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NATURAL DIET OF ZOOPLANKTON FROM AN OLIGO-MESOTROPHIC RESERVOIR (CLAVELLINOS, SUCRE STATE, VENEZUELA)

Ernesto José González Rivas

Universidad Central de Venezuela, Instituto de Biología Experimental, Calle Suapure, Colinas de Bello Monte, Caracas 1041 – Venezuela.

E-mail: ernesto.gonzalez@ciens.ucv.ve

ABSTRACT: Natural diet of zooplankton from Clavellinos reservoir (oligo-mesotrophic) was studied. A total of 631 specimens (cyclopoid copepods, nauplii, cladocerans, and rotifers) were analyzed with Hoyer's medium, which cleared animals but did not alter the gut contents. Detailed analysis of gut contents showed that particulate material was the main food item for zooplankton in the reservoir. Diatoms and green algae were consumed in high proportion. Significant differences in diets were detected between rainy and dry seasons for nauplii, *Ceriodaphnia cornuta*, *Diaphanosoma spinulosum*, *Brachionus falcatus* and *Plationus patulus*. Adult copepods (*Thermocyclops decipiens*) showed the highest values of the trophic diversity index, while *Keratella* sp. (Rotifera) and the cladoceran *Moina micrura* showed the lowest values. Further studies should focus on the origin of the consumed particulate material.

Key words: Zooplankton, natural diet, Clavellinos, tropical reservoir, trophic diversity.

RESUMEN: Se estudió la dieta natural del zooplancton del embalse Clavellinos (oligo-mesotrófico). Se analizó un total de 631 especímenes (copépodos Cyclopoida, nauplios, cladóceros y rotíferos), mediante aclaración de los organismos con medio de Hoyer, el cual no altera el contenido del tracto digestivo. El análisis detallado de los tractos digestivos mostró que el principal ítem alimenticio del zooplancton del embalse fue el material particulado. Las diatomeas y las algas verdes fueron consumidas en altas proporciones. Se determinó que hubo una elevada superposición entre las dietas de los diferentes grupos analizados. Se detectaron diferencias significativas entre las dietas de las temporadas de lluvias y de sequía para los nauplios, *Ceriodaphnia cornuta*, *Diaphanosoma spinulosum*, *Brachionus falcatus* y *Plationus patulus*. Los copépodos adultos (*Thermocyclops decipiens*) presentaron los mayores valores del índice de diversidad trófica en el embalse, mientras que *Keratella* sp. (Rotifera) y el cladócero *Moina micrura* presentaron los menores valores. Las investigaciones futuras deben enfocarse en el origen del material particulado.

Palabras claves: Zooplancton, dieta natural, Clavellinos, embalse tropical, diversidad trófica.

INTRODUCTION

Zooplankton communities constitute an important link between primary and secondary producers in the aquatic food webs (Zoppi de Roa 1972; López *et al*. 2001) in natural waters. The structure and dynamics of the zooplankton community are a result of the trophic conditions of the waterbodies (Infante & Riehl 1984; Eskinazi-Sant'Anna *et al*. 2002), and therefore, information about zooplankton is an useful tool for the analysis of the ecosystem functioning and for the establishment of lake and reservoir management policies, as well as for detecting human impacts in freshwater ecosystems (Rocha *et al*. 1995).

Generally, it is found that high zooplankton abundance is directly related with high abundance of phytoplankton, especially those species that serve as adequate food items, such as diatoms and some small green algae species, thus representing an indicator of a good nutritional quality for herbivorous zooplankton (Infante & Litt 1985; Torres *et al.* 2014). Zooplankton grazers are an essential trophic pathway by transferring organic carbon from the basis to the top of aquatic trophic webs and by recycling nutrients into the water column (Suthers *et al*. 2019). Zooplankton grazing can control the dynamics of the edible autotrophic biomass in the waterbodies, and therefore can influence the primary production (Yasuno *et al*. 1993; Köthe *et al*. 1997). Most of the time the principal role of zooplankton is to structure the prey community (Kalff 2002), and its effectiveness varies greatly among waterbodies, depending upon their trophic states (Wetzel 2001). Thus, the links between phytoplankton and zooplankton are weaker in eutrophic lakes than in oligotrophic ones (McQueen *et al*. 1986), because the predominant net phytoplankton (>50 µm) in eutrophic lakes is not extensively grazed by herbivorous zooplankton.

In spite of its key role in the aquatic food webs, considering the fact that their feeding behavior is directly involved in important processes such as nutrient cycling, energy transference, and productivity of the aquatic

ecosystems, studies on the natural diet of zooplankton in the tropical freshwaters are scarce (Infante 1973, 1978a; Cisneros *et al*. 1991; Moreno 1992; González 1998; Eskinazi-Sant'Anna *et al*. 2002; González *et al*. 2005, 2006) and knowledge about trophic relationships is inadequate (González 1998). Therefore, the aim of this study was to analyze the natural diet of the zooplankton from Clavellinos reservoir, in order to obtain a better understanding of trophic relationships in this ecosystem, where few researches relating to plankton ecology have been made.

MATERIALS AND METHODS

Study site

Clavellinos reservoir is located in North-Eastern Venezuela (Fig. 1). It was built by damming the Clavellinos stream, in Sucre state. The main morphometric features of the reservoir are shown in TABLE 1.

The reservoir is used for drinking-water supply for the populations of Margarita and Coche Islands, Cariaco and neighboring settlements (512,366 inhabitants); it is also used for irrigation of 6,200 ha (Ferraz de Reyes & Fernández-Álvarez 1988; Bernal *et al*. 2005). It was classified as oligo-mesotrophic (Merayo & González 2010).

Procedure

Monthly quantitative samples were taken from the limnetic zone of the reservoir from October 2006 to September 2007. Zooplankton specimens were taken in the water column (5–0 m) from the reservoir using a plankton net (77 µm of mesh size) (Fig. 1). Animals were anesthetized by adding carbonated water in order to prevent regurgitation (Infante 1978b) and, within 1-2 min, preserved with 4% formaldehyde (final concentration). In the laboratory, specimens were taken one by one with the help of a needle and placed on a slide, where they were cleared with Hoyer's mounting medium (30 g of Arabic gum dissolved in 50 ml distilled water, 200 g of chloral hydrate and 20 ml glycerol), for detailed examination of gut contents, according to the procedure of González (1998). The algae inside the guts were not altered by Hoyer's medium. Algae were identified using taxonomic keys from Yacubson (1972, 1974), Yacubson & Bravo (1983); Rivera *et al*. (1982), Parra *et al*. (1982a, 1982b, 1982c, 1983a, 1983b), and Infante & Riehl (1992). Zooplankton were identified using taxonomic keys from Dussart (1984), Infante (1988), Thorp & Covich (1991), Elmoor-Loreiro (1997), Fernando (2002) and Athibai *et al.* (2013).

Data analysis

Results were expressed as occurrence frequency (%) for each food item. A Chi-squared test (contingency tables) was applied to detect differences between animal diets. The X^2 coefficient was transformed into the Cramer's contingency coefficient (V) (Brown 1981):

$$V = \sqrt{\frac{X^2}{(r - 1)\,N}}$$

where r is the number of species in the original data matrix, and N is the total number of observations. This

TABLE 1. Geographic coordinates and main morphometric features of Clavellinos reservoir (Castillo *et al*. 1973).

Location: Lat. 10°20'55" N – Long. 63°36'05" W
Altitude: 291 m.a.s.l.
Area: 10.5 x 10^5 m^2
Volume: 131 x 10^6 m^3
Mean depth: 12.5 m
Discharge: 14.3 m^3/s
Residence time: 106 days

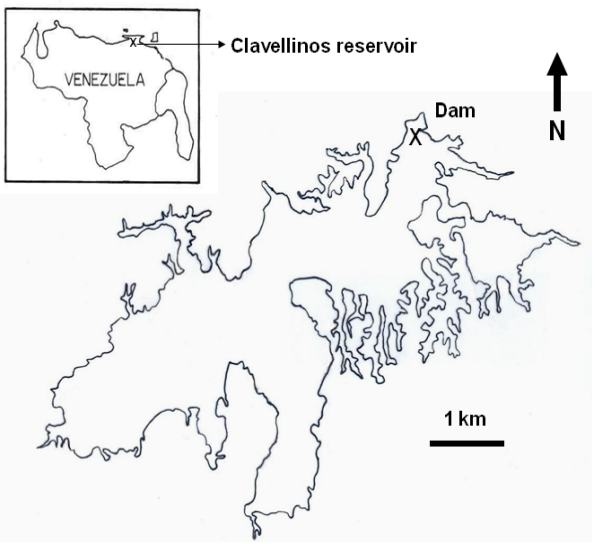

Fig. 1. Map of Clavellinos reservoir, showing the sampling site (X).

coefficient is an index of differentiation (non-overlap) between the diets of the animals. Its maximum value of 1 is achieved when all species have diets without common items; its minimum value of zero is achieved if all species consume the same items in similar proportions. The coefficient of diet overlap was calculated as O = 1 – V (Bulla 1996).

After the X^2 test, a cluster analysis (City-Block Manhattan, single linkage) (Statsoft Inc. 2004) was applied in order to determine the similarity of the gut content of the different zooplankton groups.

The Spearman coefficient test (Siegel 1988) was applied to detect differences between rainy (October – December 2006 and June – September 2007) and dry season (January to May 2007) diets. Diets of the different groups in each climatic period were compared by pairing each food item rank for each zooplankton group from rainy season with its respective equivalent in the dry season.

Finally, the trophic diversity index (D) proposed by Herrera (1976), was calculated:

$$D = - \sum_{i=1}^{s} \log \hat{p}_i$$

Where:

$\hat{p}_i$ = observed occurrence frequencies referred to unity for each food item.

i = 1, 2, ..., s = total number of qualitative food items.

RESULTS

Phytoplankton abundance was determined simultaneously during this research by González (2009), at the same sampling site where zooplankton were collected. Phytoplankton abundance ranged between $4{,}563\times10^3$ (May) and $30{,}369\times10^3$ Cells/l (January), with a mean value of $11{,}246\times10^3 \pm 7{,}334\times10^3$ Cells/l. Diatoms dominated the phytoplankton community from October 2006 to March 2007, while green algae dominated from April to September 2007. *Achnanthidium* was the diatom species which dominated the phytoplankton during almost the whole study period. Other abundant genera were *Cosmarium, Staurastrum, Staurodesmus, Tetraedron, Cyclotella, Navicula, Trachelomonas* and *Lyngbya*. Dominance of phytoplankton groups was as follow: Bacillariophyta 62.1%, Chlorophyta 21.7%, Cyanobacteria 10.0%, Euglenophyta 3.1%, Cryptophyta 1.7% and Pyrrhophyta 1.4%. Most of the phytoplankton cells were smaller than 50 µm in diameter, so they could be included within the category of nannophytoplankton.

The zooplankton community was also sampled simultaneously during this study by Merayo & González (2010). This community was composed of 16 taxa (TABLE 2). *Thermocyclops decipiens* was the dominant species during the whole study period, followed by *Brachionus falcatus, Keratella cochlearis* and *Diaphanosoma spinulosum* (Merayo & González 2010). Zooplankton abundance was low, with a mean value of 62 ± 22 Individuals/l; cyclopoid copepods accounted for up to 65.3% of total zooplankton, followed by rotifers (21.3%), cladocerans (12.9%) and other organisms as ostracods and *Chaoborus* larvae (0.4%).

In relation to the natural diet of zooplankton, a total of 631 specimens (67 empty, 10.6%) were cleared with Hoyer's medium:

•160 cyclopoid copepods (*Thermocyclops*): 11 empty (6.9%).

•101 nauplii: 13 empty (12.9%).

•234 cladocerans (91 *Ceriodaphnia,* 134 *Diaphanosoma* and 9 *Moina*): 26 empty (11.1%).

• 127 rotifers (35 *Keratella,* 54 *Brachionus* and 38 *Plationus*): 16 empty (12.6%).

• 9 ostracods: 1 empty (11.1%).

TABLE 3 shows the identified food items in the reservoir. A total of 17 food items were identified in the specimen gut contents. Excluding the particulate material, this represented 27.1% of the total phytoplankton species present in the reservoir waters. The item "particulate material" is referred to as a mixture of fragments of algae, organic matter in decomposition and mineral particles (González 1998).

Particulate material was identified in almost the 100% of the analyzed specimens which presented some food items in the gut content. Diets will be described below. Occurrence frequencies with values less than 5% will not be mentioned.

Fig. 2a shows the copepod (*Thermocyclops*) dry and rainy season diets. A total of 15 food items were identified in the cyclopoid copepod gut contents. During the dry season, copepods fed on particulate material

TABLE 2. Zooplankton taxa identified in Clavellinos reservoir.

Copepoda (Cyclopoida)
1. *Thermocyclops decipiens* (Kiefer, 1929)
Cladocera
2. *Ceriodaphnia cornuta* (Sars, 1885)
3. *Diaphanosoma spinulosum* (Herbst, 1975)
4. *Moina micrura* (Kurz, 1875)
Rotifera
5. *Anuraeopsis* sp.
6. *Brachionus falcatus* (Zacharias, 1898)
7. *Keratella cochlearis* (Gosse, 1851)
8. *Keratella tropica* (Apstein, 1907)
9. *Hexarthra intermedia* (Wiszniewski, 1929)
10. *Lecane* sp.
11. *Lepadella* sp.
12. *Plationus patulus* (Müller, 1786)
13. *Polyarthra remata* (Skorikov, 1896)
14. *Trichocerca* sp.
Others
15. Ostracoda
16. *Chaoborus* sp.

(100.0%), *Achnanthidium* (58.1%), *Monoraphidium* (17.7%), *Oocystis* (17.7%), *Peridinium* (17.7%), *Navicula* (12.9%), *Trachelomonas* (11.3%) and *Chroococcus* (6.5%). During the rainy season, copepods ingested particulate material (97.7%), *Cyclotella* (40.2%), *Peridinium* (31.0%), *Achnanthidium* (25.3%), *Navicula* (18.4%), *Oocystis* (14.9%), *Trachelomonas* (11.5%), *Monoraphidium* (8.1%), *Microcystis* (8.1%) and *Tetraedron* (5.8%).

Nauplii ingested a total of 10 items during the study period. Particulate material (84.6%), *Chroococcus* (20.5%) and *Achnanthidium* (12.8%) were found in the gut contents during the dry season, while particulate material (95.9%), *Cyclotella* (8.2%), *Achnanthidium* (6.1%) and *Oocystis* (6.1%) were the main food items ingested during the rainy season (Fig. 2b).

Ceriodaphnia specimens showed 9 food items in their gut contents (Fig. 2c). During the dry season, animals ingested particulate material (96.4%), *Achnanthidium* (50.0%), *Monoraphidium* (14.3%) and *Oocystis* (14.3%). During the rainy season, *Ceriodaphnia* included particulate material (98.2%), *Cyclotella* (22.2%), *Achnanthidium* (14.8%) and *Oocystis* (13.0%) were found to be food resources in their diets.

Diaphanosoma included 11 food resources in their diets (Fig. 2d). During the dry period, this cladoceran ingested particulate material (98.4%), *Oocystis* (42.9%) and *Achnanthidium* (28.6%), while during the rainy season showed the following items: Particulate material (100.0%), *Oocystis* (36.8%), *Cyclotella* (10.5%), *Tetraedron* (7.0%), *Trachelomonas* (7.0%) and *Achnanthidium* (5.3%).

Few *Moina* specimens were analyzed due to its scarcity. This cladoceran only ingested particulate material (100.0%) during the study period (not shown in figures).

Brachionus only showed 5 food items in their diets (Fig. 2e). In the dry season, particulate material (100.0%), *Oocystis* (20.0%), *Achnanthidium* (8.0%) and *Monoraphium* (8.0%) were present in the gut contents, while particulate material (100.0%) and *Oocystis* (23.1%) appeared in their diets during the rainy period.

Keratella (not shown in figures) only ingested 2 food items during the study period: Particulate material (100.0% in both dry and rainy seasons) and *Achnanthidium* (17.7% in the rainy season).

Plationus showed a total of 4 food items in their gut contents (Fig. 2f). During the dry season, this rotifer ingested particulate material (100.0%), *Oocystis* (50.0%) and *Achnanthidium* (25.0%); on the other hand, during the rainy season *Plationus* ingested particulate material (100.0%), *Navicula* (12.5%) and *Achnanthidium* (6.3%).

Ostracods (not shown in figures) ingested particulate material (100.0%) during the dry and rainy periods; *Navicula* (20.0%) and *Oocystis* (20.0%) appeared in the gut contents during the rainy season.

Observed and expected frequencies were contrasted using the X^2 test (contingency tables). First, diets for the global period (October 2006 – September 2007) were compared; the experimental X^2 value was 322.09, which was greater than the critical value (X^2= 102.87, α= 0.05; degrees of freedom are: c= [17 food items – 1] × r= [9

zooplankton groups – 1]), indicating that zooplankton groups had significant differences ($p<0.05$) among their diets when the whole study period was considered. Cramer's contingency coefficient (V) was 0.200 (r= 9, N= 1006 observations), so the coefficient of diet overlap (O) had a value of 0.800 (80.0% of diet overlap).

Diets were separated for dry and rainy seasons. For the dry season, experimental X^2 value was 150.47, which was greater than the critical value (X^2= 81.47, α= 0.05; c= [14 food items – 1] × r= [9 zooplankton groups – 1]), indicating that zooplankton groups had significant differences ($p<0.05$) among their diets. Cramer's contingency coefficient (V) was 0.212 (r= 9, N= 419 observations), and the coefficient of diet overlap (O) had a value of 0.788 (78.8% of diet overlap).

For the rainy season, experimental X^2 value was 208.36, which was greater than the critical value (X^2= 95.70, α= 0.05; c= [16 food items – 1] × r= [9 zooplankton groups – 1]), indicating that zooplankton groups had significant differences ($p<0.05$) among their diets. Cramer's contingency coefficient (V) was 0.211 (r= 9, N= 587 observations), while the coefficient of diet overlap (O) had a value of 0.789 (78.9% of diet overlap).

For each consideration (whole study period, dry and rainy seasons), diets were grouped according to their similarities using a cluster analysis.

For the whole study period, Fig. 3 shows that small specimens, which ingested few food items and almost exclusively particulate material, were grouped very closely (rotifers, ostracods, nauplii and *Moina*). *Ceriodaphnia* and *Diaphanosoma* were clustered in the following level of linkage, because they ingested more food items than the previous groups and showed similar diets. Finally, the last level of linkage was occupied by adult copepods, which showed more food items in their gut contents that resulted in a separate group.

During the rainy season, the cluster analysis showed a grouping pattern similar to that previously described for the whole study period, where adult copepods had different diets as compared with the rest of the zooplankton organisms analyzed (Fig. 4).

On the other hand, during the dry season, fewer similarities were found in the specimen diets (Fig. 5). *Moina* and *Keratella* just ingested particulate material in this period, and were grouped together. The rest of zooplankton groups showed differences among their diets, resulting in few similarities, probably due to the slightly greater phytoplankton abundance than during the rainy period.

Results showed that copepod diets were similar during the rainy and dry seasons (r_s= 0.609; $p<0.05$). The same was found for ostracods (r_s= 1.000; $p<0.05$). On the

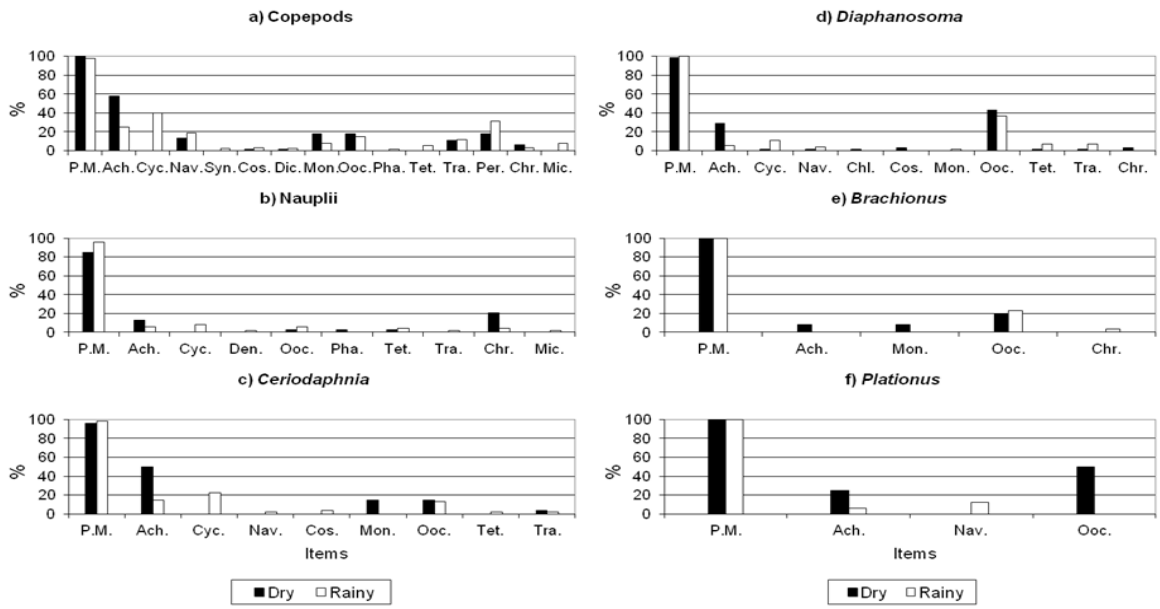

Fig. 2. Natural diet of zooplankton in Clavellinos reservoir during the rainy and dry seasons: a) Copepods, b) Nauplii, c) *Ceriodaphnia*, d) *Diaphanosoma*, e) *Brachionus*, f) *Plationus*. Legends as in Table 3.

other hand, nauplii (r_s= 0.465), *Ceriodaphnia* (r_s= 0.356), *Diaphanosoma* (r_s= 0.358), *Brachionus* (r_s= 0.684) and *Plationus* (r_s= 0.200) showed significant differences (p>0.05) between their rainy and dry season diets.

TABLE 4 shows the trophic (food item) diversity index for each zooplankton group considering the whole study period. Copepods showed the highest value while *Keratella* and *Moina* had the lowest values.

DISCUSSION

Few gut contents were empty (<11%) when animals were collected and this could indicate that zooplankton from the reservoir had sufficient and adequate food particles. Particulate material, probably associated with bacteria (González *et al*. 2006), seemed to be the most important food item for zooplankton from Clavellinos reservoir, due to its presence in all the specimens analyzed. Similar results were found in some Venezuelan reservoirs, such as El Andino (González 1998, 2000), Agua Fría, La Mariposa, Tierra Blanca and Pao-Cachinche (González *et al*. 2005), and Brazilian reservoirs such as Pampulha (Eskinazi-Sant'Anna *et al*. 2002), Broa and Barra Bonita (González *et al*. 2006).

According to Margalef (1983), food web organization in the plankton community is conditioned by an array of factors and elements, among which phytoplankton is an important constituent in the zooplankton diet, because energy enters into the system at the primary producer level. However, detritus, including its associated bacteria, represents another important food source for zooplankton. Filter-feeding animals, like cladocerans from Clavellinos, included particulate material, nannophytoplankton and small fragments of algae in their diets, and therefore they are considered herbivorous (Infante 1988; Wetzel 2001). Unlike cladocerans and calanoid copepods, which are filter-feeding animals, rotifers sediment particles (phytoplankton and detritus) inside their body walls (Horne & Goldman 1994) by using their anterior ring of cilia to direct particles to the mouth; this type of rotifers could be considered herbivorous too (Infante 1988).

Zooplankton grazing is recognized as a factor that influences carbon flow patterns in pelagic systems (Schoenberg 1990). Organic matter cropped by grazers varies from a small fraction in enriched lakes to instances in which almost all the algal production is consumed. According to Gulati (1975) and Horne & Goldman (1994), most zooplankton are filter feeders on a suspension of mixed bioseston composed of algae, bacteria, and detritus. Thus, herbivorous zooplankters include microalgae, bacteria and detritus in their diets (Edmondson 1957; Gliwicz 1969; Haney 1973; Infante 1988).

Cyclopoid copepods feed by grasping the food items rather than filtering them (Infante 1988; Horne

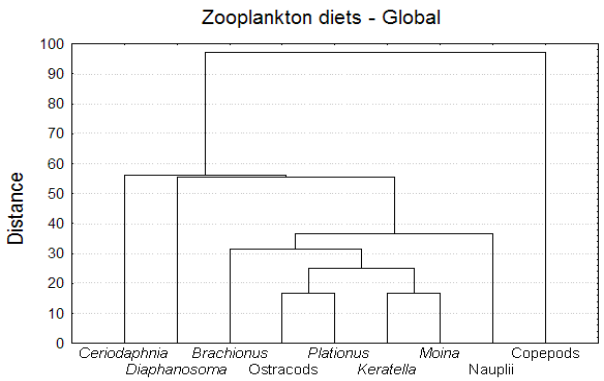

Fig. 3. Cluster analysis for zooplankton diets considering the whole study period.

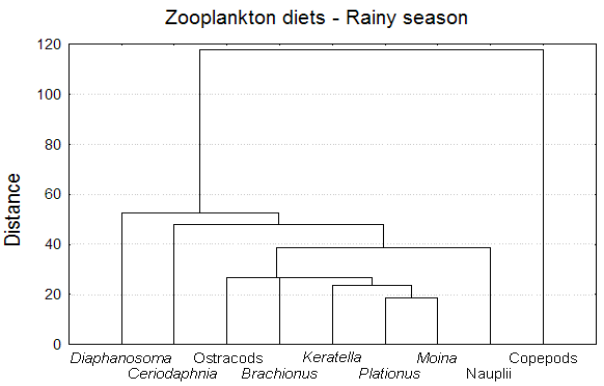

Fig. 4. Cluster analysis for zooplankton diets considering the rainy season.

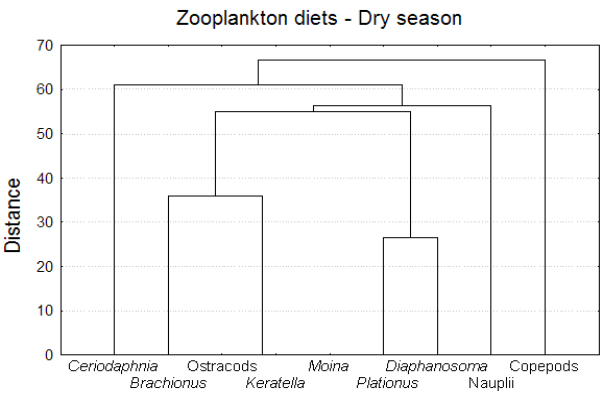

Fig. 5. Cluster analysis for zooplankton diets considering the dry season.

& Goldman 1994). This group of copepods could include animals, algae and detritus in their diets, and therefore, they can be considered as omnivorous in these ecosystems. However, in Clavellinos reservoir, no recognizable animal structures, such as rotifer mastax or any other sclerotized structure, were detected within the gut of specimens analyzed.

The small sized rotifers and nauplii limited their diets to almost exclusively small particulate material and a few phytoplankton species, which were able to be fragmented to allow their ingestion (Lampert & Sommer 1997). In the case of rotifers, they have a limited degree of food selectivity (Hotos 2002) and prefer particles of 6 µm in diameter or less (Pagano *et al*. 1999).

TABLE 3. Food items identified in the zooplankton gut contents.

1. Particulate material (P.M.)
Pyrrhophyta
2. Peridinium (Per.)
Bacillariophyta
3. Achnanthidium (Ach.)
4. Cyclotella (Cyc.)
5. Denticula (Den.)
6. Navicula (Nav.)
7. Synedra (Syn.)
Euglenophyta
8. Trachelomonas (Tra.)
Chlorophyta
9. Chlorella (Chl.)
10. Cosmarium (Cos.)
11. Dictyosphaerium (Dic.)
12. Monoraphidium (Mon.)
13. Oocystis (Ooc.)
14. Phacotus (Pha.)
15. Tetraedron (Tet.)
Cyanobacteria
16. Chroococcus (Chr.)
17. M*icrocystis* (Mic.)

The cladocerans analyzed have almost the same filtering structures (Horne & Goldman 1994), and this could be the reason why *Ceriodaphnia* and *Diaphanosoma* diets were linked together almost always in the cluster analysis. These similarities could be explained by the inter-setular distance in their thoracopods; cladoceran species show filter mesh sizes sufficiently narrow to retain fine particles, including bacteria (Villalobos & Geller 1997; Hayashi-Martins *et al.* 2017; Nevejan *et al*. 2018; Elías-Gutiérrez *et al.* 2019), with values ranging between 0.13 and 0.39 µm in *Ceriodaphnia* species (Hayashi-Martins *et al.* 2017). Also, there is evidence that cladocerans from oligotrophic waters may have shorter inter-setular distances (Villalobos 2002), although phenotypic changes in mesh widths may explain the variability of inter-setular distances found in the literature (Lampert & Brendelberger 1996).

Zooplankton diets were significantly different when they were compared between climatic periods. Possible explanations for these differences could be that: 1) The stock of phytoplankton species is different at each season; diatoms (mainly *Achnanthidium minutissimum*) dominated during the rainy season, while green algae dominated during the dry season (González 2009). 2) Phytoplankton species quality is not equivalent between rainy to dry seasons; zooplankton selected the food according to its chemical composition (Demott 1986; Infante 1988; Lampert & Sommer 1997; Eskinazi-Sant'Anna *et al*. 2002). 3) Different zooplankton filtration rates, which depend upon phytoplankton abundance (O'Brien & De Noyelles Jr. 1974).

TABLE 4. Trophic diversity index (D) for zooplankton groups.

Zooplankton groups	D
Copepods	16.53
Diaphanosoma	14.47
Nauplii	13.96
Ceriodaphnia	10.65
Rotifers	7.37
Brachionus	5.19
Plationus	3.29
Ostracods	1.81
Keratella	0.92
Moina	0.00

A high diet overlap was found in the reservoir (>75%). Similar situations had been reported in other reservoirs in Venezuela (González *et al*. 2005) and Brazil (González *et al*. 2006). This could be due to the wide food spectrum in copepod diet (Lampert & Sommer 1997; Doi *et al*. 2019), which included a higher number of food items than the other groups, and to the high percentage of guts with particulate material. The high overlap in zooplankton diets could lead to the assumption that competition is a relevant factor in the structuring of this community of planktonic animals in Clavellinos reservoir. However, this factor could be of low importance, since the zooplankton community was regulated mainly by abiotic variables, according to Merayo & González (2010), which resulted in low organism densities observed during the study period. In addition, other biotic factors, such as the different feeding habits of the species, vertical migrations and the presence of predatory fish could be more relevant than competition in the structuring of the zooplankton community (Merayo & González 2010; Doi *et al*. 2019).

Composition of particulate material must be different, according to its origin. It could be originated from allochthonous sources (Brett *et al*. 2009) that could account up to 89% of zooplankton carbon (Grey & Jones 2001), or either from autochthonous sources; in the latter case, particulate material origin could be related to the trophic state of the waterbody. Using epifluorescence analysis, González *et al*. (2006) found that cladocerans from the oligo-mesotrophic Broa reservoir showed traces of chlorophyll in their gut content, unlike cladocerans from the eutrophic Barra Bonita reservoir, which didn't show chlorophyll traces. This could indicate that most of the particulate material from Broa reservoir was directly derived from phytoplankton, whereas particulate material from Barra Bonita was mainly derived from detritus. In both cases, DAPI analysis showed bacteria attached to particulate material. In the case of the oligo-mesotrophic Clavellinos reservoir, most of the particulate material could be originated from phytoplankton and could have bacteria associated. Thus, future research should focus on the origin of this food item in studies concerning the natural diet of zooplankton.

In mesotrophic to eutrophic lakes, net phytoplankton (>50 mm) is not extensively grazed by herbivorous zooplankton, and net phytoplankton is more efficiently used by bacteria (Gliwicz 1969; Hillbricht-Ilkowska 1977; Stockner & Antia 1986). Only after partial decomposition to tiny particles of 1-2 µm in size (detritus and bacteria suspension), net phytoplankton becomes an available food source for the herbivorous zooplankton (Gliwicz 1969). Eskinazi-Sant'Anna *et al*. (2002), also found that detritus is an adequate source of carbon for cladocerans such as *Daphnia laevis*, representing the main food content during the time when peaks of these species occurred.

Apart from particulate material, green algae and diatoms were ingested in high proportions by zooplankters from Clavellinos reservoir. The same was registered for other lakes and reservoirs, such as Lake Valencia in Venezuela (Infante 1978a); Lake Washington in U.S.A. (Infante & Edmondson 1985; Infante & Litt 1985); Lake Xolotlán in Nicaragua (Cisneros *et al*. 1991); Lagartijo reservoir in Venezuela (Oliveira 1992); Lake Schöhsee in Germany (Vanni & Lampert 1992); El Andino reservoir in Venezuela (González 1998, 2000); Pampulha reservoir in Brazil (Eskinazi-Sant'Anna *et al*. 2002); Agua Fría, La Mariposa, Tierra Blanca and Pao-Cachinche reservoirs in Venezuela (González *et al*. 2005). Flagellates constitute important food items too (Infante 1988; Eskinazi-Sant'Anna *et al*. 2002). Some Cyanobacteria species could be found as a part of the zooplankton diet, as noted in this research and in some other previously cited studies (Infante & Edmondson 1985; Eskinazi-Sant'Anna *et al*. 2002; González *et al*. 2005, Tõnos *et al*. 2016), although they can pass through the digestive tract without being digested due to their mucilage, which provides protection against digestive enzymes (Gliwicz & Siedlar 1980).

Cyclopoid copepods showed the higher value of trophic diversity index, explained by the highest number of food items found in their gut contents, and it could indicate a broader food niche breadth (Herrera 1976) than that of the rest of the zooplankters in the reservoir. This could be due to the fact that cyclopoid copepods grasping their food items instead of the sieving method used by filter-feeders zooplankters such as cladocerans, in which the lower size of food spectrum is determined by the mesh size of their filter apparatus (Lampert & Sommer 1997; Doi *et al*. 2019).

According to Infante (1978), the direct analysis of the gut contents is a reliable method to determine the composition and variety of zooplankton food. However, this method, used in the present study, has the limitation that zooplankters potentially could feed on many other items which could not be recognized. For example, algae

such as *Cryptomonas erosa,* have fragile cell walls and have no identifiable structures remaining after digestion (Infante 1973, 1978; González 1998), even if they were ingested in high amounts. Probably, this limitation has influenced the scarcity of studies related to natural diet of zooplankton by the analysis of their gut contents, in favor of the use of more recent and sophisticated techniques, such as the use of pigment extraction (Oechsler-Christensen *et al*. 2012), epifluorescence (Balseiro *et al*. 2004; Joaquim-Justo *et al.* 2004; Karaköylü & Franks 2012), biomarkers (Galloway *et al*. 2014; Taipale *et al*. 2016) and prey DNA analysis (Durbin *et al*. 2012; Craig *et al*. 2016).

Although this study had the limitations already mentioned, it represents a contribution to the knowledge of the ecological dynamics of plankton, added to the previous studies carried out in this reservoir by Ferraz de Reyes & Fernández-Álvarez (1988), Bernal *et al*. (2004, 2005), González (2009) and Merayo & González (2010).

CONCLUSIONS

Particulate material was the main food item for zooplankton, followed by diatoms and green algae. Only 27.1% of the total phytoplankton species present in the reservoir was selected by herbivorous zooplankton.

No significant differences in diets were detected between rainy and dry seasons only for adult copepods and ostracods.

Copepods showed the highest values of the trophic diversity index.

Further studies should focus on the origin of the consumed particulate material as carbon source for zooplankton.

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