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DIPLOMARBEIT

Titel der Diplomarbeit

Zooplankton dynamics of two alkaline-saline lakes in the Kenyan Rift Valley

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Population of Lesser Flamingo at the shores of Lake Bogoria.

Table of content

1. Introduction to the ecology of East African salt lakes (German)

Die Salzseen des ostafrikanischen Grabenbruchs sind nicht nur durch ihre atemberaubende Landschaft einzigartig, sondern heben sich auch durch eine Reihe von Umwelt- und biologischen Faktoren von anderen Ökosystemen ab.

Ein wesentliches Charakteristikum dabei stellt die geographische Lage der Seen in Becken des Großen Afrikanischen Grabenbruchs dar. Fast ausschließlich handelt es sich um sogenannte endorheische Systeme, das heißt um Gewässer die lediglich einen Zufluss aber keinerlei Abfluss und Verbindung zum Meer besitzen. Stattdessen besteht ein Gleichgewicht zwischen zufließenden Wassermengen und Verdunstung. Folglich verbleiben gelöste Stoffe wie Kationen oder Carbonate im Wasserkörper der Seen und sorgen somit für erhöhte Leitfähigkeit und Salinität. Ein wesentliches Merkmal der Wasserchemie sind außerdem erhöhte pH-Werte, die auf die Alkalinität der Böden im Einzugsgebiet der Seen zurückzuführen sind.

Viele dieser aquatischen Systeme, wie zum Beispiel auch der im Zentrum meiner Untersuchungen stehende Lake Nakuru, sind sehr seichte Gewässer, mit einer Wassertiefe von nur wenigen Metern. Diese geringe Wassertiefe zieht eine Reihe von Konsequenzen nach sich. Zum einem bewirken die oft regelmäßig auftretenden böigen Winde eine starke Aufwirbelung des Sediments. Die dadurch erhöhte Menge an gelösten Substanzen im Wasser hat somit Auswirkungen auf die Lichtverfügbarkeit unter der Wasseroberfläche. Außerdem sind die gelösten Nährstoffe, aber auch die kleinen partikulären Substanzen im Wasser eine Voraussetzung für die reichhaltigen mikrobiellen Lebensgemeinschaften dieser Seen. Zum anderen haben durch die geringe Tiefe der Seen Schwankungen im Wasserspiegel weitreichende Konsequenzen. So kann es bei Schwankungen der Wasserzufuhr, die im Fall von Lake Nakuru durch illegale Entwaldung des Einzugsgebietes in den letzten Jahrzehnten noch verstärkt wurden, innerhalb von wenigen Monaten zu einer kompletten Austrocknung der Seen kommen.

Aber besonders herausstechend sind die biologischen Eigenheiten dieser Salzseen, für die Lake Nakuru aufgrund seiner leichten Zugänglichkeit und seiner wirtschaftlichen Wichtigkeit als Tourismusgebiet ein Modelluntersuchungsgebiet darstellt. Am augenscheinlichsten sind wohl die umfangreichen Flamingopopulationen, die diese Gewässer weit über die Grenzen von Ostafrika hinaus bekannt gemacht haben und aufgrund deren sie auch oft unter den Namen Flamingoseen zusammengefasst werden. Für den Biologen ebenso beeindruckend sind aber die Merkmale und Zyklen, denen die Planktongemeinschaften unterworfen sind. Hervorgerufen durch die extremen Standortbedingungen, sind grundsätzlich alle Ebenen des Ökosystems durch extrem hohe Biomassen der einzelnen Taxa und mit Ausnahme der mikrobiellen Zönosen durch eine sehr geringe Artenvielfalt gekennzeichnet.

Das Phyotplankton ist meist dominiert von filamentösen Blaualgen, wobei *Arthrospira fusiformis* Blüten ausbilden kann, die so sich so verdichten, dass Algenfäden an der Wasseroberfläche regelrechte Phytoplanktonteppiche bilden können. In solchen Zeiten wird die Algenbiomasse praktisch ausschließlich von dieser einen Art aufgebaut. Allerdings kommt es, möglicherweise hervorgerufen durch Virenbefall, immer wieder zu Zusammenbrüchen der Algenbiomassen und zu einer Abfolge unterschiedlicher Algengesellschaften.

Das Zooplankton dieser Seen stellt sich aus Ciliaten, Rädertieren und Kleinkrebsen zusammen, wobei letztere aufgrund von erhöhter Salinität und anderer Faktoren häufig über Jahre nur in vernachlässigbaren Dichten vorkommen. Wenn man das Mesozooplankton, bestehend aus Rädertieren und größeren Ciliaten genauer betrachtet, so ist es sehr auffällig, dass es zu gewissen Zeitpunkten zu einer Explosion der Biomassen kommt. Diese Dichten können soweit ansteigen, dass dadurch sogar die Wasserfarbe einen bräunlichen Ton annimmt, und stellen weltweit Spitzenwerte für diese Tiergruppe dar. Naturgemäß müssen solche Zooplanktonphänomene auch einen erheblichen Einfluss auf andere Fraktionen des Nahrungsnetzes dieser Seen ausüben. Doch wurden bis jetzt nur Hypothesen aufgestellt. Es gibt keinerlei Informationen, weder über Fraßverhalten und die Auswirkungen desselben, noch über die fundamentalen Muster die solchen Zooplanktonblüten zugrunde liegen.

So war es die Zielsetzung dieser Arbeit, mehr über Rhythmen und Dynamik der Zooplanktonorganismen von salinen Seen in Ostafrika herauszufinden und somit einen Baustein zum Verständnis dieser einzigartigen Ökosysteme zu liefern.

2. The role of rotifers in the food web of the saline-alkaline Kenyan Rift Valley Lake Nakuru: a snapshot of micro- and mesoplankton communities.

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Abstract

Zooplankton of saline-alkaline lakes are often dominated by rotifers but little is known about their feeding behaviour and their interaction with phytoplankton and microbial communities. In this study, the ecological niches of the two frequently dominating rotifers of Lake Nakuru (Kenya), *Brachionus dimidiatus* and *Brachionus plicatilis,* were investigated using stable isotope analysis. The larger-sized *B. pliciatilis* showed a reliance on the filamentous cyanobacteria *Arthrospira fusiformis* and *Anabaenopsis abijatae*, which indicates substantial differences of feeding behaviour within the cryptic species complex of this taxon. *B. dimidiatus* fed to a large extend on components of the microbial loop and bacterial contribution of over 40% to total rotifer nutrition belongs to the highest ever recorded *in-situ* values. Further, the comparatively high $\delta^{15}N$ value of *B. dimidiatus* implies an enrichment of $\delta^{15}N$ caused by a reliance on the microbial loop within an ecosystem which is strongly depended on recycling of nutrients originating from higher trophic levels. This underlines the necessity of a careful application of $\delta^{15}N$ values for interpreting trophic levels in such communities.

Introduction

Inland saline lakes are common in arid and semi arid regions all over the world and globally their total volume is only slightly less than that of freshwater systems (Shiklomanov, 1990). They are typically earmarked by a low biodiversity but high abundance and biomasse of both, primary producers and consumers (Oduor and Schagerl, 2007a; Talling et al., 1973; Vareschi, 1982). These characteristics turn them into very suitable systems for ecosystem studies as their food webs are relatively simple and energy fluxes can be investigated at lower levels of complexity (Vareschi and Jacobs, 1985). However, in spite of their throphic simplicity, the highly stochastic temporal dynamics in their environmental variables (Oduor and Schagerl, 2007b) and the changing interactions between communities leave many questions yet to be answered.

The world-famous Lake Nakuru, an east African saline lake, has been extensively studied in the 1970s and 80s by the research team of Vareschi (e.g. Vareschi, 1978, 1979; Vareschi and Vareschi, 1984). Their studies have resulted in a summary wherein energy pathways were investigated in detail and major parts of the ecosystem described (Vareschi and Jacobs, 1985). The phytoplankton community of L. Nakuru, which is among the most productive systems worldwide (Melack and Kilham, 1974; Oduor and Schagerl, 2007a), is able to switch between two stable state conditions which can last a few weeks up to several years lasting (Vareschi and Jacobs, 1985). One stable state is characterized by the dominance of the filamentous cyanobacterium *Arthrospira fusiformis* (Vorochinin) Komárek, which is generally common in tropical saline-alkaline lakes (Jenkin, 1936; Melack, 1981; Schagerl and Oduor, 2008; Vareschi, 1982). The alternative steady state condition is characterized by a taxonomicly more diverse community of cryptomonads and small coccoid cyanobacteria (Ballot et al., 2004; Schagerl and Oduor, 2008; Vareschi, 1982). In transitional phases between equilibrium states *Anabaenopsis abijatae* Kebede et Willénoften often shows high densities (Vareschi and Jacobs, 1985).

Zooplankton biomass is frequently dominated by various ciliate species (Yasindi et al., 2002, this study) and by the two suspension feeding rotifers *Brachionus dimidiatus* Bryce and *Brachionus plicatilis* Mueller, which constitute the typical rotifer fauna of saline lakes (Fontaneto et al., 2006; Green and Mengestou, 1991; Nogrady, 1983). Although, rotifers only play a minor role (< 5%) within the entire consumer biomass, their community ingestion rates are nearly equal to those of the huge populations of the phytoplankton grazing lesser flamingo (*Phoeniconaias minor* Geoffroy) with average numbers of around one million birds at the shore of the lake (Vareschi and Jacobs, 1985). This statement is valid independently of phytoplankton community structures and caused by high catabolic rates and low turnover times of rotifers. In terms of production rotifers are by far the most important consumers, as flamingos do not breed at Lake Nakuru (Brown, 1973; Ndetei and Muhandiki, 2005). Further, during transitional phases downright explosions of rotifer abundances frequently occur with biomass reaching dimensions usually observed only in cultures and surpassing the tenfold of normal peak densities (unpublished data). Only during these transitional phases rotifer biomass also contributes essentially to the lakes total biomass.

However, though Vareschi’s fundamental studies contribute substantially to our knowledge about tropical saline lakes, his work is affected by two major weaknesses: first, the role of the microbial loop in supply dietary energy to upper trophic levels was not incorporated, though the sheer quantity of microbial organisms point out their potential importance in such systems (Kilham, 1981; Yasindi and Taylor, 2006). Secondly, although high rotifer grazing on bacteria and detritus was suggested, actual measurements of food sources contributing to rotifer nutrition were missing.

The aim of this study was to investigate the retained food sources ecological role of the two dominant rotifer species *Brachionus dimidiatus* and *Brachionus plicatilis* of Lake Nakuru. Using stable isotopes, we attempt to differentiate their feeding niches, examine their dietary reliance on the microbial loop, and assess the impact of rotifers on the food web structure of

Lake Nakuru. To our knowledge this is the first *in-situ* stable isotope study of rotifers that investigates their role in aquatic food webs and we aimed to obtain crucial information about the ecological applicability of this technique for this group.

Material and Methods

Study area and site description

Lake Nakuru (Fig. 1; S 00°20‘E 36°05‘) is a shallow pan located in the eastern (Gregory) Rift Valley in Kenya near the town of Nakuru. It is the centrepiece of Lake Nakuru National Park, one of the major revenue sources for the whole region. This lake represents an endorheic, hypertrophic, saline-alkaline ecosystem mainly recharged by rainfall during the rainy season from April to July and short rains from October to November. Annual rainfall fluctuates between years leading to considerable changes in water depth ranging from a maximum of >4 m to a completely dried up lake basin (Schagerl and Oduor, 2008; Vareschi, 1982). Vast, illegal deforestation of the Mau Forest (Yillia and Kreuzinger, 2009), which constitutes the main catchment area of Lake Nakuru, has further added to the variability of water levels. As a matter of course, plankton communities are affected by accompanying changes in salinity and lake chemistry (Vareschi, 1982), though biological interactions also play a key role in community succession (Oduor and Schagerl, 2007b).

Sampling design and methods

Surface water samples were taken with a Schindler trap (10 L) at the central off shore station of the lake (S00°21‘12“, E036°05‘00“) in April 2009. All samples were immediately cooled until further analysis. Temperature, conductivity, salinity, pH, dissolved oxygen and Secchi depth were measured on site; water samples were collected for analysis dissolved organic carbon (DOC), nutrient concentrations, chlorophyll *a*, bacteria, protozoa, phytoplankton and zooplankton abundances. For detailed descriptions of the determination of abundance of bacteria, phytoplankton, protozoa and zooplankton see Burian et al. (2010). Total biovolumes were calculated from species abundance and average species biovolumes. Biomasses were then derived from the total biovolumes and converted to carbon using conversion factors given in Table 1.

For stable isotope analysis, water was pre-filtered through a 40 µm sieve to gather zooplankton and large, filamentous cyanobacteria. A division of cyanobacteria and the two rotifer species *B. dimidiatus* and *B. plicatilis* was achieved by a multiple subsequent filtration and a series of division chambers based on sedimentation, buoyancy and negative phototaxis. Rotifers were starved in GF/F filtered lake water for 6 hrs to facilitate gut evacuation and afterwards species separation was achieved by multiple soft filtrations through a 100 µm mesh. Phytoplankton (>40 µm) and both zooplankton samples were rinsed repeatedly with GF/F filtered lake water, concentrated on precombusted (550°C; 4 hrs) glass fibre filters (Whatman GF/F) and subsequently oven dried (60˚C; 24 hrs). For direct counts and biomass quantification of zoo- and phytoplankton, subsamples were taken from all three samples.

Furthermore, water particles were size-fractionated onto polyethylene filters: a) 20-40 µm, b) 2-20 µm, and, c) particles <2 µm were subsequently filtered on precombusted GF/F filters (0.7 µm) and dried (60˚C; 24 hrs). From each of these three size classes, subsamples were taken for biomass estimation. For DOM samples, 100 mL of GF/F filtered lake water were acidified (to pH 2) and dried. Subsequently, the collected residue was homogenized. This method was applicable because of extraordinary high DOM concentration in L. Nakuru. For sediment samples, the first centimetre of the sediment layer was collected with a corer, flushed with 1% HCl and subsequently oven dried. Additionally, several hauls with a plankton net (mesh size 250 µm) were taken to collect mesozooplankton. All individuals were separated to species level, starved for 12 h hours, pooled and dried. Samples of the only fish species occurring at L. Nakuru, *Oreochromis alcalicus grahami* Boulenger, were taken with a dip net. Muscle tissue from behind the pectoral fin was treated with chloroform for 12 hrs to remove lipids, dried and homogenized for stable isotope analysis. Additionally, the dominating macrophyte (*Cyperus laevigatus* L.) of the littoral zone was collected and water insects around the macrophytes were sweep netted. Individuals were starved, pooled at species level and dried. Close to the inflow of the Njoro River allochthonous material was collected with a 100 µm net and retained plant material (at least 50- 100 fibres per replicate) was afterwards picked with forceps and oven dried.

For carbon and nitrogen isotopic analysis, samples (triplicates) were combusted using a Flash EA 1112 series elemental analyzer (Thermo Finnigan, Italy) coupled to a Delta Plus XP IRMS (isotope ratio mass spectrometer; Thermo electron, Germany). The standard deviation for replicate samples was 0.1‰ for $\delta^{13}C$ and 0.18‰ for $\delta^{15}N$. All stable isotope values were reported in the δ notation where $\delta^{13}C$ or $\delta^{15}N$ = ([R sample / R standard] - 1)·1000, where R is ^{13}C:^{12}C or ^{15}N:^{14}N, respectively. Global standard for $\delta^{13}C$ is PeeDee Belemnite and for $\delta^{15}N$ is atmospheric nitrogen.

Data analysis

C:N ratios of sediments can be used to differentiate between organic terrestrial and aquatic organic matter (Carreira et al., 2002; Kaushal and Binford, 1999; Meyers, 1994). We used a mixing model based on N:C ratios rather than on C:N ratios as the latter ratio does not result in a linear correlation (Perdue and Koprivnjak, 2007). For quantification of zooplankton food sources, two source mixing models based on the following formula were applied:

$(V_T - F - V_{S1})/(V_{S2} - V_{S1}) \times 100 = \% V_{S1}$,

where V_{S2}, V_{S1} and V_T represented analyzed values of source one, source two and the target, respectively, and F was the isotopic fractionation factor. The same formula without F was used for the N:C based mixing model. The nitrogen isotopic enrichment factor from consumer’s diet to the body tissue of the consumer (nitrogen fractionation; ΔN) was assumed to be 3.4 ‰ (Minagawa and Wada, 1984; Post, 2002; Vander Zanden and Rasmussen, 2001), if not stated otherwise. For carbon fractionation (ΔC) 0.43 ‰, a value suggested by Grey (2001) for crustacean zooplankton was used, as a specific ΔC for rotifers was not available However, this ΔC was also in line with factors from other studies (Post, 2002; Vander Zanden and Rasmussen, 2001). Confidence intervals (95%) were calculated according to Phillips and Gregg (Phillips and Gregg, 2001).

Results

Physiochemical and biological parameters

Lake Nakuru was highly saline (35‰) with an average depth of only 1m. Dissolved oxygen was clearly oversaturated with a concentration of 19 mg O_2 L^{-1} at noon at 22°C water temperature. Lake Nakuru had very high concentrations of soluble reactive phosphorus, ammonia, nitrate, and nitrite (Table 2), with the latter dissolved nutrients resulting in low C:N ratio of lake water (Table 2).

In the raw samples, the two filamentous cyanobacteria *A. abijatae* and *A. fusiformis* accounted for 99 % of the total algae biomass with *A. abijatae* showing a heterocyte frequency of 13.5 % (35 % of *A. abijatae* biovolume). Total phytoplankton biomass was low (14.8 g C m^{-3}, Table 3), compared to rotifers, which reached 8.1 g C m^{-3} and 54.7 % of phytoplankton biomass. This zooplankton group was mainly responsible for the high consumer: producer ratio during the sampling. Among rotifers, the larger *B. plicatilis* (276 ± 26 µm body length) accounted for three quarters of biomass, the more abundant *B. dimidiatus* (Table 3; 132 ± 9 µm) made up for one quarter. Ciliates were dominated by the two large omnivores *Holophyra* and *Frontonia*. Also a couple of small bacterivorous ciliates, including the genera *Cyclidium* and *Euplotes*, were present, but in spite of huge bacterial numbers and biomass (Tab. 3), their impact on ciliate biomass was very small.

Biomass calculations of the isotope samples

The two filamentous cyanobacteria reached over 99% of biomass in three size fractions (2-20 µm, 20-40 µm, and >40 µm), but within theses samples the ratio between *A. abijatae* and *A. fusiformis* and the ^{13}C values varied. In order to calculate the species specific $\delta^{13}C$, a regression model based on the ^{13}C values and the relative biomass ratio of the two taxa was established and extrapolation led to computed values (Fig. 2 and 3). There was no significant difference in $\delta^{15}N$ of the three mixed algae samples (ANOVA; $p = 0.29$) and therefore the mean (4.2 ‰) of the mixed size classes was generally applied as $\delta^{15}N$ for filamentous cyanobacteria. The <2 µm size fraction showed a mixture of heterotrophic and mixothrophic flagellates, bacteria and picophytoplankton. The zooplankton samples showed purities of 98 % and of 94 % for *B. plicatilis* and *B. dimidiatus* respectively.

C:N ratios and stable isotope analysis

The C:N ratios of plankton (4.5 – 5.5) were lower than those of macrophytes and allochthonous plant particles (19 - 26), whereas sediment C:N ratios were 8.4. The N:C ratio based mixing model resulted in an influence of 41.5 % of terrestrial sources on sediment carbon. However, $\delta^{13}C$ signature of sediments (-18.3 ‰) were close to those of planktonic primary producers and consumers (-23.2 – -16.5 ‰), in contrast to macrophytes and allochthonous material (-12.0 – -8.8 ‰). We did not apply a mixing model based on stable isotope signatures because of possible long term temporal variability of phytoplankton signals.

The calculated $\delta^{13}C$ of the two cyanobacteria taxa represented the end points of the $\delta^{13}C$ range of planktonic signals (Fig. 3) and their $\delta^{15}N$ (4.2 ‰) was assumed to be the trophic baseline of the pelagial. The ^{13}C and ^{15}N values of the two rotifer species (Table 4) were significantly different from each other ($p<0.05$; t – test). *B. plicatilis* was one trophic level above the algal baseline, whereas *B. dimidiatus* ranged half a trophic level above *B. plicatilis*. The $\delta^{15}N$ of the < 2 µm size fraction (6.7 ‰) was also nearly one level above the algal base line and the $\delta^{15}N$ of DOM (6.1 ‰) was likewise elevated. As the <2 µm size fraction was a mixed sample of various components and a direct determination of bacterial isotopic signals was therefore not possible, we used their potential main food source DOM for calculation. Based on a ΔC for bacteria of 1 ‰ (Coffin et al., 1989) and a ΔN of 3.4 ‰, the computed isotope signals of bacteria were -16.8 ‰ for $\delta^{13}C$ and 9.5 ‰ for $\delta^{15}N$. The $\delta^{13}C$ values of the soda tilapia and the *Ephydra* larvae were both in the range of the $\delta^{13}C$ signature of *A. abijatae*, yet their $\delta^{15}N$ signatures were well below the first trophic level.

In order to calculate the contribution of possible food sources to rotifer nutrition, we established two two-source mixing models. For *B. Plicatilis*, a δ^{13}C based model with *A. fusiformis* and *A. abijatae* as possible food sources showed that, on average, 69 % of consumer's carbon originated from *A. fusiformis* (95 % confidence interval from 60 to 78 %). For *B. dimidiatus* we applied a δ^{15}N based mixing model, assuming bacteria and *A. abijatae* as possible food sources, which resulted in a dietary dependence of 47 % on bacterial nitrogen and of 53 % on nitrogen of *A. abijatae*. A 95% confidence interval could not be calculated as bacterial δ^{15}N signatures were based on calculations and a standard deviation was not available.

Discussion

During our study, L. Nakuru was characterized by low algal biomass and high bacterial numbers, compared to values commonly found in such tropical saline lakes (Ballot et al., 2004; Kilham, 1981; Oduor and Schagerl, 2007b). Two weeks before this isotope sampling, *Anabenopsis abijatae* was dominating phytoplankton (unpublished data) followed by a fast replacement by *Arthrospira fusiformis*. Together with the high rotifer abundances this scenario is typical for transitional stages of plankton communities in L. Nakuru (Vareschi, 1982).

Zooplankton was dominated by the rotifers *Brachionus plicatilis* and *Brachionus dimidiatus*, though also the large ciliates *Frontonia* and *Holophrya* were reaching considerable biomass (Tab. 3). In spite of high bacterial biomass, heterotrophic nanoflagellates and ciliates <60 µm were of minor importance (Tab. 3), which indicates a strong top town biomass control by larger omnivorous zooplankton. The high conductivity levels (49.4 mS cm^{-1}) were probably responsible for the absence of the crustacean zooplankton. *Lovenula africana*, the only copepod species of L. Nakuru, usually disappears at conductivity at conductivity levels beyond 25 mS cm^{-1} (LaBarbera and Kilham, 1974; Vareschi and Vareschi, 1984).

The N:C ratio based mixing model, which was applied to assess allochthonous and autochthonous origin of organic carbon, showed a surprisingly high contribution of allochthonous material to lake sediments. However, it is already known that due to preferential decomposition of N-compounds, the N:C ratio can be decreased in lake sediments (Sampei and Matsumoto, 2001). Considering high microbial activity (Kilham, 1981; Yasindi et al., 2002), potential N-deficiency (Oduor and Schagerl, 2007b) and regular sediment resuspension due to wind and biological activities in L. Nakuru (Vareschi, 1982; Weithoff et al., 2000) as well as the extremely high net primary production rates (Oduor and Schagerl, 2007a) and the relatively low water inflow into the lake (Yillia and Kreuzinger, 2009), the application of N:C based mixing models has to be scrutinized for such systems. The need for careful application of such models is confirmed by the stable isotope composition of the lake sediment samples. The $\delta^{13}C$ of sediments lies well within the range of planktonic ^{13}C values (Fig. 3) and quite separated isotope signatures of macrophytes and allochthonous material imply a strong reliance of the planktonic ecosystem on autochthonous production.

Although phytoplankton is often characterised by a high long-term temporal variability in their stable isotope composition (e.g. Popp et al., 2007; Post, 2002; Rolff, 2000), we used cyanobacteria as isotopic trophic baseline. This is reasonable as the rotifers are characterised by very short half lives of well below two days in L. Nakuru (Vareschi and Jacobs, 1984) and phytoplankton shows much longer turnover rates (Vareschi, 1982). Remarkably, there were only very slight differences between the $\delta^{15}N$ of plankton size fractions dominated by the two filamentous cyanobacteria (Tab. 4). This is surprising as *A. abijatae* is a atmospheric nitrogen fixer and it is commonly accepted that *Arthrospira* does not possess this ability (Vareschi, 1982; Zhang et al., 2009). N-fixing cyanobacteria are characterised by lower ^{15}N values ranging from -2.1 ‰ to 1.6 ‰ in freshwaters (Carpenter et al., 1997; Rolff, 2000; Vuorio et al., 2006). $\delta^{15}N$ for *A. abijatae* were substantially higher (4.2 ‰), although the heterocyst frequency was comparatively high (13.5 %), thus indicating nitrogen deficiency and N-fixation (Jewell and Kulasoor.Sa, 1970; Kohl and Nicklisch, 1988). We assume that intermediate $\delta^{15}N$ levels of *A. abijatae* were caused by a mixture of dissolved inorganic nitrogen uptake and nitrogen fixation. Elevated concentrations of nitrate and ammonia during our sampling, reaching nearly twice the value of means during long term monitoring (Oduor and Schagerl, 2007b) support this interpretation. Presumably, the extremely high rotifer abundances also affected nutrient concentrations as rotifers are known to play a pivotal role in nutrient recycling (Anderson et al., 2005; Vadstein et al., 2003). $\delta^{13}C$ of long-lived primary consumers *Oreochromis alcalicus grahami* and the *Ephydra sp*. were in the range of the potential food source *A. abijatae* (Vareschi, 1979). The $\delta^{15}N$ of these herbivores is well below the first trophic level (Fig. 3), indicating either alternative food sources or a lowered long term algal baseline and higher N – fixation rates.

The two Lepidoptera species collected around the macrophytes were, as was the case for *Ephydra*, recorded for the first time for saline alkaline Rift Valley lakes. Because of low abundance of Lepidoptera, individuals of both species had to be pooled and only $\delta^{13}C$ was measured. Results indicate that both species fed on a mixture of macrophyte tissue and plankton.

Based on the isotopic DOM signature, we assessed the putative bacterial stable isotope ratio. Bacterial isotope signatures are often, but not necessarily related to DOM samples (McCallister et al., 2004), but this seems likely in the case of L. Nakuru, because DOM concentrations are extremely high (Table 2) and derived from autochthonous sources indicating high food quality.

For *B. plicatilis* a mixing model based on the two filamentous cyanobacteria as possible food sources was calculated. Based on traditionally assumed mean ΔN of 3.4 ‰ (Minagawa and Wada, 1984; Post, 2002; Vander Zanden and Rasmussen, 2001) other food sources like bacteria and the plankton size fraction < 2 µm can be widely excluded as they would have led to elevated ^{15}N levels. However, recent research about ΔN has suggested lower average nitrogen enrichment factors (McCutchan et al., 2003; Vanderklift and Ponsard, 2003) and emphasised the need of group specific ΔN (Ventura and Catalan, 2008). To date, only one study investigating laboratory ΔN of rotifers is published (McClelland and Montoya, 2002) resulting in a ΔN of 2 ‰. However, even if this value and a three source model after Phillips (2001) that included the <2 µm size fraction as potential food source is used, filamentous algae still constitute the main food source of *B. plicatilis* (data not shown). Additionally, a large reliance on small ciliates, HNF and picophytoplankton seems improbable as biomass of these groups is two orders of magnitude lower than that of *B. plicatilis* (Tab. 3)and therefore not large enough to meet the high energy requirements of *B. plicatilis* (Vareschi and Jacobs, 1985). Effective grazing of *B. plicatilis* on filamentous cyanobacteria is a highly interesting result, as this species was known to have an optimal prey size range between 5 and 10 µm (Hansen et al., 1997) and the maximum prey size of *B. plicailis* was historically assumed to be 15µm (Ito and Iwai, 1957). Rotifers in the whole genus are regarded as suspension feeders commonly not grazing on filamentous cyanobacteria (Koste and Voigt, 1978; Rothhaupt, 1990). However, our findings are supported by Rothhaupt (1991) who recorded ingestion of *Anabaena flos-aquae* filaments by *Brachionus rubens* and Pagano et al. (1998), who found a food size spectrum of tropical *B. plicatilis* populations reaching probably well above 20µm. Further, Vareschi and Jacobs (1984) have observed *B. plicatilis* feeding on *A. fusiformis* by grabbing one end of a filament and pulling it spaghetti like with movements of the gizzard. Such differences in feeding behaviour might be explained by the complicated taxonomy of *B. plicatilis*, which turned out to be a cryptic complex (Ciros-Perez et al., 2001). African species are characterized by a very distinct genetic pattern (Suatoni et al., 2006) and although no accompanying study has been performed to verify that populations from L. Nakuru differ from strains used in other studies (Hansen et al., 1997; Kostopoulou and Vadstein, 2007; Montagnes et al., 2001) it seems highly likely that there exist considerable differences in the feeding behaviour of this cryptic species complex.

According to the $\delta^{13}C$, heterotrophic bacteria and *A. abijatae* are the only significant food sources for *B. dimidiatus*. As their carbon isotopic ratio did not show a large enough difference, $\delta^{15}N$ were used instead to establish mixing model leading to a reliance of over 47 % on bacteria, which is one of the highest values ever published reflecting the extreme conditions in tropical saline - alkaline Lakes. Still, the analysis is sensitive to changing fractionation factors. If the rotifer specific ΔN of 2 ‰ (McClelland and Montoya, 2002) is applied, the fraction of bacterial food increases to 73.6 %. Although the fractionation value of bacteria adds to variability of the mixing model, the dietary uptake of bacteria stays constantly above 40%. Generally, it is assumed that feeding efficiencies of rotifers on heterotrophic bacteria are low (Arndt, 1993; OomsWilms, 1997; Vadstein et al., 1993) and contribution of bacteria to rotifer nutrition of *in-situ* populations have rarely shown values of over 10 % (Agasild and Noges, 2005; Bouvy et al., 1994; Rejas et al., 2005). Nevertheless, in eutrophic lakes bacterial consumption by rotifers occasionally is increased (Work et al., 2005). Moreover Strakweather et al. (1980) have shown that *Brachionus calyciflorus* can survive and reproduce for several generations with bacteria as sole food. The high proportion of bacteria in *B. dimidiatus* food implies also high transfer efficiency from the microbial loop to higher trophic levels as protozoa play a minor and the food chain length is kept small (Sanders et al., 1989).

B. dimidiatus displayed a significantly higher level of δ^{15}N. Because of the short turn-over time of this species (Vareschi and Vareschi, 1984), age effects (Matthews and Mazumder, 2008) can be disregarded. The difference between the δ^{15}N signals of the two *Brachionus* species rather results from the stronger dependence of *B. dimidatus* on parts of the food web involved in decomposition of organic material: as protozoan and rotifers contribute considerably to total lake biomass (Tab. 3), consumer's carcasses and excrements could cause the elevated δ^{15}N signature of DOM. This leads again to higher bacterial δ^{15}N and increases in a feedback loop also δ^{15}N of *B. dimidatus*. Therefore, in systems displaying high consumer biomass and high nutrient recycling, also zooplankton related strongly to the microbial loop will show higher δ^{15}N values. However, this does not indicate a higher trophic level and demonstrates that increase in size is not necessarily related to higher trophic levels.

In stable isotope field studies frequently zooplankton bulk samples are analysed instead of species specific samples because of methodical difficulties and limited resources. Our study clearly revealed that even very closely related zooplankton species may assign very distinct ecological niches, leading to considerably different stable isotope ratios (Fig. 3). This underlines the need of species-specific sampling to more precisely interpret complex trophic interactions.

Although results of this study are based on a single time sampling, they provide detailed information about the role of rotifers in the micro- and mesoplanktonic food web of saline-alkaline lakes. Nevertheless as L. Nakuru is a highly dynamic system (Harper et al., 2003; Vareschi and Jacobs, 1985) and the microbial and algal communities of this lake frequently change substantially (Schagerl and Oduor, 2008; Yasindi et al., 2002), further research is needed to gain a better understanding of the probably highly adaptive feeding behaviour of tropical rotifers.

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List of tables and figures

Tab. 1: Conversion factors used to calculate carbon content of various biota.

Tab. 2: Physical and chemical parameters of the central off shore station in Lake Nakuru (April 7, 2009).

Tab. 3: Abundance and carbon content of the major components of the planktonic food web of Lake Nakuru (April 2009).

Tab. 4: Isotopic ratios of $\delta^{13}C$, $\delta^{15}N$ and C:N ratios of major food web components of Lake Nakuru (April 2009). Iostopic ratios are given in ‰, C:N ratios in %.

Fig. 1: Map of Africa and the eastern (Gregory) Rift Valley showing the region of Lake Nakuru in Kenya.

Fig. 2: The relative proportion of *Arthrospira fusiformis* in size fractions dominated by filamentous cyanobacteria plotted against the $\delta^{13}C$ of these size fractions. Regression line for extrapolation is shown ($y = -0.0708x – 16.107$; $r^2 = 0.9853$, $p = 0.078$).

Fig. 3: $\delta^{13}C$ versus $\delta^{15}N$ plot of major food web components of L. Nakuru. ● values have been measured ♦ computed values; 2-GFF = size fraction of < 2µm, Alloch = allochthonous material Anab = *Anabaenopsis abijatae*, Arthro = *Arthrospira fusiformis*, Bac = heterotrophic bacteria, B. dim = *Brachionus dimidiatus*, B. plic = *Brachionus plicatilis*, Chiro = *Leptochironomus deribae*, DOM = dissolved organic matter, Eph=Ephydra sp., Macroph = macrophyte tissue, Sed = sediments, Tilapia = *Oreochromis alcalicus grahami.*

Tab. 1: Conversion factors used to calculate carbon content of various biota.

Taxa	Conversion factors	References
Heterotrophic bacteria	cell number [ind] : carbon content [pg] = 15	Stenuite et al. 2009
Cyanobacteria	biovolume [mm^3] : carbon content [mg] = 0.22	Ahlgren 1983
Chlorophyta	biovolume [mm^3] : carbon content [mg] = 0.16	Lundgren 1978
Bacillariophyceae	log C [pg]=-0.610 + 0.892 (log plasma volume[µm^3])	Strathmann 1967
Other algae	biovolume [mm^3] : carbon content [mg] = 0.11	Rocha and Duncan 1985
Flagellates and ciliates	biovolume [mm^3] : carbon content [mg] = 0.14	Putt and Stoecker 1989
Rotifers	biovolume [mm^3] : dry weight [mg] = 1	Pace and Orcutt 1981
	dry weight [mg] : carbon content [mg] = 0.45	Pagano and Saint Jean 1993

Tab. 2: Physical and chemical parameters of the central off shore station in Lake Nakuru (April 7, 2009).

Parameter		Parameter	
Temp [°C]	22.1	DOC [mg L^{-1}]	344.30
O2 [mg L^{-1}]	18.8	SRP [µg L^{-1}]	899.71
pH	10.21	NH_4^+ [µg L^{-1}]	70.75
Cond [mS cm^{-1}]	49.4	NO_3^- [µg L^{-1}]	704.77
Salinity [‰]	34.9	NO_2^- [µg L^{-1}]	6.96
Coefficient of Att.	0.075	Secchi [cm]	34.75

Tab. 3: Abundance and carbon content of the major components of the planktonic food web of Lake Nakuru (April 2009).

		[Ind L^{-1}]	[mg C m^{-3}]
Bacteria		2.53E+11	3.80E+03
Ciliates	*Holophrya*	5.80E+03	5.88E+02
	Frontonia	9.60E+03	7.65E+02
	Small cilates (ESD<50µm)	3.80E+03	1.03E+01
Rotifers	*B. dimidiatus*	9.84E+04	2.14E+03
	B. plicatilis	2.40E+04	5.95E+03
	Hexarthra jenkinae	5.33E+02	1.22E+01
Algae	*A. fusiformis*	1.37E+07	1.12E+04
	A. abijatae	3.53E+07	3.22E+03
	Microalgae	9.67E+06	3.51E+02
	Chl-a [µg L-1]	-	3.64E+02

Tab. 4: Isotopic ratios of δ^{13}C, δ^{15}N and C:N ratios of major food web components of Lake Nakuru (April 2009). Iostopic ratios are given in ‰, C:N ratios in %.

	n	mean δ^{13}C	SD δ^{13}C	mean δ^{15}N	SD δ^{15}N	mean C:N	SD C:N
DOM	6	-17.83	0.07	6.13	0.09	13.92	0.24
Sediment	6	-18.28	0.48	10.63	0.32	8.37	0.47
Allochtonous material	3	-8.79	0.31	8.53	0.22	26.11	3.24
Macrophytes	3	-12.04	0.46	-2.78	0.52	19.70	0.91
Phytoplankton + 40µm	6	-22.34	0.06	4.30	0.23	4.91	0.07
40-20µm	6	-21.40	0.89	4.01	0.85	4..1	0.62
20-2µm	6	-20.17	0.59	4.42	0.64	5.64	0.25
2µm-GFF	6	-19.46	0.60	6.70	1.16	5.50	0.21
Heterortrophic bacteria	*	-16.83	-	9.53	-	-	-
Arthrospira fusiformis	*	-23.19	0.06	4.24	0.62	-	-
Anabaenopsis abijatae	*	-16.11	0.69	4.24	0.62	-	-
Brachionus dimidiatus	3	-16.47	0.14	10.14	0.91	5.48	0.06
Brachionus plicatilis	3	-20.55	0.08	8.65	1.07	5.05	0.13
Ephydra sp.	2	-16.85	0.27	4.53	0.90	4.31	014
Oreochromis a. grahami	3	-16.80	0.21	6.25	0.47	3.47	0.09
Corixidae	6	-15.40	0.45	8.01	0.72	4.16	0.15
Leptochironomus deribae	5	-17.80	0.86	9.75	0.32	4.48	0.28
Lepidoptera	2	-16.90	2.44	-	-	-	-

** calculated values, see text*

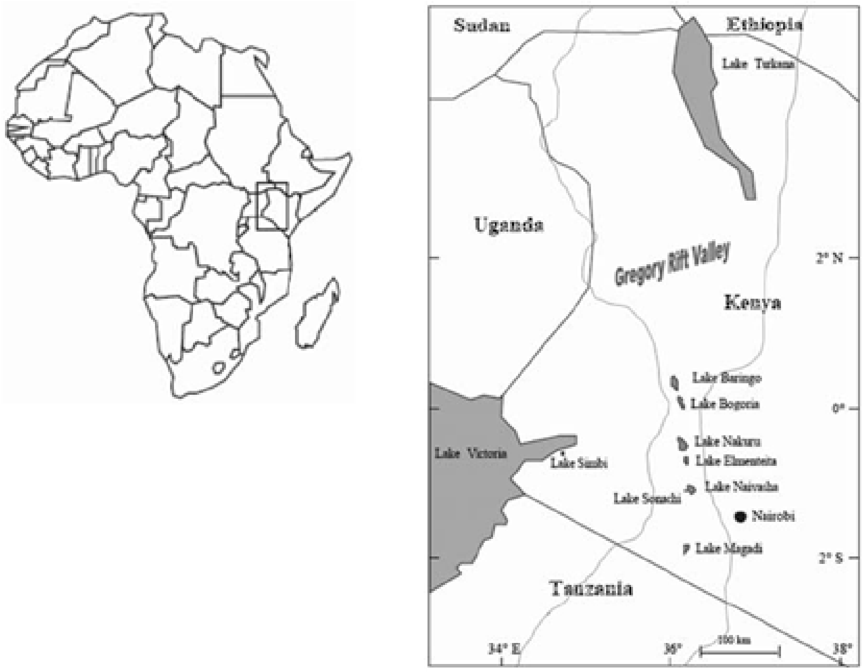

Fig. 1: Map of Africa and the eastern (Gregory) Rift Valley showing the region of Lake Nakuru in Kenya.

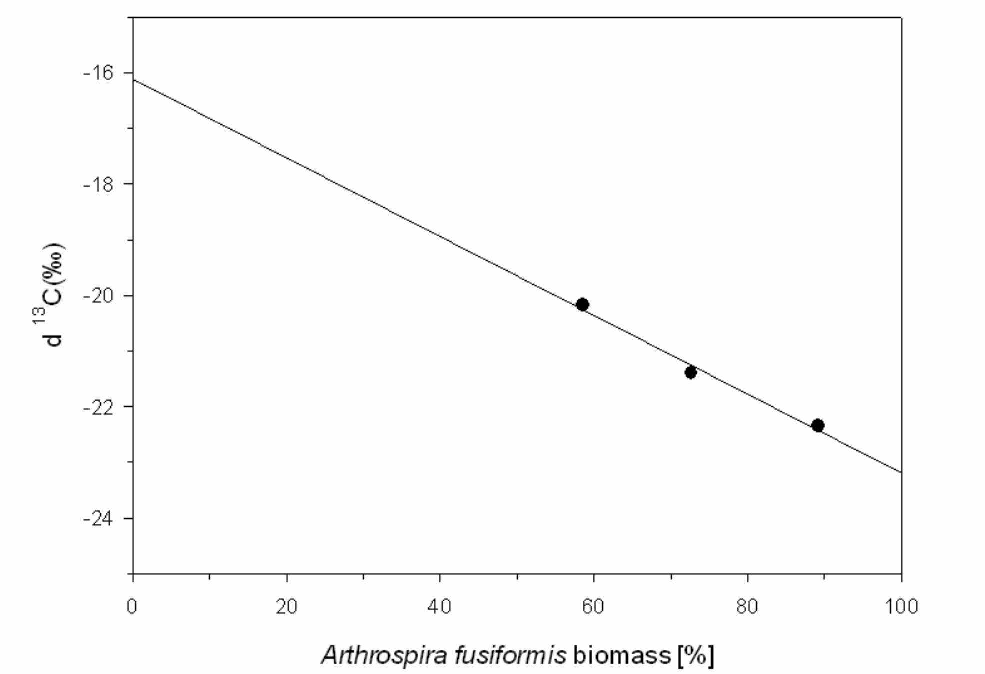

Fig. 2: The relative proportion of *Arthrospira fusiformis* in size fractions dominated by filamentous cyanobacteria plotted against the δ^{13}C of these size fractions. Regression line for extrapolation is shown ($y = -0.0708x - 16.107$; $r^2 = 0.9853$, $p = 0.078$).

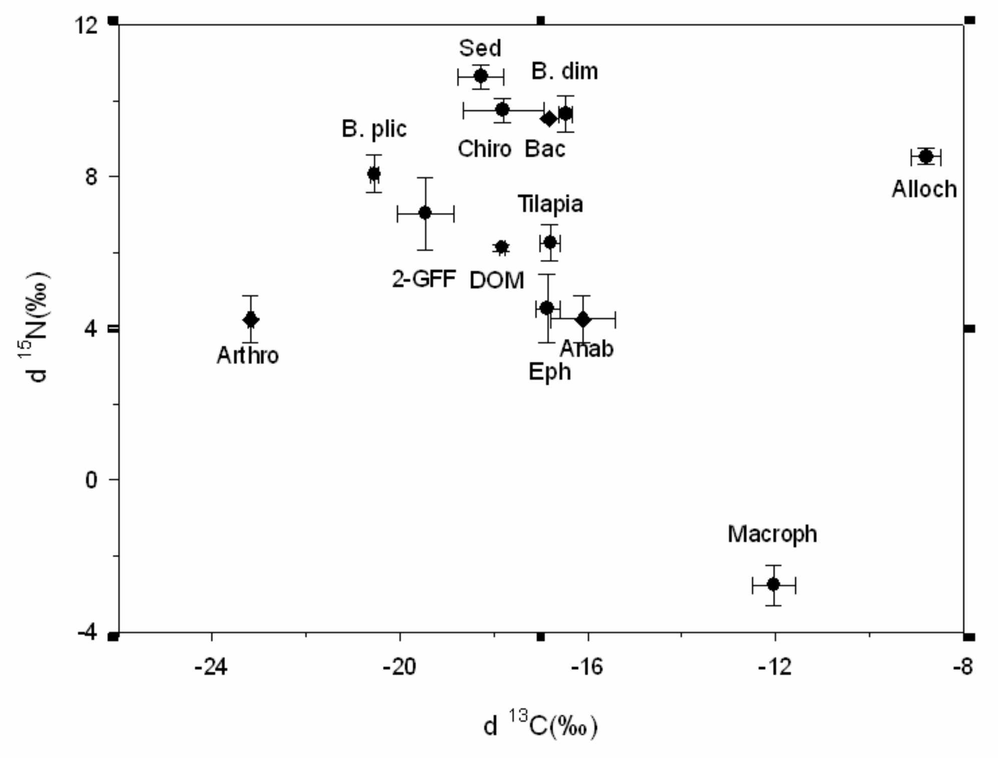

Fig. 3: δ^{13}C versus δ^{15}N plot of major food web components of L. Nakuru. ● values have been measured ♦ computed values; 2-GFF = size fraction of < 2µm, Alloch = allochthonous material Anab = *Anabaenopsis abijatae*, Arthro = *Arthrospira fusiformis*, Bac = heterotrophic bacteria, B. dim = *Brachionus dimidiatus*, B. plic = *Brachionus plicatilis*, Chiro = *Leptochironomus deribae*, DOM = dissolved organic matter, Eph=Ephydra sp., Macroph = macrophyte tissue, Sed = sediments, Tilapia = *Oreochromis alcalicus grahami.*

3. Feeding behaviour of dominant zooplankton grazers and their influence on phytoplankton and the microbial loop in saline-alkaline Kenyan Rift Valley Lakes.

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Abstract

We investigated the feeding behaviour of dominating pelagic zooplankton of saline lakes in the East African Rift Valley. A set of grazing experiments revealed extraordinary high ingestion rates of the two euryhaline rotifers *Brachionus dimidiatus* and *Brachionus plicatilis* and of the large sized omnivorous ciliates *Frontonia* and *Condylostoma magnum*. Increased feeding rates reflected the unique nature of tropical saline systems showing high water temperatures coupled with high food quantities but low food quality. The size spectrum of ingested particles was broad, and even included filamentous cyanobacteria like the commonly dominating *Arthrospira fusiformis*. Selectivity, however, showed higher values for cryptomonads and other small protozoans.

Bacterial biomass was positively influenced by presence of grazers, as small bacterivorous predators were significantly reduced in numbers, showing the cascading effect of large zooplankton on the food web structure. Overall, based on this first time study of the feeding behaviour of the mesozooplankton in East African saline lakes, a strong structuring influence of rotifers and large ciliates can be expected in times of high consumer biomass.

Introduction

Zooplankton grazing is a major factor for structuring algae, protozoan and bacterial communities in aquatic systems (Arndt, 1993; Gliwicz, 1975; Jurgens and Matz, 2002). Feeding behaviour and grazing rates are influenced by several characteristics of food particles. Prey size plays a pivotal role (Rothhaupt, 1990) but also other factors like temperature, taste, digestibility, catchability, toxicity, as well as food quantity and quality need to be considered (Demott, 1986; Mitra and Flynn, 2007; Montagnes et al., 2001). Whereas the relationships between zooplankton feeding and other pelagic communities is comparatively well studied in temperate regions, data about tropical ecosystems are very scarce (Hart and Jarvis, 1993).

Known so far, large algae forms commonly dominate the phytoplankton community of shallow tropical lakes (Fernando, 1994; Lewis, 1978; Pagano, 2008), and often a size overlap of herbivorous grazers and phytoplankton organisms can be observed (Work et al., 2005). Large-sized algae are interpreted as a strategy against grazing (Boon et al., 1994). Additionally, a tendency towards aseasonality in shallow tropical aquatic ecosystems (Talling, 2001) is observed, which consequently implies the lack of regularly disturbing environmental events. Moreover, as the impact of environmental factors is reduced (Schagerl and Oduor, 2008), internal biological components like competition and grazing pressure gain in importance for the succession of phytoplankton communities. This hypothesis is supported by the few studies on grazing of tropical rotifers, which have shown an extended size spectrum of ingested particles compared to temperate populations (Pagano, 2008; Pagano et al., 1998) and may even able to ingest filamentous algae.

The zooplankton biomass of East African saline lakes, sometimes due to their attention attracting populations of lesser flamingos (*Phoeniconaias minor* Geoffroy) also referred to as “flamingo lakes” (Matagi, 2004), is dominated by rotifers (Green and Mengestou, 1991; Iltis and Riou-Duwat, 1971) and only at times by larger crustaceans (Vareschi and Jacobs, 1985).

Apart from the two most characteristic species of rotifers *Brachionus dimidiatus* Bryce and *Brachionus plicatilis* Mueller (Nogrady, 1983; Vareschi and Vareschi, 1984), also large omnivorous ciliates like *Frontonia* can reach high densities (Yasindi and Taylor, 2006).

Phytoplankton of these lakes is typically dominated by the filamentous cyanobacterium *Arthrospira fusiformis* (Vorochinin) Komárek, which frequently forms blooms with extremely high biomass (Ballot et al., 2004; Oduor and Schagerl, 2007a). However, algal communities sometimes show high variability with rapidly changing species composition and brisk breakdowns of biomass (Schagerl and Oduor, 2008; Vareschi, 1982), whose causations and underlying patterns could not yet be explained.

In this first time investigation on the feeding behaviour of zooplankton of shallow African saline lakes, we aimed to collect basis data on selectivity and feeding rates of dominant species. Thus, this study should be the basis to evaluate grazing pressure on natural algal populations and components of the microbial loop and moreover facilitate the analysis of the potential shaping force of rotifers and large ciliates on plankton communities in such systems.

Material and methods

Two sets of grazing experiments were conducted with animals from the two saline-alkaline Kenyan Rift Valley Lakes Bogoria and Nakuru. For a detailed description of the lakes refer to Oduor and Schagerl (2007a, b). All animals used for grazing experiments were isolated from lake water, starved for 6 hours and adopted stepwise to salinity levels in case experimental conditions differed from natural conditions. All experiments were carried out under laboratory conditions in complete darkness and at a constant temperature of 22°C, which is close to the average temperature of the lakes (Harper et al., 2003; Vareschi, 1982) and the recommended temperature of 25°C for grazing experiments of *B. plicatilis* (Montagnes et al., 2001).

Bacterial samples were fixed (5 % formalin) and stained using the SYBR Gold technique (Tuma et al., 1998). Phytoplankton samples were also fixed with formalin (5 %) and counted with an inverted microscope (Nikon Diaphot, Nikon, Tokyo) following the Uthermöhl protocol (1958). Biovolumes of the various taxa were estimated using geometric formulae of the shapes of the respective phytoplankton cells (Sun and Liu, 2003). Protozoan samples were fixed with Bouin’s solution (5 %) and filtered on a gridded polycarbonate cellulose filter with warm liquid nutrient agar being added to hold organisms in position. To facilitate counting, organisms were stained using Quantitative Protargol Staining Technique (QPS) by Montagnes and Lynn (1993).

Grazing on a natural phytoplankton community of L. Nakuru

Water samples were taken during a transitional phytoplankton state of L. Nakuru as defined by Vareschi and Jacobs (1985). During the sampling, the algae composition was in the process of changing from picoplankton communities to a dominance of filamentous cyanobacteria (unpublished data). Immediately after sampling, the water was filtered through 40 µm sieves to remove large herbivorous zooplankton organisms. As the algal community at the sampling time consisted mostly of unicellular algae and small fragments of filamentous algae, the phytoplankton community structure was not significantly changed by the filtration process. All experiments started within 24 hrs after water samples were taken. For the experimental set up 30 individuals of one out of the four zooplankton species *B. dimidiatus, B. plicatilis*, *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. Triplicates for each species were prepared. Further, control experiments without introduced grazers were prepared. At the start of the experimental set up and at the end of each experiment (after 24 hrs) samples were taken for bacteria, protozoa and phytoplankton counts.

Grazing on the filamentous cyanobacterium *Arthrospira fusiformis*

Water samples were taken within 24 hours before the start of the experiments from Lake Bogoria. *B. dimidiatus*, *B. plicatilis* and *Frontonia sp.* were all isolated from surface water samples with a micropipette; *Condylostoma magnum* was abstracted from subsurface water as this species showed much higher abundances at larger depths.

As *Arthrospira fusiformis* dominated the phytoplankton community in L. Bogoria accounting for over 99% of its biomass, it was possible to obtain a pure algal concentrate (> 99.9%) from lake water using algal buoyancy and a set of filtration through 40 and 100 µm sieves to remove zooplankton and other phytoplankton species. Subsequently the algal concentrate was repeatedly flushed with GF/F filtered lake water to reduce bacterial numbers. For the grazing experiment the algal concentrate was diluted in 50 mL containers with GF/F filtered lake water at concentrations of 1300, 7500, 14000, 21500, and 43000 mg C m^{-3}. For each zooplankton species triplicates were prepared for the 5 algal concentrations by adding 25 individuals to each container. One set of triplicates was repeated without grazers as control. Zooplankton organisms were allowed to graze for 24 hrs before samples were fixed for phytoplankton counts.

Grazing rates and Selectivity

Grazing rates (G) were calculated according to the equation given by Frost (1972):

$$G = (V/n) \times ((\ln C_t - \ln C_{tf})/t) \times ((C_{tf} - C_0)/(\ln C_{tf} - \ln C_0))$$

Whereas V is the volume of the experimental containers, t the duration of the experiment, n represents 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. To evaluate the relative selectivity of different food types, we calculated the normalized forage ratio (*NFR*) after Paloheimo (1979): $NFR_i = (r_i / p_i) / \sum (r_i / p_i)$, where r_i represents the percentage of the food type i in the consumers diet and p_i for the percentage of that food type in the offered food spectrum in the experimental containers. Our selectivity calculations were based on carbon content converted from biovolume using conversion factors given in table 1.

Results

Grazing on natural phytoplankton community

At the beginning of the experiment, phytoplankton were dominated by the filamentous cyanobacterium *Anabaenopsis abijatae* Kebede et Willénoften, accounting for 9.6 g C m^{-3} or 63 % of total phytoplankton biomass (Tab. 2). *Arthrospira fusiformis*, that often is predominating in the community of saline – alkaline lakes (Melack and Kilham, 1974; Schagerl and Oduor, 2008; Vareschi, 1982) and two Cryptomonads, which were not identified to genus level (a larger from l and a smaller form s), contributed each from 8 to 15 % of phytoplankton biomass. Smaller phytoplankton species, mostly unicellular cyanobacteria accounted for less than 3 % of phytoplankton carbon and played only a minor role. Total phytoplankton biomass, relative to other biotic food sources, constituted 67 % at the start of the experiment (Fig. 1). The protozoan community was dominated by the two bacterivorous ciliates *Euplotes* and *Cyclidium*. Together the two taxa accounted for 15 % of total biomass, nearly as much as their main food source, heterotrophic bacteria (18 %).

For control experiments (no zooplankton added), the microbial community showed large reactions after 24 hrs (Fig. 2 and Fig. 3). The bacterial abundances decreased by 35 % in the control set up (t-test, $p<0.001$) and the carbon mass of bacterivorous ciliates increased significantly by over 60 % (Tab. 2). In the grazing experiments, all zooplankton species negatively affected growth of bacterivorous ciliates compared to control set-ups (t-test, $p<0.01$), although still a trend to increased ciliate biomass relative to initial values was noticeable (Fig. 3). Correspondingly, bacteria biomass reacted positively to the presences of mesozooplankton. Nevertheless, there was equally a tendency to reduced bacterial abundances compared to control values, even when mesozooplankton was present (Fig. 2).

Phytoplankton biomass did not show any significant change during the control experiments, with the exception of significantly decreased picoplankton abundance (t-test, $p<0.01$). Presence of all grazers led to significantly decreased concentrations of *A. abijatae*. However, the grazing impact of ciliates on *A. abijatae* was significantly higher than biomass reduction through rotifers ($p<0.01$, Fig. 4). There was also a clear trend of *A. fusiformis* biomass reduction due to the presence of grazers (Tab. 2). Although biomass reduction was not significant, the average filament length of the cyanobacterium decreased significantly for the two herbivorous ciliate species (t-test, $n=300$, $p<0.01$). Also cryptomonads were grazed on in various amounts with numbers and significance levels shown in table 2. Likewise bacteria, picophytoplankton biomass showed intermediate values in all experiments with mesozooplankton grazers compared to controls and initial values.

Total grazing rates on phytoplankton were much higher for herbivorous ciliates than for rotifers (Tab. 3). Among rotifers, *B. plicatilis* ingested 35 % more food per individual than *B. dimidiatus*, though if average individual biomass is considered grazing rates per unit rotifer biovolume was much higher for *B. dimidiatus*. The normalized forage ratios, based on available food particles excluding bacteria, are shown in figure 5.

Grazing on *Arthrospira fusiformis*

The highest grazing rates on *A. fusiformis* were recorded for the large heterotrich ciliate *Condylostoma magnum* (Fig. 6), which had a significant grazing impact on all offered *A. fusiformis* concentrations but the first one. Second to *C. magnum* was *B. plicatilis*, also displaying high consumption rates, especially at algal densities of 14000 and 43000 mg C m^{-3}. The other rotifer species, *B. dimidiatus* had little to no grazing impact on *A. fusiformis*, with only one significant reduction of algae abundances at intermediate algae densitiy. Also *Frontonia* had only little influence on the *A. fusiformis* concentrations with significant reductions of *A. fusiformis* only at two algae concentrations (Fig. 6).

Discussion

Methodological aspects

Overall, the main aim of this survey was to study grazing impacts of zooplankton on natural plankton populations. We therefore have avoided phytoplankton cultures, as depending on culture conditions grazing rates might be affected (Mitra and Flynn, 2007) via species specific food quality (Rothhaupt, 1995; Strojsova et al., 2009). We isolated zooplankton organisms from lake water and have chosen direct count methods to evaluate possible grazing impacts. However, direct counting has the major disadvantage that it is an extremely time consuming method and standard deviations are generally high (Rott, 1981). Isotopic or radioactive labelling and coulter counter techniques are two alternative methods frequently used to quantify grazing rates. Besides such methods are not available in many developing countries, labelling requires the incubation of food particles and coulter counting bears the risk of misinterpreting egested particle fragments and cell breakage during ingestion (Harbison and Mcalister, 1980; Peters, 1984), which influences recorded size selective patterns especially when filamentous algae are consumed. Therefore we choose direct counting as method for evaluation of grazing rates in this study.

Size spectrum of food particles

The high abundance of colonial and filamentous green algae and cyanobateria has been well documented for tropical shallow aquatic ecosystems (Fernando, 1994; Pagano, 2008; Work et al., 2005) including saline- alkaline Rift Valley lakes with frequent domination of blue- green algae filaments (Ballot et al., 2004; Schagerl and Oduor, 2008). In our experiments large phytoplankton accounted for over 70% of the algal biomass. Nevertheless, the considerable contribution of bacteria and ciliates to total lake biomass must not be neglected and underlines the importance of the microbial food web in such systems (Kilham, 1981; Yasindi et al., 2002). Further, an overlap in size between phytoplankton and dominant zooplankton primary consumers as partly also observed in our study, is a frequent phenomenon in tropical aquatic systems (Work et al., 2005). It has been suggested that an increase in algal size might be an appropriate mean to reduce the grazing pressure on phytoplankton (Boon et al., 1994). Still, in our study we observed a significant grazing impact of all investigated zooplankton organisms on large algae forms as the cyanobacterium *A. abijatae* and even small ciliates served as source of nutrition. The omnivorous ciliates *Frontonia sp.* and *C. magnum* show large physical adaptability in food ingestion. *Frontonia* has been observed to have a highly flexible cell wall (Dias and D'Agosto, 2006) and also in this study we found *Frontonia* ingesting filaments which were substantially longer than the its body dimensions. *C. magnum* shows little size restrictions feeding on phytoplankton, because of its own large body size. Sometimes, it digest several large *A. fusiformis* filaments at once and even small rotifers could be detected in a single ciliate, which has also been stated by other authors (e.g. Arndt, 1993). For suspension feeding rotifers of the genus *Brachionus,* the feeding spectrum is assumed to be concentrated on smaller size classes (Rothhaupt, 1990). Studies of temporal populations of *B. plicatilis* defined an optimum range of food size between 5 and 10 µm (Hansen et al., 1997) and food particles in this range are also commonly used in aquaculture. On the contrary Pagano et al. (1998) have shown that food selectivity of a tropical population of *B. plicatilis* reaches near to maximal values when 20 µm particles are ingested, with feeding on larger food sizes not being investigated. Correspondingly our study revealed that ingestion is not limited to small size classes (Fig. 4). Interestingly, *B. plicatilis* is obviously a cryptic species complex (Ciros-Perez et al., 2001) with African populations classified quite apart from other strains (Suatoni et al., 2006). Feeding behaviour might differ substantially within this clade (Burian et al., 2010) with African organisms specialised on larger particles (Tab. 2). Even the smaller *B. dimidatus* seems to be able to ingest *A. abijate,* but its grazing rates on *A. fusiformis* were quite low (Fig. 6), which agrees well with other studies, which exclude this species as main food source for *B. dimidatus* (Burian et al., 2010; Pourriot and Rougier, 1975).

Interactions between mesozooplankton and microbial food webs

Mesozooplankton strongly influenced abundance and biomass of microorganisms in experiments with natural plankton communities (Figs. 2 and 3). Both, rotifers and omnivorous ciliates caused cascading structural effects of the food chain by stabilizing bacterial and picophytoplankton biomass and reducing numbers of bacterivorous grazers. Even *B. dimidiatus*, which has been shown to rely at times to a considerable degree on bacterial carbon on its own (Burian et al., submitted), caused a significant impact in this respect (Tab. 2). However, the positive reaction of bacterial abundances on the presence of larger zooplankters not only might be caused by reduction of bacteriovorous predators like small ciliates and mixotrophic cryptomonads (Sanders et al., 1989), but also may be contributed to increased nutrient recycling due to metazoan presence (Anderson et al., 2005). Besides their exceptional high bacterial numbers (Kilham, 1981), saline African lakes show a stronger positive relationship between chlorophyll *a* content and bacterial abundances compared to freshwater systems (Bird and Kalff, 1984). Zinabu and Taylor (1997) have surmised that this could be due to lower abundances of bacterial grazers. This is supported by the fact that not only large ciliates (Yasindi and Taylor, 2006), but also rotifers (Iltis and Riou-Duwat, 1971; Vareschi and Vareschi, 1984) sometimes reach outstanding abundances in such ecosystems and our study pointing out the importance of both groups in controlling bacteriovorous grazers, even at low abundances present in our experiments. Overall, the characteristic zooplankton communities of saline alkaline lakes might be essential elements in supporting the extremely high bacterial biomass in such systems.

Grazing rates and selectivity of zooplankton

Grazing rates in both sets of experiments were generally high in this study (Fig. 6, tab. 3). For ciliates, to our knowledge only qualitative studies exist (Dias and D'Agosto, 2006), but for rotifers of the genus *Brachionus* and especially for *B. plicatilis*, grazing rates have been obtained several times. Most studies have been conducted with microalgae and resulted in grazing rates in the range of 2 to 4 x 10^5 µm³ ind^{-1} h^{-1} (Hansen et al., 1997; Montagnes et al., 2001). Vareschi and Jacobs (1984) did not measure grazing directly but calculated consumption based on production and a energy transfer efficiency of 0.15% with consumption rates over 6 x 10^5 µm³ ind^{-1} h^{-1}. Grazing rates of 8.2 ± 1.8 x 10^5 µm³ ind^{-1} h^{-1} obtained in this study were substantially higher. There are several explanations for increased ingestion rates under our experimental conditions: First rotifers were randomly picked from natural populations without selecting against egg carrying individuals. As egg rates were high with 0.8 for *B. plicatilis* and 0.6 for *B. dimidatus*, freshly hatched individuals might have let to increased grazing rates. Further, sloppy feeding increases with food particles size (Moller, 2005) and therefore a larger proportion of ciliates and filamentous algae in ingested food particles probably led to a higher importance for this commonly in grazing experiments disregarded factor. Moreover, also food quality, quantity and gut transition time (GTT) has to be considered as maximal zooplankton feeding can be increased by 400 % through variation of these factors (Mitra and Flynn, 2007). If quantity is high, GTT will depend on food quality as low quality food will remain for a shorter period in the gut. This physiological adaptation ensures a high gradient of essential nutrients between the digestive system and the absorbing tissue, even if low quality food is ingested (Jumars, 2000a, b; Willows, 1992). On the other hand, if quality is high grazing rates are reduced and GTT increased to achieve maximal energy efficiency (Mitra and Flynn, 2007). As 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; Lampert, 1981) leading to low population growth rates of zooplankton (Brett et al., 2006), *B. plicatilis* populations in L. Nakuru and L. Bogoria might be adopted to this condition by keeping feeding rates high and GTT low.

The selectivity index illustrated high rotifer selectivity for bacterivorous ciliates, whereas omnivorous ciliates showed rather similar selectivity values for both, phytoplankton and small zooplankton (Fig. 5). This is also reflected by total grazing rates on small ciliates, which were much higher for rotifers than for omnivorous ciliates (Tab. 3). Such variations in selectivity patterns could be caused by a number of factors ranging from specific nutrient requirements to different catchability of prey items for diverse zooplankton taxa, pointing out the need of further research in this area. Moreover, selectivity of all zooplankton species was higher for *A. abijatae* than for *A. fusiformis*. This was confirmed by an *in situ* stable isotope analysis in L. Nakuru (Burian et al., 2010) which showed a tendency for *B. plicatilis* to prefer *A. abijatae* over *A. fusiformis*. Generally *Brachionus* is considered to be only a size selective grazer without being able to select between algae of different quality (Demott, 1986; Hansen et al., 1997; Rothhaupt, 1990). Prey size might be also a factor in our study as the diameter of *A. abijatae* filaments (6.3 ± 1.0 µm) was smaller than that of *A. fusiformis* (9.9 ± 1.1 µm). On the contrary, even ciliates with a comparatively large diameter could be ingested. Snell (1998) pointed out the presence of chemoreceptors in the buccal field of this genus, which indicates that also other factors might play a role for food selectivity. Some studies of Asian populations of *B. plicatilis* have shown that selectivity cannot be explained by size alone (Hirayama et al., 1979; Zhou et al., 2009). Gilbert and Starkweather (1977) have described three mechanisms of food rejection in *Brachionus calyciflorus* Pallas, one for adjusting the maximum size of ingested particles and two others for selective rejection of single particles, connected probably to high energy costs for the grazing organism. However, food selectivity in zooplankton has been shown to increase with particle size (Demott, 1986) and also the amortization of energy intensive rejection mechanisms rises with increased particle size. Therefore the observed preference of *A. abijatae* may not only be based on size but also on food quality. This hypothesis is supported by the fact that even *C. magnum*, which because of its own large body dimensions should not be affected by different filament diameters, selected for *A. abijatae* over *A. fusiformis* (Fig. 5).

Structuring force of zooplankton

Overall, considering the high grazing rates and the sometimes outstanding abundances of rotifers (Iltis and Riou-Duwat, 1971; Vareschi and Vareschi, 1984), zooplankton in tropical saline lakes certainly has the potential to shape phytoplankton communities. Especially during transitional phases when phytoplankton community is switching between two alternative stable states, algae biomass is low (Schagerl and Oduor, 2008) and rotifer abundances are high (Vareschi and Jacobs, 1985), grazing pressure should be a major controlling factor. Nevertheless, during dominance of *A. fusiformis*, zooplankton influence should be very limited as consumer abundances are usually low and phytoplankton biomass is enormous (Vareschi, 1982). So, even high community grazing rates only would lead to small changes of phytoplankton standing stock. Therefore, phytoplankton grazers can be excluded as reason for *A. fusiformis* biomass breakdowns, which are regularly observed in saline Rift Valley lakes. Nevertheless, enhanced nutrient recycling, low selectivity of zooplankton for *A. fusiformis* and improved underwater light supply caused by grazing could play an important role for the establishment of such blooms.

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Legends

Tab. 1: Conversion factors used to calculate carbon content of various biota.

Tab. 2: Results of the grazing experiment on natural plankton communities. Initial concentrations are given under Start and final values of control experiments without mesozooplankton under End (-). Significance levels of t-test between End (-) and other experimental runs are displayed by * for $p < 0.05$, ** for $p < 0.01$ and *** for $p < 0.001$. Values are given in mg C m^{-3}, numbers in brackets indicate standard deviations.

Tab. 3: Grazing rates of mesozooplankton species on natural phytoplankton and ciliate communities. Ingestion values are given in ingested μm^3 h^{-1} ind^{-1}, numbers in brackets indicate standard deviations.

Fig. 1: Initial contribution of various plankton groups to total biomass in the natural plankton community grazing experiments.

Fig. 2: Impact of various mesozooplankton species on bacterial biomass (a) and biomass of bacteriovorus ciliates (b) in natural plankton communities of L. Nakuru.

Fig. 3: Impact of various mesozooplankton species on phytoplankton biomass in natural plankton communities of L. Nakuru.

Fig. 4: Grazing selectivity of mesozooplankton on different plankton groups in grazing experiments with natural plankton communities of L. Nakuru. Selectivity is expressed in the normalized forage ratio (NFR) and results for *B. dimidiatus* (a), *B. plicatilis* (b), *Frontonia* (c) and *Condylostoma* (d) are displayed.

Fig. 5: Final concentrations on different grazing experiments on 5 different concentrations of *A. fusiformis*. Under End (-) values for control experiments without grazing zooplankton are displayed.

Tab. 1: Conversion factors used to calculate carbon content of various biota.

Taxa	Conversion factors	References
heterotrophic bacteria	cell number [ind] : carbon content [pg] = 15	Stenuite et al. 2009
Cyanobacteria	biovolume [mm^3] : carbon content [mg] = 0.22	Ahlgren 1983
Chlorophyta	biovolume [mm^3] : carbon content [mg] = 0.16	Lundgren 1978
Bacillariophyceae	log C [pg]=-0.610 + 0.892 (log plasma volume[µm^3])	Strathmann 1967
other algae	biovolume [mm^3] : carbon content [mg] = 0.11	Rocha and Duncan 1985
ciliates	biovolume [mm^3] : carbon content [mg] = 0.14	Putt and Stoecker 1989
rotifers	biovolume [mm^3] : dry weight [mg] = 1	Pace and Orcutt 1981
	dry weight [mg] : carbon content [mg] = 0.45	Pagano and Saint Jean 1993

Tab. 2: Results of the grazing experiment on natural plankton communities. Initial concentrations are given under Start and final values of control experiments without mesozooplankton under End (-). Significance levels of t-test between End (-) and other experimental runs are displayed by * for $p < 0.05$, ** for $p < 0.01$ and *** for $p < 0.001$. Values are given in mg C m^{-3}, numbers in brackets indicate standard deviations.

	Start	End (-)	*B. plicatilis*	*B. dimidiatus*	*Frontonia sp.*	*C. magnum*
Heterotrophic bacteria	**4169 (±291)	2727 (±384)	3803 (±956)	*3461 (±166)	3973 (±776)	*3450 (±784.0)
Ciliates						
Cyclidium	***928 (±389)	1989 (±53)	***1287 (±78)	**1605 (±76)	1623 (±425)	1611 (±310)
Euplotes	**2402 (±718)	3584 (±165)	**2639 (±254)	**2706 (±256)	3874 (±1528)	3192 (±345)
Other cilates	74 (±26)	86 (±49)	68 (±13)	77 (±44)	111 (±43)	75 (±24)
Total cilate	**3405 (±1041)	5659 (±157)	***3994 (±221)	**4389 (±251)	5609 (±1979)	4880 (±533)
Phytoplankton						
A. abijatae	9563 (±652)	9276 (±174)	***7631 (±164)	*8169 (±534)	**6835 (±580)	***7111 (±90)
A. fusiformis	1394 (±155)	1285 (±108)	1210 (±99)	1225 (±167)	1205 (±239)	105 (±166)
Cryptomonas sp. (l)	1501 (±449)	1522 (±420)	1124 (±109)	1593 (±242)	854 (±40)	1027 (±321)
Cryptomonas sp. (s)	2388 (±349)	2359 (±306)	2223 (±99)	*1736 (±77)	*1787 (±257)	*1795 (±90)
Picophytoplankton	**341 (±133)	77 (±22)	140 (±50)	**269 (±77)	137 (±78)	195 (±146)
Total phytoplankton	15190 (±1044)	14522 (±977)	*12330 (±407)	12995 (±659)	*10819 (±661)	*11185 (±150)

Tab. 3: Grazing rates of mesozooplankton species on natural phytoplankton and ciliate communities. Ingestion values are given in ingested µm³ h^{-1} ind^{-1}, numbers in brackets indicate standard deviations.

	Phytoplankton	Ciliates
B. dimidiatus	6.10×10^5 (2.49×10^5)	2.22×10^5 (4.20×10^4)
B. plicatilis	8.20×10^5 (1.79×10^5)	2.89×10^5 (3.50×10^4)
Frontonia	1.49×10^6 (2.04×10^5)	-0.04×10^5 (3.70×10^5)
Condylostoma	1.32×10^6 (1.43×10^5)	1.37×10^5 (9.16×10^4)

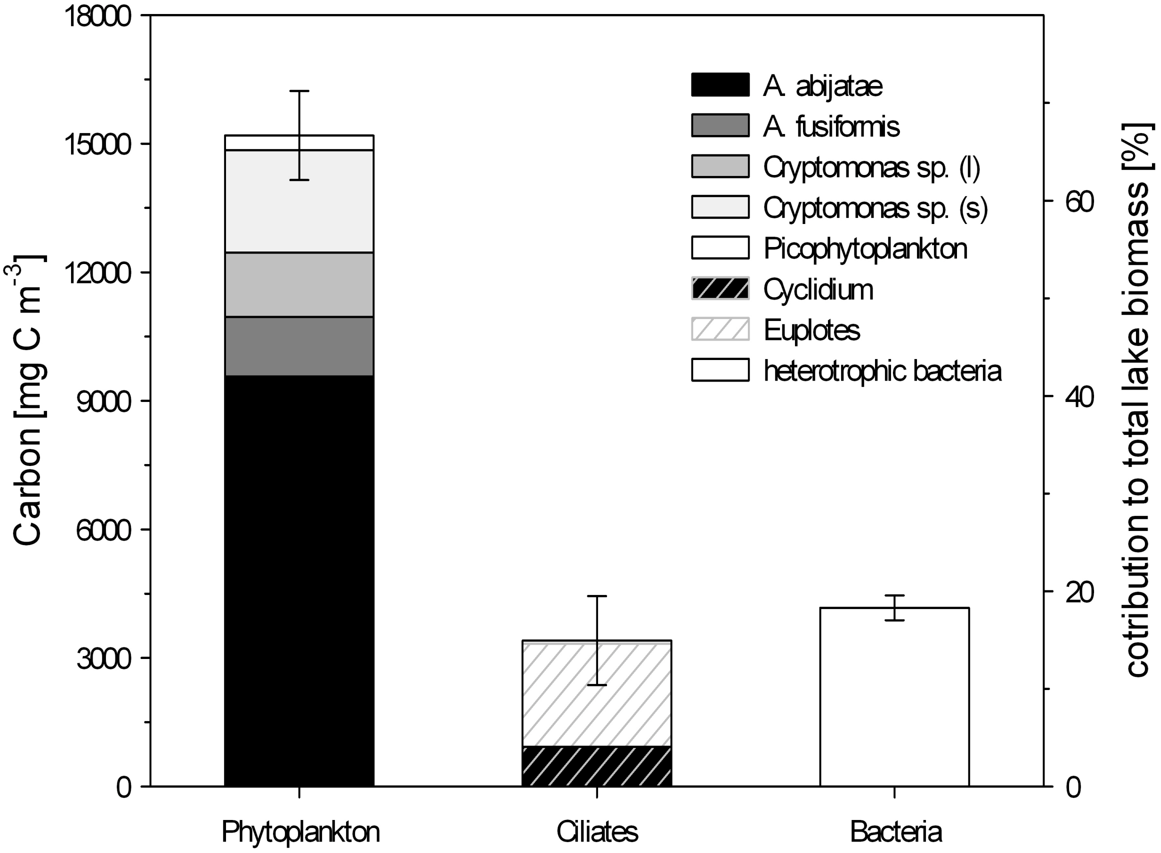
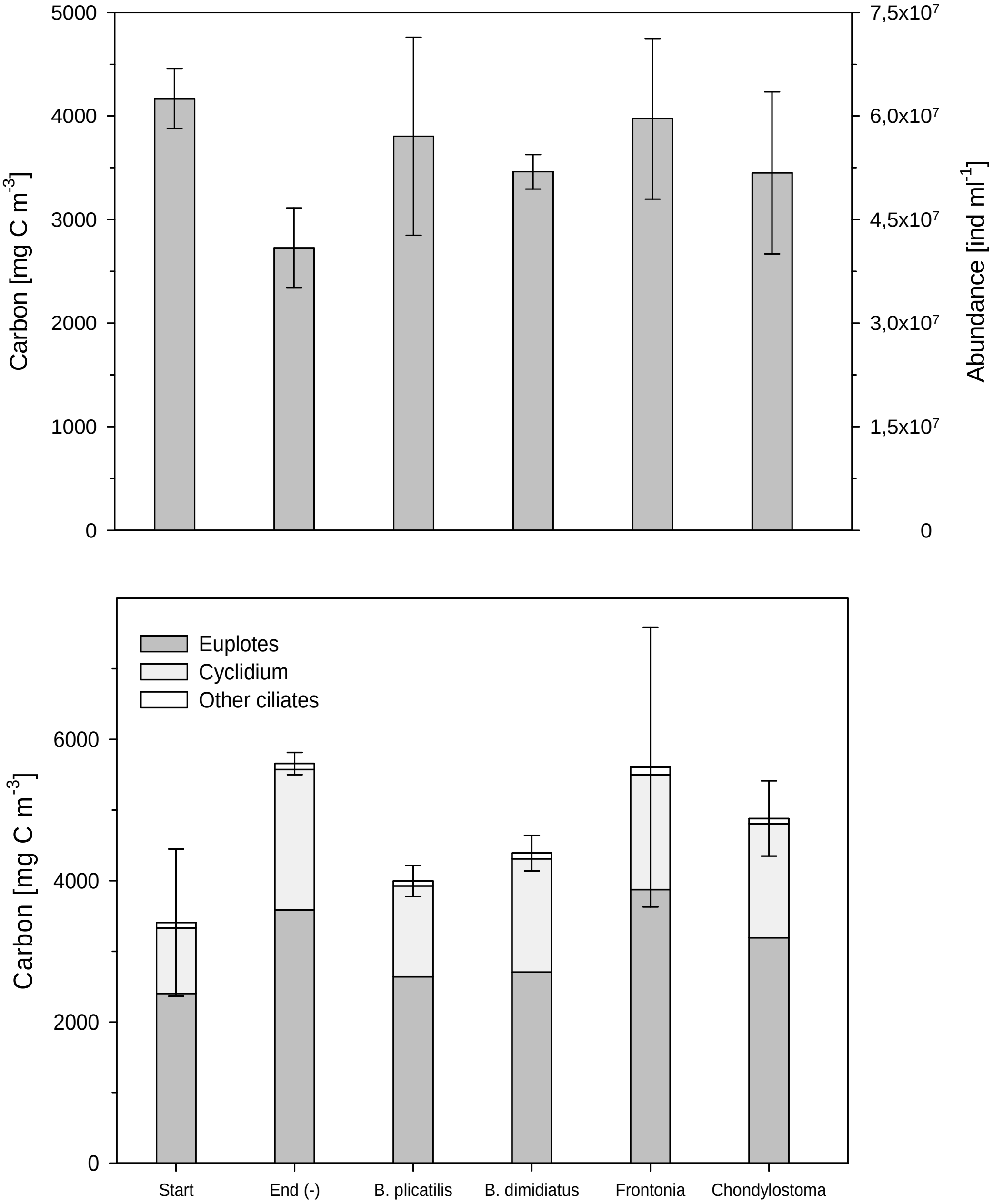


Fig. 1: Initial contribution of various plankton groups to total biomass in the natural plankton community grazing experiments.



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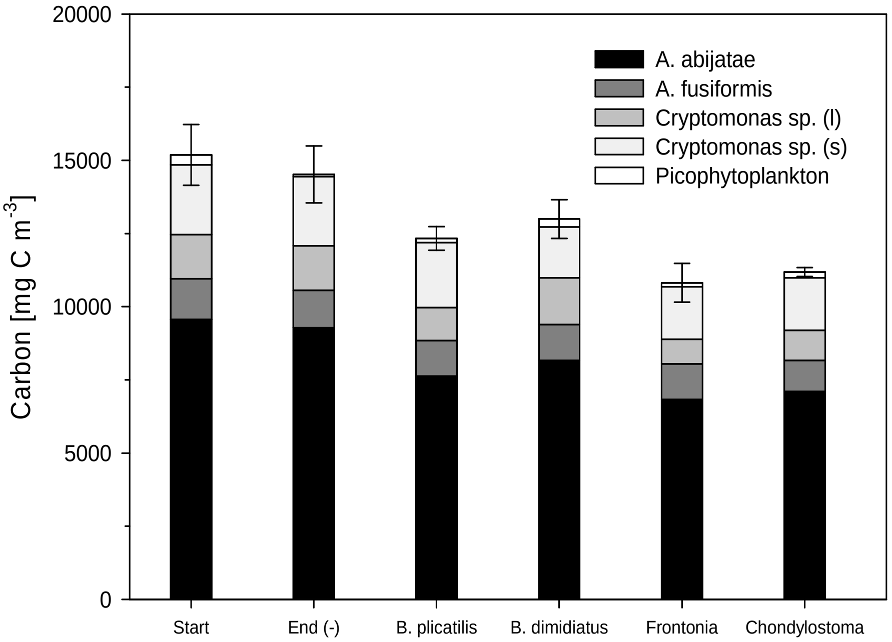

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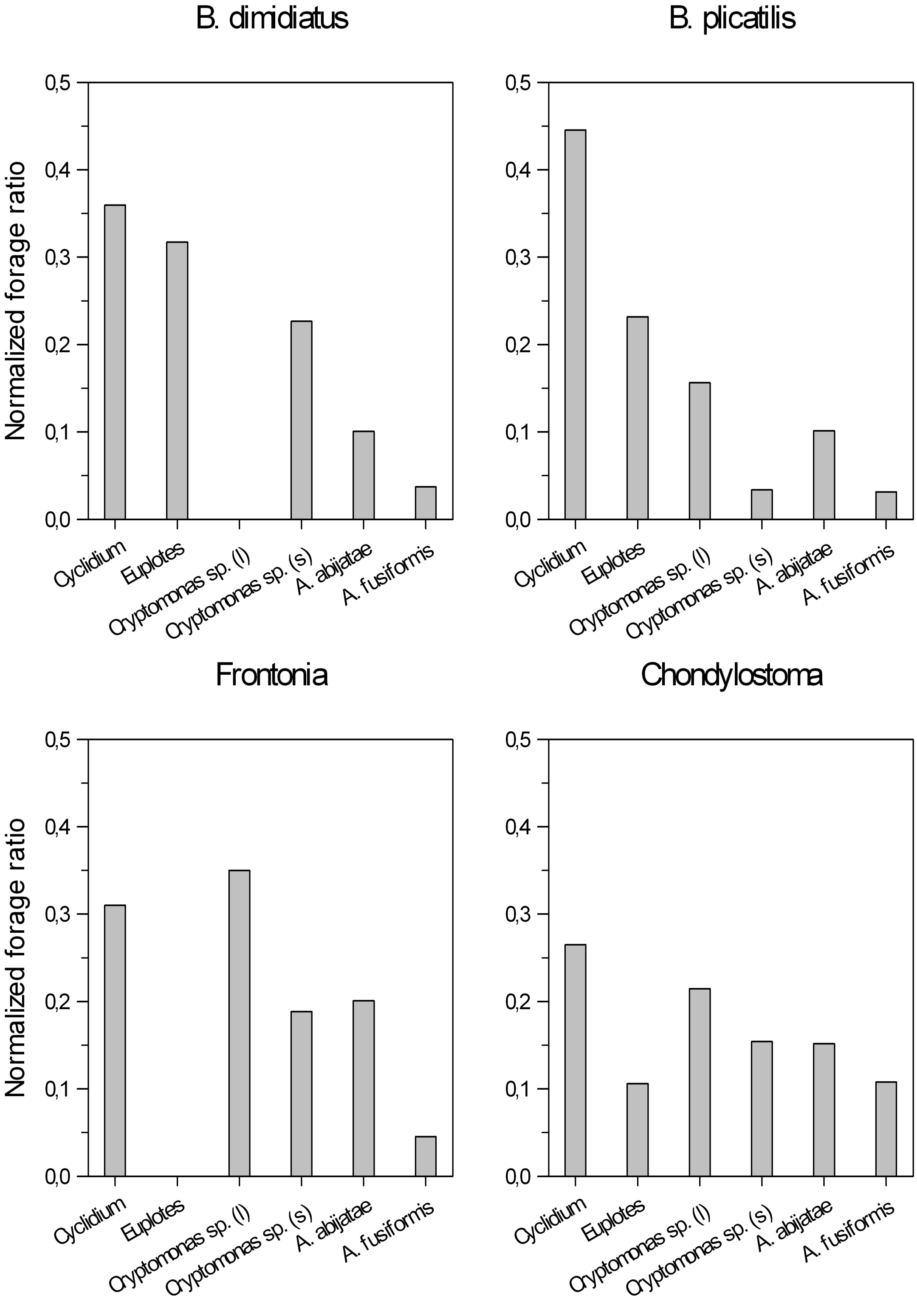

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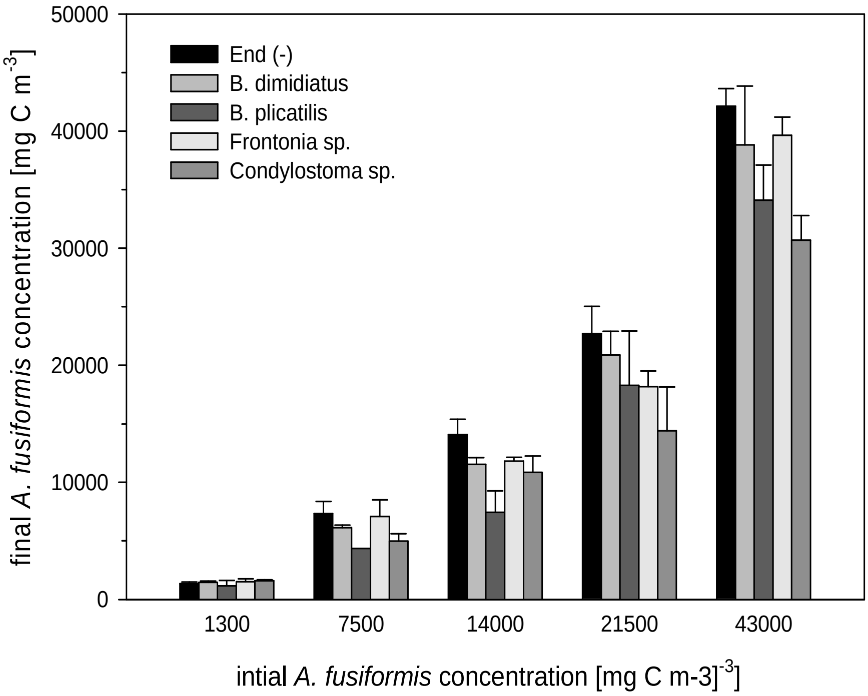

Fig. 5: Final concentrations on different grazing experiments on 5 different concentrations of *A. fusiformis*. Under End (-) values for control experiments without grazing zooplankton are displayed.

4. Zooplankton dynamics of tropical saline lakes: an analysis of rotifer biomass outbursts.

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Abstract

Underling influences on mesozooplankton dynamics of shallow, saline lakes have widely been undiscovered in spite of the ability of such communities to form blooms of exceptional high density and biomass. In our study we investigated environmental and resource based biotic factors to disclose fundamental patterns of such blooms, which are mainly formed of branchionid rotifers and large omnivorous ciliates.

Particulate matter seemed to be a key influencing factor, showing the same dynamics of zooplankton, with both variables only separated by a time lag of two weeks. Phytoplankton also played a role in sustaining high rotifer abundances, but was too low in biomass to sustain high consumer densities on its own. Contrariwise, mesozooplankton had a high impact on algae composition by facilitating the transition between a mixed community of small unicellular algae and the filamentous cyanobacterium *Anabaenopsis abijatae* to a phase of high biomass of solely *Arthrospira fusiformis*. Further a strong top down controlling force of rotifer populations on small ciliates was observed, whereas the influence of bacterial densities on zooplankton dynamics was rather limited.

Introduction

Although rotifers and other mesozooplankton play a crucial role in aquatic systems by enhancing nutrient recycling (Anderson et al., 2005) and linking the classical food web to the microbial loop (Arndt, 1993), they are systematically underrepresented in studies dealing with zooplankton dynamics (Chick et al., 2010). This might be due to the fact that rotifers need to be sampled with other sampling methods than crustacean zooplankton (Likens and Gilbert, 1970) and that though rotifers frequently dominate abundance wise, their biomass is commonly smaller than that of larger sized zooplankton groups (e.g. Gulati et al., 1992). Moreover, Bartumeus and Catalan (2008) highlighted that out of the few studies dealing with rotifer dynamics only exceptionally the impact of both, environmental and resource based biotic factors, on rotifer densities has been investigated.

Concerning Central- and East-African saline lakes the situation is even worse with most studies dating back from the last quarter of the last century (Nogrady, 1983; Vareschi, 1982), in spite of the unique patterns of rotifer dynamics in those systems. First of all, mesozooplankton frequently dominates not only abundance wise but also when biomass is considered and plays a pivotal role when it comes to total consumer's consumption and production rates (Vareschi and Jacobs, 1985). Further, especially the two euryhaline rotifers *Brachionus dimidiatus* Bryce and *Brachionus plicatilis* Mueller regularly exhibit extreme abundances with peak values of up to 600000 ind L^{-1} recorded from Lake Tchad (Iltis and Riou-Duwat, 1971). Such densities belong to the highest ever recorded values and are otherwise only reached in industrial rotifer cultures (Onal et al., 2010). Nevertheless only very little is known about the impacts of such rotifer blooms on the pelagic ecosystems. Vareschi and Jacobs (1985) established the hypothesis that these outbreaks are closely connected to break downs of the cyanobacterium *Arthrospira fusiformis* (Vorochinin) Komárek, the dominant algae in shallow saline lakes (Melack, 1981; Schagerl and Oduor, 2008). But still there exists neither information about the interactions of high rotifer biomass with members of the microbial loop, nor about direct consequences for phytoplankton community structures, nor if those rotifer outbreaks follow certain patterns, like zooplankton spring blooms and following clear water phases in temperate lakes.

Trying to fill the gap, this study focussed on collecting basic information about such phenomena and their associated environmental and biotic variables, studying the saline Lake Nakuru in the Eastern Kenyan (Gregory) Rift Valley. Further, we aimed to test existing hypotheses on the emergence of mesozooplankton biomass peaks and to evaluate the importance of such events for the dynamics of the whole ecosystem.

Material and methods

Lake Nakuru (S00°20‘, E36°05‘) is a shallow saline soda lake located in the Eastern (Gregory) Rift Valley in Kenya near the town of Nakuru. The national park around the endoreheic lake is a major tourist attraction in East Africa, world-famous mainly for its large population of the phytoplankton feeding lesser flamingo (*Phoeniconaias minor* Geoffroy). The lake has a surface area of 40 km² and a mean maximum depth of 1.1 m (Oduor and Schagerl, 2007), though its volume undergoes large fluctuations, even more since the illegal deforestation of its catchment area (Yillia and Kreuzinger, 2009). The lake ecosystem is highly eutrophic and constitutes one of the most productive systems world-wide (Melack and Kilham, 1974; Oduor and Schagerl, 2007). Its fauna and flora is generally characterised by low biodiversity but high biomass at all trophic levels (Vareschi and Jacobs, 1985), which makes it a suitable environment for food web and ecosystem research.

Weekly samplings were taken from the beginning of January to the mid of July 2009 at the central point of the lake (S00°21‘12“, E036°05‘00“). At every sampling date, temperature, conductivity, pH (all data collected with WTW 340i probes) and secchi depth were measured on site. Further, surface water was taken with a Schindler trap (10 L) and all samples were immediately cooled until further processing. Total organic carbon (TOC), dissolved organic carbon (DOC) and dissolved nitrogen (DN) were measured with a TOC-VCPH total organic carbon analyser in combination with a total nitrogen measuring unit TMN-1 by Shimadzu. Soluble reactive phosphorus (SRP) was measured using the ascorbic acid method (APHA, 1995). Samples for particulate matter were collected on precumbusted GF/F filters, oven dried (60 °C; 24 hrs), weighed and incinerated (450 °C; 6 hrs) to determine the ash free dry weight and the particulate organic matter (POM). From POM the non biotic particulate organic matter was calculated by subtracting the carbon values of bacteria, protozoa, algae and rotifers.

Chlorophyll *a* (Chl *a*) was extracted using 90 % acetone after gentle vacuum filtration on GF/F filters. The filters were stored at −20 °C for a minimum of 8 hrs to aid bursting of the cells, homogenised and covered with the extraction solvent. The absorbance of the clarified extract was measured spectrophotometrically (Talling and Driver, 1961). Additionally, from an unfiltered fixed water sample (5 % formalin) the phytoplankton taxa were quantified with an inverted microscope (Nikon Diaphot, Nikon, Tokyo) following the Uthermöhl protocol (1958). Biovolumes of the various taxa were estimated using geometric formulae of the shapes of the respective phytoplankton cells (Sun and Liu, 2003) and measurement of cell dimensions, which was carried out every two months for each taxon. Bacterial samples were also fixed (5 % formalin) and stained using the SYBR Gold technique (Tuma et al., 1998). For protozoa counts 250 mL of lake water was fixed with 50 mL Bouin's solution (final concentration of 5 %) and remained in a sedimentation chamber for at least 24 hrs. Thereupon, the top 250 mL were carefully removed with a suction pump and 1 mL of the residue was filtered on a gridded polycarbonate cellulose filter with warm liquid nutrient agar being added to hold organisms in position. To facilitate counting, organisms were stained using Quantitative Protargol Staining Technique (QPS) by Montagnes and Lynn (1993).

For rotifer samples 10 L of lake water was filtered through a 50 µm sieve and retained plankton were fixed with 5 % formalin. Smaller mesh sizes could not be used because of clogging of sieves during times of high phytoplankton biomass. Adults and eggs were counted with an inverted microscope following again the Uthermöhl protocol (1958). Biovolumes for rotifers were calculated using the formula by Vareschi and Vareschi (1984) stated for the *Brachionus* species of L. Nakuru and the formula by Ruttner-Kolisko (1977) given for the genus of *Hexarthra*. Conversion factors from biovolume to dry weight and to carbon content are shown in Table 1.

For crustacean plankton, continuously vertical tows with a 250 µm net were made, but as only the diaptomid copepod *Lovenula africana* Daday was found in very low numbers (below 50 ind. m^{-3}), this group was not included into weekly sampling routine.

Data analysis

To investigate basic plankton-community relationships between recorded environmental and biological variables a bivariate correlation matrix based on Pearson correlation coefficient and to normal distribution transformed data was used. If data could not be transformed accordingly, a non parametric Spearman-Rho correlation was used instead. Based on this analysis, variables for multivariate analysis were selected. As a high autocorrelation between conductivity, DOC, DN and SRP was observed ($r^2 > 0.6$; $p < 0.01$) a primary component analysis (PCA) was conducted and the first two main axes (cum. var. = 0.97) were used for further analysis.

The species data set contained biomass values (mg C L^{-1}) of all zooplankton species, which can potentially graze on filamentous algae and for which the collected data was sufficient for a reliable analysis. A redundancy analysis (RDA) (Terbraak, 1986) was used to demonstrate relationships between zooplankton species biomass and other biotic and environmental variables, with both data sets being z-transformed before the analysis to achieve homogeneity of variance (Leps and Smilauer, 2003). The significance of the analysis was tested with a Monte Carlo test with 499 permutations. A linear model was used, because the gradient length on the first main axis of a DCA preformed on the species data was 1.9 (Ramette, 2007). Ordinations were computed with the program CANOCO for Windows 4.5 (Terbraak and Smilauer, 2002) all other statistical test were preformed with R, version 2.11 (R Development Core Team, 2010).

Results

Trends of physical and biological parameters

During the sampling period, the volume of L. Nakuru decreased steadily, which is reflected by conductivity values showing an increase from 30 mS cm^{-3} in January to 55 mS cm^{-3} in mid July (Fig. 1). Together with salinity also dissolved nutrients concentrations went up. DOC and DN were highly autocorrelated with each other ($r^2 = 0.96$, $p < 0.001$) and with conductivity ($r^2 > 0.9$, $p < 0.001$). Also SRP showed a trend to increase within the sampling period, though two pronounced peaks within the sampling period also reflect influences of other factors (Fig. 2). The mid day water temperature of L. Nakuru with an average value of 25°C did, like the pH (10.08 ± 0.09), not show large variations within the sampling period (Table 2). Further on, there were no significant correlations of neither temperature nor pH with any other variables leading to an r^2 larger than 0.4.

Secchi disk measurements were characterised by very low values (23.6 ± 6.1 cm) with readings going down as far as to 15.5 cm, reflecting large amounts of particulate matter in the lake. Secchi depth was positively correlated with the per cent of *Arthrospira fusiformis* contributed to total phytoplankton biovolume ($r^2 = 0.56$, $p < 0.01$) and negatively with small algae (biovolume < 1500 μm^3) and *Aanbaenopsis abijatae* Kebede et Willénoften relative biomass ($r^2 > -0.55$, $p < 0.01$). Correspondingly to Secchi depth, also PM and non biotic POM showed high values with PM reaching peaks in the beginning of March and at the end of April 2009 (Fig. 2).

Bacteria abundance was generally high ($1.8 \times 10^8 \pm 6.6 \times 10^7$) tough it did not show any tight connections to other variables. Only PM ($r^2 = 0.41$, $p = 0.03$) and the ratio of eggs to adults of *Brachionus dimidiatus* ($r^2 = -0.39$, $p = 0.04$) showed significant correlations with bacterial numbers.

Total algal biomass varied between 7.7 and 48.4 mg C L^{-1} (Table 2) and was correlated significantly with a number of other variables: A positive connection existed to dissolved nutrients, conductivity ($r^2 > 0.55$, $p < 0.01$) and the relative contribution of *A. fusiformis* to total phytoplankton biomass ($r^2 = 0.63$, $p < 0.001$), whereas *A. abijatae* and small algae biomass contributions were related negatively to total algae biomass ($r^2 > 0.68$, $p < 0.001$). Further, there was also a positive correlation with the rotifers *B. plicatils* and *H. jenkinae* ($r^2 > 0.65$, $p < 0.001$) and *B. dimidiatus* ($r^2 = 0.39$, $p = 0.04$).

The algae community composition changed fundamentally during the sampling period. From January until the beginning of March biomass of small algae was high with also the filamentous cyanobacterium *A. abijatae* contributing about 50 % to total phytoplankton biomass from the beginning of February (Fig. 3). In the mid of March biomass of both groups dropped rapidly, followed by the establishment of high *A. fusiformis* biomass levels. This second filamentous algae remained community dominating (>90 % of total phytoplankton) until the end of the sampling period with only a small peak of *A. abijatae* occurring in the beginning of May. The algal composition had also a big effect on zooplankton biomass with high *A. abijatae* and small algae contribution to phytoplankton correlating negatively with the two rotifers *B. plicatilis* and *Hexarthra jenkinae* De Beauchamp ($r^2 > -0.45$, $p < 0.05$) and *A. fusiformis* correlating positively with both rotifers biomass ($r^2 > 0.74$, $p < 0.001$). *B. dimidiatus* only showed a negative relationship with small algae ($r^2 = -0.51$, $p = 0.006$).

Zooplankton dynamics

Biomass wise, small ciliates (<50 µm RSD) did not play a major role besides one pronounced peak in the time of algal community change (Fig. 3). Further, they were strongly negatively related to the two rotifers *B. plicatilis* and *H. jenkinae* ($r^2 > 0.65$, $p < 0.001$). Larger zooplankton, further referred to as mesozooplankton, were composed of the three rotifer species *B. dimidatus*, *B. plicatilis* and *H. jenkinae* and the ciliates *Frontonia sp.*, *Paradileptus sp*. and *Holophyra sp.*, with the later two only occurring occasionally and therefore not being included in further analysis. Rotifer biomass showed two peaks, a short one between the mid of March and the beginning of April and a more extended one from the beginning of May until the end of June (Fig. 4). At both occasions true outbursts of abundances and biomass were recorded, with *B. dimidatus* at one sampling reaching values close to 300000 ind L^{-1}, and a time lag between the *B. dimidiatus* and the *B. plicatils* maxima could be observed. *H. jenkinae* showed much lower average numbers (Table 3) with only one peak during the period of *A. fusiformis* dominance. *Frontia sp.* constituted 62% of total ciliate biomass over the whole sampling period and formed one pronounced peak with over 45000 ind L^{-1} shortly after the establishment of *A. fusiformis* bloom.

The PCA for the RDA based on dissolved nutrients and conductivity resulted in two primary components explaining 99 % of the variance of the variables, with DOC, DN and conductivity being loaded on the first and SRP on the second axis.

The RDA ordination of the first two axes clearly reflects the temporal change of variables during the sampling period (Figure 5A) with sampling points forming a horseshoe and first samplings influenced mainly by high biomass of small algae and small ciliates (Sampling 1 – 7). Afterwards, *A. abijatae* biomass grows in importance (8 – 13) until finally *A. fusiformis* and Secchi depth take over (14 – 28). *B. dimidiatus* was only weakly influenced by most variables, showing a different relationship to most factors in Fig. 5A and 5B. Still there seems to be a positive relationship with bacterial biomass and SRP. The picture for *B. plicatilis* and *H. jenkinae* is much clearer with both species being positively influenced by *A. fusiformis* and Secchi depth, *B. plicatilis* showing a negative connection to small algae and *H. jenkinae* to *A. abijatae*. *Frontonia sp.* does not relate closely to any environmental or biological parameter. Total mesozooplankton biomass shows a positive relation to biomass of filamentous algae with *A. fusiformis* and *A. abijatae* connected to two separated states of high consumer's biomass (compare Fig. 5A and C).

Discussion

Overall, biotic and environmental variables like bacterial abundance, ciliate and rotifer biomass and even phytoplankton biomass showed extremely high values and, if recorded, low biodiversity, reflecting the extreme conditions in saline alkaline lakes (Vareschi and Jacobs, 1985; Yasindi et al., 2002).

The transitional time between high biomass of small algae and *A. abijatae* to a dominance of *A. fusiformis*, was a period of large fluctuations of many factors, with rotifers and small ciliates forming pronounced maxima at exactly the time of the phytoplankton community change. Rotifers also developed a second peak during May and June 2009.

Interestingly, particulate matter showed a highly similar pattern to rotifer biomass, with the only main difference that rotifer biomass maxima followed PM peak values with a time lag of two to three weeks (Fig. 2). The PM was at that time only slightly influenced by biota with a combined contribution of all living organisms of maximal 20 % (mean = 13.2 ± 4.3 %). Thus, external factors like rain or strong winds, leading to an input or a resuspension of non biotic particulate matter, seem to be tightly connected to rotifer peaks. This confirms assumptions made by Vareschi and Jacobs (1984) that detritus may play an important role in rotifer nutrition. Still the question remains why there exists a time lag of more than two weeks between particulate matter and rotifer peaks, because highest zooplankton densities occur when particular matter was already returning to average values. So detritus on its own seems not to be a direct food source, but it might be after colonisation through microorganisms, a process well known from stream ecology (Meyer et al., 1998). Trophic upgrading of detritus by bacteria and small protozoa might indeed be an important factor (Bec et al., 2003; Breteler et al., 1999), but nevertheless a period of two weeks seems to be a long time span for such processes in a dynamic system like L. Nakuru, characterised by high temperature and bacterial biomass (Kilham, 1981; Vareschi, 1982).

The correlation matrix and the RDA ordination revealed tight connections between zooplankton and algae community structure. An analysis of the trends during the sampling period implies a strong controlling influence of *B. dimidiatus* on *A. abijatae* as this cyanobacterium twice built up populations of higher biomass, which were both times terminated with the beginning of the *B. dimidatus* peak. *A. abijatae* can certainly be a source of nutrition for mesozooplankton organisms of L. Nakuru (Burian et al., 2010a), and an analysis of grazing selectivity even revealed a preferred ingestion of *A. abijatae* compared to *A. fusiformis* by branchionid rotifers (Burian et al., 2010b). Nevertheless, *A. abijatae* biomass was clearly not large enough to sustain the high peak values of zooplankton, assuming a food assimilation efficiency of 20 % for *Brachionus* species (Doohan, 1973), and therefore this alga could only constitute a supplementary food source.

The first peak of soluble reactive phosphorus was overlapping exactly with the first rotifer peak in March. Considering the high nutrient recycling ability of mesozooplankton (Anderson et al., 2005; Elser and Urabe, 1999), this peak is most probably caused by excretions and sloppy feeding of rotifers. The so established conditions, high concentrations of dissolved nutrients and improved underwater light availability through increased zooplankton grazing on other algae groups, obviously created a very suitable environment for the growth of *A. fusiformis*, resulting into high densities after only a short period of time. This is supported by earlier studies, which revealed light to be a major limiting factor for phytoplankton growth (Oduor and Schagerl, 2007) and that applying the redfield ratio (Goldman, 1986) disclosed that phosphorus was clearly the limiting nutrient until the first peak of SRP. The second outburst of rotifers only lead to slightly elevated phosphorus levels, most probably because of the presence of a high standing stock of phosphorus limited algae at that time, which can absorb recycled SRP quickly for somatic growth or luxury consumption (Fu et al., 2005).

Whereas the second distinct peak of SRP was not connected with zooplankton dynamics, because it occurred one month after the end of the second mesozooplankton outburst, it seemingly was tightly related with *A. fusiformis* densities again. Though, this time the biomass of *A. fusiformis* dropped by more than 50 % from 50 to 20 mg C L^{-1}, possibly due to viral lysis (van Hannen et al., 1999), leading also to increased phosphorus levels (Fig. 2 and Fig. 3). Further, the hypothesis that rotifer blooms might be closely related to algal break downs (Vareschi and Jacobs, 1985) could not be confirmed as the second rotifer peak occurred without any major simultaneous changes in algae biomass and the most pronounced phytoplankton break down of the sampling period did not conclude into an elevation of rotifer densities.

Both the correlation matrix and the RDA showed a high connection between *H. jenkinae* and *B. plicatilis* with *A. fusiformis*. It was revealed that *B. plicatilis* can and does feed on this cyanobacterium (Burian et al., 2010a), but nevertheless *A. fusiformis* densities are hardly influenced by large rotifer biomass. This confirms the hypothesis that this algae species is normally not top down controlled by grazers (Burian et al., 2010b; Vareschi and Jacobs, 1985).

Small algae populations were tied to low abundances of all rotifers (Fig. 5A and C). It is improbable that this is due to food quality as cryptomonads and *Synechococcus*, dominating small algae communities, are generally considered to be of high nutritional value (Brett et al., 2006; Hirayama et al., 1979) and their cell dimensions are within the assumed optimum food size range of *Brachionus* species (Hansen et al., 1997; Rothhaupt, 1990). The only potential pelagic predator of rotifers is the omnivorous soda tilapia, *Oreochromis alcalicus grahami* Boulenger, which normally feeds on filamentous phytoplankton. But at times of small algae dominance it might adopt its feeding habits (Vareschi, 1979) and prey increasingly on rotifers, leading to a top down control of zooplankton. This should be facilitated by better underwater light conditions during that period, indicated by high Secchi depths. Further support for this theory comes from a shift of rotifers distribution from surface to bottom near water layers compared to periods of *A. fusiformis* blooms (data not shown) and the formation of pronounced spines of *B. dimidiatus* (personal observation), which frequently indicates high predation pressure in rotifers (Gilbert, 1980).

Bacterial abundances showed only weak connections to mesozooplankton. Only *B. dimidiatus* seems to be related to bacterial biomass, with RDA showing a weak relationship between the two and the egg ratio of *B. dimidiatus* being negatively influenced by high bacteria densities. On the one hand, this is confirmed by a one time stable isotope analysis, performed on the 7th of April 2009 in L. Nakuru, which disclosed bacteria to be one source of nutrition for this small suspension feeding rotifer (Burian et al., 2010a). On the other hand, the negative relationship between egg rate and bacterial biomass shows that bacteria, although they can be a source of food (Starkweather et al., 1980), are of rather low dietary quality (Breteler et al., 1999; Urabe, 1993). Therefore they lead to lower production rates and are only able to maintain populations and not to sustain high growth rates. This should be true, the more so as on the 7th of April, when a bacterial contribution of 40 % to *B. dimidiatus* nutrition was recorded (Burian et al., 2010a), the population of this rotifer was vastly decreasing.

Small ciliates were strongly negatively related to *B. plicatilis* and *H. jenkinae*. This was also confirmed by biomass trends throughout the sampling period. Small ciliates showed intermediate densities with a peak in the mid of March, but abundances immediately approach values close to zero as soon as *B. plicatilis* shows elevated densities (Fig. 3 and Fig. 4). This and the fact that *B. plicatilis* seems to select especially for small ciliates (Burian et al., 2010b), imply a strong top down control of small ciliates by large sized rotifers.

Moreover, *B. dimidiatus* biomass was negatively correlated with its own egg ratio. Such density dependent decrease of reproduction rates has been frequently reported for rotifers and can be the consequence of interspecific competition (Verschoor et al., 2007) or density induced sexual reproduction and self regulation mechanisms (Fussmann et al., 2007). However, for *B. plicatilis*, the other rotifer species showing pronounced biomass peaks, no such relationships could be observed, which underlines heterogeneity in behaviour even of closely related rotifer species. Such a phenomenon was also described by Carmona et al. (1994), who reported density dependent self regulation only in 6 out of 12 investigated *B. plicatilis* clades.

Frontonia sp. only showed weak connections to environmental and other biotic factors. Only PM and Chl *a* were correlated with its biomass. This might reflect an general omnivory, which has already been described before for *Frontonia* (Dias and D'Agosto, 2006), but it also could indicated that this species might rely on microbial processes which were not revealed in this investigation.

In summary, this study showed a high impact of particulate matter on rotifer densities with the exact relationship between both variables still being concealed. Nevertheless, major algae breakdowns could be ruled out as necessary driving force for rotifer biomass outbreaks. Phytoplankton community succession was closely related to zooplankton dynamics, with *A. abijatae* being top down controlled and *A. fusiformis* growth being facilitated by high nutrient recycling and improvement of underwater light conditions. This shows that rotifers can even affect competition between different phytoplankton taxa and underlines the importance of mesozooplankton in such systems.

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

Table 2: Mean values and maximal variations of environmental and biotic parameters in Lake Nakuru between January and July 2009.

Table 3: Average densities and biomass of dominant zooplankton species of L. Nakuru from January until July 2009.

Fig. 1: Trends of dissolved organic carbon, dissolved nitrogen and conductivity in Lake Nakuru from January to July 2009.

Fig. 2: Trends of particulate matter, soluble reactive phosphorus, and rotifer biomass (dry weight) in Lake Nakuru from January to July 2009.

Fig. 3: Trends of potential biotic food sources of mesozooplankton in Lake Nakuru from January to July 2009.

Fig. 4: Mesozooplankton dynamics of the four most abundant species *Brachionus dimidiatus*, *Brachionus plicatilis*, *Hexarthra jenkinae* and *Frontonia sp.* in Lake Nakuru from January to July 2009.

Fig. 5: Redundancy analysis (RDA) of environmental and biotic variables from January to July 2009. First and second main axis of RDA (**A**) and first and third axis (**B**) are displayed, showing sampling dates (numbers), dominant zooplankton species (blue arrows) and environmental and rotifer-resource based variables (red arrows). Figure **C** and **D** display the sampling dates within the ordination of the RDA, with the numbers and sizes of the pies indicating total mesozooplankton dry weight (mg L^{-1}) on the corresponding sampling date and the segments of the pie signalling the relative contribution of the four mesozooplankton species *Frontonia sp.*, *Brachionus dimidiatus*, *Brachionus plicatilis* and *Hexarthra jenkinae*. The lines symbolizing a generalized regression model of the total mesozooplankton dry weight calculated for the axis of the respective ordination.

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

Taxa	Conversion factors	References
heterotrophic bacteria	cell number [ind] : carbon content [pg] = 15	Stenuite et al. 2009
Cyanobacteria	biovolume [mm^3] : carbon content [mg] = 0.22	Ahlgren 1983
Chlorophyta	biovolume [mm^3] : carbon content [mg] = 0.16	Lundgren 1978
Bacillariophyceae	log C [pg]=-0.610 + 0.892 (log plasma volume[µm^3])	Strathmann 1967
other algae	biovolume [mm^3] : carbon content [mg] = 0.11	Rocha and Duncan 1985
ciliates	biovolume [mm^3] : carbon content [mg] = 0.14	Putt and Stoecker 1989
rotifers	biovolume [mm^3] : dry weight [mg] = 1	Pace and Orcutt 1981
	dry weight [mg] : carbon content [mg] = 0.45	Pagano and Saint Jean 1993

Table 2: Mean values and maximal variations of environmental and biotic parameters in Lake Nakuru between January and July 2009.

	mean	max	min
Temperautre [℃]	24.9 ±2.0	29.1	21.6
Conductivity [mS cm^{-1}]	42.5 ±7.0	55	30
pH	10.08 ±0.09	10.24	9.97
Dissolved organic carbon [mg L^{-1}]	339 ±68	475	227
Dissolved nitrogen [mg L^{-1}]	23.4 ±4.3	30.9	15.2
Soluble reactive phosphorus [µg L^{-1}]	771 ±568	2035	74
Secchi depth [cm]	23.6 ±6.1	38	15
Particulate organic matter [mg C L^{-1}]	61.0 ±27.4	133	28
Organic carbon (non biotic) [mg C L^{-1}]	37.1 ±26.6	102.9	0
Bacteria abundances [ind L^{-1}]	1.8×10^{8} $\pm 6.6 \times 10^{7}$	3.1×10^{8}	4.7×10^{7}
Chl a [µg L^{-1}]	385 ±155	765	197
Total algae biomass [mg C L^{-1}]	16.3 ±10.3	48.4	7.7
Anabaenopsis abijatae [%]	18.7 ±23.9	77.5	0.0
Arhtrospira fusiformis [%]	54.1 ±44.9	99.3	1.4
Small agae [%]	26.9 ±33.4	91.2	0.4
Small ciliates [mg C L^{-1}]	0.8 ±1.5	6.6	0.0
Mesozooplankton [mg C L-1]	4.1 ±4.0	14.3	0.1

Table 3: Average densities and biomass of dominant zooplankton species of L. Nakuru from January until July 2009.

	mean		max	min
Brachionus dimidiatus				
Abundace [ind L^{-1}]	48214	±70225	289275	3094
Dry weight [mg L^{-1}]	2.24	±3.21	13.13	0.16
Brachionus plicatilis				
Abundace [ind L^{-1}]	7244	±7545	24000	8,25
Dry weight [mg L^{-1}]	2.62	±3.52	13.22	0
Hexarthra jenkine				
Abundace [ind L^{-1}]	7609	±12439	45600	0
Dry weight [mg L^{-1}]	0.37	±0.74	2.84	0
Frontonia sp.				
Abundace [ind L^{-1}]	6302	±12953	51250	0
Dry weight [mg L^{-1}]	1.14	±1.95	8.69	0

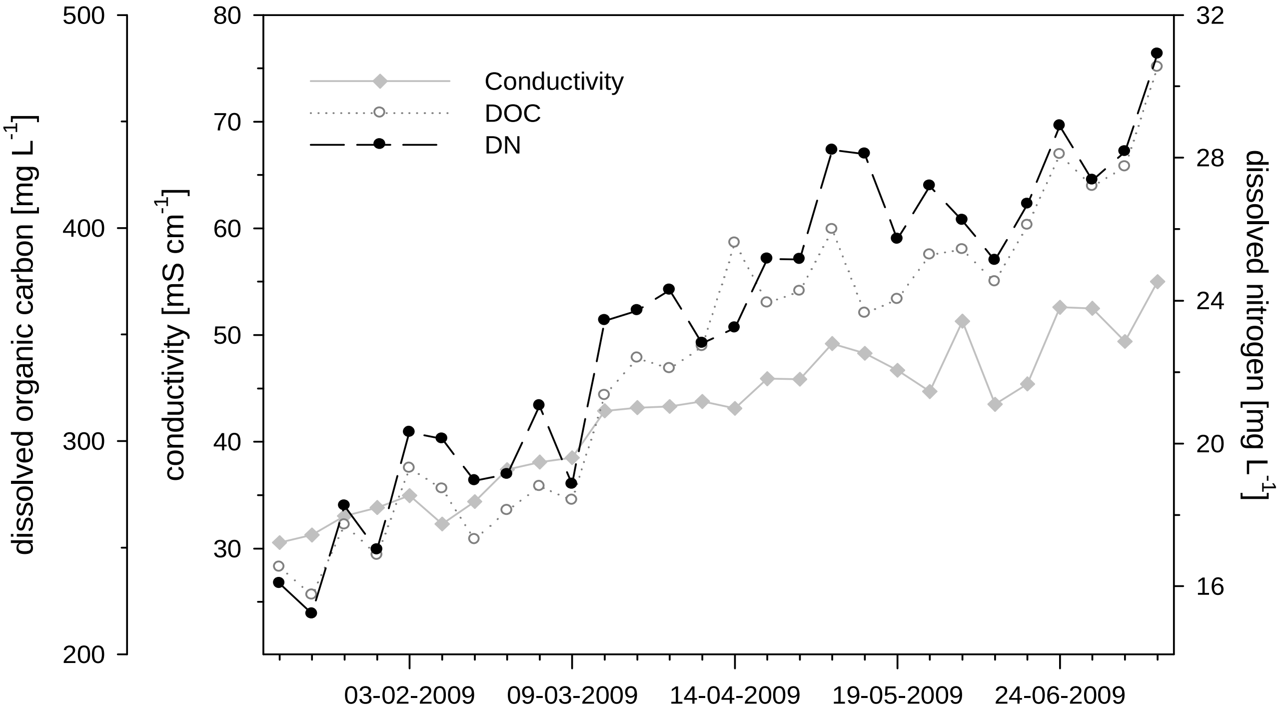

Fig. 1: Trends of dissolved organic carbon, dissolved nitrogen and conductivity in Lake Nakuru from January to July 2009.

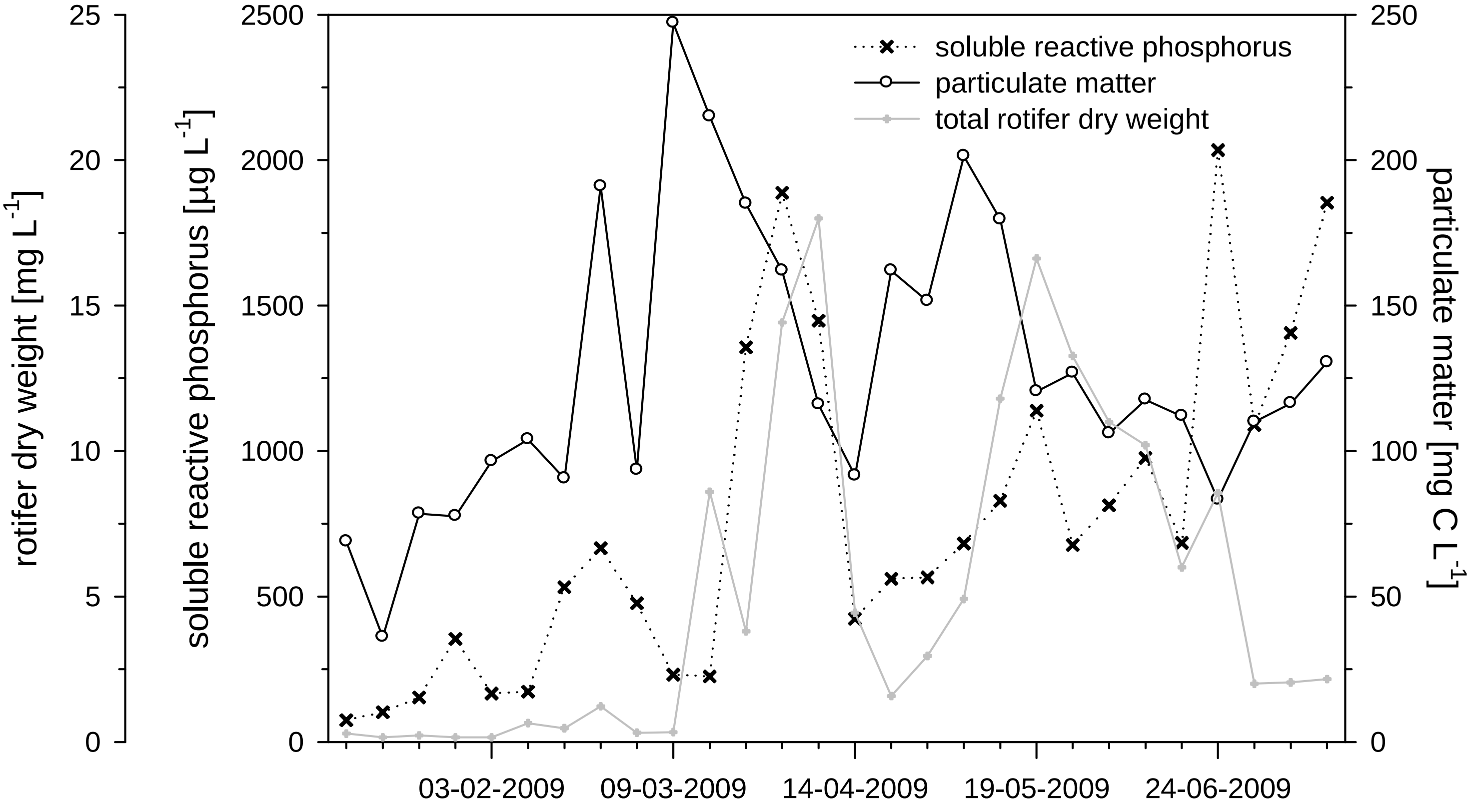

Fig. 2: Trends of particulate matter, soluble reactive phosphorus, and rotifer biomass (dry weight) in Lake Nakuru from January to July 2009.

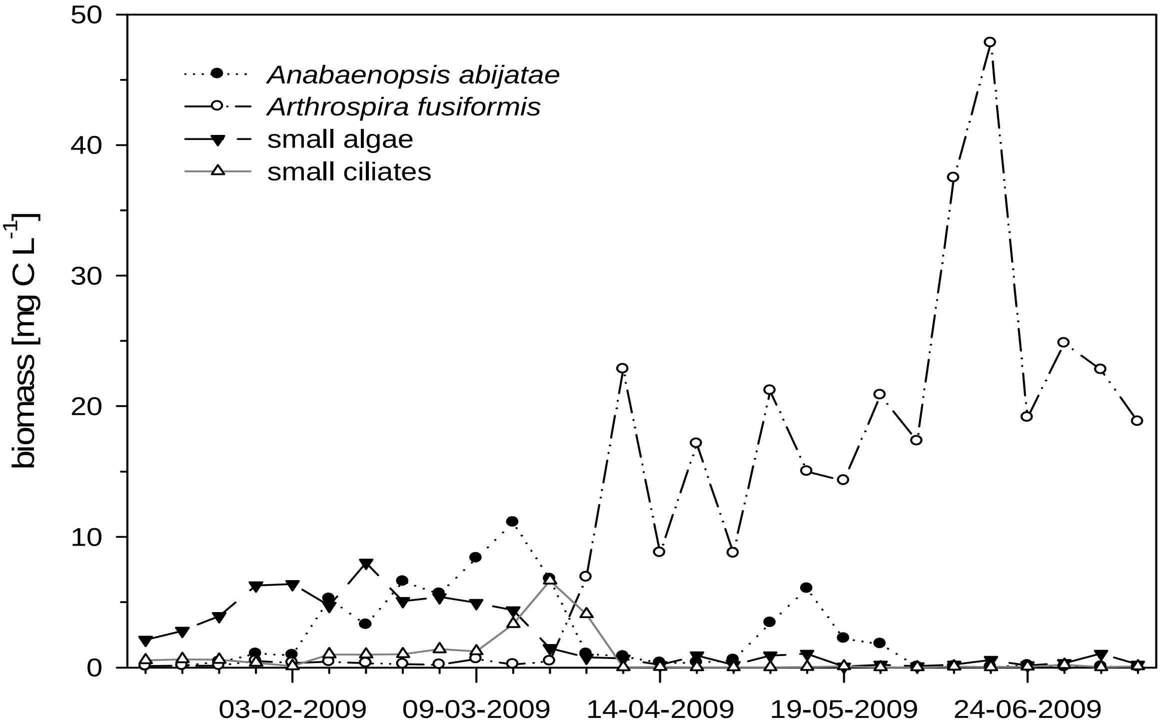

Fig. 3: Trends of potential biotic food sources of mesozooplankton in Lake Nakuru from January to July 2009.

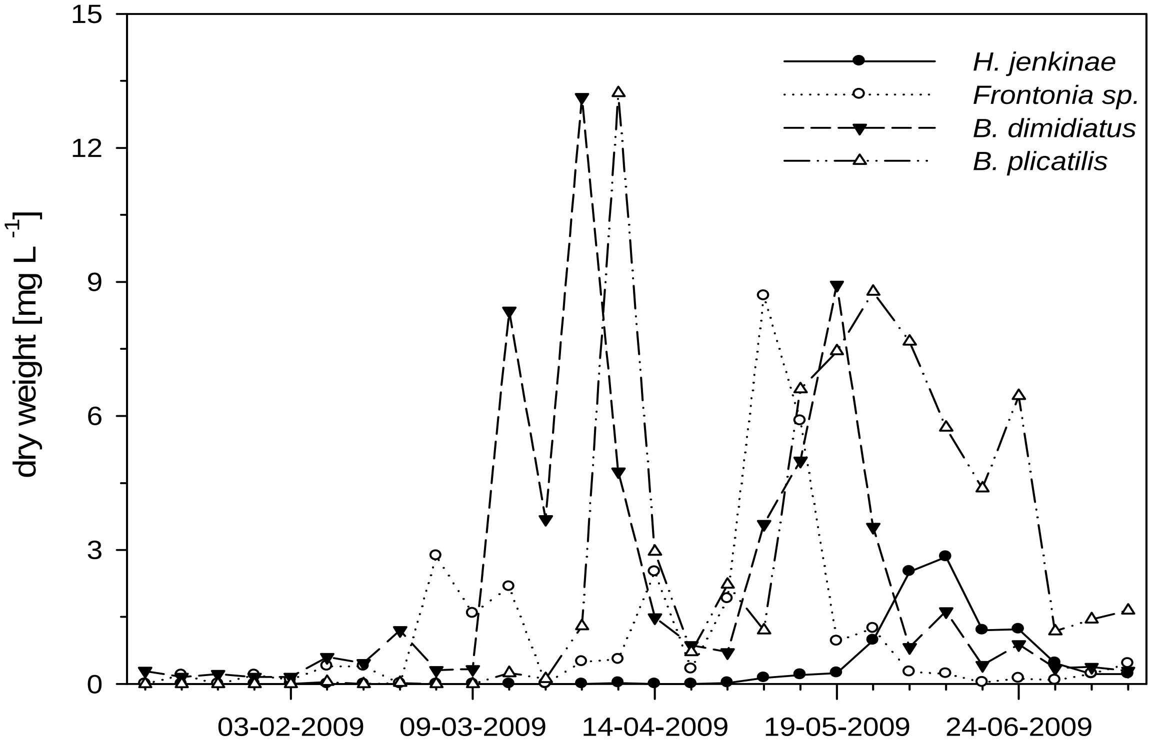

Fig. 4: Mesozooplankton dynamics of the four most abundant species *Brachionus dimidiatus*, *Brachionus plicatilis*, *Hexarthra jenkinae* and *Frontonia sp.* in Lake Nakuru from January to July 2009.

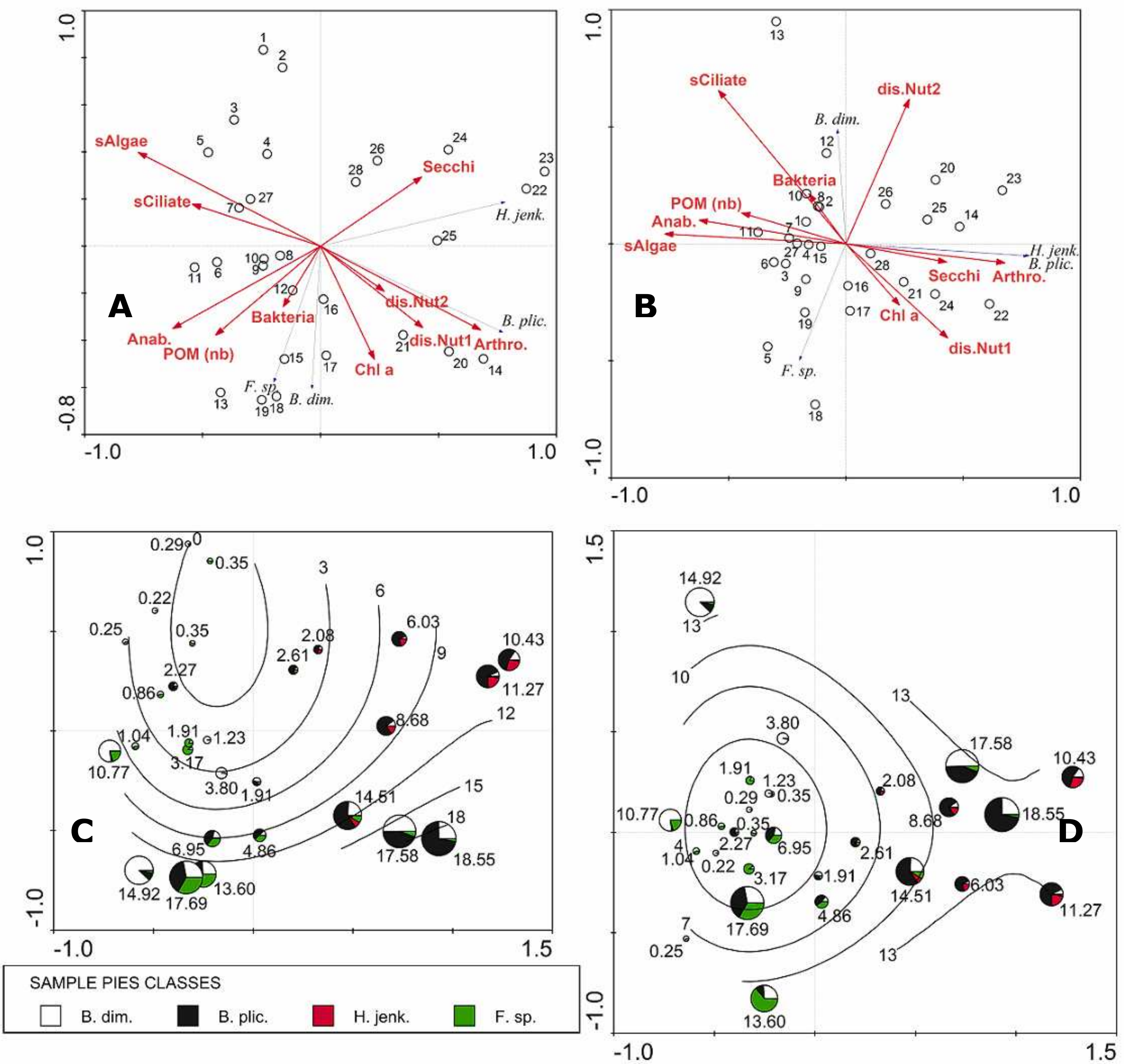

Fig. 5: Redundancy analysis (RDA) of environmental and biotic variables from January to July 2009. First and second main axis of RDA (**A**) and first and third axis (**B**) are displayed, showing sampling dates (numbers), dominant zooplankton species (blue arrows) and environmental and rotifer-resource based variables (red arrows). Figure **C** and **D** display the sampling dates within the ordination of the RDA, with the numbers and sizes of the pies indicating total mesozooplankton dry weight (mg L^{-1}) on the corresponding sampling date and the segments of the pie signalling the relative contribution of the four mesozooplankton species *Frontonia sp.*, *Brachionus dimidiatus*, *Brachionus plicatilis* and *Hexarthra jenkinae*. The lines symbolizing a generalized regression model of the total mesozooplankton dry weight calculated for the axis of the respective ordination.

5. English summary

Underling influences on mesozooplankton dynamics of shallow, saline lakes have widely been undiscovered in spite of the ability of such communities to form blooms of exceptional high density and biomass. In one of our studies we investigated therefore environmental and resource based biotic factors to disclose fundamental patterns of such blooms, which are mainly formed of branchionid rotifers and large omnivorous ciliates.

Particulate matter seemed to be a key influencing factor, showing the same dynamics of zooplankton, with both variables only separated by a time lag of two weeks. Phytoplankton also played a role in sustaining high rotifer abundances, but was too low in biomass to sustain high consumer densities on its own. Contrariwise, mesozooplankton had a high impact on algae composition by facilitating the transition between a mixed community of small unicellular algae and the filamentous cyanobacterium *Anabaenopsis abijatae* to a phase of high biomass of solely *Arthrospira fusiformis*. Further a strong top down controlling force of rotifer populations on small ciliates was observed, whereas the influence of bacterial densities on zooplankton dynamics was rather limited.

Further, the ecological niches of the two frequently dominating rotifers of Lake Nakuru (Kenya), *Brachionus dimidiatus* and *Brachionus plicatilis*, were investigated using stable isotope analysis. The larger-sized *B. pliciatilis* showed a reliance on the filamentous cyanobacteria *Arthrospira fusiformis* and *Anabaenopsis abijatae*, which indicates substantial differences of feeding behaviour within the cryptic species complex of this taxon. *B. dimidiatus* fed to a large extend on components of the microbial loop and bacterial contribution of over 40% to total rotifer nutrition belongs to the highest ever recorded *in-situ* values. Further, the comparatively high δ^{15}N value of *B. dimidiatus* implies an enrichment of δ^{15}N caused by a reliance on the microbial loop within an ecosystem which is strongly depended on recycling of nutrients originating from higher trophic levels. This underlines the

necessity of a careful application of $\delta^{15}N$ values for interpreting trophic levels in such communities.

Finally, we investigated the feeding behaviour of dominating pelagic zooplankton of saline lakes in the East African Rift Valley. A set of grazing experiments revealed extraordinary high ingestion rates of the two euryhaline rotifers *Brachionus dimidiatus* and *Brachionus plicatilis* and of the large omnivorous ciliates *Frontonia* and *Condylostoma magnum*. Increased feeding rates reflected the unique nature of tropical saline systems showing high water temperatures coupled with high food quantities but low food quality. The size spectrum of ingested particles was broad, and even included filamentous cyanobacteria like the commonly dominating *Arthrospira fusiformis*. Selectivity, however, showed higher values for cryptomonads and small protozoans.

Bacterial biomass was positively influenced by presence of grazers, as small bacterivorous predators were significantly reduced in numbers, showing the cascading effect of large zooplankton on the food web structure. Overall, based on this first time study of the feeding behaviour of the mesozooplankton in East African saline lakes, a strong structuring influence of rotifers and large ciliates can be expected in times of high consumer biomass.

6. Deutsche Kurzzusammenfassung

Grundlegende Einflüsse auf die Dynamiken des Mesozooplanktons seichter saliner Seen waren bislang weitgehend unbekannt, obwohl solche Planktongemeinschaften die Fähigkeit besitzen Blüten mit außergewöhnlich hohen Dichten und Biomasse auszubilden. In einer unserer Studien haben wir daher die basalen Umwelt und ressourcenbassierenden biologischen Faktoren untersucht, um die charakteristischen Muster solcher Blüten, die hauptsächlich von brachioniden Rotatorien und von großen, omnivoren Ciliaten gebildet werden, darzulegen.

Dabei schienen partikuläre Substanzen einen ganz zentralen Faktor darzustellen, da sie sehr ähnliche Muster wie Zooplanktonbiomassen aufwiesen. Die Spitzen beider Variablen trennte lediglich ein Zeitunterschied von zwei Wochen. Phytoplankton spielte ebenfalls eine wichtige Rolle in der Erhaltung hoher Rotatoriendichten, doch ihre Biomasse war zu gering um die einzige Nahrungsquelle darzustellen. Umgekehrt hatte aber auch das Mesozooplankton einen großen Einfluss auf die Algenzusammensetzung, indem es den Übergang zwischen einer Gemeinschaft als kleinen, einzelligen Algen und dem filamentösen Cyanobakterium *Anabaenopsis abijatae* zu einer Phase hoher Biomasse gebildet ausschließlich von *Arthrospira fusiformis* einleitete. Weiters wurde ein starker predatorischer Effekt von Rotatorien auf kleine Ciliaten festgestellt, wohingegen Bakteriendichten nur einen geringen Einfluss auf die Zooplanktondynamik hatten.

Weiters wurden die ökologischen Nischen von zwei der häufig dominierenden Rotatorienarten von Lake Nakuru, *Brachionus dimidiatus* und *Brachionus plicatilis*, untersucht. Dabei wurde eine Analyse stabiler Isotope angewandt. Der größere *B. pliciatilis* zeigte eine Abhängigkeit vom den filamentösen Cyanobakterien *Arthrospira fusiformis* und *Anabaenopsis abijatae*, was ein völlig anderes Fraßverhalten innerhalb des kryptischen Artenkomplex dieses Taxon impliziert.

B. dimidiatus stützte seine Ernährung zu einem großen Teil auf mikrobielle Organismen, mit einem Futterbeitrag von Bakterien von über 40 %. Das stellt eine der höchsten Fraßraten an Bakterien dar, die jemals *in situ* für Metazoa gemessen wurde. Außerdem lassen die hohen $\delta^{15}N$ Werte von *B. dimidiatus* auf eine durch den hohen Fraßanteil an mikrobiellen Organismen hervorgerufene Anreicherung von $\delta^{15}N$ vermuten. Das unterstreicht, besonders in Systemen die zu einem Gutteil auf der Nährstoffwiederaufbereitung durch mikrobielle Organismen beruhen, dass eine Interpretation der trophischen Ebenen basierend auf $\delta^{15}N$ Werten vorsichtig angewandt werden muss.

Schließlich untersuchten wir das Fraßverhalten von pelagischen Zooplanktonarten saliner Seen im Ostafrikanischen Grabenbruch. Ein Set von Fraßexperimenten führte zu erstaunlich hohen Fraßraten der zwei salztoleranten Rotatorien *Brachionus dimidiatus* und *Brachionus plicatilis* und der großen omnivoren *Frontonia* und *Condylostoma magnum*. Erhöhte Fraßraten weißen vermutliche auf die speziellen Bedingungen, wie hohe Temperatur, niedrige Futterqualität aber hohe Futterquantität von tropischen Salzseen hin. Das Größenspektrum gefressener Partikel war sehr weit und es wurden auch fädige Blaualgen wie zum Beispiel *Arthrospira fusiformis* aufgenommen. Dies ist besonders von Bedeutung, da diese Alge oft das Phytoplankton solcher Ökosysteme dominiert. Nichtsdestotrotz wurden aber andere Partikel wie kleine Cryptomonaden und andere Protozoa bevorzugt.

Die bakterielle Biomasse wurde positiv von der Präsenz von Mesozooplankton beeinflusst, weil Organismen, die sich ausschließlich von Bakterien ernährten in ihrer Häufigkeit abnahmen. Zusammenfassend haben diese Studien einen großen Einfluss von Mesozooplanktonarten auf andere Planktongruppen aufgezeigt, ganz besonders in Zeiten in denen diese Organismen hohe Dichten aufweisen.

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School education	
09.1994 – 06.2002	High School St. Martin, Matriculation examination in 2002
09.1990 – 07.1994	Elementary school, Villach

International Experience	
03.2009 – 05.2009	Field work for master thesis in Freshwater Ecology in Kenya
02.2009 – 03.2009	Internship at the University of KwaZulu/ Natal in S. A.
09.2008 – 01.2009	Exchange semester at the University of Egerton in Kenya
08.2008	Participant of the 2008 field course of the Tropical Biology Association in Kibale, Uganda.
12.2007	Visit of a Handicap- International- Project in Lebanon
10.2003 – 02.2005	Assistant teacher and youth attendant in KwaZulu/Natal, South Africa, fulfilling my civil service for the Austrian state.
1992, 1994, 2006, 2007	Travels to North America, Pakistan, and Great Britain.

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Personal interest	
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