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Feeding and filtration rates of zooplankton (rotifers and cladocerans) fed toxic cyanobacterium (*Microcystis aeruginosa*)

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Abstract

Microcystis aeruginosa is generally dominant in many Mexican freshwater ecosystems interacting with zooplankton species. Hence, feeding and filtration rates were quantified for three cladoceran (*Daphnia pulex*, *Moina micrura* and *Ceriodaphnia dubia*) and three rotifer species (*Brachionus calyciflorus*, *Brachionus rubens* and *Plationus patulus*) using sonicated *M. aeruginosa* alone or mixed with *Scenedesmus acutus* in different proportions (25, 50 and 75%, based on cell density), offering a combined initial density of 100,000 cells·ml^{-1}. All the three cladoceran species ingested *M. aeruginosa* (100-300 cells ind^{-1} min^{-1}) when fed exclusively with cyanobacterium. When green alga offered as exclusive diet, the number of cells ingested by the tested cladocerans varied from 80 to 400 cells ind^{-1} min^{-1}. Compared to cladocerans, rotifers in general consumed much lower quantity (< 200 cells ind^{-1} min^{-1}) of *M. aeruginosa* and *S. acutus*. The filtration rate for *Daphnia pulex* was inversely related to the proportion of green alga in the diet. For other tested cladocerans, no such clear trend was evident. In mixed treatments containing *M. aeruginosa*, the filtration rate of *Daphnia* was highest (about 220 µl ind^{-1} min^{-1}) when the medium contained 75% of *S. acutus*. Among the rotifer species, *P. patulus* filtered highest volume (100 µl ind^{-1} min^{-1} from mixed diets containing higher proportions (50 or 75%) of *M. aeruginosa*. Thus, there were species-specific differences in the filtration and feeding rates of zooplankton when offered mixed diets of green algae and toxic cyanobacteria. These probably explain the coexistence of different zooplankton species in *Microcystis*-dominant waterbodies.

Key words

Feeding and Filtration rate, Freshwater zooplankton, *Microcystis aeruginosa*, *Scenedesmus acutus*

Introduction

Mexico has many shallow eutrophic waterbodies containing permanent blooms of cyanobacteria. *Microcystis aeruginosa* is the most common cyanobacterium in most waterbodies of Central Mexico (Ramírez-García *et al*., 2002). Due to their ability to form colonial blooms, they resist feeding by zooplankton. Many strains of *M. aeruginosa* are toxic to cladocerans and rotifers causing a reduction in both survival and reproduction (Alva-Martínez *et al*., 2004; 2007a, b; Okumura *et al*., 2007). The poor nutritional quality of *M. aeruginosa* is yet another factor for the lack of dominance by daphnids and brachionids in eutrophic waterbodies (Nandini, 2000; Šejnohová and Maršálek, 2012).

Because of seasonal changes in the composition of phytoplankton, both rotifers and cladocerans are probably exposed to nearly exclusive levels of toxic cyanobacteria, edible green algae or their mixture in varying proportions (Nandini *et al*., 2000; Kardinaal and Visser, 2005; Lürling and Beekman, 2006). Therefore, rotifers and cladocerans may suffer from toxins produced by the cyanobacteria depending on the seasonal fluctuations. Some workers have thus offered mixed diets of edible algae and toxic cyanobacteria in different proportions – from exclusive cyanobacteria or exclusive green algae as well as their ratios (Lürling and Beekman, 2006; Alva-Martínez *et al*., 2007a, b; 2009). These studies have shown that zooplankton were capable of growing and reproducing on cyanobacteria when mixed with edible algae.

Feeding and filtration are the behavioral as well as physiological processes that zooplankton species display when offered a variety of diets (Lürling and Van der Grinten, 2003; Lürling and Beekman, 2006). Feeding rates are simply the quantity of particles gathered from a food suspension in a specified period of time while filtration or the clearance rates indicate the quantity of medium filtered to gather food items (Davis and Gobler, 2011; Kâ *et al*., 2012). Quantitative studies on these aspects are important in zooplankton bioenergetics. Feeding and filtration rates are dependent on both biotic (e.g., body size) and abiotic (e.g., temperature) factors (Monakov, 2003; Okumura *et al*., 2007; Pagano, 2008). Usually smaller zooplankton such as rotifers filters less volume (a few µl min^{-1}) than larger taxa, such as cladocerans (Nandini *et al*., 2000; Kâ *et al*., 2012).

The quantity of food intake measured through feeding rates of a zooplankton species is largely related to its fecundity. For example cladocerans and rotifers showed increased population abundances more or less linearly with increase in densities of *Chlorella* in the medium (Lürling and Van der Grinten, 2003; Nandini *et al*., 2007; Pagano, 2008). When non-edible or toxic phytoplankton species were offered as diet, the fecundity of zooplankton is lower due to reduced intake (Nandini, 2000; Lürling and Beekman, 2006). Besides, filtration rates are closely related to the energy spent during these processes. In other words, less food in the environment causes higher filtration rates and hence higher energetic costs. In contrast, food saturation retards swimming speed in zooplankton, mainly cladocerans because of excessive accumulation of cells on their appendices with an associated energetic cost for cleaning them (Plath, 1998; DeMott *et al*., 2001; Pagano, 2008). In most laboratory studies, the amount of food offered is specified but the quantity food actually consumed by the test zooplankton is not quantified (Nandini *et al*., 2000; Alva-Martínez *et al*., 2009).

Therefore, the aim of this work was to quantify the feeding and filtration rates of three cladoceran species (*Daphnia pulex, Moina micrura* and *Ceriodaphnia dubia*) and three rotifer species (*Brachionus calyciflorus, Brachionus rubens* and *Plationus patulus*) on sonicated (predominantly single cells) *M. aeruginosa* offered alone and together with different proportions of *Scenedesmus acutus* (25, 50 and 75%, based on cell density).

Materials and Methods

The experiments were conducted using three species of cladocerans and three species of rotifers with different body sizes. The cladoceran species (with mean length): *Daphnia pulex* (2400 µm), *Moina micrura* (500 µm) and *Ceriodaphnia dubia* (750 µm) were originally isolated from Lake Espejo de Los Lirios (Mexico City). The rotifer species were *Brachionus calyciflorus* (275 µm), *Brachionus rubens* (225 µm) and *Plationus patulus* (125 µm), isolated from Lake Xochimilco (Mexico City).

Clonal populations for each zooplankton species were established from a single parthenogenetic female and fed with green alga *Scenedesmus acutus*. The zooplankton species were cultured under laboratory conditions (see further) in moderately hard water (EPA medium) (Weber, 1993) for some months prior to experimentation. EPA medium was prepared by dissolving 96 mg $NaHCO_3$, 60 mg $CaSO_4$, 60 mg $MgSO_4$ and 4 mg KCl in one liter of distilled water. *Scenedesmus acutus* was obtained from the University of Texas, and batch-cultured using Bold's basal medium supplemented with $NaHCO_3$ (0.25 g l^{-1} every third day) (Borowitzka and Borowitzka, 1988).

Microcystis aeruginosa was freshly collected from Chapultepec Lake (Mexico City), which is dominated by this cyanobacterium throughout the year. *M. aeruginosa* was not cultured because laboratory-cultured cyanobacteria lose their toxicity (Kardinaal and Visser, 2005). *M. aeruginosa* was filtered through a 300 µm sieve to eliminate zooplankton, and then washed using EPA over a 50 µm sieve, which removed smaller phytoplankton and ciliates. Observations under microscope revealed *M. aeruginosa* free of zooplankton. The colonial *M. aeruginosa* was then sonicated in an ultrasonicator (ColePalmer Instruments Co., USA) at 20 kHz 50 Watts for 1 min. The sonicated sample was filtered through a 20 µm sieve to remove partly sonicated colonies. Microscopic examination revealed that *M. aeruginosa* contained single cells (cell diameter about 4 µm) and no lysis of individual cells.

The cell density of *S. acutus* and *M. aeruginosa* was estimated using Neubauer haemocytometer and the chosen concentration of $1X10^5$ cells ml^{-1} was obtained by adding EPA medium. The zooplankton feeding experiments were conducted in 40 ml vessels containing 10 ml of medium with one of the chosen algal-cyanobacterial combination: 100% *Scenedesmus acutus* (Sa), 75% Sa + 25% *Microcystis aeruginosa* (Ma), 50% Sa+50% Ma, 25% Sa+ 75% Ma and 100% Ma. Each test jar received five individuals of one of the three non-ovigerous cladocerans (*Daphnia pulex, Moina macrocopa* and *Ceriodaphnia dubia*) or ten individuals of non-egg bearing rotifers (*Brachionus calyciflorus*, *Brachionus rubens* and *Plationus patulus*). All zooplankton species were pre-starved for 30 min. The experiments, with six replicates per treatment, were conducted for a feeding time of 20 min. The test jars were placed on slow mode rotating system in complete dark set at 23 ± 1 °C and with pH 7.2. After feeding time, the test individuals were filtered out and the density of unconsumed cells in each jar was quantified. Phytoplankton without zooplankton served as control.

The feeding rate (f) and filtration rate (F) were estimated with the formulae given by Rigler (1971):

Feeding rate (f) = $V(C_0-C_t)/t \cdot N$ line where: V= Medium volume; C_0= Initial cell concentration; C_t= Final cell concentration; t= feeding time in min and N= number of zooplankton individuals

per jar. Filtration rate (F) = $(lnC_0\text{-}lnC_t) \cdot W/t \cdot N$ where: C_0= Initial cell concentration; *Ct*= Final cell concentration; W= Medium volume in ml; t= feeding time and N= number of test individuals per jar.

Data on the feeding and filtration rates were statistically tested (one-way statistical analyses of variance (ANOVA) with Tukey's post-hoc tests) to quantify the differences among the treatments following standard process of normality of data and homogeneity of variance (Sokal and Rohlf, 1981).

Results and Discussion

The three cladoceran species ingested *M. aeruginosa* (100-300 cells ind^{-1} min^{-1}) when fed exclusively with cyanobacteria. When green alga offered as exclusive diet, the number of cells ingested by the tested cladocerans varied from 80 to 400 cells ind^{-1} min^{-1} (Fig. 1). Statistically, diet type and combination had significant effect on the feeding rates (Table 1, F-test). For a given cladoceran species, there were significant differences in cell consumption ($p<0.05$, Tukey) depending on the

Table 1 : Results of one-way analysis of variance performed on feeding rates of *Daphnia pulex*, *Moina micrura*, *Ceriodaphnia dubia*, *Brachionus calyciflorus*, *B. rubens* and *Plationus patulus* subjected to different proportions of *Microcystis aeruginosa* and *Scenedesmus acutus*. DF: degrees of freedom; SS: sum of squares; MS: mean square; F: *F*-ratio.

Source of variation	DF	SS	MS	F	P
Daphnia pulex					
Microcystis aeruginosa					
Between groups	3	87161	29053	3.5	0.03
Residual	20	166041	8302		
Scenedesmus acutus					
Between groups	3	39266	13088	1.3	0.29
Residual	20	196666	9833		
Moina micrura					
Microcystis aeruginosa					
Between groups	3	179803	59934	12.1	<0.001
Residual	20	98875	4943		
Scenedesmus acutus					
Between groups	3	242150	80716	16.0	<0.001
Residual	20	100833	5041		
Ceriodaphnia dubia					
Microcystis aeruginosa					
Between groups	3	68645	22881	11.8	<0.001
Residual	20	38750	1937		
Scenedesmus acutus					
Between groups	3	18200	6066	8.8	<0.001
Residual	20	13666	683		
Brachionus calyciflorus					
Microcystis aeruginosa					
Between groups	3	17070	5690	8.1	<0.001
Residual	20	14041	702		
Scenedesmus acutus					
Between groups	3	24325	8108	6.9	0.002
Residual	20	23458	1172		
Brachionus rubens					
Microcystis aeruginosa					
Between groups	3	6528	2176	2.7	0.075
Residual	20	16270	813		
Scenedesmus acutus					
Between groups	3	5257	1752	11.1	<0.001
Residual	20	3156	157		
Plationus patulus					
Microcystis aeruginosa					
Between groups	3	2050	683	0.5	0.7
Residual	20	28833	1441		
Scenedesmus acutus					
Between groups	3	18212	6070	6.7	0.003
Residual	20	18083	904		

cyanobacterial-algal combination. The cell densities in controls (phytoplankton without zooplankton) remained unchanged therefore; all quantified data in this work were attributed to feeding or filtration by zooplankton tested.

Compared to cladocerans, rotifers in general consumed much lower number of cells (< 200 cells ind^{-1} min^{-1}) of *M. aeruginosa* and *S. acutus*. *Plationus patulus* consumed higher quantity (from 80 to 145 cells ind^{-1} min^{-1}) of *S. acutus* regardless of the proportion in which the alga was combined with *M. aeruginosa* (Fig. 2). The number of *M. aeruginosa* cells ingested by *B. rubens* or *P. patulus* did not vary significantly in the presence of *Scenedesmus* ($p>0.05$).

The filtration rate for *Daphnia pulex* was inversely related to the proportion of algae in the diet. For other cladocerans, no such clear trend was evident (Fig. 3). In treatments containing *M. aeruginosa*, the filtration rate of *Daphnia* was highest (about 220 µl ind^{-1} min^{-1}) when the medium contained 75% *S. acutus*. Among the rotifer species, *P. patulus* filtered highest volume (100 µl ind^{-1}

Table 2 : Results of one-way analysis of variance performed on the filtration rates of *Daphnia pulex*, *Moina micrura*, *Ceriodaphnia dubia*, *Brachionus calyciflorus*, *B. rubens* and *Plationus patulus* subjected to different proportions of *Microcystis aeruginosa* and *Scenedesmus acutus*. DF: degrees of freedom; SS: sum of squares; MS: mean square; F: *F*-ratio.

Source of variation	DF	SS	MS	F	P
Daphnia pulex					
Microcystis aeruginosa					
Between groups	3	108827	36275	14.2	<0.001
Residual	20	51140	2557		
Scenedesmus acutus					
Between groups	3	125328	41776	5.0	0.01
Residual	20	168190	8409		
Moina micrura					
Microcystis aeruginosa					
Between groups	3	23501	78340	7.5	0.001
Residual	20	20765	1038		
Scenedesmus acutus					
Between groups	3	133117	44372	8.3	<0.001
Residual	20	107483	5374		
Ceriodaphnia dubia					
Microcystis aeruginosa					
Between groups	3	28236	9412	10.7	<0.001
Residual	20	17638	881		
Scenedesmus acutus					
Between groups	3	1948	649	7.8	0.001
Residual	20	1664	83		
Brachionus calyciflorus					
Microcystis aeruginosa					
Between groups	3	2511	837	5.9	0.005
Residual	20	2857	142		
Scenedesmus acutus					
Between groups	3	1040	346	1.9	0.164
Residual	20	3675	183		
Brachionus rubens					
Microcystis aeruginosa					
Between groups	3	3727	1242	5.0	0.009
Residual	20	4959	248		
Scenedesmus acutus					
Between groups	3	1654	551	14.2	<0.001
Residual	20	773	39		
Plationus patulus					
Microcystis aeruginosa					
Between groups	3	6662	2220	2.5	0.087
Residual	20	17641	882		
Scenedesmus acutus					
Between groups	3	21117	7039	8.2	<0.001
Residual	20	17099	855		

min^{-1}) in mixed diet treatments containing higher proportions (50 or 75%) of *M. aeruginosa*. The filtration rates of *B. calyciflorus* on algae were similar in treatments containing 25% or 100% *S. acutus* (Fig. 4). Statistically, diet type and combination had significant effect on the filtration rates (Table 2, F-test).

These results indicate that the chosen rotifers and cladocerans indeed consumed cyanobacteria in large quantities when offered as an exclusive food. Our study does not permit to extrapolate if the consumed cyanobacteria were actually assimilated. For this, long term study is needed. Alva-Martínez *et al*. (2004) conducted population growth experiments of *D. pulex*

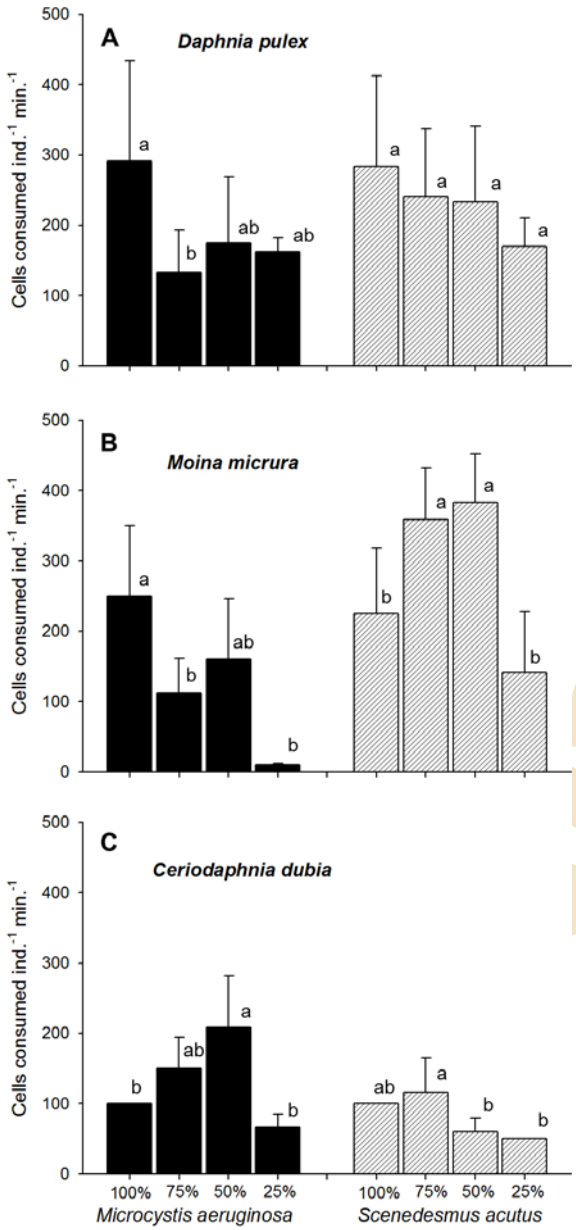

Fig. 1 : Feeding rates of *Daphnia pulex*, *Moina micrura* and *Ceriodaphnia dubia* fed different diets (*Microcystis aeruginosa*, *Scenedesmus acutus* or their proportions (%)). Bars show the mean ± standard deviation based on six replicates

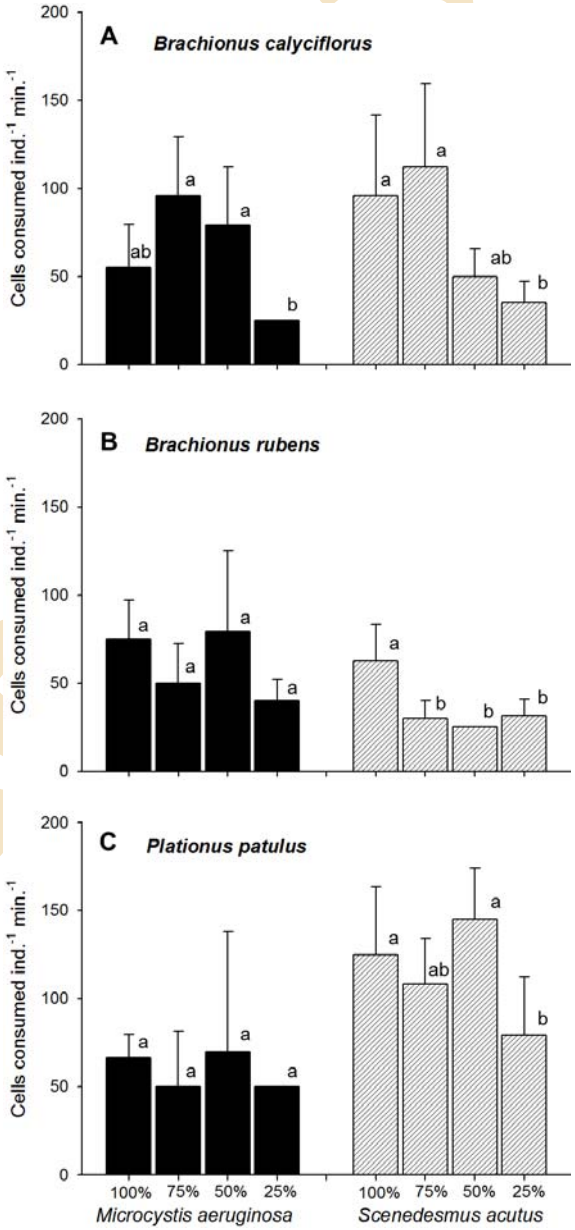

Fig. 2 : Feeding rates of *Brachionus calyciflorus*, *B. rubens* and *Plationus patulus* fed different diets (*Microcystis aeruginosa*, *Scenedesmus acutus* or their proportions (%)). Bars show the mean ± standard deviation based on six replicates

using different proportions of *M. aeruginosa* and *Chlorella*. Their results show that the population growth of *D. pulex* cultured on *M. aeruginosa* improved with increasing proportion of green algae in a mixed diet. It suggests that at least a part of the consumed cyanobacteria is assimilated. The present study complements previous observations, because the tested zooplankton species indeed consumed *Microcystis*. The adverse effects of *M. aeruginosa* on the demography of cladocerans and rotifers has been documented extensively, where the selected zooplankton died within 24 h when fed exclusively on cyanobacteria; while those in controls (no food or green algae) survived (DeMott, 1993; Lürling and Van der Grinten, 2003; Nandini *et al*., 2007).

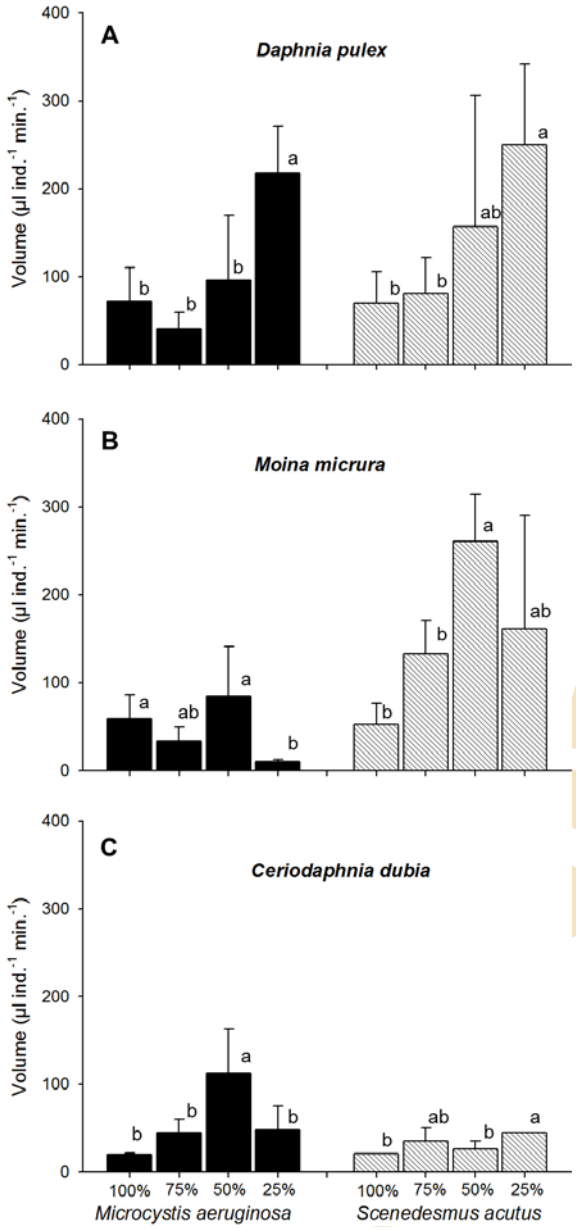

Fig. 3 : Filtration rates of *Daphnia pulex*, *Moina micrura* and *Ceriodaphnia dubia* fed different diets (*Microcystis aeruginosa*, *Scenedesmus acutus* or their proportions (%)). Bars show the mean ± standard deviation based on six replicates

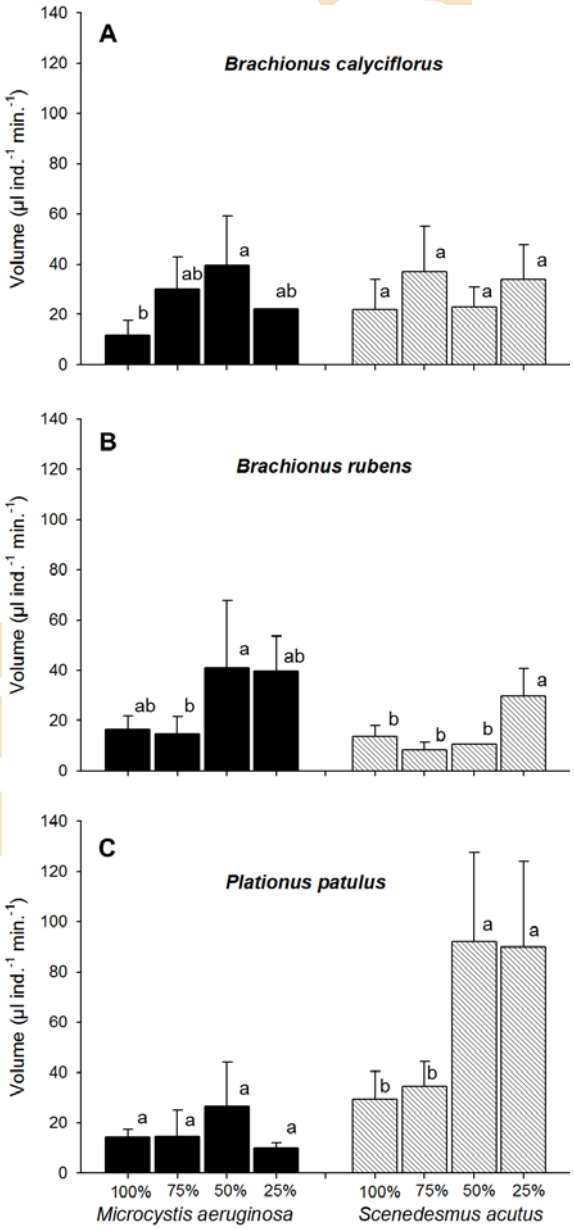

Fig. 4 : Filtration rates of *Brachionus calyciflorus*, *B. rubens* and *Plationus patulus* fed with different diets (*Microcystis aeruginosa*, *Scenedesmus acutus* or their proportions (%)). Bars show the mean ± standard deviation based on six replicates

The use of toxic *M. aeruginosa* together with a green alga as diet to zooplankton was not new. This approach has been previously employed by many workers (e.g., Nandini, 2000; Alva-Martínez *et al*., 2004). However, in most of these studies, the quantity of cyanobacteria actually consumed was not estimated. For estimating feeding rates, the tests can be conducted for as short as 20 min as to avoid the problems of gut evacuation and its influence on the quantification of uneaten cells (DeMott, 1993; Monakov, 2003). For food consumption, many approaches (automatic particle counters, radio tracer, direct microscopic observation of zooplankton gut, etc.) are suggested in literature. Counting of phytoplankton cells before and after feeding is least expensive and the most common process adapted in many works, for which exhaustive literature is available (see Monakov, 2003). This method too has many technical problems including errors in the haemocytometric quantification; however, this is routinely used because of the feasibility to conduct such tests almost in any laboratory.

The selected species of zooplankton used in this work are typical planktonic filter-feeders naturally occurring in many freshwater lakes of Mexico (Sarma, 1999; Elías-Gutiérrez *et al*., 2008). In addition, both the phytoplankton species (*Scenedesmus* and *Microcystis*) are most common in lakes of Central Mexico (Ortega, 1995). Thus, the tested zooplankton species are naturally exposed to different densities of cyanobacterial-algal combinations. As well-known from literature (Lampert and Sommer, 1997; Monakov, 2003; Kâ *et al*., 2012), feeding and filtration rates are not constant for any given herbivorous zooplankton species. These vary depending on many factors including temperature, hunger level and the proportion of phytoplankton (DeMott, 1993). The feeding rates of most zooplankton vary to a great extent from as low as <5 cells ind h^{-1} to a few thousand cells min^{-1}. Similarly, the filtration rates may vary from a few µl to ml (Lürling and Beekman, 2006; Davis and Gobler, 2011). The feeding rates reported in this work are slightly on higher side as compared to other works (DeMott *et al*., 2001; Pagano, 2008; Kâ *et al*., 2012). The most relevant aspect here is the higher rates of *Microcystis* consumption in a short duration. The cladocerans and rotifers species used in this work showed high filtration rates in presence of *Microcystis*. In this study the test jars received single-celled *Microcystis*, this probably facilitated easier filtration by zooplankton.

In conclusion, this work showed that rotifers and cladocerans ingested significant quantities of toxic *Microcystis aeruginosa* regardless of whether offered alone or in combination with green algae. In addition, there were species-specific differences in the filtration and feeding rates of zooplankton when offered identical diets. These probably explain the coexistence of different zooplankton species in *Microcystis*-dominant waterbodies. Further, our results also take into account of the importance of using several zooplankton species in feeding studies.

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