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PRIMARY RESEARCH PAPER

Can tropical freshwater zooplankton graze efficiently on cyanobacteria?

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Abstract Zooplankton may at times graze cyanobacteria. However, their top-down effects are considered to be low, particularly in tropical regions dominated by small-size grazers that may be unable to consume efficiently filamentous or colonial species. Recently, cyanobacteria blooms were reported in the Senegal River hydrosystem. We conducted feeding experiments to assess the ability of copepods (*Pseudodiaptomus hessei* and *Mesocyclops ogunnus*), cladocerans (*Moina micrura* and *Ceriodaphnia cornuta*), and rotifers (*Brachionus angularis, B. falcatus*, and *Keratella* sp.) to control different cyanobacteria (*Cylindrospermopsis raciborskii*, *Anabaena solitaria*, *A. flos-aquae*, and *Microcystis aeruginosa*). None of the zooplankton species ingested *M. aeruginosa*. *Mesocyclops ogunnus* did not consume any of the cyanobacteria. Both cladocerans consumed the smallest filaments of cyanobacteria, whereas all the rotifers and *P. hessei* consumed a broader food-size spectrum. The functional feeding responses suggest that the concentration and size of the filaments are not the sole criteria for food consumption. The high zooplankton community grazing rates, estimated by applying the clearance rates measured in the laboratory to the in situ zooplankton abundance, indicate that grazing by zooplankton potentially constitutes an important controlling factor for the filamentous cyanobacteria in the tropics.

Keywords Filamentous cyanobacteria · Copepods · Cladocerans · Rotifers · Top-down control · Freshwater

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Introduction

Harmful algal blooms occur in many water bodies all over the world as a result of increasing human activity (Hallegraeff, 1993; Anderson et al., 2002), sometimes causing serious ecological, economical or sanitary consequences (Granéli & Turner, 2006; Lehman et al., 2010). Algal blooms are also

frequently observed in African inland waters as a result of the increase in agro-industrial activities leading to eutrophication. Algal blooms have been reported regularly in various shallow water sites in the Sudano-Sahelian region (Cogels et al., 2002; Akin-Oriola, 2003). Cyanobacterial blooms have developed in several water bodies connected to the Senegal River in its lower delta region (Berger et al., 2005) because of increasing agricultural activity since the impoundment of the river (Diama and Manantali dams) in the 1980s (Cogels et al., 2002). Among the dominant cyanobacteria reported in these waterbodies, the filamentous species *Cylindrospermopsis raciborskii* and *Anabaena solitaria* are particularly abundant in Lake Guiers (LG) and the Dakar Bango Reservoir (DBR), which provide most of the drinking water for the cities of Dakar and Saint-Louis, respectively. The colonial species *Microcystis aeruginosa* is also very abundant in the ponds in Djoudj Park, the world's third largest ornithological reserve (Berger et al., 2005).

Although light conditions and nutrient availability are often critical for the development of cyanobacteria blooms (Conley et al., 2009), the subsequent success of these blooms may also be influenced by the grazing of herbivores (top-down control) including herbivorous zooplankton (Boon et al., 1994; Smayda, 2008).

Studies have been carried out to evaluate the behavior and role of zooplankton during cyanobacterial blooms (Boon et al., 1994). Several mechanisms may control the grazing pressure by zooplankton on cyanobacteria. In particular, the feeding activity of zooplankton can be inhibited by cyanotoxins (Fulton & Paerl, 1987; Agrawal, 1998), which are considered to be a defense mechanism and which are sometimes enhanced by zooplankton grazing (Jang et al., 2003). Negative impacts of cyanobacteria on zooplankton have been reported for rotifers (Rothhaupt, 1991), cladocerans (DeMott et al., 1991; Ferrão-Filho & Azevedo, 2003), and copepods (DeMott & Moxter, 1991; Kurmayer & Juettner, 1999). Moreover, these relationships can depend on the degree of exposure of zooplankton to cyanobacteria (Gustafsson & Hansson, 2004).

Another important control factor of the grazing pressure by zooplankton is the disparity between the size and nature of the cyanobacteria and the dominant grazers (Boon et al., 1994; Hambright et al., 2001; Havens, 2007). One explanation for the success of cyanobacteria species is their relative inedibility for zooplankton and fish (Gilbert, 1996; Reynolds, 1998). Many filaments or colonies are simply too large to be ingested by most zooplankters, and this can affect the feeding efficiency of filter-feeders, particularly cladocerans (Lampert, 1987; Abrusan, 2004).

The disparities between food particles and grazers are accentuated in tropical shallow freshwater ecosystems by the scarcity of large cladocerans (*Daphnia*) and calanoids, and the dominance of small grazers such as small cladocerans and rotifers (Aka et al., 2000; Fernando, 2002). Havens et al. (1996) suggested that poor control of phytoplankton biomass by herbivorous macrozooplankton may be a common feature of lowland tropical and subtropical lakes. In these ecosystems, the small size of the dominant zooplankton and their inefficient grazing on large particles may explain the abundance, and sometimes proliferation, of large phytoplankton particles, such as filamentous or colonial chlorophytes and cyanobacteria (Boon et al., 1994; Lazzaro, 1997).

There have been a few reports of large (e.g., the calanoid copepod *Boeckella* spp.) or small (e.g., rotifers of the genus *Brachionus*, cladocerans of the genera *Moina*, *Ceriodaphnia,* and *Bosmina*) tropical zooplankton grazing on filamentous or colonial cyanobacteria (Burns & Xu, 1990a, b; Boon et al., 1994; Bouvy & Molica, 1999; Bouvy et al., 2001). The relative abilities of *Boeckella* spp. to graze filamentous or colonial cyanobacteria were examined by Burns & Xu (1990a, b). Direct bacterial carbon flow to macrozooplankton was shown to be important in copepod and cyanobacteria dominated subtropical lakes (Work et al., 2005). Most of the information relative to the smaller tropical organisms was based on laboratory observations (Bouvy et al., 2001) and/or on gut examination of field collected animals (Boon et al., 1994). From these studies it was suggested that both calanoid copepods and rotifers have lower potential for controlling cyanobacterial blooms than large cladocerans. However, more detailed experimental studies on the feeding behavior and the functional feeding responses of tropical zooplankters are still needed to really evaluate the ability of copepods and rotifers to consume effectively cyanobacteria and to control their blooms.

In a previous work, Pagano (2008) showed that tropical cladocerans (*Moina micrura*) and rotifer

(*Brachionus calyciflorus*) had potential to control large colonial chlorophytes. In this work, we examine the potential of tropical freshwater zooplankton to control cyanobacterial bloom development. For the grazing experiments, we have chosen dominant species (copepods, cladocerans, and rotifers) as target species because they were present during cyanobacterial blooms in the water bodies of the Senegal River Hydrosystem (Kâ et al., 2006; Mendoza-Vera et al., 2008). Our goals were (1) to determine whether these zooplankters are potentially able to consume colonial or filamentous cyanobacteria and (2) to assess whether the zooplankton communities are able to exert an effective top-down control on the cyanobacterial blooms.

Materials and methods

Grazing experiments were performed with seven zooplankton species: the calanoid copepod *Pseudodiaptomus hessei* (adult stages), the cyclopoid copepod *Mesocyclops ogunnu*s (adults or nauplii), the cladocerans *Moina micrura* (adults) and *Ceriodaphnia cornuta* (adults) and the rotifers *Brachionus angularis*, *B. falcatus*, and *Keratella* sp. Eleven food suspensions were tested: natural water from Lake Guiers (LG) and Dakar Bango Reservoir (DBR), monospecific cultures of chlorophytes (*Cosmarium impressulum*) or cyanobacteria (*Cylindrospermopsis raciborskii*, *Anabaena solitaria*, *A. flos-aquae,* and *Microcystis aeruginosa*), natural LG or DBR water mixed with pure cultures of *C. raciborskii* or the unicellular cyanobacteria *Synechococcus* sp.

Our strategy was to test as many food-zooplankton combinations in single species experiments as possible, if possible replicated in time and at different food concentrations when organisms were available. For technical reasons (availability of zooplankton species and/or food suspensions), only 38 food–zooplankton combinations could be tested at 13 different dates (Table 1). Many combinations (e.g., *Mesocyclops ogunnus* vs. *Microcystis aeruginosa*) could not be tested, while other combinations were run one or several times, giving a total of 78 experiments (Table 1).

All experiments were performed with wild zooplankton collected at DBR. Collections were performed at night using cylindro-conical nets: opening diameter 30 cm, length 80 cm, and mesh sizes 200 μm for crustaceans and 60 μm for rotifers. After collection, animals were diluted in 20-l containers

Table 1 Feeding experiments: summary of the food–zooplankton combinations tested at different dates (the 13 dates are illustrated by numbers 1–13)

Food	*P. hessei*	*M. ogunnus*		*M. micrura*	*C. cornuta*	*B. angularis*	*B. falcatus*	*Keratella* sp.
		Nauplii	Adults					
Natural (DBR)	1, 3, 4, 5			3, 4, 5				
Natural (LG)	1							
DBR + *Synechococcus* sp.	2							
DBR + *C. raciborskii*	2							
LG + *Synechococcus* sp.	2							
LG + *C. raciborskii*	2							
Cosmarium impressulum	3, 4, 5			3, 4, 5				
C. raciborskii	3, 4, 5, 7, 9	13	10	3, 4, 5, 6, 7, 9, 11	10, 11	11, 12, 13	12	13
A. solitaria	3, 4, 5, 7	13	10	3, 4, 5, 6, 7, 11	10, 11	11, 12, 13	12	13
A. flos-aquae	8, 9	13	10	8, 9, 11	10, 11	11, 12, 13	12	13
Microcystis aeruginosa	9			9, 11	11	12	12	

DBR Dakar Bango Reservoir, *LG* Lake Guiers

1 = 1 April 03, 2 = 5 April 03, 3 = 17 May 04, 4 = 18 May 04, 5 = 19 May 04, 6 = 23 January 06, 7 = 6 February 06, 8 = 14 February 06, 9 = 28 March 06, 10 = 9 May 06, 11 = 16 May 06, 12 = 22 May 06, 13 = 29 May 06

filled with filtered DBR or LG water and kept for several hours before experiments. The cyanobacteria and algae used in the experiments came from the Paris Museum Collection (PMC, Muséum National d'Histoire Naturelle, MNHN): *Cylindrospermopsis raciborskii* (strain PMC 118, origin: LG, Senegal), *Anabaena flos-aquae* (PMC 207, DBR, Senegal), *A. solitaria* (PMC 202, DBR, Senegal), *Microcystis aeruginosa* (PMC 155, Djoudj, Senegal), *Synechococcus* sp. (PMC 98.17, Villeret, France), and *Cosmarium impressulum*. The cultures were grown in sterile medium (Z8X for the cyanobacteria, F2 for the chlorophyte) and kept in thermo-regulated enclosures at a constant temperature of 24°C with illumination at 20 µE and a 12–12 h photoperiod.

Water was collected during the daytime, at the surface (using a bucket) and passed through a 60 µm sieve to eliminate zooplankton grazers. LG samples were dominated by cyanobacteria (>90% of the total abundance, with *C. raciborskii* and *Lyngbya versicolor* as dominant species), chlorophytes (ca. 10%, mainly *Oocystis lacustris*) and diatoms (ca. 2%, mainly *Fragilaria* sp.), and had concentrations around 15×10^9 µm^3 biovolume (40 µg chlorophyll l^{-1} or 2 mg C l^{-1}). DBR samples were dominated by cyanobacteria (>85%, mainly *A. solitaria*), diatoms (ca. 7%; mainly *Melosira granulata*) and chlorophytes (ca. 4%, mainly *Coelastrum* spp.) and had concentrations around 8×10^9 µm^3 biovolume (20 µg chlorophyll l^{-1} or 1 mg C l^{-1}).

Before each grazing experiment (food/zooplankton combination), the food suspension tested was prepared. For monospecific suspensions, algae or cyanobacteria, cultures were diluted into 0.2-µm filtered in situ water (from DBR) in a 1/10 (vol/vol) proportion. For mixed suspensions, cyanobacteria culture (*C. raciborskii* or *Synechococcus* sp.) was diluted into 60 µm filtered lake water (LG or DBR) in a 1/10 (vol/vol) proportion. The food concentration in the suspensions tested varied from 1.4 to 25.4×10^9 µm^3 biovolume (8–161 µg chlorophyll l^{-1} or 0.5–9.6 mg C l^{-1}) according to the experiments (see Tables 2, 3, 4, 5, 6). After preparation, the food suspension was homogeneously poured in six jars (550 ml volume for copepod or cladoceran experiments, 55 ml for nauplii or rotifers). Homogeneous monospecific sets of the target species were then constituted by sorting specimens from the zooplankton assemblage, using a dropper under a dissecting microscope. Pre-sieving (200 µm) was used to separate crustacean and rotifers. Light behavior (phototaxis) also helped to separate the taxa. Three sets of the tested species were thus constituted and immediately introduced into three of the jars (called experimental jars). The three remaining jars without zooplankton served as controls (control jars). The flasks were placed on rotating wheels (1 rd mn^{-1}, 0.3 m rotation diameter) to prevent the settlement of food particles and incubated in the dark (to limit algal growth) at ambient temperature (24–25°C) for 24-h.

At the end of the experiments, water samples were collected in each jar in order to measure the chlorophyll-*a* concentration, the concentration and size distribution of total particles and the lengths of filaments. The chlorophyll-*a* concentrations (cells retained on Whatman GF/F filters, 25 mm diameter) were determined on 5–10 ml subsamples after methanol extraction (Yentsch & Menzel, 1963) using a Turner Design AU-5 fluorometer. The particle concentration and size distribution (size expressed as equivalent spherical diameter, ESD) were determined using a Coulter Multisizer II equipped with a 70 µm aperture tube. If necessary, subsamples were diluted with 0.22 µm filtered Isoton to maintain the coincidence level below 2% (maximal dilution factor = 5). For each subsample, 12 successive analyses were performed with the Multisizer with 2 ml as analytical volume. In the experiments with filtered LG or DBR water, the dominance of the phytoplankton species was roughly evaluated from a lugol preserved water sample (Utermöhl's method). Animals from the experimental jars were transferred to a 5% buffered formalin solution, for subsequent enumeration and measurements ($N = 30$ for each taxa) to determine the exact densities and biomass. Animals were enumerated under a dissecting microscope using a Dolfuss chamber. The individual carbon weights were calculated using length–dry weight relationships from Jerling & Wooldridge (1991) for *P. hessei* and from Bottrell et al. (1976) for the other taxa. Dry weights were converted into carbon weights using an average carbon:dry weight ratio of 45% (Pagano & Saint-Jean, 1993). The mean zooplankton densities in the experimental jars were: 16 ind l^{-1} (150 µg C l^{-1}) for *P. hessei* (adults), 80 ind l^{-1} (144 µg C l^{-1}) for *M. ogunnus* (mixture of copepodites and adults), 100 ind l^{-1} (149 µg C l^{-1}) for *M. micrura* (adult females), 300 ind l^{-1} (150 µg C l^{-1})

Table 2 Experiments with *Pseudodiaptomus hessei*: concentration (Conc.) and peak size range of the different food tested and *t* tests results (significance of *P*) to compare the difference in particle volume between experimental and control flasks (triplicates), within three size classes (peak range, larger, and smaller) after 24-h incubation

Food	Date	Conc. ($\mu g\ l^{-1}$)	Peak range (μm ESD)	*t* Tests			
				Total	Smaller	Peak	Larger
Monospecific							
C. raciborskii	3	1.31	5–9	ns	+	−	ns
	4	0.49	2–5	ns	+	ns	ns
	5	0.88	5–9	+++	++	−−	ns
	7	3.96	6–11	ns	+++	−−	ns
	9	9.09	6–11	−	+++	−−−	ns
A. solitaria	3	0.57	10–12	ns	+	−	ns
	4	1.20	16–24	ns	+++	−−	ns
	5	2.03	14–23	+++	++	ns	ns
	7	2.40	6–11	−−−	+++	−−−	ns
A. flos-aquae	8	9.50	8–14	ns	+++	−−	ns
	9	9.67	6–12	ns	++	ns	ns
Cosmarium impressulum	3	0.79	11–15	−−	+++	−−−	ns
	4	0.59	11–15	−−−	+++	−−−	ns
	5	0.81	11–15	−	+	−	ns
M. aeruginosa	9	1.85	7–9	+++	+++	−	++
Natural							
DBR	1	1.20	2–10	−	++	−	ns
	3	0.93	3–10	−−−	++	−−−	ns
	4	0.88	3–10	−	+++	−−−	ns
	5	1.19	3–10	−−	+	−−	−
LG	1	2.28	4–10	−−−	+++	−−−	−−−
Mixed							
DBR + *Synechococcus* sp.	2	1.25	3–15	−−−	+++	−−−	−
DBR + *C. raciborskii*	2	2.33	3–15	−−−	−−−	−−−	−−−
LG + *Synechococcus* sp.	2	5.55	5–10	−−	+++	−−−	−
LG + *C. raciborskii*	3	4.82	5–10	−−−	+++	−−−	−−

Degree of freedom = 4. −, −−, and −−− = significant negative differences (i.e., particle removing) at $P < 0.05$, $P < 0.01$, and $P < 0.001$, respectively. +, ++, and +++ = significant positive differences (i.e., particle "production") at $P < 0.05$, $P < 0.01$, and $P < 0.001$, respectively. *ns* no significant difference ($P > 0.05$), *DBR* Dakar Bango Reservoir, *LG* Lake Guiers. Date numbers as in Table 1

Table 3 Experiments with *Mesocyclops ogunnus:* concentration (Conc.) and peak size range of the different food tested and *t* tests results (significance of *P*) to compare the difference in particle volume between experimental and control flasks (triplicates), within three size classes (peak range, larger, and smaller) after 24-h incubation

Food	Date	Conc. ($\mu g\ l^{-1}$)	Peak range (μm ESD)	*t* Tests			
				Total	Smaller	Peak	Larger
Copepodites and adults							
C. raciborskii	10	3.69	6–11	ns	ns	+	ns
A. solitaria	10	2.30	5–11	ns	−−	ns	ns
A. flos-aquae	10	3.25	6–11	ns	ns	ns	ns
Nauplii							
C. raciborskii	13	4.26	6–12	ns	++	−	ns
A. solitaria	13	5.96	6–12	ns	ns	ns	ns
A. flos-aquae	13	4.83	5–12	ns	−−−	ns	ns

Degree of freedom = 4. −, −−, and −−− = significant negative differences (i.e., particle removing) at $P < 0.05$, $P < 0.01$, and $P < 0.001$, respectively. +, ++, and +++ = significant positive differences (i.e., particle "production") at $P < 0.05$, $P < 0.01$, and $P < 0.001$, respectively. *ns* no significant difference ($P > 0.05$). Date numbers as in Table 1

Table 4 Experiments with *Moina micrura*: concentration (Conc.) and peak size range of the different food tested and *t* tests results (significance of *P*) to compare the difference in particle volume between experimental and control flasks (triplicates), within three size classes (peak range, larger and smaller) after 24-h incubation

Food	Date	Conc. ($\mu g\ l^{-1}$)	Peak range (μm ESD)	*t* Tests			
				Total	Smaller	Peak	Larger
Monospecific							
C. raciborskii	3	1.31	5–9	ns	ns	−−	ns
	4	0.49	2–5	−−	ns	−−−	ns
	6	2.64	2–10	ns	ns	−−−	ns
	7	3.96	6–11	−−−	−−−	−−	ns
	9	9.09	6–11	ns	ns	−	ns
	11	3.31	6–11	−	−	−	ns
A. solitaria	3	0.57	10–12	−−	−−−	−−	−
	4	1.20	16–24	−	−−−	ns	ns
	5	2.03	14–23	ns	ns	ns	+
	6	2.55	6–12	−	−−	−	ns
	7	2.40	6–11	−−−	−−−	−−−	ns
	11	2.30	6–11	−	ns	−	−
A. flos-aquae	8	9.50	8–14	ns	ns	ns	ns
	9	9.67	6–12	ns	++	ns	ns
	11	3.48	6–11	ns	+	−	ns
Cosmarium impressulum	3	0.79	11–15	ns	ns	ns	ns
	5	0.81	11–15	ns	ns	ns	ns
M. aeruginosa	9	1.85	7–9	ns	ns	−	++
	11	3.29	2–5	ns	−−	ns	ns
Natural							
DBR	3	0.93	3–10	−	ns	−−−	ns
	4	0.88	3–10	−−	ns	−−−	ns
	5	1.19	3–10	−−	ns	−−−	ns

Degree of freedom = 4. −, −−, and −−− = significant negative differences (i.e., particle removing) at $P < 0.05$, $P < 0.01$, and $P < 0.001$, respectively. +, ++, and +++ = significant positive differences (i.e., particle "production") at $P < 0.05$, $P < 0.01$, and $P < 0.001$, respectively. *ns* no significant difference ($P > 0.05$), *DBR* Dakar Bango Reservoir. Date numbers as in Table 1

for *C. cornuta* (adult females), 3000 ind l^{-1} (150 μg C l^{-1}) for nauplii of *M. ogunnus*, 4000 ind l^{-1} (136 μg C l^{-1}) for *B. falcatus*, 6000 ind l^{-1} (123 μg C l^{-1}) for *Keratella* sp., and 10,000 ind l^{-1} (130 μg C l^{-1}) for *B. angularis*.

All the differences between control and experimental flasks (triplicates), in total particle volume or within different size classes corresponding to the phytoplankton peaks were tested using *t* tests (SigmaStat version 3.5). Three size classes were considered (peak range, larger, and smaller). Peak range values for each experiment are shown in Tables 2, 3, 4, 5, and 6. Upper and lower limits of the peak were determined graphically by examining the size distribution of particulate volumes in the control flasks at the end of incubation.

Ingestion rates (I, μm^3 ind^{-1} h^{-1} or μm^3 ng C^{-1} h^{-1}) and clearance rates (F, ml of water cleared of particles ind^{-1} h^{-1} or mg C^{-1} h^{-1}) were calculated from the difference in total particle volume (when statistically significant) between control and experimental flasks assuming zero algal growth in a flask, owing to darkness:

$$I = (C_c - C_e) * V/(B * t)$$

$$F = ((\ln C_c - \ln C_e)/t) * V/B$$

Table 5 Experiments with *Ceriodaphnia cornuta*: concentration (Conc.) and peak size range of the different food tested and *t* tests results (significance of *P*) to compare the difference in particle volume between experimental and control flasks (triplicates), within three size classes (peak range, larger, and smaller) after 24-h incubation

Food	Date	Conc. (μg l^{-1})	Peak range (μm ESD)	*t* Tests			
				Total	Smaller	Peak	Larger
C. raciborskii	10	3.69	6–11	ns	ns	ns	ns
	11	3.31	6–11	−	ns	−	ns
A. solitaria	10	2.30	5–11	−−−	−−	−−−	ns
	11	3.77	6–11	−−	ns	−−	ns
A. flos-aquae	10	3.25	6–11	−−−	ns	−−−	ns
	11	3.48	6–11	ns	ns	−	ns
M. aeruginosa	11	3.29	2–5	ns	ns	ns	ns

Degree of freedom = 4. −, −−, and −−− = significant negative differences (i.e., particle removing) at $P < 0.05$, $P < 0.01$, and $P < 0.001$, respectively. +, ++, and +++ = significant positive differences (i.e., particle "production") at $P < 0.05$, $P < 0.01$, and $P < 0.001$, respectively. *ns* no significant difference ($P > 0.05$). Date numbers as in Table 1

Table 6 Experiments with rotifers: concentration (Conc.) and peak size range of the different food tested and *t* tests results (significance of *P*) to compare the difference in particle volume between experimental and control flasks (triplicates), within three size classes (peak range, larger, and smaller) after 24-h incubation

Food	Date	Conc. (μg l^{-1})	Peak range (μm ESD)	*t* Tests			
				Total	Smaller	Peak	Larger
B. angularis							
C. raciborskii	11	3.31	6–11	−−	ns	−−	ns
	12	2.29	6–11	−−−	−−−	−−−	+
	13	4.26	6–12	−	ns	−	ns
A. solitaria	11	2.30	6–11	ns	−−−	+	ns
	12	5.15	6–11	ns	−−−	+	ns
	13	5.96	6–12	ns	ns	ns	ns
A. flos-aquae	11	3.48	6–11	ns	++	ns	ns
	12	3.44	6–11	ns	−−−	ns	ns
	13	4.83	5–12	ns	−−−	ns	ns
M. aeruginosa	11	3.29	2–5	ns	−−	ns	+
	12	2.06	3–5	ns	ns	+	ns
B. falcatus							
C. raciborskii	12	2.29	6–11	−−	−−−	−−	+
A. solitaria	12	5.15	6–11	−−−	−−−	−−−	−
A. flos-aquae	12	3.44	6–11	−−	−−−	−−	ns
M. aeruginosa	12	2.06	3–5	ns	ns	ns	+
Keratella sp.							
C. raciborskii	13	4.26	6–12	ns	+++	−	+
A. solitaria	13	5.96	6–12	−	ns	−	ns
A. flos-aquae	13	4.83	5–12	−	ns	−−	ns

Degree of freedom = 4. −, −−, and −−− = significant negative differences (i.e., particle removing) at $P < 0.05$, $P < 0.01$, and $P < 0.001$, respectively. +, ++, and +++ = significant positive differences (i.e., particle "production") at $P < 0.05$, $P < 0.01$, and $P < 0.001$, respectively. *ns* no significant difference ($P > 0.05$). Date numbers as in Table 1

where C_c and C_e are the particle biovolume (μm^3 ml^{-1}) at the end of the incubation in the control and experimental flasks, respectively (C_c is taken to be the initial concentration), V is the experimental flask volume (ml), B is the zooplankton concentration (expressed as number of individuals or as carbon biomass) in the flask, and t is the incubation time (hours). The ingestion rates are also expressed in µg Chl or µgC μgC^{-1} day^{-1} using the chlorophyll to particulate volume ratios measured in the flasks and a ratio C:Chl of 60 (Båmstedt et al., 2000).

The grazing rates of the zooplankton communities (ZCG in day^{-1}) were estimated for several sites in the lower delta of the Senegal River sampled in 2004–2005 in a previous study (Mendoza-Vera et al., 2008). They were estimated by summing the products of the specific clearance rates (F from this study) and the in situ biomass of the various zooplankton species (data from Mendoza-Vera et al., 2008). Estimations were made for each of the cyanobacteria considered in this study. The selected ingestion rates were the maximum values obtained for each zooplankton species/cyanobacteria species combination, which gave an estimate of the maximum grazing rate for the population considered. The clearance rates of the zooplankton species not studied in this work were estimated by analogy with the morphologically closest species studied (e.g., *P. hessei* for other calanoid species).

Results

Analysis of size spectra modifications by zooplankton

Copepods

In monoculture experiments, *Pseudodiaptomus hessei* reduced significantly the total particle volume, always for *Cosmarium impressulum* and occasionally, for *A. solitaria* and *C. raciborskii* (Table 2). In most cases, it significantly reduced the cell volume in the most abundant size fraction (peaks range) and increased the relative contribution of small cells (Fig. 1A–C; Table 2). In both natural and mixed seston experiments, *P. hessei* decreased significantly the total and the peak particle volumes (Table 2; Fig. 1D–F). It also provoked an increase of small cells volume, except for DBR + *C. raciborskii* mixtures (see Fig. 1F).

Mesocyclops ogunnus caused no significant variation in the total particulate volume of the different filamentous cyanobacteria tested and had little impact on their size spectra (Table 3).

Cladocerans

In monoculture experiments, *Moina micrura* did not modify the total and peak volumes when the peak range corresponded to large particles: e.g., 14–24 µm ESD for *A. solitaria* and 6–14 µm ESD for *A. flos-aquae* (Fig. 2A, B; Table 4), 11–15 µm for *C. impressulum* (Table 4). However, a significant reduction in the peak was observed when the cultures were composed of smaller particles (generally <10 µm ESD; Fig. 2C) leading sometimes to elimination of the peak for very small particles (*C. raciborskii*, 2–5 µm ESD; Fig. 2D; Table 4). In presence of *M. aeruginosa*, *M. micrura* did not modified the total particulate volume despite significant modification of the size spectrum was observed (Fig. 2E; Table 4). In experiments with natural seston from DBR, *M. micrura* caused significant reductions in total and peak volumes (Fig. 2F; Table 4).

Ceriodaphnia cornuta had larger effects on the size spectra of *A. solitaria* and *A. flos-aquae* than on *C. raciborskii* (Fig. 3A–C; Table 5) and it had no significant effect on *M. aeruginosa* (Fig. 3D; Table 5).

Rotifers

In the three experiments carried out with *C. raciborskii*, *B. angularis* induced a significant decrease of the total particulate volume and the particle peak (Fig. 4A; Table 6). This rotifer induced neither significant variation in particle volume nor a clear impact on the size structure of *A. solitaria*, *A. flos-aquae* (Fig. 4B) and *M. aeruginosa* (Table 6).

Brachionus falcatus caused a clear reduction in the total and peak volumes of the three filamentous cyanobacteria tested (*C. raciborskii*, *A. solitaria,* and *A. flos-aquae*) (Fig. 4C, D; Table 6).

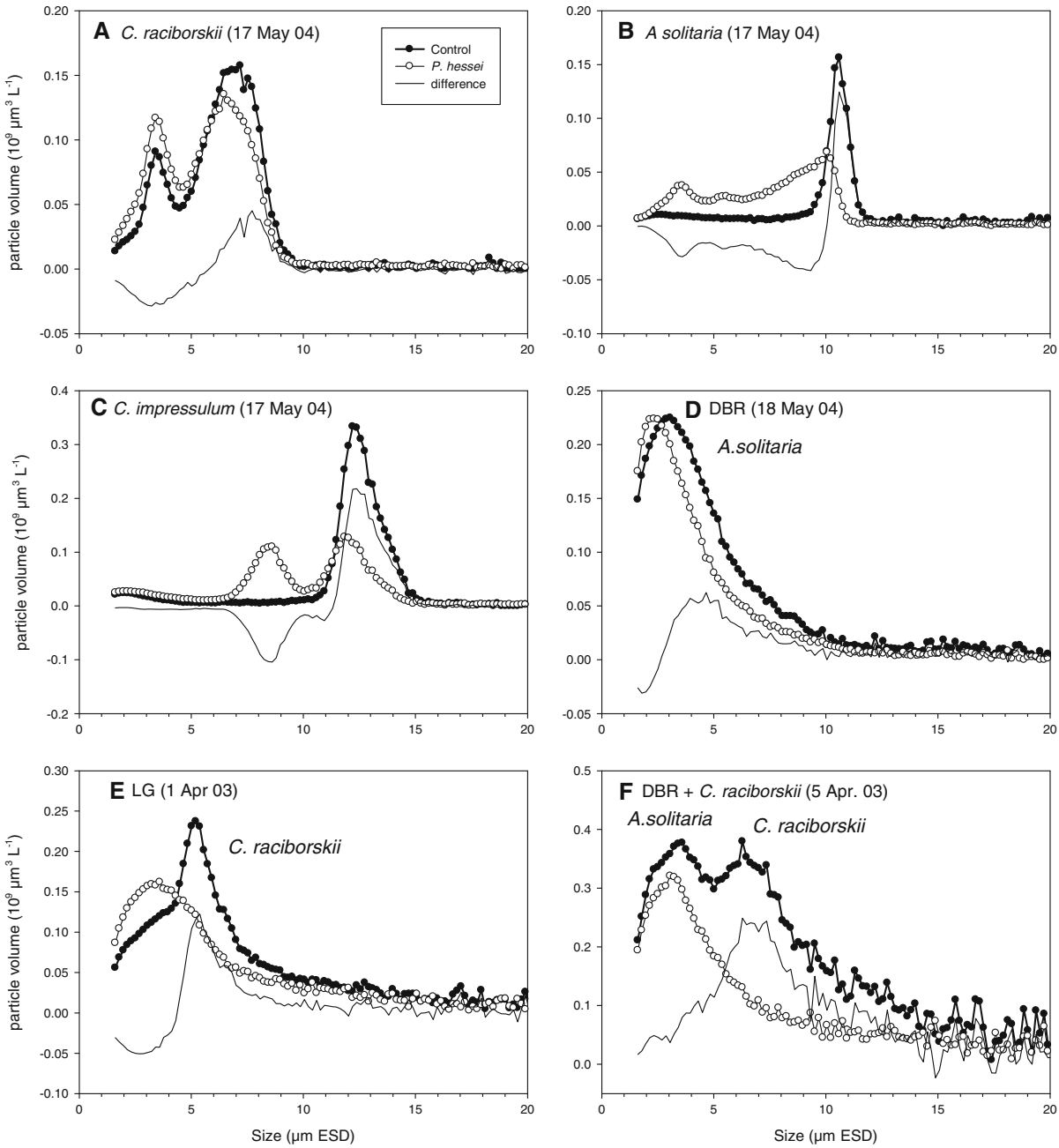

Fig. 1 Mean size distributions (size as equivalent spherical diameter, ESD) of particulate volumes (Coulter Counter measurement) in control (*solid dots*) and experimental (*open dots*) flasks and difference between experimental and control flasks (*solid line*) at the end of incubation period in experiments with *Pseudodiaptomus hessei* adults fed with monospecific suspensions of *C. raciborskii* (**A**), *Anabaena solitaria* (**B**), and *Cosmarium impressulum* (**C**) or with natural particles from DBR (**D**) or LG (**E**) or with mixtures of natural particles and *C. raciborskii* (**F**). For natural particles, the main phytoplankton species explaining particle peaks are indicated

However, this rotifer did not have a significant impact on the non-filamentous species *M. aeruginosa* (Table 6).

Keratella sp. caused significant reduction in the total particulate volumes and particle peaks of *A. solitaria* and *A. flos-aquae* (Fig. 4D, E; Table 6).

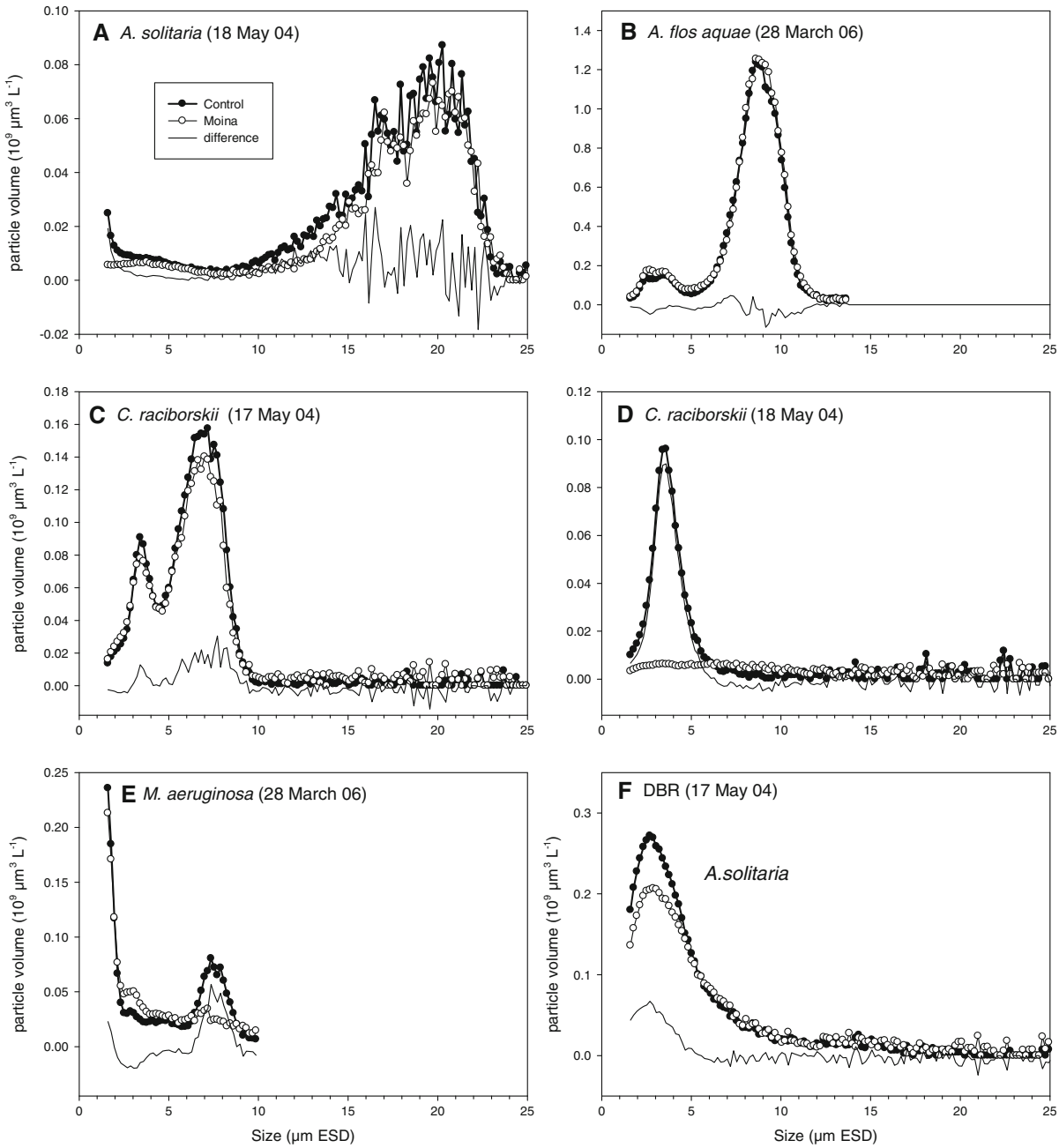

Fig. 2 Mean size distributions (size as equivalent spherical diameter, ESD) of particulate volumes (Coulter Counter measurement) in control (*solid dots*) and experimental (*open dots*) flasks and difference between experimental and control flasks (*solid line*) at the end of incubation period in experiments with *Moina micrura* fed with monospecific suspensions of *Anabaena solitaria* (**A**), *A. flos-aquae* (**B**), *Cylindrospermopsis raciborskii* (**C**, **D**), or *Microcystis aeruginosa* (**E**) or with natural particles from DBR (**F**). For natural particles, the main phytoplankton species explaining the particle peak is indicated

Ingestion and clearance rates

Mean ingestion and clearance rates of *P. hessei* varied from 0.03 to 0.19 µgC µgC^{-1} day^{-1} and from 0.4 to 5.1 ml mgC^{-1} h^{-1}, respectively (Table 7). Mean ingestion and clearance rates of *M. micrura* were much higher than those of *P. hessei*. The highest values were obtained with *A. solitaria*, whereas *A. flos-aquae* was

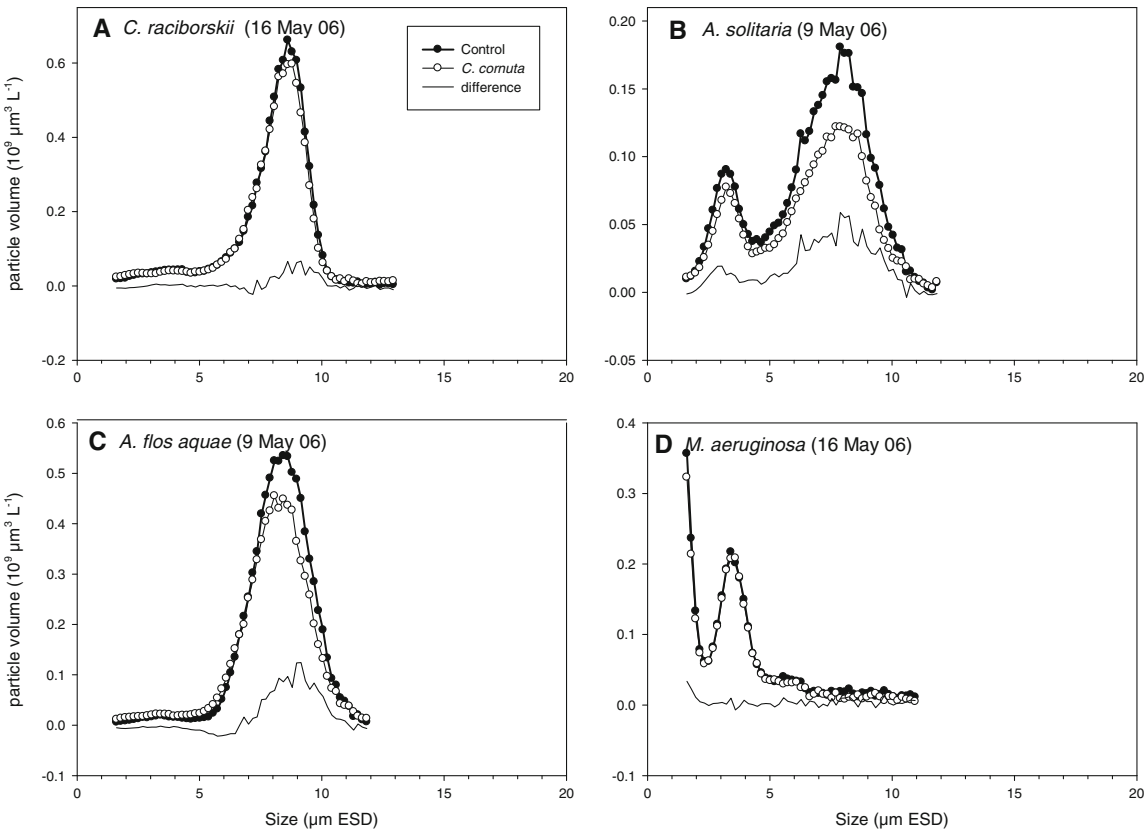

Fig. 3 Mean size distributions (size as equivalent spherical diameter, ESD) of particulate volumes (Coulter Counter measurement) in control (*solid line*) and experimental (*black circles*) flasks and difference between experimental and control flasks (*white circles*) at the end of incubation period in experiments with *Ceriodaphnia cornuta* fed with monospecific suspensions of *Cylindrospermopsis raciborskii* (**A**), *Anabaena solitaria* (**B**), *A. flos-aquae* (**C**), and *Microcystis aeruginosa* (**D**)

not consumed. The mean rates of *C. cornuta* were of the same order of magnitude. Only the largest rotifers species (*B. falcatus*) consumed all three filamentous cyanobacteria. *B. angularis* did not consume *A. solitaria*, whereas *Keratella* sp. did not consume *C. raciborskii*. The ingestion and clearance rates were comparable for the two *Brachionus* species and the highest values were observed for *Keratella* sp.

For all the zooplankton species considered, the ingestion rates were low or zero at low particle concentrations ($<5 \times 10^9$ µm^3 l^{-1}), but highly variable at higher particle concentrations (Fig. 5).

Zooplankton community grazing rates on the filamentous cyanobacteria

The potential grazing rates of the zooplankton communities on *A. flos-aquae*, *A. solitaria*, and *C. raciborskii* varied between 0.01 and 15.40% day^{-1}, between 0.04 and 49.40% day^{-1}, and between 0.04 and 12.80% day^{-1}, respectively. The plots of cyanobacteria abundance vs. grazing pressure showed a wide range of abundance values with high maxima for the low grazing values and always low (or zero) abundance at higher grazing values (>10% day^{-1}) (Fig. 6).

Discussion

Our results indicate that *Pseudodiaptomus hessei*, *Moina micrura*, *Ceriodaphnia cornuta*, *Brachionus angularis*, *B. falcatus,* and *Keratella* sp. can consume and/or modify the size structure of filamentous cyanobacteria, with a varying degree of efficiency depending on the zooplankton species and the nature of the food offered. The exception is an apparent lack of control of *Microcystis aeruginosa*.

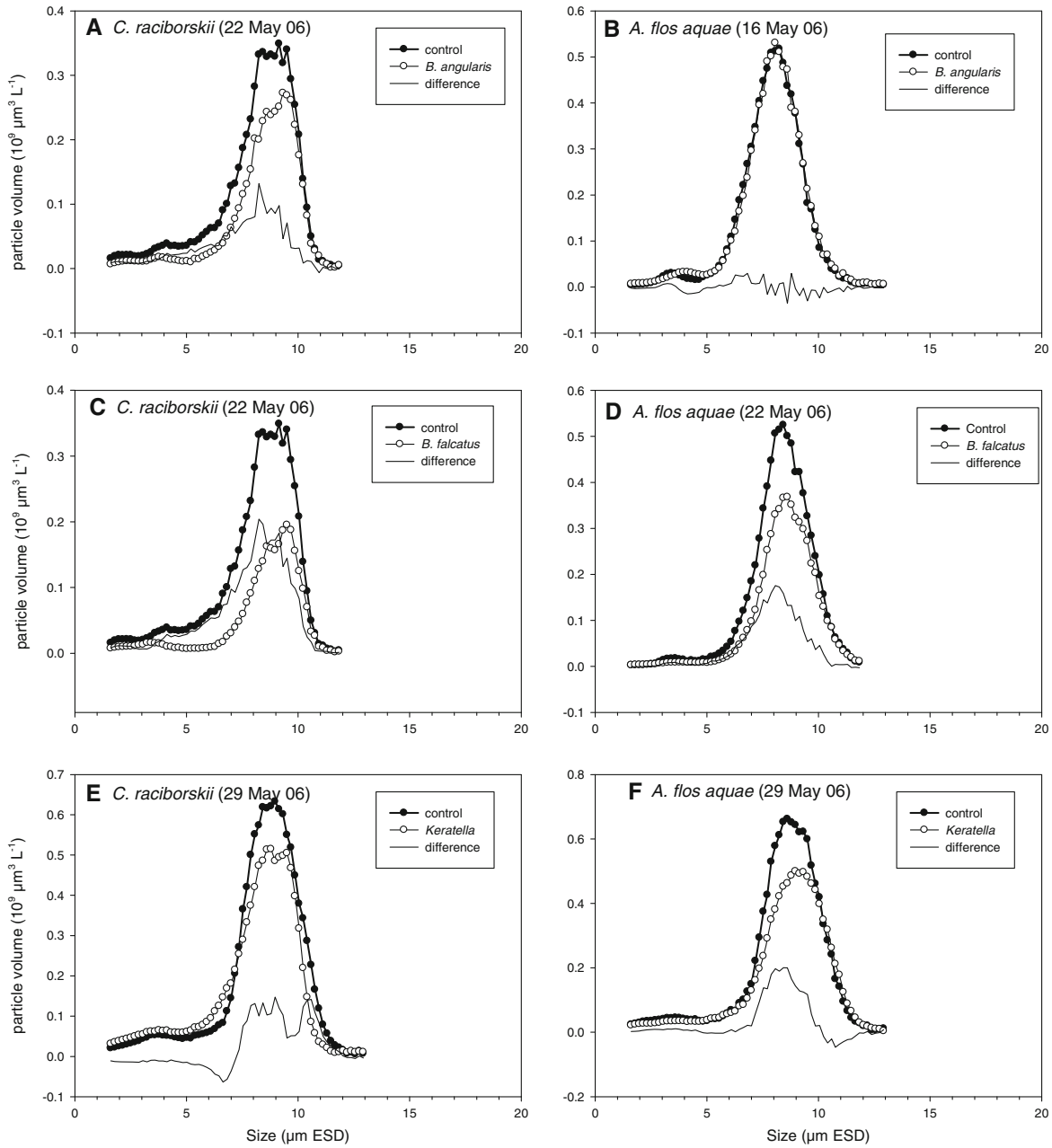

Fig. 4 Mean size distributions (size as equivalent spherical diameter, ESD) of particulate volumes (Coulter Counter measurement) in control (*solid line*) and experimental (*black circles*) flasks and difference between experimental and control flasks (*white circles*) at the end of incubation period in experiments with *Brachionus angularis* (**A**, **B**), *B. falcatus* (**C**, **D**), and *Keratella* sp. (**E**, **F**) fed with monospecific suspensions of *Cylindrospermopsis raciborskii* (**A**, **C**, **E**) and *Anabaena flos-aquae* (**B**, **D**, **F**)

Inedibility of the colonial cyanobacterium *Microcystis aeruginosa* for zooplankton

Microcystis aeruginosa was only tested with *P. hessei*, *Moina micrura*, *C. cornuta*, *B. angularis,* and *B. falcatus*. The results indicate that these zooplankters do not consume *Microcystis* colonies.

Fulton & Paerl (1987) also observed that *M. aeruginosa* (unicellular form as well as colonial) was not consumed by the calanoid copepod,

Table 7 Mean values (±SE) of the food concentration (Food conc.) and of the individual and weight-specific ingestion, and clearance rates for the various tested zooplankton species and foods

Zooplankton food	*n*	Food conc.	Ingestion rates		Clearance rates	
		mgC l^{-1}	ngC ind^{-1} h^{-1}	µgC µgC^{-1} day^{-1}	µl ind^{-1} h^{-1}	µl µgC^{-1} h^{-1}
Pseudodiaptomus hessei						
DBR	4	1.3 ± 0.3	23.7 ± 7.9	0.07 ± 0.0	29.3 ± 12.9	3.7 ± 1.6
LG	1	2.3	16.5	0.05	9.7	1.2
DBR + *C. raciborskii*	1	2.3	42.5	0.13	28.8	3.6
LG + *C. raciborskii*	1	4.8	11.4	0.03	2.9	0.4
DBR + *Synechococcus* sp.	1	1.3	17.7	0.05	21.3	2.7
LG + *Synechococcus* sp.	1	5.6	51.8	0.16	12.8	1.6
Cosmarium impressalum	3	0.7 ± 0.1	21.8 ± 3.9	0.07 ± 0.0	40.8 ± 6.9	5.1 ± 0.9
M. aeruginosa	1	1.8	0.0	0.00	0.0	0.0
A. flos-aquae	2	9.6 ± 0.1	0.0 ± 0.0	0.00 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
A. solitaria	4	1.5 ± 0.4	62.0 ± 338.1	0.19 ± 1.0	36.2 ± 272.3	4.5 ± 34.0
C. raciborskii	5	3.1 ± 1.6	23.8 ± 23.8	0.07 ± 0.1	3.2 ± 3.2	0.4 ± 0.4
Moina micrura						
Naturel DBR	3	1.0 ± 0.1	49.4 ± 17.3	0.72 ± 0.4	67.6 ± 17.9	41.2 ± 10.9
Cosmarium impressalum	2	0.8 ± 0.0	0.0 ± 0.0	0.00 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
M. aeruginosa	2	2.6 ± 0.7	0.0 ± 0.0	0.00 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
A. flos-aquae	3	7.5 ± 2.0	0.0 ± 0.0	0.00 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
A. solitaria	5	1.8 ± 0.4	110.9 ± 62.0	1.62 ± 2.0	99.2 ± 49.9	60.5 ± 30.4
C. raciborskii	6	3.5 ± 1.4	40.5 ± 16.5	0.59 ± 0.6	24.9 ± 10.2	15.2 ± 6.2
Ceriodaphnia cornuta						
M. aeruginosa	1	3.3	0.0	0.00	0.0	0.0
A. flos-aquae	2	3.4 ± 0.1	41.2 ± 41.2	1.98 ± 2.0	16.3 ± 16.3	32.6 ± 32.6
A. solitaria	2	3.0 ± 0.7	122.8 ± 96.5	5.89 ± 4.6	47.4 ± 33.3	94.9 ± 66.6
C. raciborskii	2	3.5 ± 0.2	10.3 ± 10.3	0.50 ± 0.5	3.8 ± 3.8	7.7 ± 7.7
Brachionus angularis						
M. aeruginosa	2	2.7 ± 0.6	0.0 ± 0.0	0.00 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
A. flos-aquae	3	3.9 ± 0.5	1.1 ± 1.1	1.98 ± 2.0	0.1 ± 0.1	10.6 ± 10.6
A. solitaria	3	4.5 ± 1.1	0.0 ± 0.0	0.00 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
C. raciborskii	3	3.3 ± 0.6	2.2 ± 0.9	4.07 ± 1.8	0.6 ± 0.1	48.5 ± 9.0
Brachionus falcatus						
M. aeruginosa	1	2.1	0.0	0.00		0.0
A. flos-aquae	1	3.4	1.1	0.81	0.5	13.9
A. solitaria	1	5.1	3.2	2.26	1.1	31.2
C. raciborskii	1	2.3	3.1	2.17	2.3	67.9
Keratella sp.						
A. flos-aquae	1	4.8	5.1	5.88	0.7	32.5
A. solitaria	1	6.0	6.3	7.26	0.7	33.5
C. raciborskii	1	4.3	0.0	0.00		0.0

n number of measurements, *DBR* Dakar Bango Reservoir, *LG* Lake Guiers

Eurytemora affinis. The authors suggested that this copepod avoided or rejected *M. aeruginosa* on some basis other than particle size, most likely owing to toxic or unpalatable chemicals associated with *M. aeruginosa* cells, consistent with the known chemosensory abilities of copepods (Poulet & Marsot,

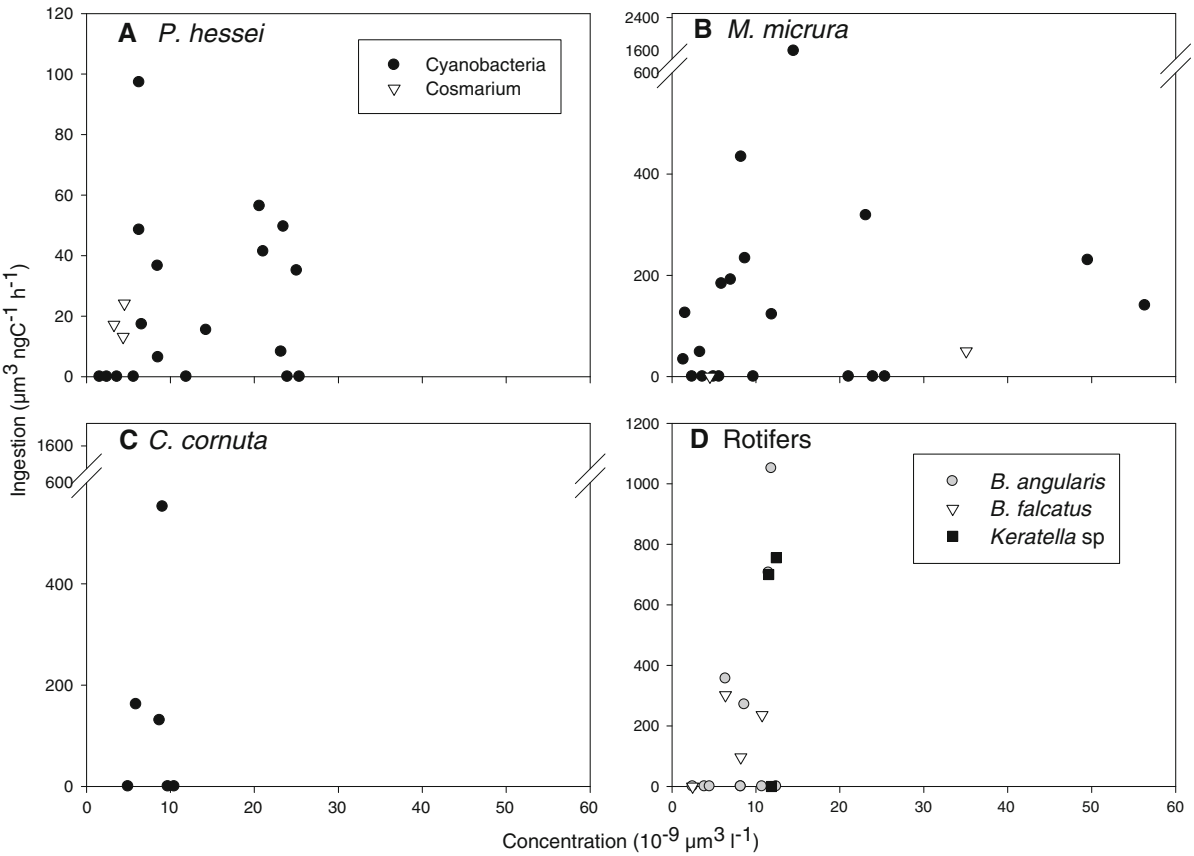

Fig. 5 Variations of the weight-specific ingestion rates with particle concentration during the grazing experiments with *Pseudodiaptomus hessei* (**A**), *Moina micrura* (**B**), *Ceriodaphnia cornuta* (**C**), and rotifers (**D**) fed with cyanobacteria or with *Cosmarium impressalum* (**A**)

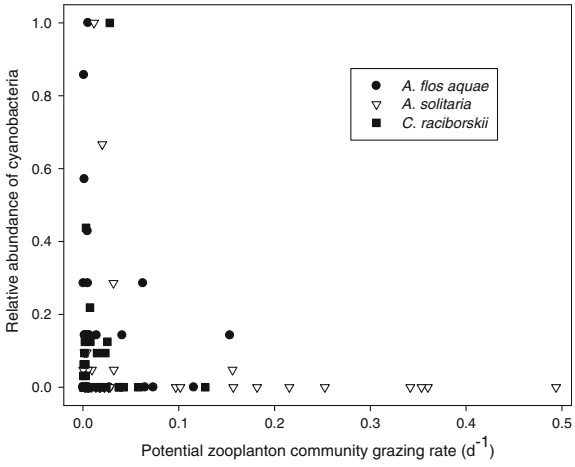

Fig. 6 Relationship between the in situ cyanobacteria relative concentrations (concentration/maximal concentration; data from Mendoza-Vera et al., 2008) and the potential zooplankton community grazing rate (see "Materials and methods" section for details on the calculation) in the lower delta of the Senegal River

1978). However, the inedibility of *M. aeruginosa* for cladocerans and rotifers is undoubtedly partly related to the colonial form of the cultures offered in our experiments. Fulton & Paerl (1988) showed that unicellular forms are generally better ingested than colonial forms by cladocerans (*Bosmina longirostris*) and rotifers (*Brachionus calyciflorus*). However, substances that are excreted by *Microcystis* and that limit protease activity also may reduce consumption by *Moina macrocopa* (Agrawal et al., 2001).

Field observations suggested that blooms of colonial or filamentous cyanobacteria were linked to the decline of large organisms (*Daphnia*) and the parallel increase of small organisms (rotifers) (e.g., Gliwicz, 1977). More recently, Ferrão-Filho et al. (2000) showed that the food inhibition by *M. aeruginosa* varied according to the strain offered and the type of grazer. They found that the two small tropical cladocerans, *Ceriodaphnia cornuta* and *Moinodaphnia*

macleayi, were less sensitive than large temperate cladocerans. Other studies showed significant ingestion of *M. aeruginosa*, without any negative effects, by various species such as the cladocerans *C. cornuta*, *Simocephalus vetulus* (Nandini, 2000) and *Daphnia* spp. (Barros et al., 2001), or the calanoid copepods *Acartia tonsa* (Schmidt & Jónasdóttir, 1997) and *Arctodiaptomus salinus* (Tolomeyev, 2002). *Daphnia* spp. are able to control blooms of *M. aeruginosa* (Pani & Wanganeo, 2000; Chen & Xie, 2003), perhaps due to lower feeding inhibition when *Microcystis* is mixed with more palatable food particles, such as *Scenedesmus* (Chen & Xie, 2003; Ghadouani et al., 2004).

Zooplankton feeding behavior with the filamentous cyanobacteria

The consumption and/or size structure modification of filamentous cyanobacteria by copepods, cladocerans, or rotifers reported in this study are consistent with the preliminary results reported by Bouvy & Molica (1999). They showed, from laboratory experiments, that several groups of zooplankton (classified according to their size) were able to cut and reduce the mean size of the filaments, and to consume the smallest filaments of *Cylindrospermopsis raciborskii*. This is also consistent with the study by Fulton (1988) which demonstrated that most herbivorous species (including cladocerans, copepods, and rotifers) were able to consume filamentous species (diatoms, chlorophytes, and cyanobacteria) efficiently. Work & Havens (2003) also showed that a wide range of macrozooplankton can graze filamentous and colonial cyanobacteria, despite other phytoplankton (diatoms) may be preferred.

In this study, *P. hessei* consumed filamentous cyanobacteria (*C. raciborskii* and *A. solitaria*) with weight-specific daily ingestion rates (7 and 19% of C body, respectively) comparable with those obtained on natural seston or on *Cosmarium impressulum* (7% for both). However, these rates are low compared to the values in the literature for calanoid copepods and in particular compared to the values reported for *P. hessei* by Pagano et al. (2003) in a tropical lagoon (13–100%). This study also shows that *P. hessei* can cut and shorten the largest filaments during the ingestion process, as illustrated by the significant increase of the smallest particles and reduction of the average length of the filaments during incubation. This copepod could, therefore, play an important role in the control of algal blooms, by direct consumption and/or the fragmentation of the largest filaments. Calanoid copepods can detect, capture, and handle large particles (such as large diatoms or cyanobacteria) before ingesting or rejecting them (Paffenhofer et al., 1982; Turner et al., 1998). During "handling", they damage or break particles with their mouth parts ("sloppy feeding"). The calanoid copepod *Diaptomus leptopus* has been observed capturing the trichomes of cyanobacteria (*Oscillatoria limnetica*, *O. planktonica*, and *Anabaena* sp.) and then consuming a segment, the remainder being lost or rejected (Schaffner et al., 1994). This behavior is also shown in this study for *P. hessei* feeding on natural particles as well as on chlorophytes (*C. impressulum*) or on filamentous cyanobacteria (*A. solitaria*, *A. flos-aquae*, and *C. raciborskii*). This confirms that calanoid copepods are able to cut the filaments of filamentous cyanobacteria, shortening them to an edible size for other zooplankton species, such as small cladocerans, as shown in other studies on freshwater (Burns & Xu, 1990a, b; Bouvy et al., 2001) and coastal marine water (Turner et al., 1998). As emphasized by these last authors, this phenomenon can have considerable ecological consequences that are generally underestimated, with a larger portion of the phytoplankton assemblage being affected by the grazers than is accounted for by ingestion and clearance rates, based only on the removal of filaments. Besides, the fragmentation of filaments by zooplankton can also indirectly affect the population growth of cyanobacteria through impact on physiological processes, as shown by Chan et al. (2004) for heterocystous species (*Anabaena* spp.). They showed that heterocyst formation and N fixation were lower in populations that experienced fragmentation by zooplankton.

Unlike *P. hessei*, *Mesocyclops ogunnus* did not consume the filamentous cyanobacteria tested in this study. So far as we are aware, few studies if any have been carried out on the feeding behavior of the cyclopids on filamentous cyanobacteria. The non-ingestion of the filaments by *M. ogunnus* observed in this study is consistent with the studies reported by Kurmayer & Juettner (1999) who observed zero filtration rates for *Cyclops* sp. on *Planktothrix rubescens* filaments. However, they observed significant ingestion rates with filaments previously treated (extraction with methanol) to limit inhibition by microcystins.

In our experiments, both small cladocerans *M. micrura* and *C. cornuta* consumed filamentous cyanobacteria with ingestion rates (50–600% of body C day^{-1}), sometimes higher than that observed for *M. micrura* fed with natural seston (70% body C day^{-1}). These ingestion rates are comparable with those previously measured for *M. micrura* fed with natural phytoplankton (40–800% body C day^{-1}) (Pagano, 2008). In this study, *M. micrura* consumed small filaments in preference to larger filaments (significant consumption below the peak size and no consumption above the peak). This preference for the smallest filaments is in agreement with Fulton (1988) who showed that the ingestion of filamentous species (diatoms, chlorophytes, and cyanobacteria) by *M. micrura* and another small cladoceran, *Diaphanosoma brachyurum* was limited by the size of the filaments. It is well known that cladocerans have a filter apparatus that is better adapted to capturing small rather than large particles (DeMott & Moxter, 1991; Pattinson et al., 2003). Boon et al. (1994) showed that cladocerans consume filamentous species less efficiently than calanoid copepods, mainly because their filter apparatus becomes clogged. However, Dawidowicz (1990) showed that *Daphnia magna* incubated in the water of a hypereutrophic lake rich in filamentous cyanobacteria, significantly reduced the density of the filaments as well as their mean size. Soares et al. (2009) also showed that this species was able to consume filaments of *C. raciborskii*, but feeding efficiency decreased as the proportion of the cyanobacteria in the food offered increased.

This study shows that *B. angularis*, *B. falcatus*, and *Keratella* sp. are able to consume filamentous cyanobacteria with high daily ingestion rates ranging from 80 to 700% of body C, comparable with the literature values for rotifers fed with non-filamentous algae ($\sim$220% for *B. calyciflorus*, Rothhaupt, 1990; 212–486% for *B. plicatilis*, Pagano et al., 1999), or filamentous algae (100–600% for *Euchlanis dilatata*, Gulati et al., 1993). These high ingestion rates for filamentous cyanobacteria are consistent with several studies showing the efficiency of capture of the filamentous species by large brachionid rotifers such as *E. dilatata* (Gulati et al., 1993) and *B. calyciflorus* (Starkweather & Kellar, 1983; Fulton, 1988). However, small rotifers also seem to be able to deal with filaments as shown by Fabbro & Duivenvoorden (1996) who observed specimens of *B. angularis* ingesting entire straight trichomes of *C. raciborskii*. This is confirmed in our study, with the observation of very high ingestion rates (equivalent to 4–7 times their body weight per day) for *B. angularis* on *C. raciborskii* and for *Keratella* sp. on *Anabeana* spp.

The functional feeding responses to the concentration and the nature of food particles observed in this study for the six species (*P. hessei*, *M. micrura, C. cornuta, B. angularis, B. falcatus*, and *Keratella* sp.) that consumed filamentous cyanobacteria are very variable. Several cases of zero ingestion were observed: *A. flos-aquae* for *P. hessei* and *M. micrura*, *A. solitaria* for *B. angularis*, and *C. raciborskii* for *Keratella* sp. Other factors besides the nature (shape and size) and concentration of the cyanobacteria offered may influence the feeding behavior and food ration, and thus contribute to the variability observed. The heterogeneity of the functional feeding responses was probably also related to differences in the nutritional quality of the particles offered as observed by Rothhaupt (1988) for *B. calyciflorus*. The low or zero ingestion rates sometimes observed in this study suggest the influence of inhibiting effects related to cyanotoxins or other substances produced by the cyanobacteria (Rothhaupt, 1991; Paerl et al., 2001).

Potential grazing impact of zooplankton grazing on cyanobacteria

Our ZCG estimates combine own laboratory results (clearance rates of the dominant species) and field data (in situ biomass of zooplankton) from Mendoza-Vera et al. (2008), leading to potential inaccuracies associated with scaling up from laboratory to field studies. Nevertheless, these ZGC estimates suggest that grazing by the zooplankton could be an important factor for controlling filamentous cyanobacteria in the hydrosystem of the lower delta of the Senegal River.

The maximum values of the potential ZCG were relatively high, since they accounted for 13, 15, and 49% per day of the field concentration of *C. raciborskii*, *A. flos-aquae,* and *A. solitaria*, respectively. But, in absence of these cyanobacteria growth rate estimates, we cannot evaluate the real impact on cyanobacteria production. However, the relationships between the in situ concentration of the filamentous cyanobacteria and the potential ZCG

showed that high cyanobacteria densities (of the three species considered) were always observed when the ZCG was low or zero.

Little evidence of a direct top-down effect of the zooplankton community on the cyanobacteria is reported in the literature. The role of grazing is generally suggested indirectly by the analysis of the dynamics of phyto- and zooplankton communities in situ or in mesocosms (Hunt et al., 2003; Smith & Lester, 2006; Zhang et al., 2007). Recently, Fey et al. (2010) using both in situ mesocosm experiments and laboratory incubations showed that crustacean zooplankton (*Daphnia pulex*, *Holopedium gibberum*, *Ceriodaphnia quadrangula*, and *Bosmina longirostris*) damaged the colonies of the large colonial cyanobacteria *Gloeotrichia echinulata* and thus, could have efficient top-down impact on this species. However, they could not clearly demonstrate ingestion on this cyanobacterium, except, indirectly, by *D. pulex*.

The high community grazing rates estimated in this study are consistent with the mesocosm study by Sinistro et al. (2007) showing that large filamentous cyanobacteria decreased as large herbivorous species increased. However, these results are contrary to previous observations which suggested that the top-down control of the filamentous cyanobacteria by zooplankton is negligible, either because of the scarcity of large sized grazers, themselves controlled by fish predation (Wang et al., 2007; Zhang et al., 2007), or because of the inability of these large grazers (*Daphnia*) to consume efficiently filamentous cyanobacteria (Degans & De Meester, 2002). In this study, filamentous cyanobacteria seemed able to develop only when the potential grazing pressure was low.

Conclusion

Our results indicate that a variety of zooplankton in tropical lakes may have the ability to consume and control the populations of cyanobacteria. This finding was not expected based on earlier work conducted mainly in temperate and subtropical systems, and suggests a need for further research to elucidate the suite of biotic and abiotic factors that control tropical phytoplankton.

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