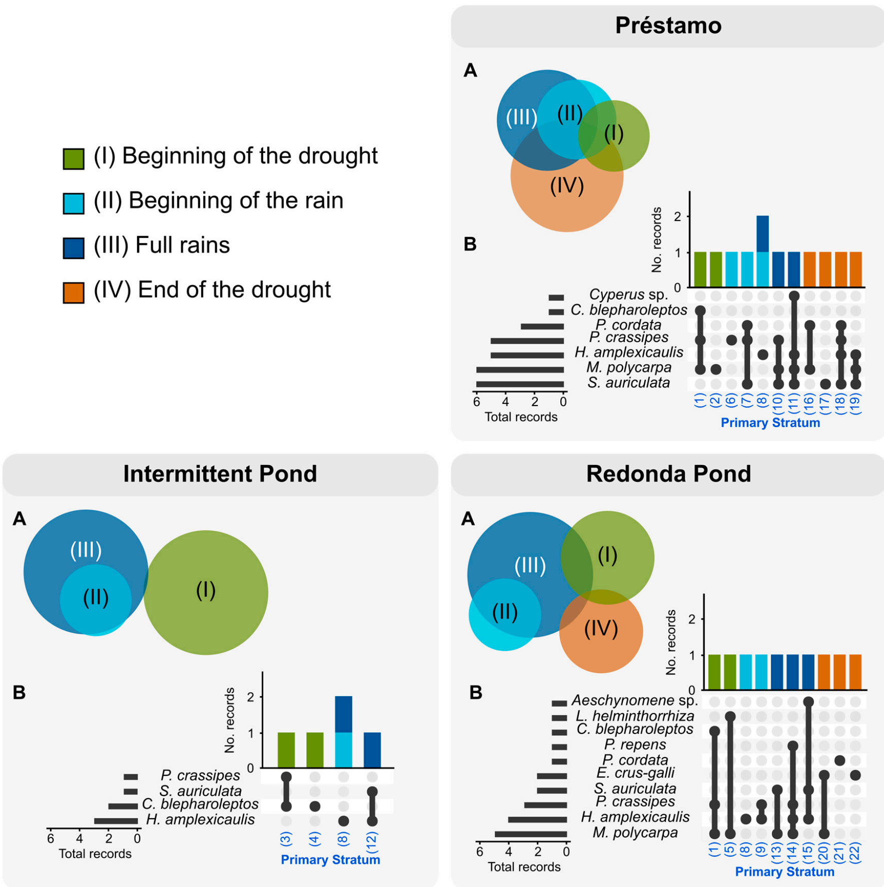

Figure 3. (**A**) Representation of the number of similar secondary strata per pond in each sampling period. The size of the circles is indicative of the number of macrophyte species in each sampling. (**B**) Number of records of primary and secondary strata obtained during the study. The vertical bars represent the primary strata by sampling date; below are the species that comprise each primary stratum. The horizontal bars on the left show the total number of records registered in each secondary stratum throughout the study period.

3.2. Composition and Taxa Richness of Rotifers

Identifying periphytic and planktonic rotifers associated with littoral aquatic vegetation yielded a list of 102 taxa. The list of identified taxa, occurrence in plankton or associated with each macrophyte species, geographical distribution, and seasonal occurrence is given in Table 1.

Table 1. List of rotifer taxa found in the three studied ponds and their geographic distribution (GD), occurrence in the sampled strata, and climatic season. (*) = First report in South America; (**) = first report in Venezuela; UD = Uncertain Distribution; PT = Pantropical; NT = Neotropical; C = Cosmopolita (pl) plankton; (a) *Cyperus blepharoleptos*; (b) *Pontederia crassipes*; (c) *Marsilea polycarpa*; (d) *Pontederia cordata*; (e) *Salvinia auriculata*; (f) *Hymenachne amplexicaulis*; (g) *Cyperus* sp.; (h) *Ludwigia helminthorrhiza*; (i) *Paspalum repens*; (j) *Aeschynomene* sp.; (k) *Echinochloa crus-galli*.

Taxa	GD	Secondary Strata	Season
Brachionus ahlstromi Lindeman, 1939	PT	pl	IV
Brachionus bidentatus Anderson, 1889	PT	pl	I
Brachionus dolabratus Harring, 1914	NT	pl	IV
Brachionus mirus Daday, 1905	NT	pl	I, IV
Brachionus quadridentatus Hermann, 1783	C	pl, e, f, h	I, III, IV
Cephalodella forficula (Ehrenberg, 1838)	C	d, e, k	IV
Cephalodella gibba (Ehrenberg, 1830)	C	c, d, e, f, k	I, II, IV
Colurella colurus (Ehrenberg, 1830)	C	f	III
Colurella obtusa (Gosse, 1886)	C	b, c, f	III
Colurella uncinata (Müller, 1773)	C	d	IV
** *Colurella uncinata bicuspidata* (Ehrenberg, 1830)	C	pl, b, c, d, e	I, II, III, IV
** *Dicranophorus forcipatus* (Müller, 1786)	C	pl, a, b, f	I, II, III
Dicranophorus sp.		b, d	I, II, IV
* *Dipleuchlanis ornata* Segers, 1993	UD	pl, b, c	II
Dipleuchlanis propatula (Gosse, 1886)	C	pl, b, c, d, e, f	III, IV
Euchlanis dilatata Ehrenberg, 1830	C	pl, b, f, k	I, II, III, IV
Euchlanis dilatata lucksiana Hauer, 1930	C	pl, a, b	I, II, IV
Euchlanis incisa Carlin, 1939	C	pl, a, b, e	I, II, III
Filinia opoliensis (Zacharias, 1898)	PT	pl, c	I, IV
Filinia terminalis (Plate, 1886)	C	pl, c, d	I
Hexarthra intermedia (Wiszniewski, 1929)	C	pl, c, d	I
Hexarthra intermedia brasiliensis (Hauer, 1953)	PT	pl	I, II
Keratella americana Carlin, 1943	PT?	pl, f	I, IV
Keratella cochlearis (Gosse, 1851)	C	pl, c, e, f	I, II
Keratella lenzi Hauer, 1953	PT	pl	II
Keratella procurva (Thorpe, 1891)	PT	pl, c	I, IV
Keratella tropica (Apstein, 1907)	C	pl	I, II, III
Lecane arcula Harring, 1914	C	pl, b, c, d, f, g, j, k	III, IV
Lecane bulla (Gosse, 1851)	C	pl, a, b, c, d, e, f, g, i	I, II, III, IV
Lecane closterocerca (Schmarda, 1859)	C	pl, a, b, c, d, e, f, i, j, k	I, III, IV
Lecane cornuta (Müller, 1786)	C	pl, a, b, c, d, e, f, g, i, j, k	I, II, III, IV
Lecane crepida Harring, 1914	PT	pl, b, f, g	III
Lecane curvicornis nitida (Murray, 1913)	PT	pl, a, b, c, d, e, f, g, i, k	I, II, III, IV
Lecane decipiens (Murray, 1913)	C	pl, b, d, e, f	I, II, III, IV
Lecane doryssa Harring, 1914	PT	c, f, g, i	II, III
** *Lecane elegans* Harring, 1914	PT	a, b, c, d, f, i	I, II, III, IV
Lecane elongata Harring & Myers, 1926	PT	f	III
Lecane furcata (Murray, 1913)	C	a, b, c, d, f, i, k	I, II, III, IV
Lecane haliclysta Harring & Myers, 1926	PT	pl, a, b, c, e, f, g, i	I, II, III
Lecane hamata (Stokes, 1896)	C	pl, a, b, c, d, e, f, g, i, k	I, II, III, IV
Lecane hastata (Murray, 1913)	C	pl, b, c, f, k	I, II, IV
Lecane hornemanni (Ehrenberg, 1834)	C	pl, b, f	I, III
Lecane inermis (Bryce, 1892)	C	pl, b, c, e, f, g, i, j, k	II, III, IV
Lecane leontina (Turner, 1892)	C	pl, a, b, c, d, e, f, g, h, i	I, II, III, IV

Table 1. *Cont.*

Taxa	GD	Secondary Strata	Season
Lecane levistyla (Olofsson, 1917)	C	g	III
Lecane ludwigii (Eckstein, 1883)	C	pl, b, d, g	I, II, III, IV
Lecane lunaris (Ehrenberg, 1832)	C	pl, a, b, e, f, h	I, II, III
Lecane monostyla (Daday, 1897)	C	pl	III
Lecane papuana (Murray, 1913)	PT	pl, b, c, e, f, h, k	I, II, III, IV
Lecane proiecta Hauer, 1956	NT	pl	IV
Lecane punctata (Murray, 1913)	C	d	IV
** *Lecane pusilla* Harring, 1914	C	b, c, f	III
Lecane pyriformis (Daday, 1905)	C	pl, a, b, c, d, f, g, k	I, II, III, IV
Lecane quadridentata (Ehrenberg, 1830)	C	pl, d, e, f, i	I, II, III, IV
Lecane rhytida Harring & Myers, 1926	PT	b, c, d, e, f, i	I, III, IV
Lecane signifera ploenensis (Voigt, 1902)	C	pl, b, c, d, e, f, i	I, II, III
Lecane ungulata (Gosse, 1887)	C	pl, a, b, c, e, f, g, k	I, II, III, IV
Lepadella cf. *heterodactyla* Fadeev, 1925	C	f	III
Lepadella acuminata (Ehrenberg, 1834)	C	e	IV
Lepadella dactyliseta (Stenroos, 1898)	C	h	I
** *Lepadella donneri* Koste, 1972	NT	pl, c, d, e, f, g	I, III, IV
Lepadella imbricata Harring, 1914	C	c, d, f	III, IV
Lepadella latusinus (Hilgendorf, 1899)	PT	d, e, f	III, IV
Lepadella ovalis (Müller, 1786)	C	b, c, d	I, IV
Lepadella patella (Müller, 1773)	C	pl, c, d	I, II, III, IV
** *Lepadella quinquecostata* (Lucks, 1912)	C	pl, c, k	III, IV
Lepadella rhomboides (Gosse, 1886)	C	pl, b, c, h	I, III, IV
Lepadella triptera (Ehrenberg, 1830)	C	pl, c	III
Macrochaetus collinsii (Gosse, 1867)	C	pl, b, e	I, III
Macrochaetus sericus (Thorpe, 1893)	C	pl, b, e, f	III
Monommata maculata Harring & Myers, 1930	C	pl, b, c, e, f	I, II, III, IV
Mytilina bisulcata (Lucks, 1912)	C	pl	IV
Mytilina michelangellii Reid & Turner, 1988	PT	pl, b, f	I, III
** *Mytilina unguipes* (Lucks, 1912)	C	pl, d, f	III, IV
Mytilina ventralis (Ehrenberg, 1830)	C	pl, b, c, d, e, g	II, III, IV
Plationus patulus (Müller, 1786)	C	pl	I, II, III, IV
Plationus patulus macracanthus (Daday, 1905)	PT	pl, e, f	I, II, III
Platyias leloupi Gillard, 1957	PT	pl, d	II, IV
Platyias quadricornis (Ehrenberg, 1832)	C	pl, b, c, d, e, f	II, IV
Polyarthra dolichoptera Idelson, 1925	C	pl	I, IV
Polyarthra remata Skorikov, 1896	C	pl	I, II, III, IV
Polyarthra vulgaris Carlin, 1943	C	pl	III
Scaridium longicauda (Müller, 1786)	C	pl, b, c, e	I, II, III, IV
Synchaeta stylata Wierzejski, 1893	C	pl	IV
** *Taphrocampa* cf. *annulosa* Gosse, 1851	C	d, e	IV
** *Taphrocampa* cf. *selenura* Gosse, 1887	C	pl, b, c, d, e	I, II, III, IV
Testudinella mucronata (Gosse, 1886)	C	pl, b, c	III
Testudinella mucronata haueriensis Gillard, 1967	PT	pl, b	I, II, III
Testudinella patina (Hermann, 1783)	C	pl, a, b, c, e, f, g, k	I, II, III, IV
Testudinella patina dendradena Beauchamp, 1955	C	pl, a, b, c, d	I, III, IV
Trichocerca bicristata (Gosse, 1887)	C	pl, b, e	I
Trichocerca bidens (Lucks, 1912)	C	pl, b, d, e, f	I, III, IV
Trichocerca braziliensis (Murray, 1913)	PT	pl, b, c, e, g, k	II, III, IV
Trichocerca insignis (Herrick, 1885)	C	pl	I
** *Trichocerca* cf. *kostei* Segers, 1993	PT	d, e	IV
Trichocerca mucosa (Stokes, 1896)		pl, b, c, d, f, k	I, II, III, IV
Trichocerca myersi (Hauer, 1931)	C	pl	III
Trichocerca pusilla (Jennings, 1903)	C	pl, e	III, IV
Trichocerca similis grandis Hauer, 1965	NT	pl	I, III, IV
Trichocerca tenuior (Gosse, 1886)	C	pl, a, e, f	I, II, III
Trichocerca tigris (Müller, 1786)	C	pl, b, c, d, f, h	I, II, III, IV
Trichotria tetractis (Ehrenberg, 1830)	C	pl, a, b, e, f	I, II, III, IV
Sessile org.			I, II, III, IV

The rotifer taxocenosis consisted of a prevalence of species of the genera *Lecane* (31%), *Lepadella* (11%), and *Trichocerca* (10%). From a zoogeographical point of view, cosmopolitan taxa (72%) dominated, followed by pantropical (23%) and neotropical (5%) taxa.

Typical euplanktonic and semiplanktonic taxa such as *Brachionus bidentatus*, *B. mirus*, *Filinia opoliensis*, *F. intermedia*, *Hexarthra intermedia*, *H. intermedia brasiliensis*, *Keratella americana*, *K. cochlearis*, *K. lenzi*, *K. tropica*, *Polyarthra dolichoptera*, *P. remata*, and *P. vulgaris* were found among the littoral planktonic samples in at least one of the three ponds. However, some were also found among periphytic rotifer fauna (Table 1).

3.3. Frequency of Occurrence of Rotifers

Seven taxa belonging to the *Lecane* genus showed values of frequency of occurrence higher than 25%, considering all data of the sampling dates. Of these, only *Lecane leontina* and *L. cornuta* exceed 50% frequency of occurrence (constant species), while *L. bulla*, *L. haliclysta*, *L. hamata*, *L. curvicornis nitida*, and *L. inermis* showed values between 25% and 49% (common species).

Only 24 species were present in all the sampling periods in at least one of the ponds (permanent species), with the *Lecane* genus being the most represented with 13 species (Figure 4). At P, the highest number of permanent species with 15 species was recorded, of which 7 belong to the genus *Lecane*. *Taphrocampa* cf. *selenura* was only recorded in this pond among different species of macrophytes. Seven permanent species were recorded at IP and at RP only two were reported.

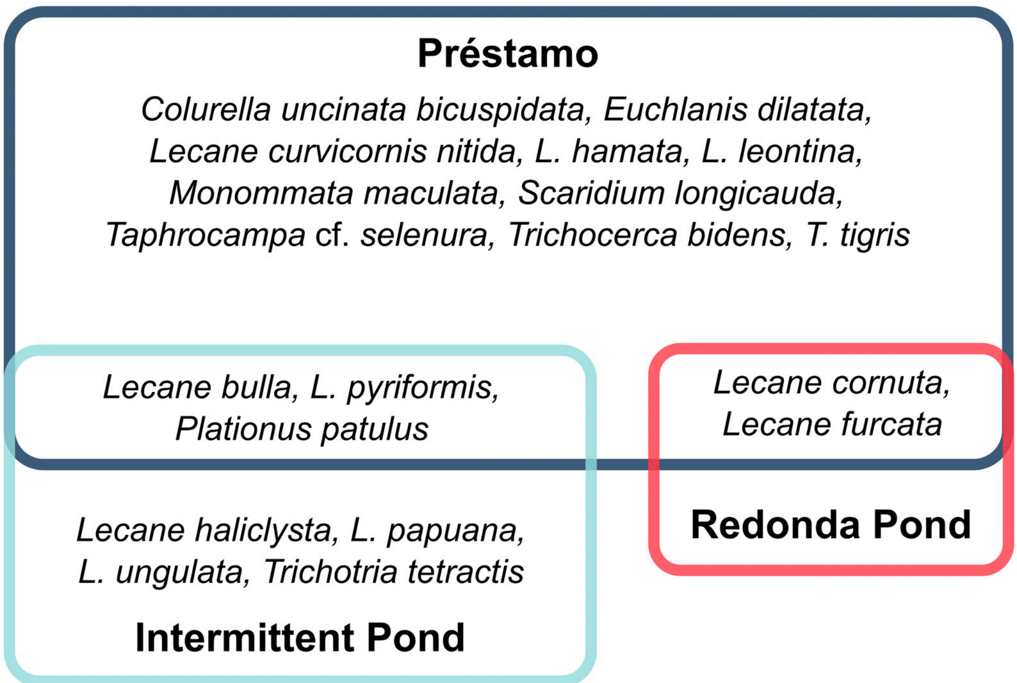

Figure 4. Permanent rotifer taxa at each pond.

Some taxa showed higher values of frequency of occurrence on one or several sampling dates, which indicates a particular relationship with seasonality (Table 2).

Very few rotifer taxa were ubiquitous. Most belong to the genus *Lecane*. The species with the highest degree of ubiquity, found in eleven of the twelve secondary strata, was *Lecane cornuta*, followed by *L. closterocerca*, *L. curvicornis nitida*, *L. hamata*, and *L. leontina*, recorded in ten of the twelve secondary strata.

Table 2. Frequency percentages of rotifer taxa occurrence associated with seasonality.

Taxa	Beginning of the Drought	Beginning of the Rain	Full Rains	End of the Drought
Euchlanis incisa	44	5	9	0
Lecane bulla	64	26	61	19
Lecane cornuta	78	42	33	67 *
Lecane haliclysta	33	16	82	0
Lecane hastata	44	21	49	38
Lecane inermis	0	16	49	19
Lecane leontina	83	63	36	48 *
Lecane papuana	33	42	3	10
Lecane rhytida	11	0	18	43 *
Taphrocampa cf. *selenura*	6	5	3	43 *

* Particularly important during this period in Préstamo.

3.4. Relative Numerical Frequency of Rotifers

The relative numerical frequency of each rotifer taxa was highly variable among the different types of samples analyzed. In each of the macrophyte species and the planktonic samples associated with them, between four and seven taxa showed higher values of relative numerical frequency in each climatic season (Table 3).

Table 3. Rotifer taxa with Relative Numerical Frequency values ≥ 30% among the associated macrophytes and planktonic samples. P: Prestámo, IP: Intermittent Pond, RP: Redonda Pond.

Season	Taxa	Habitats	P	IP	RP
Beginning of the drought	*Lecane curvicornis nitida*	*M. polycarpa*	50		
	Lecane bulla	*C. blepharoleptos*		44	
	Plationus patulus	Plankton		41	
	Lecane cornuta	*C. blepharoleptos*			46
Beginning of the rain	*Lecane cornuta*	*P. crassipes*	67		
		P. cordata	50		
	Lecane leontina	*P. crassipes*	50		
		P. crassipes			50
		Plankton			75
	Polyarthra remata	Plankton	84		
	Keratella cochlearis	*H. amplexicaulis*		50	
	Lecane haliclysta	*H. amplexicaulis*		50	
	Lecane inermis	*H. amplexicaulis*			100
	Lecane papuana	Plankton		40	
Full rains	*Lecane cornuta*	*S. auriculata*	53		
	Lecane closterocerca	*Aeschynomene* sp.			33
	Lecane haliclysta	*P. crassipes*	100		
	Lecane inermis	*M. polycarpa*	38		
		H. amplexicaulis	70	61	38
		M. polycarpa			39
	Testudinella patina	*H. amplexicaulis*			43
	Plationus patulus macracanthus	Plankton	34	32	
End of the drought	*Lecane arcula*	*P. cordata*			33
	Lecane cornuta	*S. auriculata*	33		
	Lecane leontina	*S. auriculata*	33		
	Lecane proiecta	Plankton			55
	Lecane quadridentata	*S. auriculata*	30		
	Lecane rhytida	*S. auriculata*	33		
		M. polycarpa	30		
	Synchaeta stylata	Plankton			41

3.5. The Richness of Taxa of Periphytic and Planktonic Rotifers

The total taxa richness of periphytic and littoral planktonic rotifers, by pond for each sampling season is shown in Figure 5A. P presented the highest number of rotifer taxa in all sampling seasons compared to the other two ponds. The values of taxa richness in all the ponds increased considerably in the season of maximum rains, especially those corresponding to IP and RP. At the beginning of the rain, these last ponds showed the lowest values of species richness (6 and 12 taxa, respectively). This coincided with the lower depth values and a low coverage and low richness of macrophyte species recorded in these ponds compared to the P, whose rotifer taxa richness was much higher (49 spp.).

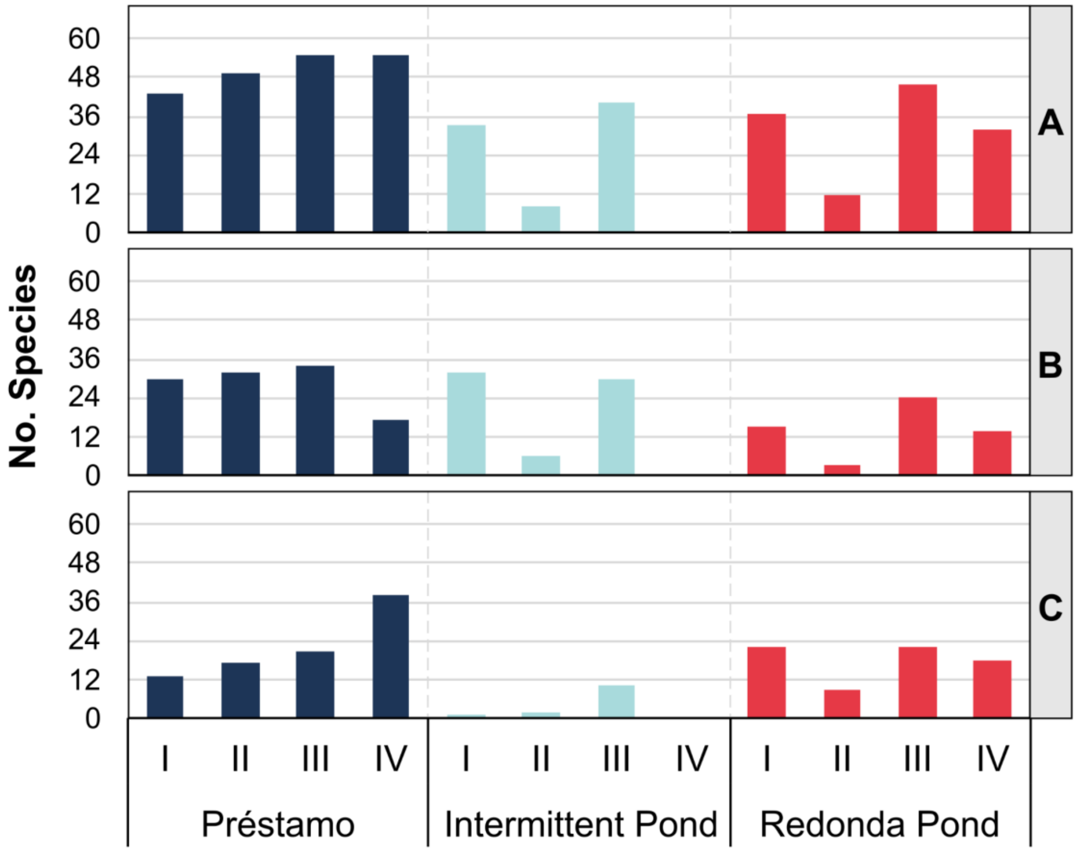

Figure 5. (**A**) Total richness of planktonic and periphytic littoral rotifers in each pond and climatic season. (**B**) Richness of planktonic littoral rotifers common to both types of environments in each pond and climatic season. (**C**) Richness of exclusively periphytic rotifers in each pond and climatic season. I: beginning of the drought; II: beginning of the rains; III: full rains; IV: end of the drought.

Of the total taxa recorded during this study, 81 were found among the plankton associated with the vegetation and 84 among the different aquatic macrophytes, with 62 taxa being common to both habitats. P, with 96 total taxa, contributed the greatest number of periphytic and littoral planktonic taxa, followed by RP (78 taxa) and IP (62 taxa).

Regarding seasonality, the highest total taxa richness was recorded in full rain (74 spp.) and the lowest at the beginning of the rain (53 spp.).

When the results obtained by each pond on each collection date are considered as the total data, it was observed that each water body showed differences regarding the richness of planktonic rotifers associated with vegetation and periphytic ones in each of the samplings (Figure 5B,C).

Among the total taxa (102 taxa), 23 taxa were found exclusively among the macrophytes (Table 4).

Table 4. Species of periphytic (V) and planktonic rotifers associated with vegetation (PL) that were not common to both habitats throughout the study period.

Taxa	V	PL
Brachionus ahlstromi		X
Brachionus bidentatus		X
Brachionus dolabratus		X
Brachionus mirus		X
Cephalodella forficula	X	
Cephalodella gibba	X	
Colurella colurus	X	
Colurella obtusa	X	
Colurella uncinata	X	
Dicranophorus sp.	X	
Dipleuchlanis ornata	X	
Hexarthra intermedia brasiliensis		X
Keratella lenzi		X
Keratella tropica		X
Lecane doryssa	X	
Lecane elegans	X	
Lecane elongata	X	
Lecane levistyla	X	
Lecane monostyla		X
Lecane proiecta		X
Lecane punctata	X	
Lecane pusilla	X	
Lecane rhytida	X	
Lepadella acuminata	X	
Lepadella dactyliseta	X	
Lepadella heterodactyla	X	
Lepadella imbricata	X	
Lepadella latusinus	X	
Lepadella ovalis	X	
Lepadella rhomboides	X	
Lepadella triptera		X
Mytilina bisulcata		X
Plationus patulus		X
Platyias quadricornis		X
Polyarthra dolichoptera		X
Polyarthra remata		X
Polyarthra vulgaris		X
Synchaeta stylata		X
Taphrocampa cf.*annulosa*	X	
Trichocerca insignis		X
Trichocerca cf. *kostei*	X	
Trichocerca myersi		X
Trichocerca similis grandis		X

3.6. Rotifer Taxa Richness in Each Species of Aquatic Macrophyte

The analysis of the total number of rotifer taxa found in each of the macrophyte species throughout the study period is presented in Table 5.

A direct relationship was observed between the most frequent macrophyte species between the ponds and sampling dates and the number of rotifer taxa. Thus, *P. crassipes*, *H. amplexicaulis*, *M. polycarpa*, and *S. auriculata* presented between 46 and 56 rotifer taxa. However, *P. cordata* (rooted) stood out as an exception since, despite being present only in P and RP in dry seasons, it had a total richness of 45 rotifer taxa.

On the other hand, the analysis of the number of rotifer taxa found between the roots and leaves and/or stems of some macrophytes provided variable results (Table 5). In *H. amplexicaulis*, *P. cordata*, and *Cyperus* sp., the numbers of rotifer species found among the different parts of the plant were very similar to each other. On the contrary, the roots of *M. polycarpa* and *P. crassipes* showed a greater number of rotifer taxa.

Table 5. Total number of rotifer taxa recorded in each macrophyte species' roots, stems, and leaves throughout the study period.

Macrophyte	All Plant	Number of Taxa Roots	Stems/Leaves
Aeschynomene sp.	5		
Cyperus sp.	19	12	13
Pontederia crassipes	56	38	13
Echinochloa crus-galli	18		
Hymenachne amplexicaulis	52	40	38
Ludwigia helminthorrhiza	7		
Marsilea polycarpa	51	25	18
Cyperus blepharoleptos	21		
Pontederia cordata	45	30	33
Paspalum repens	15		
Salvinia auriculata	46		

3.7. The Similarity between Strata

The application of the Jaccard Coefficient to the total number of rotifer species present in each of the strata in all ponds and climatic seasons, with few exceptions, resulted in low faunal similarity values. The highest values recorded correspond to the comparisons of the rotifer assemblages of *P. crassipes*, *H. amplexicaulis*, *M. polycarpa*, *S. auriculata*, *P. cordata*, and littoral planktonic samples with those corresponding to the total macrophytes, with similarity values between 0.6 and 0.7. Other similarity values $\geq$ 0.5 were obtained by comparing the rotifer fauna found in *P. crassipes* with that of *M. polycarpa* (0.52), with that of *H. amplexicaulis* (0.54), and with that of the associated plankton (0.5) (Table 6).

Table 6. Faunal similarity values (Jaccard Coefficient) resulting from the comparison of total richness between secondary strata in which similarity values $\geq$ 0.40 were obtained.

	All Plants	Plankton	*P. crassipes*	*M. polycarpa*	*P. cordata*	*S. auriculata*	*H. amplexicaulis*
All plants	1.00						
Plankton	0.57	1.00					
P. crassipes	0.67	0.50	1.00				
M. polycarpa	0.61	0.42	0.52	1.00			
P. cordata	0.54	0.30	0.36	0.47	1.00		
S. auriculata	0.55	0.38	0.44	0.36	0.40	1.00	
H. amplexicaulis	0.62	0.41	0.54	0.44	0.38	0.44	1.00

The comparison of the rotifer assemblages between roots and leaves and/or stems of the same macrophyte species, independent of the pond and sampling date, resulted in similarity values of 0.32 between the different parts of *Cyperus* sp.; 0.34 for *P. crassipes*; 0.48 for *M. polycarpa*, and 0.5 for *H. amplexicaulis* and *P. cordata*.

3.8. The Similarity of the Total Richness of Rotifers between Ponds and between Sampling Seasons

The greatest Jaccard Coefficients were obtained for P at the different collection dates, with a maximum value of 0.5 between the samplings at the beginning of drought and beginning of rain, and a minimum value of 0.31 between the samplings at the beginning of drought and the end of the drought. Similar values were obtained when comparing the total rotifer fauna of IP (0.34) and RP (0.3) at the beginning of drought and maximum rainfall. The rest of the faunal comparisons resulted in very low similarity values.

Likewise, the ponds were segregated based on their respective rotifer assemblages according to seasonality. The highest similarity values were obtained between the three ponds during the maximum rainy season (between 0.44 and 0.58). This highest similarity value was obtained by comparing the rotifers assemblages of P and IP, when the ponds were connected by the overflow of the Falcón stream close to both ponds.

3.9. The Correlation of the Fauna of Littoral and Periphytic Planktonic Rotifers by Pond and Strata in Each Sampling Season

Spearman's Rank Correlation Coefficient was calculated for the littoral planktonic rotifer communities and those associated with different aquatic plants in each littoral zone and stratum on each collection date (Figure 6 and Supplementary Materials). With some exceptions, significant differences ($\alpha < 0.05$) were found between littoral planktonic and periphytic rotifer communities. Among the recorded exceptions, moderate positive correlations dominated (ρ between 0.4 and 0.6) and may be independent of the pond, the macrophyte species, and the primary stratum.

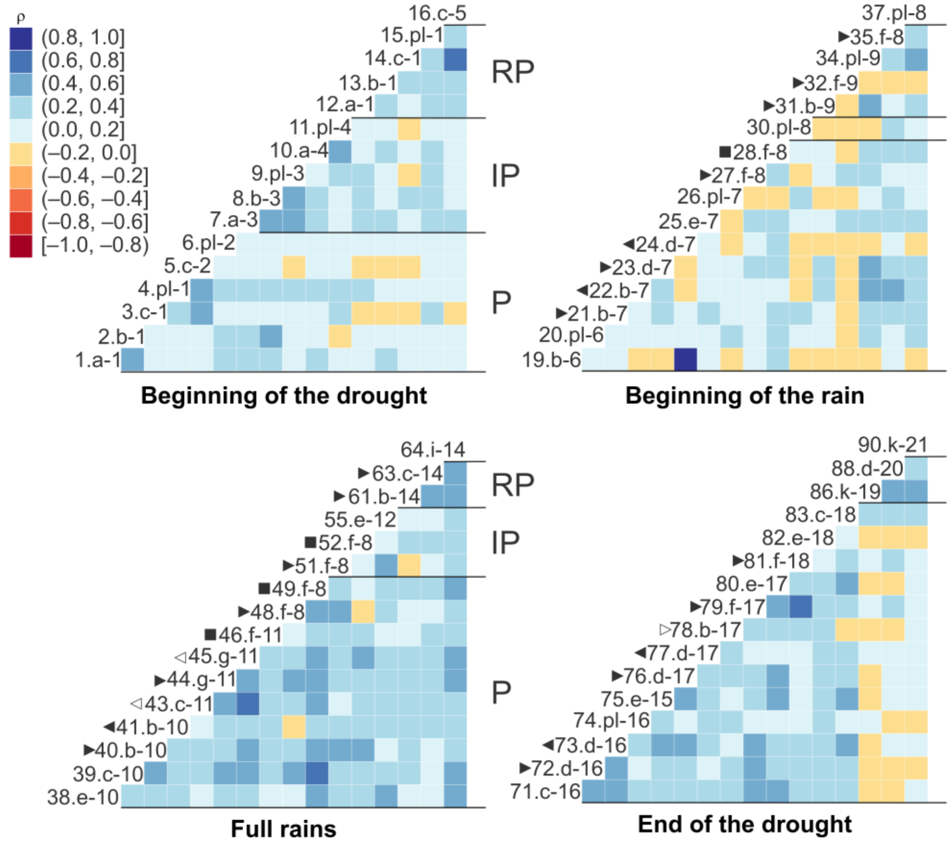

Figure 6. Representation of Spearman's Correlation Coefficients of planktonic and periphytic littoral rotifer communities on each coastline and stratum in the climatic periods evaluated. Only the cases with the highest correlation coefficients are shown; all cases are included in the Supplementary Materials. P: Préstamo, IP: Intermittent Pond, RP: Redonda Pond. The first number represents the case identifier (1–91). The letter represents the secondary stratum: (pl) plankton, (a) *Cyperus blepharoleptos*, (b) *Pontederia crassipes*, (c) *Marsilea polycarpa*, (d) *Pontederia cordata*, (e) *Salvinia auriculata*, (f) *Hymenachne amplexicaulis*, (g) *Cyperus* sp., (i) *Paspalum repens*, (j) *Aeschynomene* sp., (k) *Echinochloa crus-galli*. The number after the hyphen indicates the primary stratum. The symbols represents the part of the plant analyzed: (▶) roots, (◀) stems, (■) leaves, (▷) roots and stems, (◁) stems and leaves.

The highest correlation value found in the sampling during the maximum drought corresponded to the rotifer fauna associated with *P. crassipes* and the stems of *P. cordata* collected in different strata of P (0.9). The full rains registered the largest number of cases with moderate (ρ between 0.4 and 0.6) and strong (0.6 and 0.8) correlation values. The end of the drought also presented an important number of cases with moderate correlation values.

Of all the comparisons of the recorded planktonic and periphytic rotifer assemblages, within and between ponds on the same and different collection dates (Spearman's Coefficient, Supplementary Materials), those associated with *H. amplexicaulis* presented the highest number of cases with correlation values greater than 0.4 compared to those associated with littoral planktonic samples and with the other studied macrophytes.

4. Discussion

The current study provides an update on the rotifer community in Venezuelan freshwater bodies. *Dipleuchlanis ornata* was reported for the first time in South America. The genus *Taphrocampa* with two species, *T.* cf *annulosa* and *T.* cf *selenura*, in addition to *Colurella uncinata bicuspidata*, *Dicranophorus forcipatus*, *Lecane elegans*, *L. pusilla*, *Lepadella donneri*, *L. quinquecostata*, *Mytilina unguipes*, and *Trichocerca* cf. *kostei* were reported for the first time in Venezuela. With these new species, the rotifer fauna for Venezuela has risen to 260 species and 46 genera [50].

Pardo and Zoppi de Roa [33] recorded 50 pelagic taxa for these same ponds. Only five taxa were not found in the littoral zone (*Asplanchna sieboldi*, *Brachionus falcatus*, *B. urceolaris*, *Filinia longiseta*, and *Trichocerca elongata)*, thus resulting in 107 rotifer taxa that were known up to now for the Esteros de Camaguán. The geographic distribution *of Euchlanis dilatata lucksiana*, *Lecane decipiens*, and *Lepadella imbricata* was extended, which had not been previously mentioned for the Orinoco River basin [50,51]. Moreover, the presence of *Trichocerca tigris*, previously registered by Hauer [52], *Euchlanis dilatata lucksiana* by Infante [53], *Mytilina michelangelli* and *Trichocerca myersi* by Michelangelli et al. [23], *Lepadella acuminata* and *L. latusinus* by Medina and Vásquez [54], *Synchaeta stylata* by Saunders and Lewis [55], and *Cephalodella forficula*, *Trichocerca braziliensis*, and *Lecane decipiens* by Zoppi et al. [25] should be highlighted since these taxa have not been cited again since their first report in the country. This number of taxa found is incomplete because some specimens could not be identified at the genera level, such as soft-bodied and sessile species. Additionally, some unusual taxa of the genera *Lecane*, *Colurella*, *Lepadella*, and *Trichocerca*, among others, were found in an abundance of one or two individuals, which made their identification impossible. Comparatively, the richness found during the present study represented 71.8% of the rotifer fauna known for the floodplains of Mantecal, a region of the Venezuelan plains in Apure state, that has been subject to intensive zooplankton research since 1980 [19,23,25], for which a total of 149 taxa have been recorded to date, including littoral pelagic and planktonic monogonont species, as well as some species of bdelloids. From the regional point of view, the total richness corresponds to 41.2% of the total Venezuelan fauna and 18.9% of the total fauna registered for the Neotropical region (according to data from Segers [6]) and is comparable with results obtained by other authors in flood-prone areas of South America [13,16,20,45,56–58].

The predominance of species of the genera *Lecane*, *Lepadella*, and *Trichocerca* was similar to that recorded in studies which sampled littoral areas with vegetation [19,43,45,58–60]. From the zoogeographic point of view, it is also common for this group to record a higher proportion of cosmopolitan species, followed by pantropical and neotropical forms [6,45,61–63].

The differences recorded in the richness of rotifer species between the ponds seemed to confirm the important role played by littoral vegetation in the richness of these organisms, as has also been observed in other water bodies by authors such as José de Paggi [57], Pontin and Shiel [17], Lansac-Toha et al. [64], and Andrade-Sossa et al. [20], among others. The structural complexity offered by the macrophytes in floodplain ponds directly influences the species richness [11,57], which is reflected in the characteristics of the studied ponds. As indicated, P maintained a littoral zone with abundant aquatic macrophytes and total or almost full coverage. IP and RP presented greater variations in richness, composition, and coverage of aquatic macrophytes between samplings. The seasonal cycle had a more severe influence on these ponds with gently sloping marginal edges that somehow seemed to affect the growth and maintenance of aquatic vegetation, which was reflected in lower values of rotifer taxa richness.

In contrast to Pardo and Zoppi de Roa [33] regarding planktonic rotifers in these same ponds, the highest richness of rotifer taxa was obtained in the rainy season. At this time, the ponds were completely flooded; dense formations of *H. amplexicaulis* dominated and covered the entire IP including the pelagic zone. In P and RP, large extensions of *S. auriculata*, *M. polycarpa*, *H. amplexicaulis*, and *P. crassipes* dominated and bordered the entire littoral zone.

A greater richness in littoral rotifer assemblages during the rainy season is attributable to factors such as an increase in nutrients from the decomposition of vegetation, the invasion of alien taxa resulting from the overflow of rivers [56,64–67], faunal exchange between pelagic and littoral regions [68,69], and faunal homogenization between ponds [20,64]. The connectivity between environments during the rainy period influences the richness of taxa, the density, and the renewal in the composition of zooplankton communities [70]. Additionally, the seasonal growth cycles of macrophytes affect the rotifer assemblages associated with them [11], with an interesting aspect being related to the age of the plant. Pontin and Shiel [17] found a greater richness of taxa associated with "older" specimens of *Myriophyllum crispatum* Orchard than with "younger" specimens, as well as a greater number of species found exclusively among the former. In older plants, the development of a greater diversity and abundance of periphytic algae that serve as food for rotifers is a factor that could explain these variations [11].

The lowest total taxa richness of rotifers was obtained at the beginning of the rainy season. P with diverse and abundant littoral vegetation yielded a total of 49 species. On the contrary, the area and depth of IP were drastically reduced, suggesting that it dried up completely during the previous months (maximum drought). The presence of small and incipient patches of *H. amplexicaulis* was characteristic. The sampling reflected only eight rotifer taxa: *Keratella cochlearis*, *Lecane bulla*, *L. curvicornis nitida*, *L. haliclysta*, *L. papuana*, *L. ungulata*, *Plationus patulus*, and *Trichotria tetractis*. RP also showed a very low density and richness of macrophytes. *H. amplexicaulis* and *P. crassipes*, whether associated or not, were not very abundant, and the depth of the littoral zone also decreased. The rotifer richness in this pond and season consisted of 12 taxa; *Lecane papuana* and *L. ungulata* were the only taxa common to this pond. A lower richness in the dry season has been recorded in other investigations that include littoral areas with vegetation and have been attributed to factors such as less environmental heterogeneity due to decreased development of littoral vegetation and reduction in the size and depth of the water body or the influence of local factors or factors specific to each body of water [20,66,71]. The results obtained for the richness in IP and RP are consistent with the shallower depth of the littoral zone and the lower development of vegetation in this zone, and confirm what was previously expressed about the effect of seasonal changes in aquatic vegetation on the community of rotifers.

Comparatively, the total richness of littoral planktonic and periphytic taxa gave very similar results (81 and 84 taxa, respectively), with 62 taxa common to both types of strata and 23 exclusively periphytic. Each sampling date, as well as the total richness, yielded a variable but an important number of exclusively periphytic species that had not been recorded in short- and long-term studies. There are few similar investigations to allow for comparisons. Lucena-Moya and Duggan [18], using artificial plants with three increasing levels of structural complexity (L1 < L2 < L3), found significant differences in the richness of benthic taxa (associated with surfaces) between L3 and L1 but not between L3 and L2. However, they did not find differences in the richness of planktonic rotifer taxa (associated with the water column) or benthic-planktonic rotifer taxa (present on macrophytes and in the water column) concerning the level of complexity. Since non-sessile periphytic taxa are free to move [11], it is quite probable to collect individuals of the same species in both strata when they break off to migrate from one substrate to another.

The relative abundance of rotifers in the different macrophyte species was also highly variable. Of the total number of rotifer taxa recorded, only 18 taxa stood out for their relatively dominant numerical frequencies in certain secondary strata and sampling dates. None of them reflected a trend towards a greater increase in density due to substrate, pond, or seasonality. *Lecane cornuta* was the only taxa that showed a variable but high abundance in different strata on all sampling dates. This was also one of the few taxa with higher occurrence frequency percentages in the entire study, and showed higher degrees of ubiquity. Pardo and Zoppi de Roa [33] recorded it as characteristic and common among the assemblages of pelagic rotifers in these same ponds. Pontin and Shiel [17] also found that of the 55 taxa of periphytic rotifers, four of these were the most abundant. Still, their densities showed significant differences between macrophyte species at the same sampling time. The differences were attributed to dissimilarities in the surface area, structure, or chemical environment of the plants. Additionally, Duggan et al. [11] found significant differences in the abundances of the rotifer species *Euchlanis dilatata*, *Lecane closterocerca*, and *L. lunaris* between *Myriophyllum propinquum* A. Cunn., *Eleocharis sphacelata* R. Br., and *Egeria densa* Planch regardless of their proximity. Therefore, they ruled out the influence of chemical or physical conditions on the variations found between plant species. For these authors, the influence of aquatic vegetation in the structuring of periphytic rotifer communities was evident. The spatial variability of their abundance is related to factors such as plant characteristics, food supply, chemical factors, and degree of protection against predators.

Our findings showing a high taxa richness and only a few numerically dominant taxa coincide with studies of rotifers carried out in Venezuela along the Orinoco River [24,72], Apure River [55], and Mantecal floodplains [23] and in other systems of tropical and subtropical floodplains of South America, such as the Amazon [20,64,71] and Paraná [57,61] and temperate regions [9].

Regarding the littoral zone specifically, Segers [6], referring to the great diversity of monogonont and bdelloid rotifers recorded by Myers [73], concluded that the surprisingly high diversity at low abundances of rotifers in littoral and benthic environments may be attributable to fractional niche use by rotifers in combination with high habitat heterogeneity at micro and macro levels in these types of environments. Of the 18 rotifer taxa that showed the highest relative abundance values in our study, 15 correspond to P strata, a pond that presented greater spatial heterogeneity in the littoral zone throughout the study.

The variations observed in spatial and seasonal composition and richness of rotifer taxa are reflected in the low values of faunal similarity obtained through the Jaccard and Spearman Coefficients and highlight the observed environmental heterogeneity. Among the ponds, P was the only one that reflected relatively high values of faunal similarity between sampling dates.

On the contrary, the other two ponds presented the greatest variations in plant development between the different dates, evidenced by the greatest variations in the richness and structure of the rotifer assemblages.

Regarding seasonality, the highest values of faunal similarity were obtained in the samplings corresponding to full rains (flood period), the date on which the ponds were connected as a consequence of the flooding, as mentioned above. Although dissimilar, the highest value of similarity obtained (0.58) corresponds to the comparison of the rotifer fauna of the “Préstamo” and IP, ponds closer to each other and similarly flooded by the overflow of the Falcón stream. According to Paggi and José de Paggi [61], nearby lakes with the influence of the same hydrological resource during floods must present a high faunal similarity in the composition of rotifers. The connectivity between environments resulting from flood pulses allows the homogenization of faunas [20,60,64]. José de Paggi [60] pointed out a faunal similarity of less than 40% in 82% of the ponds studied in Argentinian fluvial littoral zones before and after the flood period due to changes in faunal composition.

Contrary to other studies on periphytic rotifers in which selectivity for particular aquatic macrophyte species is evidenced [15,17,18], the few cases of faunal similarity found in this study between the same or different plant species and between different parts of the same plant (roots, stems, and submerged leaves) do not allow inferring preferences or associations of rotifer species to any particular macrophyte species or part thereof.

An alternative is that the few comparisons that resulted in faunal affinities may also be indicating the need for more intensive sampling (greater number of samples and higher sampling frequency).

Even so, Pejler [74] stated that most periphytic rotifers are eurytopic and do not show evident selectivity for particular macrophytes. Duggan [11] stated that unlike sessile rotifers dependent on the substrate to which they are fixed, freely mobile periphytic species can migrate to different classes of favorable substrates. Therefore, their dependence on a specific substrate may be less rigorous.

The results indicate the indiscriminate use of the spatial heterogeneity offered by aquatic macrophytes by rotifers. This is reflected in a wide dispersion among the different available niches and, consequently, in a particular and variable faunal composition imposed by the hydrological cycle and by the particular characteristics of each pond, which ultimately promote the particular development of marginal aquatic vegetation, and sustenance of the fauna of periphytic rotifers and littoral planktonic associated with them.

The variations in the composition and coverage of the different macrophyte species in the littoral areas of the ponds suggest that the replacement of one macrophyte by another, the growth of the same macrophyte species during the seasonal cycle, or the association with different aquatic plants, should more frequently promote the colonization and recolonization of microenvironments by rotifers. Segers [6] stated that local diversity may represent an important part of regional diversity due to colonization processes and the dispersal capacity of rotifers. Available niches, even in temporary environments, are quickly filled by incorporating resting eggs. As indicated by Pontin and Shiel [17], the same structure cannot be expected in the rotifer assemblages when the environment and substrates where they develop undergo seasonal changes.

Littoral rotifer assemblages in fluctuating environments such as floodplains are influenced by many factors not considered in this study. However, the few variables that were accounted for allow us to infer at least that the degree of development of the littoral aquatic vegetation and the flood cycle have direct effects on the structure of the rotifer assemblages that developed in the littoral zone of these three ponds. Likewise, the importance and necessity of periphytic rotifer sampling and long-term studies to obtain a better estimate of the local and regional rotifer fauna were verified. It is also considered necessary to standardize similar sampling strategies that allow or facilitate comparisons between results obtained when conducting studies of littoral aquatic communities.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/d15050590/s1, Spearman's Rank Correlation Coefficient.

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