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SHALLOW LAKE ECOSYSTEMS

Microzooplankton feeding behaviour: grazing on the microbial and the classical food web of African soda lakes

Alfred Burian · Michael Schagerl · Andrew Yasindi

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Abstract We investigated the feeding behaviour of the dominant microzooplankton of saline lakes in the East African Rift Valley. A set of grazing experiments revealed high ingestion rates of the two euryhaline rotifers *Brachionus dimidiatus* and *Brachionus plicatilis* and of the large-sized omnivorous ciliates *Frontonia* sp. and *Condylostoma magnum* reflecting the unique nature of tropical saline systems. The size spectrum of ingested particles was broad and even included filamentous cyanobacteria such as the commonly dominating *Arthrospira fusiformis*. Feeding selectivity on cyanobacteria, however, was rather low showing higher values for cryptomonads and small ciliates. Bacterial biomass was favoured by the presence of grazers, as small bacterivorous predators were reduced at an average of 13.9%, showing the cascading effect of large zooplankton on the food web structure. Overall, based on this first-time study of the microzooplankton feeding behaviour in East African soda lakes, a strong structuring effect of rotifers and large ciliates on microbial plankton communities is assumed, especially in times of high consumer biomass.

Keywords Zooplankton selectivity · Phytoplankton · Bacteria · Ingestion rate · Cascading effects · Saline lakes · *Brachionus* · Omnivorous ciliates

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A. Burian (✉) · M. Schagerl
Department of Limnology, University of Vienna, Althanstraße 14, 1090 Vienna, Austria
e-mail: flinserl@hotmail.com

A. Yasindi
Egerton University, P.O.Box 536, Njoro, Kenya

Introduction

Grazing of zooplankton is a major factor structuring plankton communities (Gliwicz, 1975) and influencing biomass, competitiveness, growth rates and morphology of prey organisms (Arndt, 1993; Jurgens & Matz, 2002; Verschoor et al., 2007). Zooplankton in the size class 250–100 µm (hereafter referred to as microzooplankton) consists mainly of rotifers, nauplliae and large ciliates and is able to ingest a wide range of food particles. Most studies have focused on the grazing impact on phytoplankton (Rothhaupt, 1990; Hansen et al., 1997). Nevertheless, microzooplankton is also important in channelling energy from the microbial loop to higher trophic levels because it ingests protozoans (Azam et al., 1983; Arndt, 1993) and even bacteria, although with lower efficiencies (Vadstein et al., 1993; Oomswilms, 1997). Feeding behaviour and grazing rates are influenced by several characteristics of food particles. Factors such as food quantity and quality, temperature, taste, digestibility,

catchability and toxicity can play important roles (Demott, 1986; Montagnes et al., 2001; Mitra & Flynn, 2007). For rotifers, prey size is often considered most important (Rothhaupt, 1990; Hansen et al., 1997).

In shallow tropical lakes and especially in alkaline-saline (soda) lakes, phytoplankton communities are frequently dominated by large forms (Lewis, 1978; Fernando, 1994; Oduor & Schagerl, 2007a). This leads to an overlap in size between herbivorous grazers and phytoplankton (Vareschi & Jacobs, 1985; Work et al., 2005). Blooms of large-sized algae may be supported by a higher grazing resistance (Boon et al., 1994; Gragnani et al., 1999) and the lack of regular disturbance events (Talling, 2001).

Schagerl & Oduor (2008), however, demonstrated a relatively low impact of environmental factors on the phytoplankton community structure of soda lakes, which implies an increased importance of biological features. This indicates that, besides allelopathy and resource-competition, grazing by microzooplankton—the most important planktonic consumers in soda lakes (Vareschi & Jacobs, 1985)—could also play a fundamental role, despite the dominance of large-sized photoautotrophs.

Another feature of shallow soda lakes is their high abundance of microbial organisms. Bacterial densities often reach 10^8 ind ml^{-1} (Kilham, 1981), and the biomass of pelagic ciliates ranges among the highest values recorded worldwide (Finlay et al., 1987; Yasindi et al., 2002). Protozoan biomass is commonly dominated by large herbivorous and carnivorous ciliates, whereas bacterivorous protozoa only occasionally reach high abundances. Zinabu & Taylor (1997) argue that carnivorous microzooplankton could be a major reason for the characteristic microbial community structure in tropical saline lakes. They discovered a stronger correlation between chlorophyll *a* values and bacterial numbers in soda lakes than in freshwater systems and hypothesised that bacterial biomass in soda lakes is bottom up controlled. Top down predation pressure could be reduced because of the heavy rotifer and ciliate grazing on heterotrophic nanoflagellates (HNF).

So far, grazing impacts of microzooplankton in tropical soda lakes have not been studied empirically; they were calculated based on either assumptions (Vareschi & Jacobs, 1984) or the subject of speculations (Zinabu & Taylor, 1997). Trying to fill this gap, we conducted grazing experiments under controlled laboratory conditions and focused on two central aspects of mircozooplankton community interactions: First, we tested the hypothesis that dominating filamentous cyanobacteria serve as a food source for microzooplankton in African soda lakes. We investigated ingestion rates on filamentous cyanobacteria and determined the selectivity of microzooplankton taxa when a variety of natural food particles are offered simultaneously. Second, we explored the shaping force of four commonly dominating microzooplankton taxa of tropical African soda lakes on protozoan and bacterial populations. By measuring changes of near-natural communities under the presence and absence of microzooplankton grazers, we monitored the interactions between different members of the microbial loop.

Materials and methods

General

Two sets of grazing experiments were conducted with animals from the two saline-alkaline Kenyan Rift Valley Lakes Bogoria and Nakuru. Both lakes represent typical examples of hypersaline tropical soda lakes and have been used as model systems before (Vareschi & Jacobs, 1985; Harper et al., 2003). For a detailed description of their physical and chemical properties refer to Oduor & Schagerl (2007a, b). All animals used for grazing experiments were isolated from lake water, starved for 6 h and acclimated stepwise to conductivity levels in case experimental conditions differed from natural conditions (change rate of 5 mS cm^{-1} h^{-1}). Experiments were conducted in complete darkness with a constant conductivity of 45 mS cm^{-1} at 22°C, which is close to the average lake temperature (Vareschi, 1982; Harper et al., 2003) and the recommended temperature of 25°C for grazing experiments of *B. plicatilis* (Montagnes et al., 2001).

Bacterial samples were fixed (5% formalin), stained using the SYBR Gold technique (Tuma et al., 1998) and counted under a compound microscope (Motic BA 400, Nikon, Tokyo) equipped with an epifluorescence device. Phytoplankton samples were fixed (5% formalin) and counted using an inverted microscope (Nikon Diaphot, Nikon, Tokyo) according to Utermöhl (1958). Two magnifications, one for pico and

nanoplankton (1000×) and one for larger forms (200×), were used. Biovolumes of the various taxa were estimated using geometric formulae of the shapes of the respective phytoplankton cells (Sun & Liu, 2003). Protozoan samples were fixed with Bouin's solution (5%) and stained using the Quantitative Protargol Staining Technique (QPS) by Montagnes & Lynn (1993) to facilitate counting.

We used direct counts to evaluate grazing impacts even though it is time-consuming and often associated with relatively high-standard deviations (Rott, 1981) because this method still yields the most detailed species-specific results when dealing with diverse plankton communities. Furthermore, other methods such as isotopic or radioactive labelling and coulter counter techniques bear the risk of delays because of incubation times, altering microbial community structure or leading to a misinterpretation of egested particle fragments and cell breakage occurring during ingestion (Harbison & Mcalister, 1980; Peters, 1984). We also avoided culturing because in vitro conditions can affect important factors such as food quality or colony size (Rothhaupt, 1995; Verschoor et al., 2007). We worked with organisms freshly isolated from the lakes to guarantee near-natural conditions.

Grazing on the natural phytoplankton community of L. Nakuru

Water samples were taken from an offshore station in L. Nakuru. Immediately after sampling, lake water was filtered through 40-μm sieves to remove large herbivorous zooplankton. As the phytoplankton community consisted mostly of unicellular algae and small fragments of filamentous cyanobacteria, the phytoplankton community structure was not significantly changed by the filtration process. All experiments started in triplicates within 24 h after water samples were taken. Thirty individuals of one of the four zooplankton taxa *Brachionus dimidiatus* Bryce, *Brachionus plicatilis* Mueller, *Frontonia* sp. (all isolated freshly from L. Nakuru) or *Condylostoma magnum* Spiegel (isolated from L. Bogoria) were placed in 50 ml of prefiltered lake water. Control experiments without added microzooplankton were conducted ($n = 3$). At the start and end of each experiment (after 24 h), samples were taken for bacteria, protozoa and phytoplankton counts.

Grazing on the filamentous cyanobacterium *Arthrospira fusiformis*

Dilution experiments were used to test the ingestion of filamentous cyanobacteria. Water samples from Lake Bogoria were taken because *A. fusiformis* (Vorochinin) Komárek, the phytoplankter commonly predominating in soda lakes, accounted for more than 90% of total plankton biomass in this lake. *B. dimidiatus*, *B. plicatilis* and *Frontonia* sp. were isolated from surface water samples with a micropipette; *C. magnum* was abstracted from subsurface water because this species showed much higher abundances at greater depths. A monospecific cyanobacteria concentrate of *A. fusiformis* (>99.9% biomass) was attained through multiple sieving through 40- and 100-μm sieves and sedimentation chambers making use of phytoplankton buoyancy. This concentrate was diluted in 50-ml containers with GF/F filtered lake water to concentrations of 1.3, 7.5, 14.0, 21.5 and 43.0 g C m^{-3}, reflecting the natural spectrum of *A. fusiformis* densities in tropical soda lakes. To set up the grazing experiments, triplicates for each zooplankton taxon and each dilution approach were prepared by adding 25 individuals to every container. One set of triplicates without introduced grazers served as control. Experiments started within 24 h after lake water sampling, and zooplankton were allowed to graze for 24 h before samples were fixed for phytoplankton counts.

Grazing rates and selectivity

Grazing rates (G) were calculated according to the equation given by Frost (1972): $G = (V/n) \times ((\ln C_t - \ln C_{tf})/t) \times ((C_{tf} - C_0)/(\ln C_{tf} - \ln C_0))$, where V is the volume of the experimental containers, t is the duration of the experiment and n is the number of grazing individuals added. C_0, C_t and C_{tf} correspond to the initial particle concentration, the final concentration in the control and the final concentration in vessels with grazers, respectively.

We calculated the normalised forage ratio (NFR) after Paloheimo (1979) to evaluate the relative selectivity of different food types: $NFR_i = (r_i/p_i)/\sum (r_i/p_i)$, where r_i represents the biomass percentage of the food type i in the consumers diet and p_i is the percentage of that food type in the total offered food spectrum. We included only food particles that were predominantly grazed by the introduced zooplankton. Our

Table 1 Conversion factors used to calculate carbon content of various biota

Taxa	Conversion factors	Reference
Heterotrophic bacteria	Cell number [ind]: carbon content [pg] = 25	Bell (1993)
Cyanobacteria	Biovolume [mm^3]: carbon content [mg] = 0.22	Ahlgren (1983)
Protist plankton	Log C [pg $cell^{-1}$] = log −0.665 + 0.939 × log V [μm^3]	Menden-Deuer & Lessard (2000)
Bacillariophyceae	Log C [pg $cell^{-1}$] = −0.610 + 0.892 × (log plasma V [μm^3])	Strathmann (1967)
Rotifers	%C [dry mass] = 7.8 × V [10^6 μm]$^{-0.37}$	Telesh et al. (1998)

calculations were based on carbon content converted from biovolume with taxon-specific conversion factors (Table 1).

We tested the statistical significance of grazing impact with ANOVAs, followed by post hoc tests with FDR adjusted *p* values (Benjamini & Yekutieli, 2001). Data were transformed to achieve homogeneity of variance, if necessary. If data could not be transformed accordingly, Kruskal–Wallis one-way analysis of variance was used instead of ANOVA. All tests were performed with R, version 2.11 (R Development Core Team, 2010).

Results

Grazing on the natural phytoplankton community of L. Nakuru

At the beginning of the experiment, heterotrophic bacteria biomass was 6.9 g C m^{-3}, contributing 22.2% to the total biomass of the plankton community <40 µm (Fig. 1). Protozoans accounted for 13.7% and phytoplankton for 64.1% or 20.1 g C m^{-3}. Among protozoans, the omnivorous ciliate *Euplotes* and the bacterivorous ciliate *Cyclidium* dominated the biomass, although HNF also played a considerable role with a biomass of 0.9 g C m^{-3}, equivalent to 12.9% of the biomass of heterotrophic bacteria, their major food source. Phytoplankton was dominated by the filamentous cyanobacterium *Anabaenopsis abijatae* Kebede et Willénoften, accounting for 9.6 g C m^{-3} or 46.6% of phytoplankton biomass (Table 2). Two *Cryptomonas* species, picophytoplankton (mainly 1–2.5 µm) and the cyanobacterium *A. fusiformis* were the other important taxa, contributing 28.2, 18.2 and 7.0% of phytoplankton biomass, respectively.

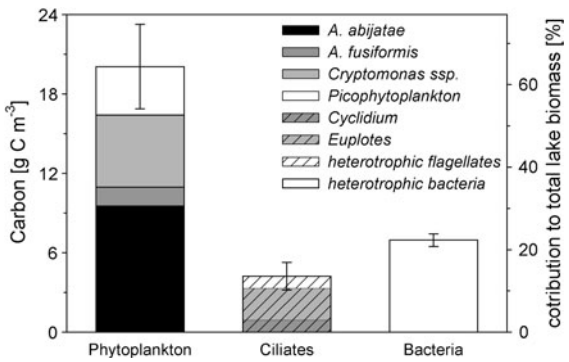

Fig. 1 Biomass of plankton groups at the start of the grazing experiments on a natural plankton community. *Error bars* refer to the standard deviation of the whole compartment ($n = 6$)

The microbial community in the control experiments changed significantly within 24 h (Fig. 2). The bacterial abundances decreased by 35% in the control setup (FDR post hoc test, $P < 0.05$), and the biomass of ciliates significantly increased by more than 60% (FDR post hoc test, $P < 0.01$). The introduction of grazers to experiments reduced the biomass of small ciliates in comparison to final values of controls (see Table 2 for statistics), although a trend to increased ciliate biomass relative to start values was still noticeable (Fig. 2B). In contrast, bacteria were favoured by the presence of introduced grazers compared with controls. Nevertheless, also in experiments with large microzooplankton, final bacterial biomass was always lower than the initial values (Fig. 2A). HNF (all <7 µm) showed the highest biomass at the beginning of the experiment. Controls and experiments with microzooplankton did not differ significantly.

Phytoplankton biomass showed no substantial change in the control treatments. All grazing experiments led to significantly decreased concentrations of *A. abijatae*, with the grazing impact of large ciliates being significantly higher than that of rotifers (FDR post hoc

Table 2 Results of the grazing experiment on natural plankton communities

	Start	End (−)	*B. plicatilis*	*B. dimidiatus*	*Frontonia*	*Chondylostoma*
Heterotrophic bacteria	6949.9* (±486.0)	4546.4 (±641.3)	6338.9 (±1593.9)	5769.1 (±278.0)	5750.2 (±1306.7)	6622.6 (±1294.1)
Protoza						
Heterotrophic flag.	897.7 (±339.3)	637.2 (±164.4)	632.3 (±553.4)	653.5 (±140.8)	841.0 (±574.2)	870.3 (±272.9)
Cyclidium	928.1** (±389.3)	1989.5 (±53.3)	1287.4** (±78.2)	1605.5** (±76.7)	1623.7 (±425.0)	1611.8 (±310.9)
Euplotes	2402.8* (±718.0)	3584.0 (±165.7)	2639.1* (±254.7)	2706.6* (±256.3)	3874.2 (±1528.7)	3192.5 (±345.0)
Other ciliates	74.3 (±26.3)	86.2 (±49.4)	68.0 (±13.0)	77.2 (±44.9)	111.3 (±43.0)	75.6 (±24.2)
Total ciliates	3405.3** (±1041.6)	5659.7 (±157.9)	3994.6* (±221.5)	4389.2* (±251.1)	5609.2 (±1979.2)	4880.0 (±533.5)
Phytoplankton						
A. abijatae	9563.7 (±652.1)	9276.8 (±174.0)	7631.2** (±164.2)	8169.3* (±534.8)	6835.1* (±580.8)	7111.8** (±90.3)
A. fusiformis	1394.4 (±155.8)	1285.4 (±108.2)	1210.8 (±99.6)	1225.7 (±167.9)	1205.1 (±239.9)	1054.5 (±166.5)
Cryptomonas sp. large	2017.8 (±604.0)	2046.3 (±565.0)	1510.8 (±146.7)	2142.1 (±325.0)	1148.6 (±53.8)	1381.4 (±432.7)
Cryptomonas sp. small	3429.4 (±502.4)	3388.3 (±439.4)	3192.2 (±143.3)	2493.6* (±111.9)	2566.5* (±369.2)	2577.7* (±130.6)
Picophytoplankton	3660.8* (±1508.6)	1817.4 (±884.2)	1855.5 (±708.1)	1689.1 (±92.9)	1917.6 (±1352.9)	2446.4 (±461.6)
Total phytoplankton	20066.3 (±3188.1)	17814.3 (±954.2)	15400.5* (±579.8)	15719.8 (±654.0)	13672.0*** (±910.6)	14571.0** (±855.9)

Initial concentrations are given under Start and final values of control experiments without large microzooplankton under End (–). Significance levels of post hoc tests between End (–) and other experimental runs/start values are displayed by * $P < 0.05$, ** $P < 0.01$ and *** $P < 0.001$. Values are given in mg C m^{-3}, numbers in brackets indicate standard deviations

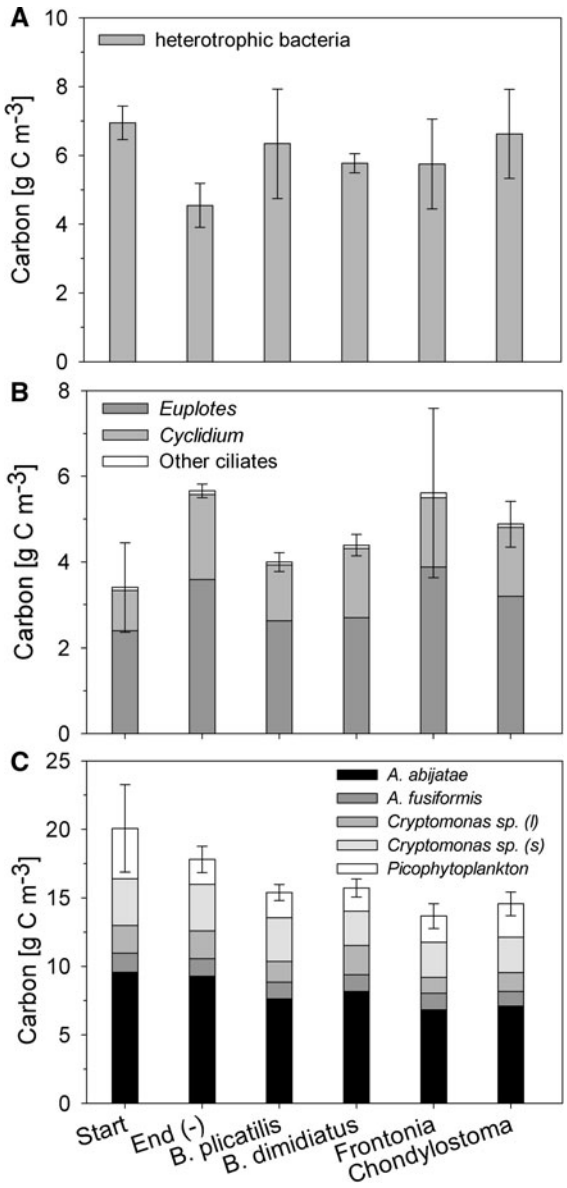

Fig. 2 Impact of various large microzooplankton species on the biomass of heterotrophic bacteria (**A**), small ciliates (**B**) and phytoplankton (**C**) in grazing experiments with natural plankton communities of L. Nakuru

test, $P < 0.05$, Fig. 2C). There was also a clear trend of *A. fusiformis* biomass reduction because of the presence of grazers (Table 2). Although biomass reduction was not significant, the average filament length of the cyanobacterium significantly decreased in the presence of the two large ciliate taxa (FDR post hoc test, $n = 300$, $P < 0.05$). Cryptomonads were grazed on to various extents, with the smaller species showing significantly reduced concentrations (Table 2). Like HNF, picophytoplankton biomass had the highest values at the start of the experiment and a reduced biomass in all setups, including controls.

The grazing rates on phytoplankton were much higher for large ciliates than for rotifers. Among rotifers, *B. plicatilis* ingested 35% more food per individual than *B. dimidiatus*. The ciliate grazing rates were even higher, nearly double those of rotifers. When ingestion per unit grazer biomass was calculated, however, the small-bodied *B. dimidiatus* and *Frontonia* showed clearly higher grazing rates; values reached by *B. plicatilis* and *C. magnum* were one order of magnitude lower (Table 3).

Selectivity indices for the different microzooplankton groups showed some accordance within microzooplankton taxa. The two *Brachionus* species both showed preferences for small bacterivorous ciliates, whereas filamentous cyanobacteria had lower selectivity values. The two ciliates, especially *C. magnum*, exhibited a more uniform ingestion, with a wide range of particles ingested at similar rates. Notably, when selectivity between filamentous cyanobacteria was compared, values for *A. fusiformis* were always lower than for *A. abijatae* (Fig. 3).

Grazing on *Arthrospira fusiformis*

The highest grazing rates on *A. fusiformis* were recorded for the large heterotrich ciliate *C. magnum*, which had a significant grazing impact (FDR post hoc test, $P < 0.05$) on the highest four *A. fusiformis* concentrations (Fig. 4). *B. plicatilis* also displayed high consumption rates, especially at *A. fusiformis* densities of 14.0 and 43.0 g C m^{-3}. The other rotifer, *B. dimidiatus*, had little to no grazing impact on *A. fusiformis*, with only one significant reduction of *A. fusiformis* at intermediate phytoplankton densities.

Grazing rates on *A. fusiformis* concentrations of 1.3 g C m^{-3} were lowest for all microzooplankton organisms. All grazers, except *C. magnum*, showed no significant differences in grazing rates between the highest four *A. fusiformis* concentrations. This implies that the incipient limiting level of *Frontonia* and the two rotifers ranged between 1.3 and 7.5 g C m^{-3}. Grazing rates of *C. magnum* significantly increased (FDR post hoc test, $P < 0.05$) until the second highest cyanobacterial biomass. Even highest *A. fusiformis* densities did

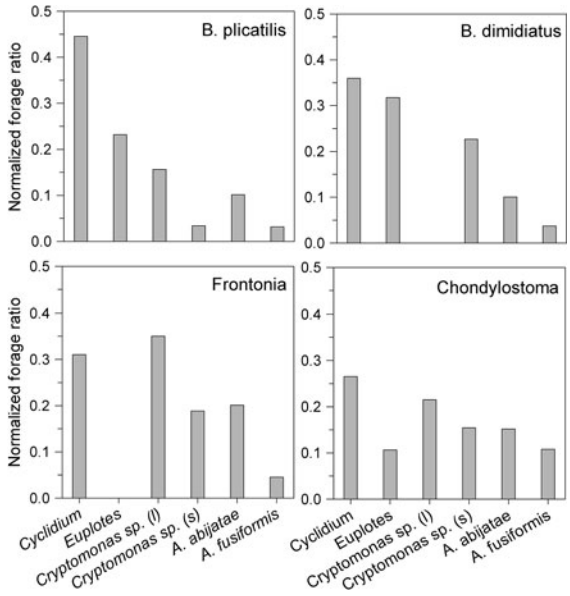

Fig. 3 Grazing selectivity of microzooplankton on different plankton groups in grazing experiments with natural plankton communities of L. Nakuru. Selectivity is expressed in the NFR, and results for *B. dimidiatus*, *B. plicatilis*, *Frontonia* and *Condylostoma* are displayed

not result in inhibitory effects on microzooplankton: None of the grazers showed significantly lower ingestion rates at highest cyanobacteria densities. Grazing rates measured in the two different sets of experiments were not significantly different for all microzooplankton taxa (FDR post hoc test, $P > 0.05$).

Discussion

Size spectrum of food particles and selectivity

High abundance of filamentous cyanobacteria is well documented for tropical soda lakes (Ballot et al., 2004; Schagerl & Oduor, 2008). In our experiments based on the natural plankton community of L. Nakuru, filaments of two cyanobacteria also accounted for 54.6% of phytoplankton biomass. The overlap in size between phytoplankton and dominant primary consumers, a typical phenomenon in shallow tropical lakes (Work et al., 2005), was also observed in our study. We showed that filamentous cyanobacteria can be ingested by microzooplankton despite their large dimension and coiled colony forms.

The two large ciliates *Frontonia* sp. and *C. magnum* showed high physical adaptability in food ingestion. *Frontonia* has a flexible cell wall (Dias & D'agosto, 2006) and we observed this species ingesting filaments substantially longer than its own body. *C. magnum* shows few size restrictions feeding on phytoplankton because of its own large body size. Sometimes *C. magnum* digested several large *A. fusiformis* filaments at once, and this genus is even known to occasionally ingest small rotifers (Arndt, 1993). It is commonly assumed that small food dominate the feeding spectrum of the suspension-feeding rotifer genus *Brachionus* (Rothhaupt, 1990). Studies on *B. plicatilis* from temperate regions defined an optimum food size between 5 and 10 μm (Hansen et al., 1997), and food particles in this range are also commonly used in aquaculture. In contrast, Pagano et al. (1998) showed that food selectivity of a tropical population of *B. plicatilis* reached almost maximum values when 20-μm particles were ingested (feeding on larger particles was not studied). Furthermore, tropical rotifer populations of *Brachionus calyciflorus* Pallas are able to ingest the filamentous cyanobacterium *Cylindrospermopsis raciborskii* Woloszynska (Soares et al., 2010), and Bouvy et al. (2001) measured high *B. calyiflorus* biomass when phytoplankton consisted nearly 100% of *C. raciborskii*. This indicates that brachionid rotifers populations in eutrophic tropical systems might have adapted to the dominance of large phytoplankton forms.

Selectivity indices, however, illustrated a lower selectivity of rotifers and *Frontonia* sp. for filamentous cyanobacteria. Especially *B. plicatilis* and *B. dimidiatus* preferred small ciliates over cyanobacteria. Variations in selectivity patterns could be caused by a number of factors ranging from specific nutrient requirements and food quality to prey catchability and the cell surface of prey items (Mohr & Adrian, 2000; Plath & Boersma, 2001). Nonetheless, size did not seem to be a factor limiting the ingestion of cyanobacteria in our study, as bacterivorous ciliates grazed by microzooplankton were considerably bigger.

Brachionus is often considered to be a size-selective grazer, unable to distinguish between particles of different quality (Demott, 1986; Rothhaupt, 1990, 1995; Hansen et al., 1997). In contrast, Snell (1998) pointed out the presence of chemoreceptors in the buccal field of this genus, indicating

Table 3 Grazing rates of microzooplankton species on natural phytoplankton and ciliate communities

	Phytoplankton		Ciliates	
	Prey μm^3 predator (ind^{-1})	Prey μm^3 predator (ng^{-1})	Prey μm^3 predator (ind^{-1})	Prey μm^3 predator (ng^{-1})
B. dimidiatus	6.10×10^5 (2.49×10^5)	1.33×104 (5.43×103)	2.22×10^5 (4.20×10^4)	4.84×103 (9.15×102)
B. plicatilis	8.20×10^5 (1.79×10^5)	4.48×103 (9.78×102)	2.89×10^5 (3.50×10^4)	1.58×103 (1.92×102)
Frontonia	1.49×10^6 (2.04×10^5)	1.71×104 (2.34×103)	-0.04×10^5 (3.70×10^5)	-4.58×101 (4.24×103)
Condylostoma	1.32×10^6 (1.43×10^5)	1.02×103 (1.11×102)	1.37×10^5 (9.16×10^4)	1.06×102 (7.10×101)

Ingestion values are given in ingested μm^3 h^{-1} ind^{-1}, numbers in brackets indicate standard deviations

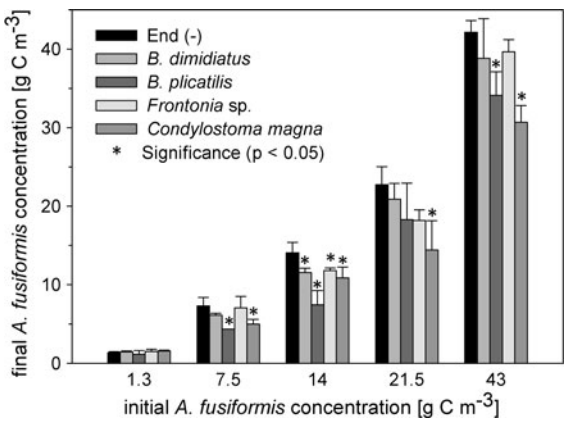

Fig. 4 Results of the grazing experiments with *A. fusiformis* as sole food source. Control experiments without grazing zooplankton are displayed as *End* (–). Significant results of post hoc tests between *End* (–) values and other experimental runs are displayed

that other factors might also play a role for food selectivity. Some studies of Asian *B. plicatilis* populations have shown that selectivity cannot be explained by size alone (Hirayama et al., 1979; Zhou et al., 2009), and according to Kirk & Gilbert (1992), *Brachionus* can avoid toxic cyanobacteria via sensitive taste receptors. This seemed to be confirmed by another study (Lurling & Verschoor, 2003), which showed varying selectivity of *Brachionus* on *Microcystis*, depending on ratios between *Microcystis* and other available food particles. Gilbert & Starkweather (1977) have described three mechanisms of food rejection in *B. calyciflorus*: one for adjusting the maximum size of ingested particles and two others for selective rejection of single particles, probably connected to high energy costs for the grazing organism. Nonetheless, food selectivity in zooplankton has been shown to increase with particle size (Demott, 1986). Probably the amortization of energy-intensive rejection mechanisms may rise with increased particle size, leading to increased importance of other factors influencing selectivity patterns.

Interactions between microzooplankton and microbial food webs

Microzooplankton strongly influenced the abundance and biomass of other microorganisms in experiments with natural plankton communities (Fig. 2). Both rotifers and large ciliates caused cascading structural effects on the food chain by reducing numbers of bacterivorous grazers and thus stabilising bacterial biomass. Additionally, the positive reaction of bacterial abundances might also be attributed to other factors such as increased nutrient recycling because of metazooplankton presence (Guildford & Taylor, 2011). The biomass of an intermediate size group consisting of HNF and picophytoplankton decreased in both the control and experimental setups. This is because large microzooplankton and small ciliates feed on this particle size (Rothhaupt, 1990; Cheng et al., 2004). The increasing abundances of small omnivorous ciliates probably compensated the absence of large microzooplankton grazers in control vessels.

The positive effect of large microzooplankton grazers on heterotrophic bacteria, by reducing the biomass of bacterivorous protozoans, supports the hypothesis of Zinabu & Taylor (1997) that bacterial biomass in soda lakes is generally bottom up controlled. This is confirmed by the fact that large microzooplankton forms commonly occur in soda lakes at much higher densities than in our grazing experiments (Iltis & Riou-Duwat, 1971; Vareschi & Vareschi, 1984). A long-term investigation of

microbial communities would provide a more detailed insight into this topic.

Grazing rates and structuring forces of zooplankton

Grazing rates in both sets of experiments were generally high. To our knowledge, only qualitative studies have been conducted on *Frontonia* sp. (Dias & D'agosto, 2006); grazing rates, however, have been reported for rotifers of the genus *Brachionus* and especially for *B. plicatils*. Most studies have been conducted with nanoalgae cultures and yielded rates in the range of 2–5 $\times$ 10^5 μm^3 ind^{-1} h^{-1} (Hansen et al., 1997; Navarro, 1999; Montagnes et al., 2001). Vareschi & Jacobs (1984) did not directly measure grazing but calculated consumption based on the production and an energy transfer efficiency of 0.15%, with consumption rates more than 6 $\times$ 10^5 μm^3 ind^{-1} h^{-1}. Interestingly, the grazing rates of 8.2 $\pm$1.8 $\times$ 10^5 μm^3 ind^{-1} h^{-1} obtained in this study were substantially higher, which could be because of several factors. First, 24-h incubation times could have increased microzooplankton densities. Rotifers were randomly picked from natural populations without selecting against egg-carrying individuals. As egg rates (eggs $females^{-1}$) were high, with 0.8 for *B. plicatilis* and 0.6 for *B. dimidatus*, and embryonic development time is low (Vareschi & Jacobs, 1984), freshly hatched individuals might have increased grazing rates. Second, sloppy feeding increases with food particle size (Moller, 2005). Accordingly, a larger proportion of ciliates and filamentous cyanobacteria in ingested food particles probably increased the importance of this factor, which is usually neglected in grazing experiments. Third, also food quality, quantity and gut transition time (GTT) have to be considered: maximum feeding rates can be increased by a factor of four through variation of these variables (Mitra & Flynn, 2007). If the quantity is high, GTT will depend on food quality because low-quality food remains shorter in the gut. This physiological acclimation ensures a high gradient of essential nutrients between the digestive system and the absorbing tissue, even if low-quality food is ingested (Willows, 1992; Jumars, 2000a, b). Conversely, if quality is high, then grazing rates are reduced and GTT is increased to maximise energy efficiency (Mitra & Flynn, 2007). Phytoplankton communities in tropical saline-alkaline lakes are commonly dominated by filamentous cyanobacteria, which are mostly considered as low-quality food (e.g. Arnold, 1971) leading to low zooplankton population growth rates (Brett et al., 2006). Thus, *B. plicatilis* populations in L. Nakuru and L. Bogoria might be adapted to this condition by keeping feeding rates high and GTT low.

When weight-specific grazing instead of individual rates is investigated, the two smaller species *B. dimidiatus* and *Frontonia* sp. display much higher ingestion rates. This might reflect higher metabolic requirements and higher production rates of the smaller microzooplankton taxa and is in line with Vareschi & Jacobs (1984), who found higher production rates for *B. dimiatus* than for *B. plicatilis*.

To estimate in situ community grazing rates, we multiplied microzooplankton of L. Bogoria and L. Nakuru at the sampling dates (Table 4) with grazing rates of rotifers and large ciliates in near-natural plankton communities. This yielded community grazing rates of 3.0 g C m^2 day^{-1} for L. Nakuru, reflecting comparatively high microzooplankton densities (Vareschi & Vareschi, 1984), and 0.8 C day^{-1} for L. Bogoria, which had average to low densities at the sampling date. If community grazing is related to the average daily gross primary production rates of the two lakes (Oduor & Schagerl, 2007a), then rotifers and large ciliates consumed 45 and 17% of the daily autotrophic production of L. Nakuru and L. Bogoria, respectively.

Overall, we identified three different effects of the large microzooplankton on plankton communities: a negative one on large phytoplankton and small ciliates because of direct grazing, a neutral effect on HNF and picophytoplankton because microzooplankton consumption compensates reduced grazing pressure by small ciliates and finally a positive effect on heterotrophic bacteria (<1 μm).

Considering the high grazing rates and the sometimes outstandingly abundant rotifer populations (Iltis & Riou-Duwat, 1971; Vareschi & Vareschi, 1984), microzooplankton in tropical soda lakes certainly has the potential to shape phytoplankton communities. Especially during transitional phases—when phytoplankton biomass is low, rotifer abundances high and the phytoplankton community is switching between two alternative stable states (Vareschi & Jacobs, 1985)—grazing pressure might be a major controlling factor. Nevertheless, when *A. fusiformis* dominates,

Table 4 Microzooplankton densities of Lake Bogoria and Lake Nakur at the time of sampling for grazing experiments in April 2009

	Bogoria	Nakuru
Frontonia sp.	2,692	565
B. dimidiatus	817	3,230
B. plicatilis	583	584
C. magnum	575	0

Abundances are displayed in ind l^{-1}

the influence of zooplankton should be very limited because of low consumer densities and a very high phytoplankton biomass (Vareschi, 1982). During such periods, even high community grazing rates would only minimally change the phytoplankton standing stock. Therefore, phytoplankton grazers can be excluded as the sole reason for *A. fusiformis* biomass breakdowns, which are observed stochastically in saline Rift Valley lakes. Nonetheless, enhanced nutrient recycling, lower selectivity of zooplankton for *A. fusiformis* and improved underwater light supply caused by grazing could play key roles in establishment of such blooms.

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