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PRIMARY RESEARCH PAPER

Grazing impacts of rotifer zooplankton on a cyanobacteria bloom in a shallow temperate lake (Vancouver Lake, WA, USA)

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Abstract Grazing by microzooplankton has been shown to significantly impact freshwater cyanobacteria blooms; however, the contribution of rotifers to the overall effect of microzooplankton grazing is not well understood. We conducted monthly microzooplankton community grazing (dilution) experiments June–October 2019, concurrent with incubations of field-collected rotifers feeding upon the natural assemblage of microplankton prey < 75 µm in Vancouver Lake (Washington State, USA), a lake annually affected by cyanobacteria blooms. Our results showed that just days after a large bloom, the microzooplankton community grazing impact on phytoplankton biomass was exceptionally high (> 1000% d^{-1}), yet the impact by rotifers was low (< 1% d^{-1}). As the bloom diminished in September and October, the grazing impact of rotifers increased dramatically, specifically consuming substantial dinoflagellate (≤ 574%) and ciliate (≤ 382%) biomass daily. Analysis of rotifers in Vancouver Lake during these months showed the presence of large, carnivorous *Asplanchna* spp., which indicates multi-trophic grazing dynamics within the rotifer assemblage. We conclude that non-rotifer micro-grazers (i.e., ciliates) were likely responsible for the initial dissipation of cyanobacteria just after the bloom peak, while rotifers primarily removed micro-grazers later in autumn. This study highlights the trophic roles of micro-grazers in controlling harmful cyanobacteria blooms and quantifies the specific grazing contributions of rotifers.

Keywords Harmful algal blooms · *Brachionus* · *Keratella* · Ingestion rate · Clearance rate · Selectivity

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Introduction

Cyanobacteria are ecologically important, naturally occurring components of freshwater planktonic communities (Díez & Ininbergs, 2014). However, harmful cyanobacteria blooms have become a major challenge to aquatic system health worldwide (Rabalais et al., 2009; Paerl et al., 2011; Kosten et al., 2012), as they present a threat to humans and wildlife through the production of cyanotoxins (Chorus et al., 2000;

Carmichael & Boyer, 2016; Chorus & Welker, 2021), diminish overall water quality, reduce biodiversity, and change the flow of energy in aquatic systems (Paerl et al., 2001). There is also growing evidence that climate change will likely lead to increases in occurrence and magnitude of cyanobacteria blooms in the future (Paerl et al., 2011; Kosten et al., 2012; O'Neil et al., 2012).

Harmful cyanobacteria blooms are often associated with nutrient enrichment, increased temperature or light, and hydrodynamics (i.e., mixing, flushing) (Elser, 1999; Paerl et al., 2001; Yang et al., 2008; Kosten et al., 2012); however, the influence of biotic factors is also important. For instance, mesozooplankton taxa (200 µm–2 mm in size), such as large cladocerans, have been observed to graze directly on cyanobacteria cells, significantly reducing cyanobacterial biomass (e.g., Sterner, 1989; Gobler et al., 2007). Conversely, copepods have been shown to facilitate cyanobacterial dominance by selectively avoiding the consumption of these inedible and/or toxic cells in favor of algal or diatom competitors (Fulton & Paerl, 1987; DeMott & Moxter, 1991; Kurmayer, 1999; Rollwagen-Bollens et al., 2013; Ger et al., 2016, 2019).

In comparison, microzooplankton grazers (20–200 µm in size; e.g., heterotrophic protists, small bosminid cladocerans, and rotifers) are more resistant to cyanobacterial defenses, often co-existing with cyanobacteria under bloom conditions (Fulton & Paerl, 1987; Gilbert, 1990; Hansson et al., 2007; Davis et al., 2012; Ger et al., 2016). Indeed, multiple microzooplankton community grazing studies have shown the ability of these grazers to actively consume cyanobacterial cells (Gobler et al., 2007; Agasild et al., 2007), which can control cyanobacteria blooms in some cases (Davis et al., 2012; Rollwagen-Bollens et al., 2018). Despite this evidence for substantial grazing impact of the microzooplankton community as a whole, the impact of specific micro-grazer assemblages on freshwater cyanobacteria blooms has been less well studied, especially for rotifers.

Individuals in the phylum Rotifera are ubiquitous in freshwater (Segers, 2008; Wallace et al., 2015) and can be the numerically dominant zooplankton in lakes and reservoirs (Hillbricht-Ilkowska, 1983; Mazumder et al., 1992; Rodríguez & Matsumura-Tundisi, 2000; Li et al., 2017). Yet, rotifers are generally under-represented in zooplankton feeding studies, especially in relation to cyanobacteria blooms, in part due to the challenge of sampling them in ways that accurately assess their abundance, composition, and feeding without body damage (Orcutt & Pace, 1984; James, 1991; Muirhead et al., 2006; Chick et al., 2010; Thomas et al., 2017). In the few published field studies of rotifer grazing, rotifers were responsible for a substantial fraction of total zooplankton grazing impact on phytoplankton communities. For instance, the rotifer assemblage in Lake Pavin (France), dominated by *Kellicottia longispina* (Kellicott, 1879), accounted for 20–95% of the daily grazing impact by the entire zooplankton community, far exceeding the contribution of cladocerans (Quiblier-Lloberas et al., 1996). Similarly, rotifers in Lake Võrtsjärv (Estonia) contributed on average 68% of the total grazing impact on non-cyanobacterial phytoplankton < 30 µm (Agasild et al., 2007) and in Lake Aydat (France) mean summertime grazing impacts of *Keratella* sp. ranged from 5 to 70% of the total phytoplankton biomass per day (Lair & Oulad Ali, 1990).

In addition to their impact on phytoplankton communities, rotifers in laboratory experiments have been found to prefer and consume small heterotrophic and mixotrophic organisms. Specifically, *Asplanchna girodi* (Guerne 1880), *Synchaeta pectinata* (Ehrenberg, 1832), and *Brachionus calyciflorus* (Pallas, 1766) rotifers each consumed 10–50 cultured ciliates individual^{-1} d^{-1} and preferred *Tetrahymena* sp. ciliates over *Strobilidium* sp. ciliates (Gilbert & Jack, 1993). Large raptorial-feeding rotifers such as *Asplanchna* sp. and *Ascomorpha* sp. are also known predators of mixotrophic dinoflagellate genera, like *Ceratium* and *Peridinium* (Pourriot, 1977; Stelzer, 1998; Chang et al., 2010), in some instances consuming up to 0.025 µg C individual^{-1} d^{-1} of *Ceratium* (Stelzer, 1998).

Specific to cyanobacteria, a small set of studies have found rotifers to be significantly associated with the occurrence of cyanobacteria blooms, more so than other zooplankton taxa (i.e., Hansson et al., 2007; Ger et al., 2016). Rotifers may even thrive under these conditions, whether due to an evolved tolerance to cyanobacterial defenses, suppression of competitors or predators, or the availability of alternative nutrition (e.g., parasitic zoospores) (Gilbert, 1990; Frenken et al., 2018; Horppila et al., 2019).

In addition, laboratory studies using cultured rotifers and/or cultured cyanobacteria and algal

strains demonstrate that rotifers may directly consume cyanobacteria. For example, cultured *Euchlanis* rotifers from a lake in the Netherlands (Gulati et al., 1987), as well as field-collected *Brachionus angularis* (Gosse, 1851) and *Keratella* sp. from Senegalese lakes (Kâ et al., 2012), were all found to graze upon and at times prefer filamentous cyanobacteria taxa (*Aphanizomenon*, *Cylindrospermopsis,* and *Anabaena* spp.) in laboratory grazing experiments. In a combined field and modeling study using stable isotopes, Burian et al. (2014) reported that filamentous *Arthrospira fusiformis* (Komárek & Lund, 1990) was selected by *Brachionus plicatilis* (Müller, 1786) in tropical, shallow Lake Nakuru (Kenya), comprising 48% of their diet. *Brachionus calyciflorus* was similarly shown in laboratory experiments to select and thrive upon filamentous *Anabaena flos-aquae* (Bornet & Flahault 1888) even when provided a 'more nutritious' food source (*Euglena gracilis* [Klebs, 1883]) (Starkweather, 1981; Starkweather and Kellar, 1983). Conversely, Kirk and Gilbert (1992) found *Keratella* avoided *Anabaena* sp. and instead showed near-complete preference for *Cryptomonas* sp. in laboratory experiments, and Fulton (1988) showed cultured *Brachionus calyciflorus* from the Potomac River avoided *Aphanizomenon flos-aquae* (Bornet & Flahault, 1888) and *Anabaena planktonica* (Brunthaler, 1903).

To the best of our knowledge, only two published studies report grazing rates for field-collected rotifers feeding upon naturally occurring phytoplankton. Lionard et al. (2005) found that the microzooplankton community (composed largely of *Brachionus, Trichocerca,* and *Synchaeta* rotifers) grazed up to 84% of the available ambient phytoplankton community in the Schelde Estuary, Belgium/Netherlands, which was usually dominated by diatoms. Conversely, in the Potomac River, VA, USA, Sellner et al. (1993) reported that before, during, and after a cyanobacteria bloom peak, rotifers consumed cyanobacteria at rates 5–10 times less than other phytoplankton taxa, with no detectable grazing impact on available cyanobacteria biomass.

Although the former studies are informative, the role of rotifer grazing in shaping cyanobacteria bloom dynamics remains unclear. We aimed to fill this knowledge gap by pairing a comprehensive assessment of the ambient rotifer assemblage with a set of experimental grazing studies using field-collected rotifers over the course of a cyanobacteria bloom in a well-studied, shallow, eutrophic lake (Vancouver Lake, WA, USA). We sought to answer three primary research questions:

(1) What are rotifers' preferred prey and at what rates do they consume various microplankton prey categories?
(2) What is the temporal variation in rotifer prey selection and consumption?
(3) How might rotifers' grazing dynamics affect the duration and magnitude of a cyanobacteria bloom?

By studying natural populations of rotifers from Vancouver Lake and experimentally measuring rotifer grazing behavior, this research provides new insight into rotifer seasonal abundance, prey preference, and grazing impact in the context of a cyanobacteria bloom and builds a more comprehensive basis for using Vancouver Lake as a model system for studying the influence of planktonic grazers on cyanobacteria bloom dynamics.

Materials and methods

We took a three-pronged methodological approach to address our research questions. First, we collected water samples to describe the rotifer assemblage and the microplankton community (i.e., cyanobacteria, autotrophic, and heterotrophic protists) before, during, and following a large cyanobacteria bloom in Vancouver Lake during summer 2019. Second, we conducted a series of monthly dilution experiments to measure microzooplankton community (i.e., rotifers and heterotrophic protists) grazing rates over the same time period, which provided context for our third approach, in which we conducted bottle incubation experiments to measure the prey preferences, feeding rates, and grazing impact of the rotifer assemblage.

Study site and sampling location

Vancouver Lake, located in southwestern Washington State (USA), is a shallow freshwater lake (depth ~ 1.2 m; surface area ~ 9.2 km^2) located in the floodplain of the lower Columbia River (Fig. 1). Cyanobacteria blooms were first recorded in Vancouver Lake in 1967 (Bhagat & Osborn, 1971) and since

Fig. 1 Vancouver Lake, Washington, USA and sampling location (●). Inset map shows location of study area within the northwest USA. Map created in ArcGIS® using publicly available data from Esri and U.S. agencies

then blooms composed of filamentous *Aphanizomenon* sp. and/or *Anabaena* sp. occur with increasing frequency (Boyer et al., 2011; Rollwagen-Bollens et al., 2013; Lee et al., 2015a, b, 2016). *Microcystis* sp. individuals and colonies have also been observed in Vancouver Lake, although their relative abundance has never been observed to be more than 1% of the overall cyanobacteria community. Blooms typically form in mid- to late July, last for 3–4 weeks and then rapidly decline in late August due to the combination of decreased nutrient availability and strong grazing pressure from the microzooplankton community (Rollwagen-Bollens et al., 2018). The lake is a popular site for outdoor recreation in the region throughout the year; however, intense annual cyanobacteria blooms (Boyer et al., 2011; Rollwagen-Bollens et al., 2013; Lee et al., 2015a, b) often result in poor water quality and closures of the lake to recreational use (Rollwagen-Bollens et al., 2018).

All sampling for water quality, chlorophyll (chl) *a* concentration, plankton abundance, and incubation experiments was conducted from a dock located on the eastern shore of Vancouver Lake (Fig. 1). Vancouver Lake is well mixed vertically and horizontally throughout the year, and this sampling site has been shown to be geographically representative

of Vancouver Lake as a whole, based on quarterly sampling of the lake over a full calendar year at eight locations widely distributed throughout the lake (Bollens & Rollwagen-Bollens, 2009).

Water quality and chl *a* concentration

From May to October 2019, we performed bi-weekly sampling of surface water to measure temperature, dissolved oxygen, and conductivity using a YSI 85 sonde, and deployed a Secchi disk. Additionally, we collected triplicate surface water samples using a clean, acid-washed bucket, from which we measured in situ phycocyanin concentration using a Turner Designs AquaFluor Model 8000-010 handheld fluorometer. We also removed sub-samples for later measurement of extracted chl *a* concentration. We filtered aliquots of 5–25 ml from each sub-sample through GF/F filters, froze them for at least 24 h (but not exceeding 7 days), and measured chl *a* concentration via the acidification method (Arar & Collins, 1997) using a Turner Model 10 AU fluorometer.

Ambient microplankton and rotifer abundance, biomass, and composition

We sampled the microplankton, here defined as unicellular protists and cyanobacteria < 200 µm in size, from Vancouver Lake in conjunction with four monthly feeding incubation experiments conducted between July and October 2019 (described below). Using a clean bucket, we collected triplicate surface samples from the lake and preserved 200-ml sub-samples in amber bottles containing 5% Lugol's iodine solution. We then settled 0.111 ml from each sample in a nanoplankton chamber (PhycoTech, Inc.) and examined at 200 × with a Leica DMI 4000B inverted microscope to enumerate and identify microplankton taxa. For each replicate, we counted and sized all cells in 30 randomly selected fields along transects and categorized them into the following taxonomic groups: diatoms, dinoflagellates, flagellates, ciliates, chlorophytes, or cyanobacteria. We calculated biovolume for each cell based on geometric shape (Hillebrand et al., 1999), which we used to estimate carbon biomass (Menden-Deuer & Lessard, 2000).

To characterize the ambient assemblage of rotifers, on each of the four experiment dates we collected triplicate 3-L samples of 300 µm-screened surface lake water using a clean bucket. Although rotifers are capable of maintaining vertical heterogeneity in the water column (Stewart & George, 1987; Ignoffo et al., 2005; Karabin & Ejsmont-Karabin, 2005), we considered surface sampling to represent their water column abundance due to the consistent vertical mixing in this shallow lake (Lee et al., 2015a). We reverse filtered each 3-L sample through a 20-µm sieve to a concentrated volume of ~ 200 ml. Following Thomas et al. (2017), we narcotized the concentrated water samples by adding an antacid tablet to prevent distortion of soft-bodied (illoricated) species and preserved the samples in 4% sucrose-buffered formalin for microscopical analysis. We added Rose Bengal stain to aid in distinguishing rotifers during microscopical examination.

To identify and enumerate the rotifers, we rinsed the stained formalin-preserved samples in deionized water, sub-sampled using a 1-ml Stempel pipette, placed the sub-samples into a welled slide, and examined them using an Olympus CK-40 inverted scope at 100–200x. We repeated this process until at least 300 individuals were counted. We identified rotifers to genus and species where possible, using Stemberger (1979), Wallace & Snell (2010), and Haney et al. (2013).

Microzooplankton community grazing experiments

We conducted five monthly dilution experiments (Landry & Hassett, 1982; Landry et al., 1995) from June to October 2019 to measure the grazing rates of the full microzooplankton community (e.g., heterotrophic protists and rotifers), as well as the growth rate of the ambient phytoplankton community before, during, and after the summer cyanobacteria bloom in Vancouver Lake.

We prepared particle-free lake water by collecting water from the lake surface using an acid-washed carboy and filtering through 75-µm, 35-µm, and 20-µm sieves in succession and then passed through 1.2-µm and 0.22-µm cellulose membrane filters using a peristaltic pump. We also collected unfiltered lake water in a separate acid-washed carboy immediately before incubation. Each experiment consisted of three dilution treatments prepared in triplicate, with each 500-ml polycarbonate bottle filled with a portion of unfiltered ambient lake water and a portion of filtered

lake water in the following ratios: 1:0, 0.5:0.5, and 0.1:0.9. We added 114 µl of 85 g mol^{-1} $NaNO_3$ and 210 µl of 225 g mol^{-1} $NaH_2PO_4 \cdot H_2O$ to each incubated bottle to ensure nutrient-replete conditions for optimal growth (Boyer et al., 2011). We immediately sub-sampled a set of three replicate initial control bottles of each of three dilution levels (n = 9) for later chl *a* analysis as described above and then incubated the three replicate treatment bottles of each of three dilution levels (n = 9) for 24 h on a rotating plankton wheel (0.5–1 rpm) at ambient temperature and diel light:dark cycle conditions. Subsamples of chl *a* from each treatment bottle were immediately collected at the end of incubation and then processed and analyzed as described above.

The change in chl *a* concentration over the course of the 24-h incubation, assuming exponential growth, was used to estimate net phytoplankton community growth rates in each dilution treatment. Linear regression of net growth rates relative to dilution level were then used to estimate intrinsic phytoplankton growth rates (indicated by the y-intercept in the regression equation) and microzooplankton community grazing rates (indicated as the regression slope * −1) according to Landry and Hassett (1982), Landry et al. (1995), and Boyer et al. (2011). We interpreted regression slopes that were significantly ($P < 0.05$) different from 0 to indicate a biological effect of grazers. Statistics were performed using R version 4.0.4 statistical software (R Core Team, 2021).

Rotifer assemblage grazing experiments

We conducted a set of four monthly incubation experiments with field-collected rotifers feeding upon the natural assemblage of microplankton prey July–October 2019, concurrent with the dilution experiments, to measure rotifer grazing dynamics during and after the cyanobacteria bloom. We employed an experimental approach modified from Rollwagen-Bollens et al. (2013) and Rose et al. (2017). On the day of each experiment, we gently collected 15 L of surface lake water with a clean bucket covered with 300-µm Nitex mesh and then concentrated the samples by reverse filtration through a 75-µm sieve. We hand-picked individual live rotifers from the concentrated sample and transferred them into 25-ml glass scintillation vials containing lake water pre-screened over a 75-µm sieve, to reach a density of 5 individual rotifers per ml. We chose this grazer density based on published filtering rates estimated from laboratory studies (i.e., Starkweather, 1980; Fulton & Paerl, 1987; Gulati et al., 1993) to result in ~ 30–60% reduction of prey abundance in each vial by the end of the incubation. We attempted to select rotifers for incubation in a manner representative of the ambient rotifer assemblage and without targeting a particular species due to (1) our interest in the potential trophic impacts of the entire rotifer assemblage, and (2) to minimize the time to select and sort these small and fragile live organisms.

For each experiment, we prepared a triplicate set of initial control vials containing only lake water with the natural assemblage of planktonic prey < 75 µm in size, which we immediately sub-sampled for chl *a* analysis and preserved the remainder in 4% Lugol's solution to be analyzed using the microscopical methods described above for microplankton. We filled a triplicate set of final controls (prey assemblage < 75 µm only) and a triplicate set of final treatments (prey assemblage < 75 µm plus rotifers) and incubated these at ambient lake temperature for 12 h overnight under ambient diel light:dark cycle conditions on a rotating plankton wheel (0.5–1 rpm). When incubation was complete, we passed the water from all final treatment vials over a 75-µm screen to remove the rotifers and then preserved in formalin as noted above and later examined microscopically. We sub-sampled and preserved the incubation water from both the final treatment and final control vials, as was done for the initial controls.

Rotifer feeding metrics

To determine whether a rotifer incubation experiment resulted in a feeding effect, we employed *t* tests assuming unequal variance to assess for significant ($P < 0.05$) differences in mean chl *a* concentration, microplankton abundance, and/or carbon biomass in the final treatments compared to the final controls. We interpreted a lack of significant change across all measurements in any experiment as evidence of no feeding effect of added rotifers and thus did not include results of that experiment in further analyses.

For all experiments where a significant feeding effect was observed, we calculated rotifer clearance rate (CR; ml $rotifer^{-1}$ h^{-1}) and ingestion rate (IR; µg C $rotifer^{-1}$ h^{-1}) for each prey type in each experiment

according to Marin et al. (1986). We then assessed whether rotifers demonstrated selective feeding behavior in each experiment using two approaches. First, we used 1-way ANOVA and post hoc Tukey's test to assess the differences in CR among prey types. Conformance to assumptions of normality and homoscedasticity were verified using Shapiro–Wilk and Bartlett's test, respectively. For those experiments in which data did not meet these assumptions, we used a Kruskal–Wallis rank sum test (for which assumptions of homoscedasticity were met based on a Fligner–Killeen test) and a post hoc Dunn's multiple comparisons test. Statistics were performed using R version 4.0.4 statistical software (R Core Team, 2021). We interpreted a significant ($P < 0.05$) difference among CR between prey categories as evidence of selective feeding effort by rotifers, with greater effort expended upon those prey types with the highest CR values.

As a second method, we calculated electivity indices (E*) (Vanderploeg & Scavia, 1979a, 1979b), which compare the proportion of a particular prey type available in Vancouver Lake to the proportion of that prey consumed by the rotifers. See Rollwagen-Bollens et al. (2013) for a detailed description of this approach. E* values range from − 1 to + 1, where + 1 indicates complete preference, 0 indicates neutral preference, and − 1 represents complete avoidance. We interpreted E* values significantly ($P < 0.05$) different from 0 (based on 2-tailed *t* tests) to be evidence of selection for (positive values) or avoidance of (negative values) particular prey taxa.

Grazing impact

Finally, we estimated the overall grazing impact of microzooplankton in Vancouver Lake for the entire community, as well as the rotifer assemblage separately. Overall microzooplankton community grazing impact upon phytoplankton (% d^{-1}) was calculated as the ratio of daily grazing rate to phytoplankton growth rate obtained from each dilution experiment, multiplied by 100. The grazing impact (% prey consumed d^{-1}) of the rotifer assemblage upon the < 75-µm microplankton community was calculated from the incubation experiment results by multiplying the observed per capita rotifer IR in each experiment by the standing stock of rotifers in Vancouver Lake present on the experiment day, dividing by the biomass of < 75-µm microplankton prey in the lake, and multiplying by 100.

Results

Water quality

Surface water temperatures in Vancouver Lake from May to August 2019 were generally stable near 20°C and then decreased steadily through September and October to 13°C (Fig. 2). Dissolved oxygen concentrations at the lake surface remained ~ 8–10 mg l^{-1} in May and early June, after which concentrations fluctuated from 4.6 to 13.2 mg l^{-1} from July to October (Fig. 2). Secchi depth was deepest (~ 1–2 m) in May but shallowed in early June to ~ 0.3 m and remained at this level throughout the summer and early autumn (Fig. 2).

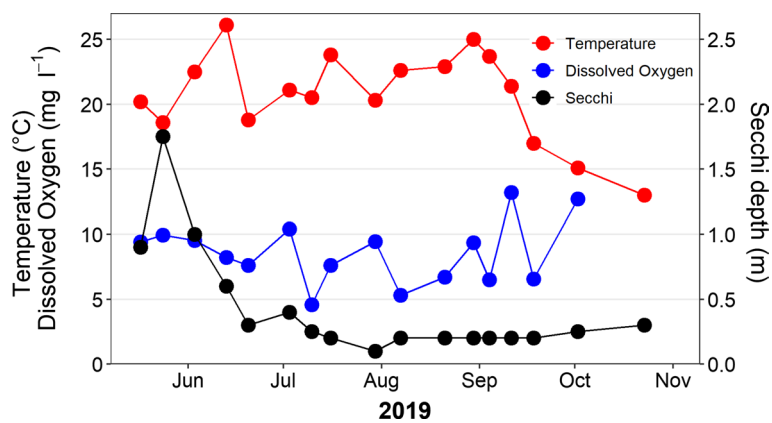

Fig. 2 Surface water temperatures, dissolved oxygen concentrations, and Secchi depths measured in Vancouver Lake, WA, from May to October 2019

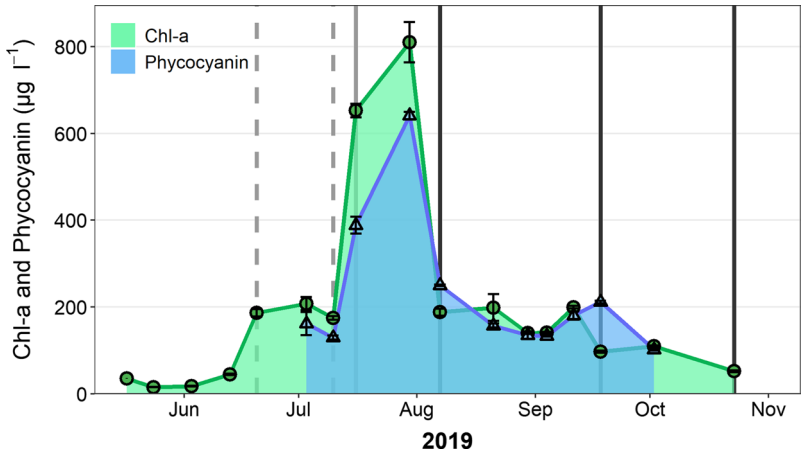

Fig. 3 Mean chl *a* (green circular symbols and shading) and phycocyanin (blue triangular symbols and shading) concentrations measured in Vancouver Lake from May to October 2019. Error bars represent one standard error. Vertical dashed lines represent dates when microzooplankton community grazing (dilution) experiments were performed. Solid gray lines represent dates when rotifer grazing experiments were performed. Solid black lines represent dates when both rotifer and dilution experiments were performed

Chl *a* concentrations in Vancouver Lake measured between May and October 2019 showed that phytoplankton biomass was lowest in late spring (~ 14–48 µg chl l^{-1}) and autumn (~ 50 µg chl l^{-1}), with a substantial bloom that extended for several weeks in July, ranging in magnitude from 200 to 900 µg chl l^{-1} (Fig. 3). The high levels of phycocyanin pigment present during the July bloom period (~ 400–650 µg l^{-1}) indicate that this bloom was dominated by cyanobacteria biomass (Fig. 3).

Ambient microplankton abundance, biomass, and composition

Abundance and biomass of the microplankton community in Vancouver Lake were highest in August, just after the peak of the cyanobacteria bloom and lowest in July and October (Fig. 4). Throughout the June to October sampling period, cyanobacteria taxa, notably *Anabaena* spp. and/or *Aphanizomenon* sp., represented > 87% of the microplankton community abundance and biomass, with maxima of 7.6×10^6 cells ml^{-1} and 40.6 µg C ml^{-1}, respectively, in August (Fig. 4). The next most abundant microplankton taxa averaged across all months were

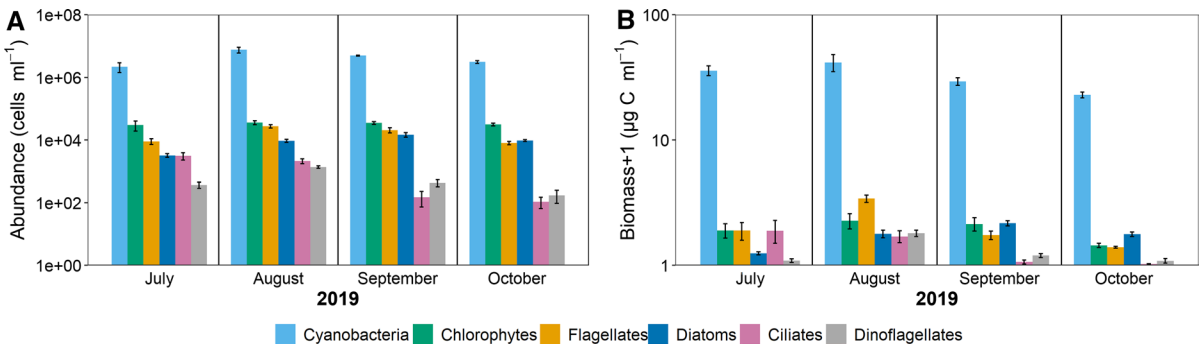

Fig. 4 Mean abundance (**A**) and carbon biomass (**B**) of major taxonomic categories of the microplankton community in Vancouver Lake at the time of each monthly feeding experiment from July to October 2019. Error bars represent one standard error

chlorophytes (~0.9% of the total assemblage), followed by flagellates (~0.4%), diatoms (~0.2%), ciliates (~0.04%), and dinoflagellates (~0.01%). In terms of relative biomass, the sub-dominant taxa were flagellates (~2.9%), followed by chlorophytes (~2.6%), diatoms (2.3%), ciliates (~1.0%), and dinoflagellates (~0.7%) (Fig. 4).

Ambient rotifer abundance and composition

Rotifer abundance in Vancouver Lake varied over the course of the bloom cycle, with a minimum of 0.17 rotifers ml^{-1} (±0.06 SE) coinciding with the cyanobacteria bloom in July and the highest abundance (6.0 rotifers ml^{-1} ± 0.25 SE) in September (Fig. 5). At the height of the cyanobacteria bloom, the rotifer assemblage was dominated by *Brachionus* spp. (46%) and *Polyarthra* spp. (25.7%), but shifted to dominance by *Keratella* spp. (43.7%) and *Pompholyx sulcata* (Hudson, 1885) (37%) in August. During September and October, the assemblage was dominated by *Keratella* spp. (72% and 57.4%, respectively) followed by *Polyarthra* spp. (18.5% and 41.2%, respectively). *Asplanchna* spp. and *Synchaeta* spp. were the least abundant rotifer genera observed in Vancouver Lake throughout the sampling season (Fig. 5).

Microzooplankton community feeding rates

Microzooplankton community grazing (dilution) experiments were conducted in June, July, August, September, and October 2019; however, only the experiments conducted in June, August, and October resulted in regression slopes significantly ($P < 0.05$) different from zero (Supplementary Fig. 1). Therefore, only the results of these three experiments are discussed further. Intrinsic phytoplankton growth rates were highest in June (0.73 d^{-1}), lowest in August just after the peak of the cyanobacteria bloom (0.13 d^{-1}), and moderately high in October (0.42 d^{-1}) (Fig. 6). By contrast, microzooplankton community grazing rates were lower than estimated phytoplankton growth rates before the cyanobacteria bloom (in June), extremely high in August (1.39 d^{-1}) just after the bloom peak, and equal to estimated growth rates after the bloom in October (Fig. 6).

Rotifer prey selectivity

We conducted four feeding incubation experiments with field-collected rotifers and the natural assemblage of plankton < 75 µm from Vancouver Lake, concurrent with microzooplankton community

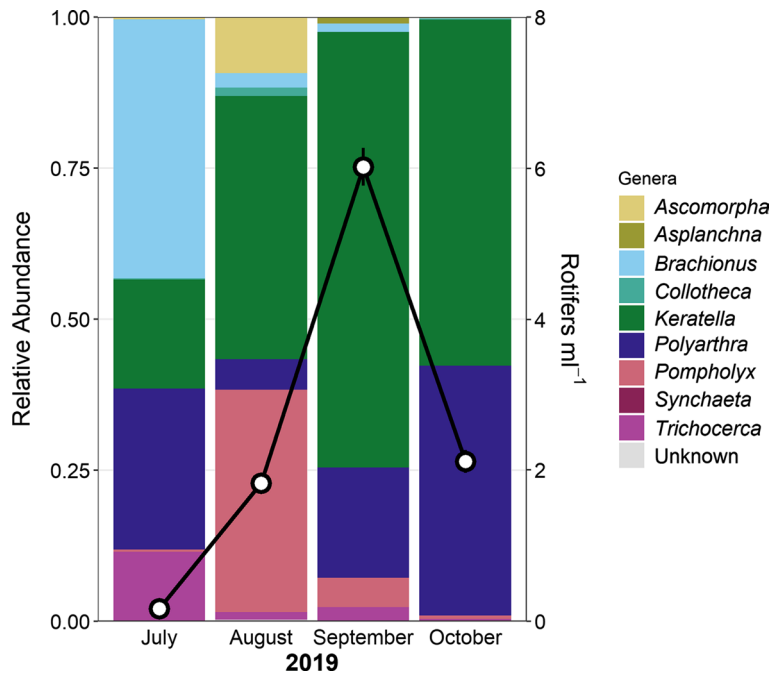

Fig. 5 Mean rotifer abundance (open circles) and relative abundance of rotifer genera (stacked bars) present in Vancouver Lake at the time of each monthly feeding experiment conducted from July to October 2019. Error bars represent one standard error

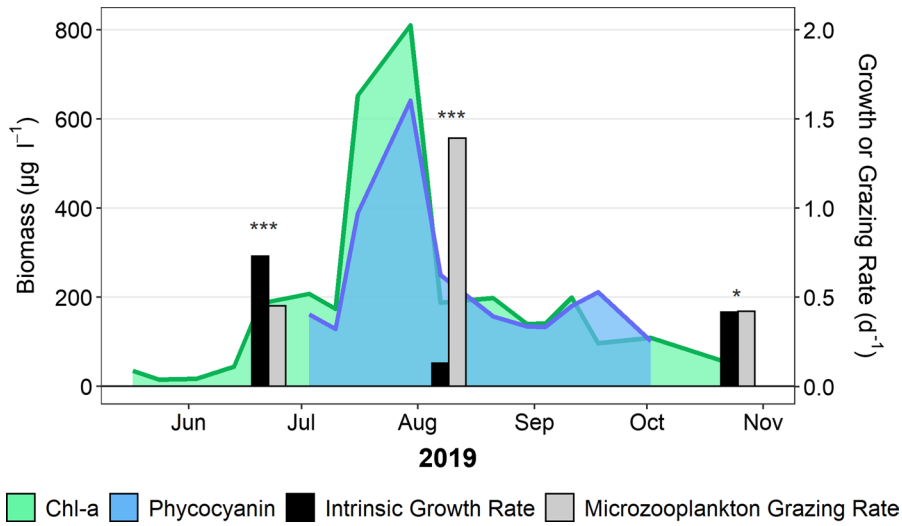

Fig. 6 Chl *a* concentrations (green shading), phycocyanin concentrations (blue shading), intrinsic phytoplankton growth rates (black columns), and microzooplankton community grazing rates (gray columns) measured in Vancouver Lake from June to October 2019. Microzooplankton community grazing experiments in which regression slopes were significantly different from zero are represented with asterisks (*$P<0.05$, **$P<0.01$, ***$P<0.001$)

grazing (dilution) experiments in July, August, September, and October 2019. We observed a significant ($P<0.05$) reduction in either the microplankton prey abundance, carbon biomass, or chl *a* concentration after the 12-h incubation in each experiment except July and therefore were able to calculate and report rotifer assemblage feeding rates from the August, September, and October experiments.

The abundance and biomass of < 75-µm microplankton prey at the start of each experiment was highest in July during the cyanobacteria bloom but fell dramatically in August just after the bloom peak, with continued decline through October (Fig. 7). In each month, the microplankton community was overwhelmingly dominated by cyanobacteria in terms of both abundance and biomass, with the remainder of the prey taxa each accounting for < 1.5% of the total abundance and < 9% of the total biomass (Fig. 7).

We estimated rotifer feeding selectivity in two ways. First, we compared the clearance rates of rotifers on each major taxonomic category of < 75-µm microplankton available during each experiment. Clearance rates will be negative if the grazing coefficient (g, h^{-1}) measured in an incubation experiment is negative, which occurs whenever the growth rate of a prey taxon in the grazer treatments is higher than the growth rate of that prey taxon in the non-grazer-amended controls over the incubation period. A negative clearance rate can therefore be interpreted as avoidance of that prey taxon by the grazer and/or the

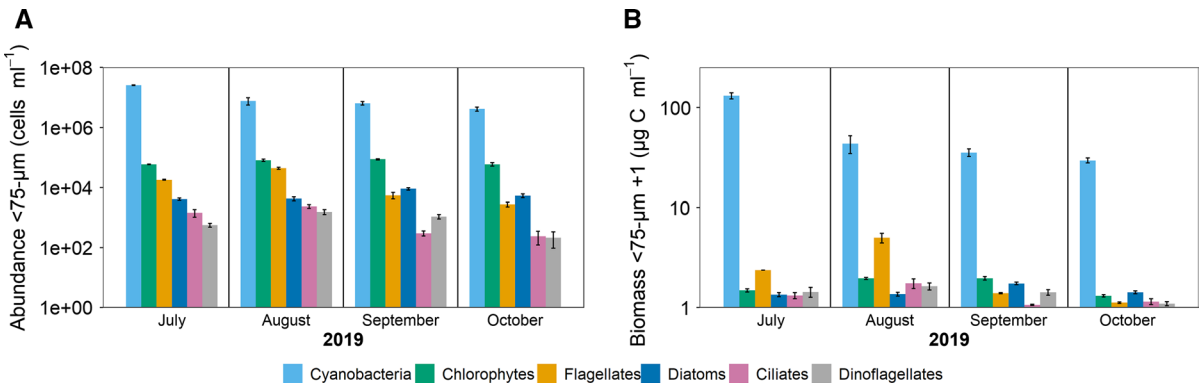

Fig. 7 Mean abundance (**A**) and biomass (**B**) of microplankton prey taxa < 75 µm in size that were initially present in each rotifer feeding experiment. Error bars represent one standard error

cascading effect of the added grazers consuming a different taxon which releases the target prey from grazing pressure in the treatment bottles. In the August experiment, immediately after the peak in cyanobacteria abundance, we observed significant differences among clearance rates (ANOVA: F-value = 2.9, $P = 0.063$), and a Tukey's multiple comparison test indicated that rotifers cleared dinoflagellates at a significantly higher rate than cyanobacteria ($P < 0.05$) (Fig. 8). However, during the September experiment, no significant differences in clearance rates were observed among the prey groups (Fig. 8). In October, clearance rates differed significantly among prey categories (ANOVA: F-value = 4.4, $P < 0.05$) and once again a Tukey's test showed that clearance rates were highest on dinoflagellates; although in this case, these rates were significantly higher than those for chlorophytes and ciliates ($P < 0.05$) (Fig. 8).

Second, we calculated E* values for rotifers feeding upon each category of microplankton prey < 75 µm in size. In August, rotifers exhibited a significant avoidance of cyanobacteria ($t << -0.001$, $P << 0.001$) (Fig. 9). Rotifers continued to strongly avoid cyanobacteria in September ($t << -1$, $P < 0.0001$) but also strongly avoided ciliates ($t << -1$, $P = 0.001$) and chlorophytes ($t << -1$, $P < 0.0001$). Conversely, in October, rotifers showed a significant selection for cyanobacteria ($t >> 1$, $P < 0.0001$) (Fig. 9). Although the mean rotifer E* value for dinoflagellates was higher than that for cyanobacteria in October, t tests showed these values were not significantly different from 0 ($t = 3.8$, $P = 0.06$) (Fig. 9).

Rotifer ingestion rates

Biomass ingestion rates of the rotifer assemblage on < 75-µm prey were the lowest immediately

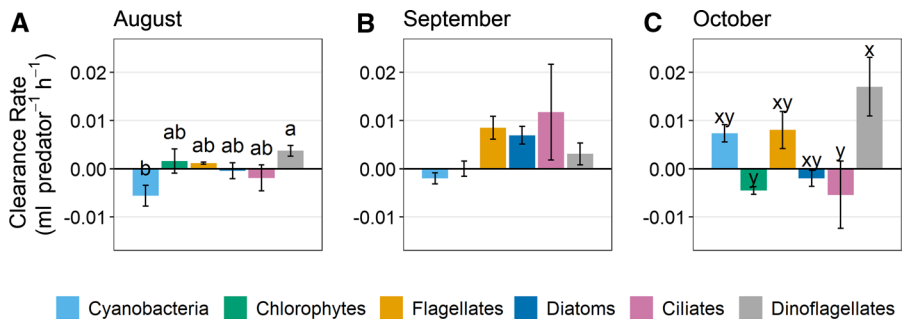

Fig. 8 Mean clearance rates of rotifers incubated for 12 h with microplankton taxa < 75 µm in size in monthly experiments August–October 2019. Error bars represent one standard error. Clearance rates with different letter designations are significantly different from each other (Tukey's test, $P < 0.05$)

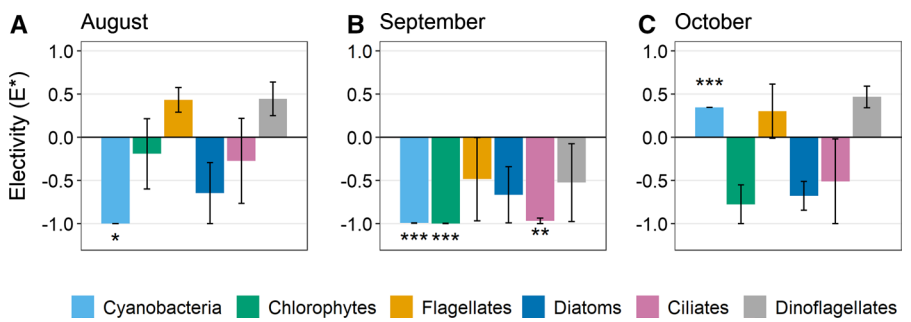

Fig. 9 Mean electivity (E*) of rotifers incubated for 12 h with microplankton taxa < 75 µm in size in monthly experiments August–October 2019. Error bars represent one standard error. E* values significantly different from zero are represented with asterisks (*$P < 0.05$, **$P < 0.01$, ***$P < 0.001$)

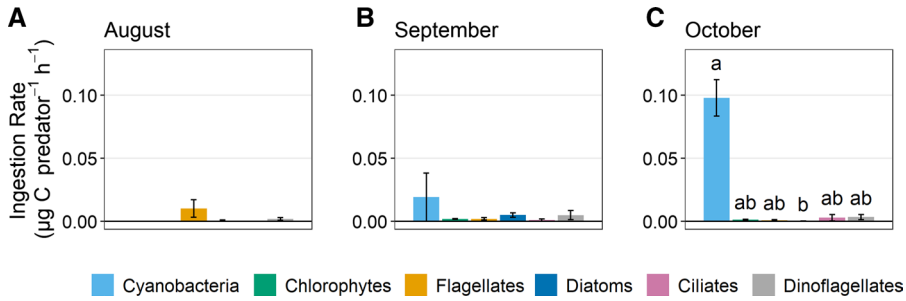

Fig. 10 Mean biomass ingestion rates of rotifers incubated for 12 h with microplankton < 75 µm in size in monthly experiments August–October 2019. Error bars represent one standard error. Ingestion rates with different letter designations are significantly different from each other (Dunn's test, $P < 0.05$)

following the peak in cyanobacteria biomass in August (< 0.01 µg C rotifer^{-1} h^{-1}) with a modest increase in September (0.03 µg C rotifer^{-1} h^{-1}) and were highest in October (0.1 µg C rotifer^{-1} h^{-1}) (Fig. 10). We found no significant differences in ingestion rates among prey groups during the August and September rotifer feeding experiments, when ingestion rates were relatively low overall. In October, however, we found that rotifers ingested cyanobacteria at a significantly higher rate (0.098 µg C rotifer^{-1} h^{-1}) than other prey items, particularly diatoms (Dunn's Test: $z = 3.02$, $P < 0.05$) (Fig. 10).

Rotifer grazing impact

Rotifer assemblage grazing impact in Vancouver Lake, measured as the percent of prey biomass available that was consumed by rotifers per experiment day, indicated that rotifers could have been removing a substantial proportion of the ambient microplankton biomass (< 75 µm), especially in September and October (Fig. 11). In August, just after the 2019 bloom peak, rotifer grazing impact upon the entire (< 75-µm) microplankton prey community was extremely low (< 1% d^{-1}), but when measured on particular prey categories the grazing impact ranged from undetectable (for cyanobacteria and chlorophytes) up to 20% (for flagellates) of available biomass per day (Fig. 11). In September, rotifer grazing impact increased, estimated as 13.3% of the total available microplankton biomass (< 75 µm) per day, with 513% of dinoflagellate biomass and 154% of ciliate biomass consumed daily (Fig. 11). In October, rotifer grazing impact further increased to 21.9% of the total available microplankton biomass (< 75 µm). Rotifer grazing in October was particularly impactful upon dinoflagellates (574% biomass consumed d^{-1}) and ciliates (382% biomass consumed d^{-1}) and with rotifer impact on ciliates significantly higher than on diatoms (Dunn's Test: $z = 2.95$, $P < 0.05$) (Fig. 12).

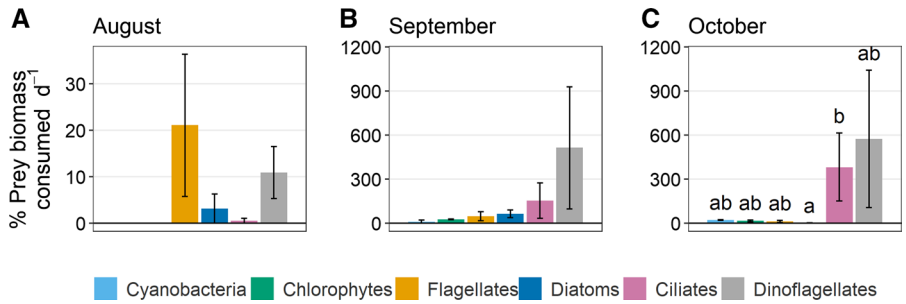

Fig. 11 Mean daily grazing impact of rotifers upon microplankton < 75 µm in Vancouver Lake during August, September, and October 2019. Note y-axis scales differ. Error bars represent one standard error. Grazing impact values with different letter designations are significantly different from each other (Dunn's test, $P < 0.05$)

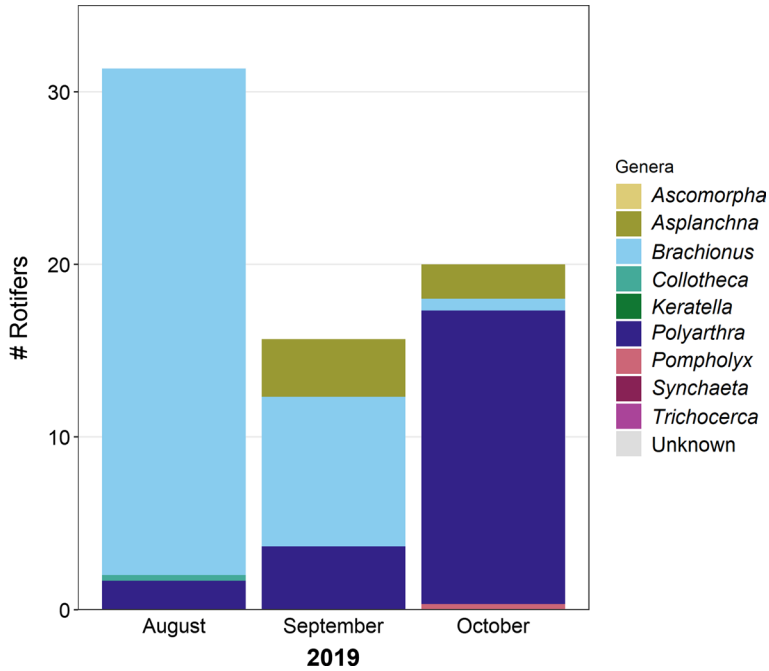

Fig. 12 Mean number and taxonomic composition of rotifers recovered at the end of each monthly feeding experiment conducted August–October 2019. Note: 125 individuals were added to each treatment bottle at the start of each incubation experiment

Discussion

Our results demonstrate that grazing by non-rotifer microzooplankton strongly and directly influences the initial decline of the cyanobacteria bloom and that rotifers play an important role in modulating the abundance and composition of the microzooplankton community in the weeks following the bloom. This study was the first to conduct concurrent and complementary, feeding experiments to assess the influence of the microzooplankton community as a whole, as well as the specific impact of the natural rotifer assemblage, on the dynamics of a large cyanobacteria bloom in a shallow, temperate lake.

Micro-grazer community structure in Vancouver Lake

Our results align closely with previous studies that showed the microzooplankton (< 200 µm) community in Vancouver Lake to be composed of mixotrophic and heterotrophic taxa assemblages, including high abundances of flagellates, dinoflagellates (i.e., *Ceratium* sp., and assorted athecate taxa), and ciliates (i.e., *Strombidium* spp. and assorted oligotrichs) (Boyer et al., 2011; Rose et al., 2017), as well as less abundant rotifers, copepod nauplii, copepodites, and small bosminids (Boyer et al., 2011; Lee et al., 2015a). More specifically, Boyer et al. (2011) reported low mean ciliate abundance in early summer and very high ciliate abundance (~2,800 cells ml^{-1}) just prior to the bloom peak in 2008, aligning with ciliate abundances we observed before the bloom peak in 2019 (~2,900 cells ml^{-1}). Ciliate abundance was also high during the 2019 bloom (~3,100 cells ml^{-1}) and dropped to very low levels in the fall (< 200 cells ml^{-1}).

With respect to rotifer abundance and composition, our finding that the assemblage in Vancouver Lake during 2019 was dominated by brachionid rotifers (i.e., *Brachionus angularis* and *Keratella cochlearis* (Gosse, 1851)), and to a lesser degree *Polyarthra* sp., also aligned closely with reports from other temperate lakes. For instance, high rotifer abundance was observed in the eutrophic lower basin of Lake Biwa (Japan), of which ~ 50% were *Keratella tecta* (Gosse, 1851), while the oligotrophic upper basin featured low rotifer abundance and only ~ 1% were *K. tecta* (Hillbricht-Ilkowska, 1983). Similarly, in eutrophic Lake Chaohu (China), > 80% of the zooplankton assemblage was composed of *Keratella* spp. and *Brachionus* spp. (Li et al., 2017); and in Lake Oglethorpe (Georgia, USA), rotifers accounted for > 69% of zooplankton biomass in the summer, with two brachionid

groups (*Keratella* spp., *Kellicottia* sp.), *Polyarthra* sp., and *Trichocerca* sp. as the most abundant genera (Orcutt & Pace, 1984).

Further, our examination of the rotifer assemblage in Vancouver Lake supports other studies showing that lakes, such as Lake Caldonazzo (Italy), Lago Maggiore (Italy), and Lake Washington (WA, USA), are often dominated by a single rotifer functional group at a time (Obertegger et al., 2011; Obertegger & Manca, 2011; Obertegger & Flaim, 2015, 2018). The rotifer assemblage in Vancouver Lake was dominated by microphagous feeders such as *Brachionus* spp., *Keratella* spp., and *Pompholyx sulcata* (~55–80% of total rotifer individuals) rather than raptorial feeders, such as *Polyarthra* spp. and *Trichocerca* spp., particularly in August and September 2019. The majority of rotifer taxa observed in our study were also small bodied, which are predictably the dominant grazers in systems of poor food quality/quantity (Stemberger & Gilbert, 1985) (i.e., cyanobacteria blooms), low food concentrations (Bogdan & Gilbert, 1982; Stemberger and Gilbert, 1987), and small prey sizes (Gilbert & Bogdan, 1984) because small grazers are more efficient food collectors than larger zooplankton and have a lower threshold for a minimum food concentration supporting population growth (Stemberger & Gilbert, 1985).

Microzooplankton community grazing over a bloom cycle

The pattern of grazing rates upon phytoplankton biomass by the entire microzooplankton community during 2019 closely matched the microzooplankton community grazing rates measured in Vancouver Lake during the summer bloom cycles of 2008 and 2009 (Boyer et al., 2011; Rollwagen-Bollens et al., 2018). Grazing rates were lowest during the pre-bloom and post-bloom periods (i.e., June and October 2019, respectively) and exceptionally high immediately following the bloom peak (i.e., August 2019). In each of the three years studied, community grazing rates were substantially higher than phytoplankton growth rates just after the bloom peak and remained high late into the autumn well after the blooms dissipated, particularly upon cyanobacteria (as indicated by microscopical analysis in 2008 by Boyer et al., 1971). These interannual patterns indicate that rotifers, ciliates, heterotrophic dinoflagellates, and other micro-grazers were together removing more phytoplankton biomass than was being created after the peak of each bloom and thus were largely responsible for the blooms' dissipation.

Rotifer grazing behavior in Vancouver Lake

Based on the historical record of cyanobacteria bloom timing in Vancouver Lake, we scheduled our rotifer grazing experiments to occur in early July to coincide with the formation of the expected bloom, in August during the bloom peak, and in September and October when we expected the bloom to be in decline and eventually dissipated (respectively). However, while the magnitude and duration of the 2019 cyanobacteria bloom was typical for Vancouver Lake, the bloom developed in late June and reached maximal levels in early July, several weeks earlier than had been previously observed (Bhagat & Orsborn, 1971; Boyer et al., 2011; Lee et al., 2016; Rollwagen-Bollens et al., 2018). This earlier timing was unexpected and thus prevented us from performing rotifer grazing experiments in the pre-bloom period. However, results of our August, September, and October experiments allow us to assess the role of rotifer grazing in the rapid decline and eventual dissipation of the cyanobacteria bloom in Vancouver Lake in 2019.

Our clearance rate and electivity results demonstrated that rotifers were often, but not always, selective feeders with a preference for dinoflagellates and usually avoided cyanobacteria. A notable exception, however, was in October when cyanobacteria were preferred in addition to small (> 75 µm) dinoflagellates and flagellates—taxonomic groups that potentially included heterotrophic micro-grazers in addition to autotrophic cells. However, measurements of actual rotifer consumption show that just after the bloom peak in August 2019, rotifer biomass ingestion rates were at their lowest overall, but were highest on flagellates, and to a lesser extent on their preferred dinoflagellate prey. Notably, rotifers did not measurably consume cyanobacteria biomass in August. However, in September and October rotifer ingestion rates increased and were significantly higher for cyanobacteria biomass over all other prey types. These higher ingestion rates aligned with rotifers' preference for

cyanobacteria in October, as well as the high relative abundance of cyanobacteria cells in the autumn and together could be viewed as evidence that cyanobacteria may have been more easily consumed by rotifers compared to August. The susceptibility of cyanobacteria to rotifer consumption may be pronounced at the end of the bloom period due to a variety of factors, including filament fragmentation due to former grazing by other grazers, nutrient deficiency, or parasitism (see Gerphagnon et al., 2013), reductions in ambient cyanotoxin concentrations potentially inhibitory to grazing by micro-grazers, or changes to the composition of the cyanobacteria assemblage to species more susceptible to grazing.

To our knowledge no other published studies report feeding rates of field-collected rotifers on natural assemblages of prey during a cyanobacteria bloom in a lake system. However, two such studies have been conducted in estuaries. Sellner et al. (1993) found rotifers in the Potomac River estuary, VA, USA, to consume very little, if any, cyanobacteria throughout the bloom cycle, 1.65 µl rotifer^{-1} h^{-1}, which is less than the maximum clearance rate we report for cyanobacteria in Vancouver Lake (~10 µl rotifer^{-1} h^{-1}). Importantly, Sellner et al. (1993) also found the assemblage of rotifers had greater clearance rates (~0.098–5.38 µl rotifer^{-1} h^{-1}) and grazing impact (< 0.17% d^{-1}) on the non-cyanobacteria assemblage than on the cyanobacteria assemblage (0.004–1.65 µl rotifer^{-1} h^{-1} and < 0.034%, respectively) at each measured stage of the cyanobacteria bloom. This finding is consistent with our study in that rotifers had a negligible effect on the cyanobacteria assemblages regardless of bloom stage and that rotifers largely prefer non-cyanobacteria prey. In the second field study, conducted in the Schelde Estuary in western Europe, Lionard et al. (2005) estimated clearance rates (0.008–0.763 ml rotifer^{-1} h^{-1}) of the natural rotifer assemblage on a phytoplankton community dominated by diatoms (< 10% cyanobacteria) that were within the range of our own measurements (−0.01–0.03 ml rotifer $^{-1}$ h^{-1}).

Our observations also align with a laboratory study by Soares et al. (2010) who found ingestion by cultured *Brachionus calyciflorus* rotifers of cyanobacteria isolated and cultured from the Funil Reservoir, Brazil, to increase as cyanobacteria concentrations increased, although the maximum rotifer ingestion rates for cyanobacteria reported in our study (< 0.1 µg C rotifer^{-1} h^{-1} for the whole cyanobacteria assemblage) are less than the maxima reported by these investigators (0.2 and 0.5 µg C rotifer^{-1} h^{-1} for *Microcystis* and *Cylindrospermopsis*, respectively). Although cultured *B. calyciflorus* have been reported to consume *Microcystis* sp. (Fulton & Paerl, 1987, 1988; Soares et al., 2010), low consumption rates are typical as *Microcystis* sp. cannot sustain rotifer population growth as a sole food source (Fulton & Paerl, 1987). On the other hand, Burian et al. (2014) showed that *Brachionus* spp. consumed filamentous cyanobacteria genera (*Arthrospira* and *Anabaenopsis*) in Lake Nakuru, Kenya and cultured *Keratella cochlearis* were found to consume cultured *Anabaena affinis* (Lemmerman, 1898) (Kirk & Gilbert, 1992). In this case, *Keratella* consumed *Anabaena* at an ingestion rate of 5–9 cells rotifer^{-1} h^{-1} (Kirk & Gilbert, 1992), which were within but on the low end of the range we observed in Vancouver Lake.

Although rotifers in Vancouver Lake consumed cyanobacteria biomass more than any other taxonomic group during the autumn of 2019 (up to 0.098 µg C rotifer^{-1} h^{-1}), they also ingested small amounts of ciliate, dinoflagellate, and diatom biomass (0.05–5 ng C rotifer^{-1} h^{-1}) and cleared up to 20 µl of water per rotifer h^{-1} to do so. The clearance rates we measured for rotifers grazing on these prey are within range of those found in other studies. For example, clearance rates of *Keratella* spp. in an in situ mesocosm study in Star Lake, VT, USA, on various prey ranged from 0 to 9.8 µl rotifer^{-1} h^{-1}, with the highest clearance rates on flagellates (Gilbert & Bogdan, 1984). Similarly, *Polyarthra* spp. have been shown to prefer flagellates, particularly cryptomonads and *Euglena* at clearance rates from 0.2 to 4.3 µl rotifer^{-1} h^{-1} (Pourriot, 1977; Bogdan & Gilbert, 1982, 1984), which are rates in range with those we found for rotifers grazing on flagellates in Vancouver Lake (1–8 µl rotifer^{-1} h^{-1}).

Grazing impact of rotifers and the entire microzooplankton community over a bloom cycle

In our assessment of the overall grazing impact of rotifers in Vancouver Lake, we found that even though hourly rotifer per capita ingestion rates were the highest for cyanobacteria compared to other prey, cyanobacteria biomass in the lake at the time of these experiments was sufficiently high enough that rotifer

grazing impact was lowest for cyanobacteria (0–23% d^{-1}) (except in October when grazing impact upon diatoms was <1% d^{-1}). This finding indicates that the rate of consumption of cyanobacteria by rotifers was not high enough to directly influence the bloom. Furthermore, impact of rotifer grazing on the total microplankton prey assemblage was lowest (0%) in August yet increased as the bloom dissipated (up to ~ 22% in October). These daily grazing impacts on the prey community are less than those estimated by Lionard et al. (2005), who found the natural rotifer assemblage's grazing impact on the total phytoplankton community in the Schelde Estuary to range 33–84% d^{-1}.

However, the grazing impact of rotifers on small ciliates and dinoflagellates was extremely high (~ 150–575% d^{-1}) during September and October. Grazing impacts of > 100% are possible when the experimentally derived per capita ingestion rates of rotifers are sufficiently high that when applied to the ambient abundance of rotifers in the lake on the experiment date, the ratio of overall grazing rate to prey availability becomes greater than 1. This suggests that rotifer grazing in the lake during autumn was likely resulting in negative ciliate and dinoflagellate growth rates, thus controlling the populations of these two prey groups as the cyanobacteria bloom waned.

It is important to note that our measurements of rotifer grazing rates and grazing impacts were based on the number and composition of the rotifers added to each experimental treatment bottle, which upon examination of the preserved samples after incubation were found to differ from the natural rotifer assemblage in Vancouver Lake (Fig. 12). In all three experiments where a detectable grazing effect was observed, we recovered only 11–40 individuals (of the 125 added) from each bottle after each incubation. In terms of taxonomic composition, in August and September, *Brachionus* spp. comprised the majority of recovered rotifers (92% and 54% respectively), but the ambient rotifer assemblage in the lake at the time of those experiments was dominated by *Keratella* spp. and to a lesser extent *Polyarthra* spp. and *Pompholyx* sp. In October, the recovered assemblage was dominated by *Polyarthra* spp. (83%), yet the ambient assemblage was approximately evenly composed of both *Polyarthra* and *Keratella* species.

We speculate that the low numbers and altered assemblage composition of the remaining rotifers in the September and October incubation bottles are likely due to the presence of *Asplanchna* spp., a rotiferan genus well known to prey upon other rotifers, dinoflagellates, and ciliates (Pourriot, 1977; Chang et al., 2010). The abundances of these rotiferan predators were 0.13 and 0.08 *Asplanchna* ml^{-1} at the end of the September and October experiments, respectively—abundances comparable to what we directly observed in Vancouver Lake in those months (0.62 and 0.003 *Asplanchna* ml^{-1}, respectively). As the most abundant rotifer genus in Vancouver Lake from August to October, we believe that *Keratella* individuals were likely the majority of rotifers added to the treatment bottles; however, since *Keratella* spp. are often highly preferred by *Asplanchna*, it is also likely that individual *Asplanchna* rotifers efficiently removed all *Keratella* individuals within each experimental treatment bottle. Indeed, *Asplanchna* clearance rates have been estimated to be up to ~ 0.5 ml $rotifer^{-1}$ h^{-1} (Conde-Porcuna & Sarma, 1995), which in our experiments would account for ~ 24% of the incubated volume over the entire incubation period, per predator. Thus, only ~ 4 *Asplanchna* individuals would have been required to clear ~ 100% of the volume in each treatment bottle over the 12-h incubations. This is further supported by our microscopical observation of *Keratella* spp. individuals within the stomachs of most of the recovered *Asplanchna* spp. individuals, in addition to *Brachionus* spp. and loricate ciliates. Thus, we also postulate that the very strong grazing impact on dinoflagellates and ciliates in the post-bloom period may have been largely due to predatory *Asplanchna* spp. individuals. Notably, *Polyarthra* sp. individuals were largely still present at the end of incubations, likely due to their ability to effectively evade *Asplanchna* predation (Gilbert, 1985). Why we observed a change in the number and diversity of rotifers remaining in the treatment bottles during the August experiment, despite a lack of *Asplanchna*, has no obvious explanation and remains an open question.

When we considered rotifer grazing in the context of the entire microzooplankton community over three cyanobacteria bloom cycles (2008, 2009, and 2019), we found that just after the peak of the bloom, when total microzooplankton community grazing impact was typically extremely high (> 1000% d^{-1}) rotifer

grazing impact on the total microplankton community < 75 µm was negligible (< 1% d^{-1}); although in October, the grazing impacts of these two groups were much more similar (100% and 22%, respectively). Note that direct comparisons between these grazing impacts may be misleading, as impact by the whole microzooplankton community was upon chl *a* biomass, while the rotifer assemblage grazing impact was calculated using the carbon biomass of each microplankton prey assemblage in the incubation bottles (i.e., autotrophic phytoplankton and heterotrophic protists). Nevertheless, our results further substantiate other assertions that grazing by microzooplankton communities generally, and rotifers specifically, can have a substantial impact on phytoplankton community biomass and composition (i.e., Bogdan & Gilbert, 1982; Lair & Oulad Ali, 1990; Quiblier-Lloberas et al., 1996; Agasild et al., 2007; Burian et al., 2014).

Implications for Vancouver Lake cyanobacteria blooms and the planktonic food web

We found that overall microzooplankton community grazing impact was low in the spring, well before the cyanobacteria bloom, which suggests rotifer grazing on the phytoplankton community was also minimal in this period, although this should be tested in future studies. Further, during the peak of the cyanobacteria bloom in July, the microzooplankton community grazing impact remained low, and we also did not find a significant grazing effect by rotifers. However, immediately after the bloom peak in August, the grazing impact by the entire microzooplankton community was exceptionally high, while rotifers' contribution to this overall grazing impact was low, suggesting that grazing impact was mostly due to non-rotifer micro-grazers. Indeed, because ciliates were in very high abundance immediately following the blooms in 2008, 2009, and 2019 and *Asplanchna* rotifer abundance was extremely low during August 2019, we assert that these micro-grazers are likely the most significant contributor to the decline of cyanobacteria biomass in Vancouver Lake.

In contrast, in the weeks following the initial decline of the cyanobacteria bloom, predation by *Asplanchna* sp. (and possibly other large rotifers) upon ciliates, small rotifers, and other heterotrophic microplankton was occurring and may help to explain the low microzooplankton community grazing rates we measured during this period. Specifically, in September 2019, the abundance of *Asplanchna* was at its highest in Vancouver Lake and may have reduced the abundance of ciliates, dinoflagellates, and small rotifers sufficiently enough to prevent a significant grazing effect during the dilution experiments conducted in that month. Whereas in October, overall rotifer abundance was low but with a relatively high proportion of *Polyarthra* sp., which are effective at avoiding predation by *Asplanchna* and also documented consumers of phytoplankton. This may explain why we observed low, but significant, microzooplankton community grazing rates in the October dilution experiment.

Overall, our results indicate that ciliates, dinoflagellates, flagellates, rotifers, and other heterotrophic microplankton together greatly influence the dynamics of cyanobacteria blooms in Vancouver Lake, with ciliates most likely responsible for the initial decline in cyanobacteria biomass, followed by rotifers acting to change the composition of the micro-grazer community, with cascading effects on phytoplankton biomass. These results also reinforce the need to consider the distinct trophic roles of the many assemblages that comprise the microzooplankton community, as well as the interactions among them (e.g., intra-guild predation, top-down vs. bottom-up influences), in well-studied model systems, such as Vancouver Lake.

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Author contribution KS and GRB contributed to the conceptualization and design of this study. Material preparation, experimentation, and data collection were performed by KS and GRB with guidance from SEH. KS conducted microscopical and statistical analyses. The manuscript was written by KS; GRB and SEH provided comprehensive reviews of subsequent versions of the manuscript.

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Data availability Data are available under supporting data.

Code availability Available upon request.

Declarations

Conflict of interest The authors declare they have no conflicts of interest.

Ethical approval Not required.

Consent to participate All authors read and approved the final manuscript and consent to peer review.

Consent for publication All authors consent the final manuscript to be published.

References

Agasild, H., P. Zingel, I. Tõnno, J. Haberman & T. Nõges, 2007. Contribution of different zooplankton groups in grazing on phytoplankton in shallow eutrophic Lake Võrtsjärv (Estonia). Hydrobiologia 584: 167–177.

Arar, E. J., & G. B. Collins, 1997. In vitro determination of chlorophyll a and phaeophytin a in marine and freshwater algae by fluorescence, Method 445.0. National Exposure Research Laboratory, US Environmental Protection Agency, Cincinnati, OH.

Bhagat, S. K. & J. F. Orsborn, 1971. A Summary Report on Water Quantity and Quality Studies of Vancouver Lake, Washington State University, Pullman, WA, Washington:

Bogdan, K. G. & J. J. Gilbert, 1982. Seasonal patterns of feeding by natural populations of *Keratella*, *Polyarthra*, and *Bosmina*: clearance rates, selectivities, and contributions to community grazing. Limnology and Oceanography 27: 918–934.

Bogdan, K. G. & J. J. Gilbert, 1984. Body size and food size in freshwater zooplankton. Proceedings of the National Academy of Sciences of the United States of America 81: 6427–6431.

Bolam, B. A., G. Rollwagen-Bollens & S. M. Bollens, 2019. Feeding rates and prey selection of the invasive Asian clam, *Corbicula fluminea*, on microplankton in the Columbia River, USA. Hydrobiologia 833: 107–123.

Bollens, S. M., & G. Rollwagen-Bollens, 2009. Biological Assessment of the Plankton in Vancouver Lake, WA: Year One Annual Report. Washington State University Vancouver. http://www.vancouverlakepartnership.org/MapsMaterials/WSUYr1Report_Text.pdf.

Bornet, B. & C. Flahault, 1888. Annales des Sciences Naturelles. Botanique VII 7: 228.

Boyer, J., G. Rollwagen-Bollens & S. Bollens, 2011. Microzooplankton grazing before, during and after a cyanobacterial bloom in Vancouver Lake, Washington, USA. Aquatic Microbial Ecology 64: 163–174.

Brunthaler, J., 1903. Sitzungsberichte Kaiserliche Akademie der Wissenschaften in Wien, Mathematisch-naturwissenschaftliche Klasse. Abteilung I, Mineralogie, Krystallographie, Botanik, Physiologie Der Pflanze 112: 289–293.

Burian, A., M. J. Kainz, M. Schagerl & A. Yasindi, 2014. Species-specific separation of lake plankton reveals divergent food assimilation patterns in rotifers. Freshwater Biology 59: 1257–1265.

Carmichael, W. W. & G. L. Boyer, 2016. Health impacts from cyanobacteria harmful algae blooms: Implications for the North American Great Lakes. Harmful Algae 54: 194–212.

Chang, K., H. Doi, Y. Nishibe & S. Nakano, 2010. Feeding habits of omnivorous *Asplanchna*: comparison of diet composition among *Asplanchna herricki, A. priodonta* and *A. girodi* in pond ecosystems. Journal of Limnology 69: 209–216.

Chick, J. H., A. P. Levchuk, K. A. Medley & J. H. Havel, 2010. Underestimation of rotifer abundance a much greater problem than previously appreciated. Limnology and Oceanography: Methods 8: 79–87.

Chorus, I., I. Falconer, H. Salas & J. Bartram, 2000. Health risks caused by freshwater cyanobacteria in recreational waters. Journal of Toxicology and Environmental Health, Part B 3: 323–347.

Chorus, I. & M. Welker (eds), 2021. Toxic Cyanobacteria in Water: A Guide to Their Public Health Consequences, Monitoring and Management., 2nd ed. CRC Press, London, World Health Organization.

Conde-Porcuna, J. M. & S. S. S. Sarma, 1995. Prey selection by *Asplanchna girodi* (Rotifera): the importance of prey defence mechanisms. Freshwater Biology 33: 341–348.

Davis, T. W., F. Koch, M. A. Marcoval, S. W. Wilhelm & C. J. Gobler, 2012. Mesozooplankton and microzooplankton grazing during cyanobacterial blooms in the western basin of Lake Erie. Harmful Algae 15: 26–35.

De Guerne, J., 1888. Excursions zoologiques dans les Isles de Fayal et de San Miguel (Açores). VII. Note monographique sur les rotifères de la famille Asplanchnidae. Campagnes scientifiques du yacht monégasque l'Hirondelle. Gauthier-Villars et Fils, Imprimeurs-Libraires, Paris (pp. 50–65).

DeMott, W. R. & F. Moxter, 1991. Foraging cyanobacteria by copepods: responses to chemical defense and resource abundance. Ecology 72: 1820–1834.

Díez, B. & K. Ininbergs, 2014. Chapter 3: Ecological services rendered by cyanobacteria: an economic perspective, Wiley, Somerset (pp. 43–63).

Ehrenberg, C. G., 1832. Über die Entwickelung und Lebensdauer der Infusionsthiere; nebst ferneren Beiträgen zu einer Vergleichung ihrer organischen Systeme. Abhandlungen der königlichen Akademie der Wissenschaften zu Berlin (für 1831) (pp. 1–154).

Elser, J. J., 1999. The pathway to noxious cyanobacteria blooms in lakes: the food web as the final turn. Freshwater Biology 42: 537–543.

Frenken, T., J. Wierenga, E. van Donk, S. A. J. Declerck, L. N. de Senerpont Domis, T. Rohrlack & D. B. Van de Waal, 2018. Fungal parasites of a toxic inedible cyanobacterium provide food to zooplankton: chytrid zoospores

support rotifer growth. Limnology and Oceanography 63: 2384–2393.
Fulton, R. S., 1988. Grazing on filamentous algae by herbivorous zooplankton. Freshwater Biology 20: 263–271.
Fulton, R. S., III. & H. W. Paerl, 1987. Toxic and inhibitory effects of the blue-green alga *Microcystis aeruginosa* on herbivorous zooplankton. Journal of Plankton Research 9: 837–855.
Fulton, R. S. & H. W. Paerl, 1988. Effects of the blue-green alga *Microcystis aeruginosa* on zooplankton competitive relations. Oecologia 76: 383–389.
Ger, K. A., S. Naus-Wiezer, L. De Meester & M. Lürling, 2019. Zooplankton grazing selectivity regulates herbivory and dominance of toxic phytoplankton over multiple prey generations. Limnology and Oceanography 64: 1214–1227.
Ger, K. A., P. Urrutia-Cordero, P. C. Frost, L.-A. Hansson, O. Sarnelle, A. E. Wilson & M. Lürling, 2016. The interaction between cyanobacteria and zooplankton in a more eutrophic world. Harmful Algae 54: 128–144.
Gerphagnon, M., D. Latour, J. Colombet & T. Sime-Ngando, 2013. Fungal parasitism: life cycle, dynamics and impact on cyanobacterial blooms. PLoS ONE 8: e60894.
Gilbert, J. J., 1985. Escape response of the Rotifer *Polyarthra*: a high-speed cinematographic analysis. Oecologia 66: 322–331.
Gilbert, J. J., 1990. Differential effects of *Anabaena affinis* on Cladocerans and Rotifers: mechanisms and implications. Ecology 71: 1727–1740.
Gilbert, J. J., & K. G. Bogdan, 1984. Rotifer grazing: in situ studies on selectivity and rates (pp. 97–133). In: D. G. Meyers and J. R. Strickler, editors. Trophic Interactions Within Aquatic Ecosystems. AAAS Selected Symposium.
Gilbert, J. J. & J. Jack, 1993. Rotifers as predators on small ciliates. Hydrobiologia 255(256): 247–253.
Gobler, C. J., T. W. Davis, K. J. Coyne & G. L. Boyer, 2007. Interactive influences of nutrient loading, zooplankton grazing, and microcystin synthetase gene expression on cyanobacterial bloom dynamics in a eutrophic New York lake. Harmful Algae 6: 119–133.
Gosse, P. H., 1851. A catalogue of Rotifera found in Britain; with description of five new genera and thirty-two new species. The Annals and Magazine of Natural History 8: 197–203.
Gulati, R. D., J. Ejsmont-Karabin & G. Postema, 1993. Feeding in *Euchlanis dilatata lucksiana* Hauer on filamentous cyanobacteria and a prochlorophyte. Hydrobiologia 255: 269–274.
Gulati, R. D., J. Rooth & J. Ejsmont-Karabin, 1987. A laboratory study of feeding and assimilation in *Euchlanis dilatata lucksiana*. Hydrobiologia 147: 289–296.
Haney, J. F., R. S. Stemberger, M. A. Aliberti, E. Allan, S. Allard, D. J. Bauer, W. Beagen, S. R. Bradt, B. Carlson, S. C. Carlson, U. M. Doan, J. Dufrense, W. Godkin, S. Greene, A. Kaplan, E. Maroni, S. Melillo, A. Murby, J. Smith, B. Ortman, J. Quist, S. Reed, T. Rowin, M. Schmuck, & B. Travers, 2013. An Image-Based Key to the Zooplankton of North America, version 5.0. http://cfb.unh.edu/cfbkey/html/index.html.
Hansson, L.-A., S. Gustafsson, K. Rengefors & L. Bomark, 2007. Cyanobacterial chemical warfare affects zooplankton community composition. Freshwater Biology 52: 1290–1301.
Hillbricht-Ilkowska, A., 1983. Response of Planktonic Rotifers to the Eutrophication Process and to the Autumnal Shift of Blooms in Lake Biwa, Japan. Japanese Journal of Limnology (rikusuigaku Zasshi) 44: 93–106.
Hillebrand, H., C.-D. Dürselen, D. Kirschtel, U. Pollingher & T. Zohary, 1999. Biovolume calculation for Pelagic and Benthic Microalgae. Journal of Phycology 35: 403–424.
Horppila, J., L. Härkönen, N. Hellén, S. Estlander, Z. Pekcan-Hekim & A. Ojala, 2019. Rotifer communities under variable predation-turbulence combinations. Hydrobiologia 828: 339–351.
Hudson, C. T., 1885. On four new species of the genus Floscularia, and five new species of Rotifera. Journal of the Royal Microscopical Society 5: 608–614.
Ignoffo, T. R., S. M. Bollens & A. B. Bochdansky, 2005. The effects of thin layers on the vertical distribution of the rotifer, *Brachionus plicatilis*. Journal of Experimental Marine Biology and Ecology 316: 167–181.
James, M. R., 1991. Sampling and preservation methods for the quantitative enumeration of microzooplankton. New Zealand Journal of Marine and Freshwater Research 25: 305–310.
Kâ, S., J. M. Mendoza-Vera, M. Bouvy, G. Champalbert, R. N'Gom-Kâ & M. Pagano, 2012. Can tropical freshwater zooplankton graze efficiently on cyanobacteria? Hydrobiologia 679: 119–138.
Karabin, A. & J. Ejsmont-Karabin, 2005. An evidence for vertical migrations of small rotifers – a case of Rotifer community in a Dystrophic Lake. Hydrobiologia 546: 381–386.
Kellicott, D. S., 1879. A new rotifer. The American Journal of Microscopy and Popular Science 4: 19–20.
Kirk, K. L. & J. J. Gilbert, 1992. Variation in herbivore response to chemical defenses: zooplankton foraging on toxic Cyanobacteria. Ecology 73: 2208–2217.
Klebs, G., 1883. Über die Organisation einiger Flagellatengruppen und ihre Beziehungen zu Algen und Infusorien. Untersuchungen aus dem Botanischen Institut zu Tübingen 1: 233–362, pls II, III.
Komárek, J. & J. W. G. Lund, 1990. What is *Spirulina platensis* in fact? Algological Studies 58: 1–13.
Kosten, S., V. Huszar, E. Becares, L. Costa, E. Van Donk, L.-A. Hansson, E. Jeppesen, C. Kruk, G. Lacerot, N. Mazzeo, L. Meester, B. Moss, M. Lürling, T. Noges, S. Romo & M. Scheffer, 2012. Warmer climates boost cyanobacterial dominance in shallow lakes. Global Change Biology 18: 118–126.
Kurmayer, R., 1999. Strategies for the co-existence of zooplankton with the toxic cyanobacterium *Planktothrix rubescens* in Lake Zurich. Journal of Plankton Research 21: 659–683.
Lair, N. & H. Oulad Ali, 1990. Grazing and assimilation rates of natural populations of planktonic rotifers *Keratella cochlearis, Keratella quadrata* and *Kellicottia longispina* in a eutrophic lake (Aydat, France). Hydrobiologia 194: 119–131.

Landry, M. R. & R. P. Hassett, 1982. Estimating the grazing impact of marine micro-zooplankton. Marine Biology 67: 283–288.

Landry, M. R., J. Kirshtein & J. Constantinou, 1995. A refined dilution technique for measuring the community grazing impact of microzooplankton, with experimental tests in the central equatorial Pacific. Marine Ecology Progress Series 120: 53–63.

Lee, T. A., G. Rollwagen-Bollens, & S. M. Bollens, 2015a. The influence of water quality variables on cyanobacterial blooms and phytoplankton community composition in a shallow temperate lake. Environmental Monitoring and Assessment 187.

Lee, T. A., G. Rollwagen-Bollens, S. M. Bollens & J. J. Faber-Hammond, 2015b. Environmental influence on cyanobacteria abundance and microcystin toxin production in a shallow temperate lake. Ecotoxicology and Environmental Safety 114: 318–325.

Lee, T. A., S. M. Bollens, G. Rollwagen-Bollens & J. E. Emerson, 2016. The effects of eutrophication and invasive species on zooplankton community dynamics in a shallow temperate lake. Fundamental and Applied Limnology/archiv Für Hydrobiologie 188: 215–231.

Lemmerman, E., 1898. Beitrag zur Algenflora von Schlesien. Abhandlungen Naturwissenschaftlicher Verein Bremen 14: 1–520.

Li, J., K. Yang, F. Chen, W. Lu, T. Fang, X. Zhao, H. Li & K. Cui, 2017. The impacts of crustacean zooplankton on a natural ciliate community: a short-term incubation experiment. Acta Protozoologica 2017: 289–301.

Lionard, M., F. Azémar, S. Boulêtreau, K. Muylaert, M. Tackx & W. Vyverman, 2005. Grazing by meso- and microzooplankton on phytoplankton in the upper reaches of the Schelde estuary (Belgium/The Netherlands). Estuarine, Coastal and Shelf Science 64: 764–774.

Mazumder, A., D. R. S. Lean & W. D. Taylor, 1992. Dominance of small filter feeding zooplankton in the Lake Ontario food web. Journal of Great Lakes Research 18: 456–466.

Menden-Deuer, S. & E. J. Lessard, 2000. Carbon to volume relationships for dinoflagellates, diatoms, and other protist plankton. Limnology and Oceanography 45: 569–579.

Muirhead, J. R., J. Ejsmont-Karabin & H. J. Macisaac, 2006. Quantifying rotifer species richness in temperate lakes. Freshwater Biology 51: 1696–1709.

Müller, O.F., 1786. 367. *Brachionus plicatilis*. In Animalcula infusoria fluviatilia et marina, quæ detexit, systematice descripsit et ad vivum delineari curavit (pp. 344–345). Typis Nicolai Molleri Aulæ Regias Typographi, Hauniæ.

Obertegger, U. & G. Flaim, 2015. Community assembly of rotifers based on morphological traits. Hydrobiologia 753: 31–45.

Obertegger, U. & G. Flaim, 2018. Taxonomic and functional diversity of rotifers, what do they tell us about community assembly? Hydrobiologia 823: 79–91.

Obertegger, U. & M. Manca, 2011. Response of rotifer functional groups to changing trophic state and crustacean community. Journal of Limnology 70: 231.

Obertegger, U., H. A. Smith, G. Flaim & R. L. Wallace, 2011. Using the guild ratio to characterize pelagic rotifer communities. Hydrobiologia 662: 157–162.

O'Neil, J. M., T. W. Davis, M. A. Burford & C. J. Gobler, 2012. The rise of harmful cyanobacteria blooms: the potential roles of eutrophication and climate change. Harmful Algae 14: 313–334.

Orcutt, J. D. & M. L. Pace, 1984. Seasonal dynamics of rotifer and crustacean zooplankton populations in a eutrophic, monomictic lake with a note on rotifer sampling techniques. Hydrobiologia 119: 73–80.

Paerl, H. W., R. S. Fulton, P. H. Moisander & J. Dyble, 2001. Harmful freshwater algal blooms, with an emphasis on cyanobacteria. The Scientific World Journal 1: 76–113.

Paerl, H. W., N. S. Hall & E. S. Calandrino, 2011. Controlling harmful cyanobacterial blooms in a world experiencing anthropogenic and climatic-induced change. Science of the Total Environment 409: 1739–1745.

Pallas, P. S., 1766. V. Brachionus. In Elenchus zoophytorum sistens generum adumbrationes generaliores et specierum cognitarum succinctas descriptiones, cum selectis auctorum synonymis (pp. 89–105). Hagae-Comitum, Netherlands.

Pourriot, R., 1977. Food and Feeding Habits of Rotifera (pp. 243–260). Proceedings of the First International Rotifer Symposium. Archiv für Hydrobiologie–Beiheft Ergebnisse der Limnologie, Lunz, Austria.

Quiblier-Lloberas, C., G. Bourdier, C. Amblard & D. Pepin, 1996. Impact of grazing on phytoplankton in Lake Pavin (France): Contribution of different zooplankton groups. Journal of Plankton Research 18: 305–322.

Rabalais, N. N., R. E. Turner, R. J. Diaz & D. Justic, 2009. Global change and eutrophication of coastal waters. ICES Journal of Marine Science 66: 1528–1537.

Rodríguez, M. P. & T. Matsumura-Tundisi, 2000. Variation of density, species composition and dominance of Rotifers at a shallow tropical reservoir (Broa reservoir, SP, Brazil) in a short scale time. Revista Brasileira De Biologia 60: 01–09.

Rollwagen-Bollens, G., S. M. Bollens, A. Gonzalez, J. Zimmerman, T. Lee & J. Emerson, 2013. Feeding dynamics of the copepod *Diacyclops thomasi* before, during and following filamentous cyanobacteria blooms in a large, shallow temperate lake. Hydrobiologia 705: 101–118.

Rollwagen-Bollens, G., T. Lee, V. Rose & S. Bollens, 2018. Beyond eutrophication: Vancouver Lake, WA, USA as a model system for assessing multiple, interacting biotic and abiotic drivers of harmful cyanobacterial blooms. Water 10: 757.

Rose, V., G. Rollwagen-Bollens & S. Bollens, 2017. Interactive effects of phosphorus and zooplankton grazing on cyanobacterial blooms in a shallow temperate lake. Hydrobiologia 788: 345–359.

Segers, H., 2008. Global diversity of rotifers (Rotifera) in freshwater. Hydrobiologia 595: 49–59.

Sellner, K. G., D. C. Brownlee, M. H. Bundy, S. G. Brownlee & K. R. Braun, 1993. Zooplankton grazing in a Potomac River Cyanobacteria bloom. Estuaries 16: 859–872.

Soares, M. C. S., M. Lürling & V. L. M. Huszar, 2010. Responses of the rotifer *Brachionus calyciflorus* to two tropical toxic cyanobacteria (*Cylindrospermopsis*

raciborskii and *Microcystis aeruginosa*) in pure and mixed diets with green algae. Journal of Plankton Research 32: 999–1008.

Starkweather, P., 1980. Aspects of the feeding behavior and trophic ecology of suspension-feeding rotifers. Hydrobiologia 73: 63–72.

Starkweather, P. L., 1981. Trophic relationships between the rotifer *Brachionus calyciflorus* and the blue-green alga *Anabaena flos-aquae*. SIL Proceedings 1922–2010(21): 1507–1514.

Starkweather, P. L. & P. E. Kellar, 1983. Utilization of cyanobacteria by *Brachionus calyciflorus*: *Anabaena flos-aquae* (NRC-44-1) as a sole or complementary food source. Hydrobiologia 104: 373–377.

Stelzer, C.-P., 1998. Feeding behaviour of the rotifer *Asco-morpha ovalis*: functional response, handling time and exploitation of individual *Ceratium* cells. Journal of Plankton Research 20: 1131–1144.

Stemberger, R. S., 1979. A Guide to Rotifers of the Laurentian Great Lakes. US Environmental Protection Agency, Washington DC.

Stemberger, R. S. & J. J. Gilbert, 1985. Body size, food concentration, and population growth in planktonic rotifers. Ecology 66: 1151–1159.

Stemberger, R. S. & J. J. Gilbert, 1987. Rotifer threshold food concentrations and the size-efficiency hypothesis. Ecology 68: 181–187.

Sterner, R. W., 1989. Resource competition during seasonal succession toward dominance by cyanobacteria. Ecology 70: 229–245.

Stewart, L. J. & D. G. George, 1987. Environmental factors influencing the vertical migration of planktonic rotifers in a hypereutrophic tarn. Hydrobiologia 147: 203–208.

Thomas, S. M., J. H. Chick & S. J. Czesny, 2017. Underestimation of microzooplankton is a macro problem: one size fits all zooplankton sampling needs alterations. Journal of Great Lakes Research 43: 91–101.

Vanderploeg, H. A. & D. Scavia, 1979a. Two electivity indices for feeding with special reference to zooplankton grazing. Journal of the Fisheries Board of Canada 36: 362–365.

Vanderploeg, H. A. & D. Scavia, 1979b. Calculation and use of selectivity coefficients of feeding: zooplankton grazing. Ecological Modelling 7: 135–149.

Wallace, R. L., & T. W. Snell, 2010. Rotifera (pp. 173–235). In: Thorp, J. & A. Covich, editors. Ecology and Classification of North American Freshwater Invertebrates. Third edition. Elsevier.

Wallace, R. L., T. W. Snell & H. A. Smith, 2015. Chapter 13 - Phylum Rotifera. In Thorp, J. H. & D. C. Rogers (eds), Thorp and Covich's Freshwater Invertebrates 4th ed. Academic Press, Boston: 225–271.

Yang, X., X. Wu, H. Hao & Z. He, 2008. Mechanisms and assessment of water eutrophication. Journal of Zhejiang University Science B 9: 197–209.