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PRIMARY RESEARCH PAPER

Feeding dynamics of the copepod *Diacyclops thomasi* before, during and following filamentous cyanobacteria blooms in a large, shallow temperate lake

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Abstract Cyanobacteria blooms are an increasing problem in temperate freshwater lakes, leading to reduced water quality and in some cases harmful effects from toxic cyanobacteria species. To better understand the role of zooplankton in modulating cyanobacteria blooms, from 2008 to 2010 we measured water quality and plankton abundance, and measured feeding rates and prey selectivity of the copepod *Diacyclops thomasi* before, during and following summertime cyanobacteria blooms in a shallow, eutrophic lake (Vancouver Lake, Washington, USA). We used a combined field and experimental approach to specifically test the hypothesis that copepod grazing was a significant factor in establishing the timing of cyanobacteria bloom initiation and eventual decline in Vancouver Lake. There was a consistent annual succession of zooplankton taxa, with cyclopoid copepods (*D. thomasi*) dominant in spring, followed by small cladocerans (*Eubosmina* sp.). Before each cyanobacteria bloom, large cladocerans (*Daphnia retrocurva, Daphnia laevis*) peaked in abundance but quickly disappeared, followed by brief increases in rotifers. During the cyanobacteria blooms, *D. thomasi* was again dominant, with small cladocerans abundant in autumn. Before the cyanobacteria blooms, *D. thomasi* substantially consumed ciliates and dinoflagellates (up to 100% of prey biomass per day), which likely allowed diatoms to flourish. A shift in copepod grazing toward diatoms before the blooms may have then helped to facilitate the rapid increase in cyanobacteria. Copepod grazing impact was the highest during the cyanobacteria blooms both years, but focused on non-cyanobacteria prey; copepod grazing was minimal as the cyanobacteria blooms waned. We conclude that cyclopoid copepods may have an indirect role (via trophic cascades) in modulating cyanobacteria bloom initiation, but do not directly contribute to cyanobacteria bloom decline.

Keywords Copepod grazing · Cyanobacteria bloom · *Diacyclops thomasi* · Harmful algae

Introduction

Seasonal blooms of cyanobacteria and other phytoplankton are natural occurrences in lakes of varying morphology and location; however, increasing evidence demonstrates that lakes are becoming increasingly eutrophied due to human activity, through sewage and fertilizer inputs, deforestation, road construction, real estate development and other disturbances in lake watersheds, and this eutrophication is

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contributing to an increase in frequency and intensity of cyanobacteria blooms (e.g., Elser et al., 1990; Dokulil & Teubner, 2000; Sellner et al., 2003; Paerl, 2008).

Excessive abundance of cyanobacteria may have detrimental effects on lake ecosystems and water quality, including development of surface scums, depleted oxygen levels, and (in some cases) production of toxins that can negatively affect aquatic life and humans (Carmichael, 1992; Codd, 1995; Sellner et al., 2003). Moreover, several recent studies suggest that increased eutrophication under conditions of a warming climate may result in increased dominance of cyanobacteria in aquatic systems (Paerl & Huisman, 2008; Wagner & Adrian, 2009; Kosten et al., 2012; O'Neill et al., 2012) and may actually favor harmful cyanobacterial taxa over non-toxic forms (Paerl & Huisman, 2009). This phenomenon is of great concern to water resource managers, particularly with respect to human health, as well as to the public whose use and enjoyment of these environments may be prohibited as a result.

Excessive nutrient availability is commonly considered to be a necessary precursor for cyanobacteria bloom formation, measured either as total phosphorus or total nitrogen (Downing et al., 2001), while some studies point to the importance of low ratios of dissolved inorganic nitrogen to phosphorus (N:P) for cyanobacteria blooms to occur (Elser et al., 2000; Paterson et al., 2002). However, a multiplicity of physical factors may influence the timing, frequency, and intensity of individual cyanobacteria blooms (e.g., elevated temperature, water column stratification, etc.) (Paerl 1988; Dokulil & Teubner, 2000; Paerl & Fulton, 2006).

Recently, increased attention has been directed toward the impact of biotic factors on cyanobacteria bloom dynamics, in particular the composition and structure of the pelagic food web and the role of planktonic grazers in mediating or controlling cyanobacteria growth and bloom formation. Historically, the focus in freshwater lakes has been on the trophic role of crustacean zooplankton, namely large cladocerans and to a much lesser degree small cladocerans and copepods. But despite numerous laboratory and field studies across a wide range of systems, there is still substantial disagreement about how these zooplankton groups may contribute to the formation, persistence, and decline of cyanobacteria blooms.

For example, Elser (1999) predicted that cladoceran zooplankton (e.g., *Daphnia*) control cyanobacteria blooms, either through altering the stoichiometric balance of nitrogen and phosphorus (e.g., Elser et al., 2000) and/or through selective grazing (e.g., Paterson et al., 2002), and that if cladoceran abundance is reduced (for example, via predation by planktivorous fish), then noxious cyanobacteria will bloom. Indeed, additional studies have shown that cladocerans do have the capacity to effectively graze cyanobacteria (Oberhaus et al., 2007) and may limit cyanobacterial blooms in some environments (Kasprzak et al., 1999; Chan et al., 2004).

Conversely, a range of laboratory and field studies have shown that cyanobacteria are poor food for cladocerans, and may in fact inhibit feeding either through mechanical interference (Lampert, 1982, 1987; Fulton, 1988; Gilbert & Durand, 1990; Gliwicz, 1990; DeMott et al., 2001) and/or through exposure to toxins (DeMott et al., 1991; De Mott, 1999; Ghadouani et al., 2003; Dao et al., 2010).

In addition to cladocerans, copepods may also influence cyanobacteria populations. Studies of copepod grazing in relation to cyanobacteria blooms are fewer in number, but are similarly mixed as to the effect of copepods on bloom dynamics. Burns & Xu (1990) found *Boeckella* spp. copepods to effectively consume large colonies of *Anabaena flos-aquae* and *Nostoc* sp. in a New Zealand lake. Similarly, *Notodiaptomus iheringi* copepods in a Brazilian reservoir were found to consume cyanobacteria, although they were more selective for smaller colonies (Panosso et al., 2003). Koski et al. (2002) also examined copepod feeding on diets dominated by *Nodularia spumigena* in mesocosms, and showed that *Acartia bifilosa* and *Eurytemora affinis* had high ingestion rates on cyanobacteria. And Hambright et al. (2007) found the copepod *Skistodiaptomus pallidus* fed selectively on large colonial and filamentous cyanobacteria taxa, including *Aphanocapsa* and *Anabaena*. On the other hand, Fulton (1988) observed *Diaptomus reighardi* and *Eurytemora affinis* copepods to have clearance rates near zero on filamentous cyanobacteria in the Potomac River, USA. And in laboratory experiments, DeMott & Moxter (1991) found *Diaptomus* copepods to have low-clearance rates on *Anabaena flos-aquae*, particularly the toxic forms of this species, while Ger et al. (2010) found the consumption of *Microcystis* cells to cause substantial

mortality among the calanoid copepods *Pseudodiaptomus forbesi* and *Eurytemora affinis*.

Clearly, considerable uncertainty remains regarding whether and how grazing by crustacean zooplankton generally and copepods in particular may control or modulate the timing, intensity, and degradation of cyanobacteria blooms in lake ecosystems. Yet, the pressure to find explanations for and solutions to the problem of harmful cyanobacteria blooms in lakes with particular value to human populations remains high. Therefore, we expanded an existing research program focused on the plankton ecology of a large, popular urban lake in southwest Washington state (USA) to specifically quantify the role of zooplankton grazing on cyanobacteria blooms, to better understand the bloom dynamics of this and other shallow temperate lakes, and to provide managers with information that may assist in mitigating future bloom events.

In this article, we present the results of a two-year field and experimental study to assess seasonal zooplankton abundance and diversity, and specifically copepod grazing impact on intense summertime cyanobacteria blooms that occur annually in Vancouver Lake, WA, USA. Our project had two main objectives: (1) to measure the temporal variability in abundance and composition of the protists and metazoan zooplankton community, and (2) to measure the diet and feeding selectivity of the cyclopoid copepod *Diacyclops thomasi* before, during and following two filamentous cyanobacteria blooms that occurred in the summers of 2008 and 2009. We specifically aimed to test the hypothesis that copepod grazing was a significant factor in establishing the timing of cyanobacteria bloom initiation and eventual decline. Thus, we conclude the article with an estimate of copepod grazing impacts and the role of food web dynamics in modulating cyanobacteria blooms in Vancouver Lake and possibly other shallow, eutrophic, and temperate lakes.

Materials and methods

Study area

Vancouver Lake is a large (9.3 km^2 = 930 ha), shallow (mean depth 1 m, range 1–6 m), and highly turbid lake located in the floodplain of the Columbia River in the southwest corner of Washington state, USA (Fig. 1). Vancouver Lake is situated within the city limits of Vancouver, Washington, which is part of a large metropolitan area (human population 2.2 million) that includes Portland, Oregon. Vancouver Lake is popular for boating, fishing (primarily catfish, crappies, and white perch) and other recreational activities, and is also an important habitat for a range of wildlife, particularly migrating and resident waterfowl, raptors, and songbirds. However, over the past two decades the lake has been experiencing intense summertime blooms of filamentous cyanobacteria (primarily *Anabaena flos-aquae* and *Aphanizomenon flos-aquae*), and from 2004 to 2010 cyanobacteria abundance was high enough to force closure of the lake to all water contact for several weeks each August.

Field collections

Field sampling for measurement of water quality variables, phytoplankton and zooplankton abundance was conducted over a two-year period from March 2008 to February 2010 on a weekly (June–September),

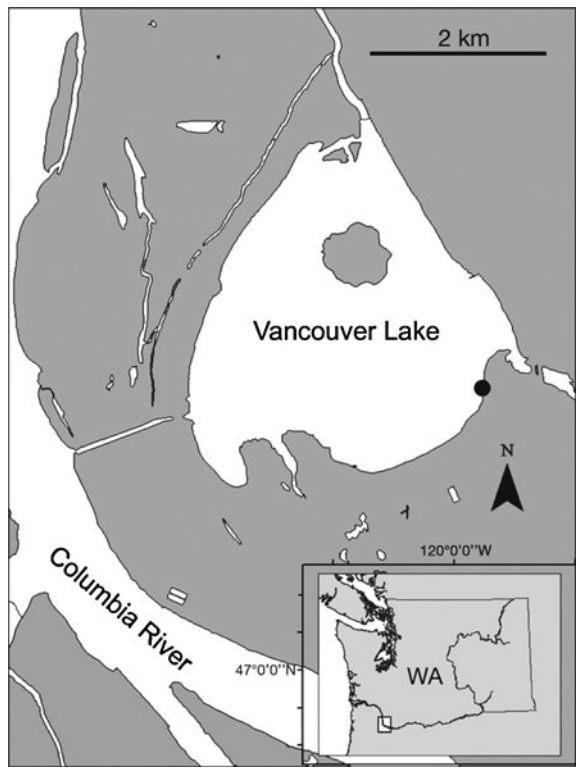

Fig. 1 Map of Vancouver Lake, Washington, USA, showing the location of sampling

bi-weekly (April–May and October–November), and monthly (December–March) basis from a dock located on the southeast shore of Vancouver Lake (Fig. 1). A single station (water depth ~2 m) was sampled to represent lake-wide patterns, since quarterly sampling of water quality and plankton abundance at eight stations throughout Vancouver Lake over the previous year demonstrated no significant horizontal variability in any measured parameter (G. Rollwagen-Bollens, unpublished data).

Water quality

At each sampling time, temperature and dissolved oxygen profiles from the surface to the bottom were obtained using a YSI 85 probe, and relative water clarity was estimated by measuring the Secchi depth. In addition, triplicate water samples were collected from the surface using a clean, acid-washed bucket, and subsamples were taken for later laboratory analyses of chlorophyll *a* concentration. Subsamples of 20–100 ml were filtered through GF/F filters, and the filters wrapped in foil and immediately frozen. Upon return to the laboratory, thawed GF/F filters were placed in vials containing 20 ml of 90% acetone for 24 h. The concentration of chlorophyll *a* suspended in the acetone after incubation was measured on a Turner Model 10 AU fluorometer, using the acidification method (Strickland & Parsons, 1972).

Plankton abundance, biomass and composition

At all sampling times, triplicate water samples were collected from the surface using a clean bucket and 200 ml subsamples preserved in 5% acid Lugol's solution, for enumeration and identification of cyanobacteria and all protist (i.e., unicellular eukaryotic) plankton. In addition, triplicate vertical tows from surface to bottom were conducted with a 0.5-m diameter, 73-μm mesh zooplankton net (with each tow sampling ~1.5 m^3 of lakewater), and the contents concentrated and preserved in 5–10% buffered formalin.

To determine the abundance and composition of planktonic protists and cyanobacteria, 1–10 ml aliquots of the Lugol's preserved water samples were settled overnight in Utermohl chambers, and the chambers examined using an Olympus CK-40 inverted microscope at 200–400×. All individuals were identified to genus (and species when possible) and sized using an ocular micrometer, and biovolume calculated based on geometric shape (Hillebrand et al., 1999). Carbon biomass was then estimated using the algorithms of Menden-Deuer & Lessard (2000).

The abundance and composition of the metazoan zooplankton (e.g., cladocerans, copepods, rotifers) were determined by examining 5–25 ml aliquots of the formalin-preserved zooplankton net samples using a Leica MZ-6 stereomicroscope, following Pennak (1989). Aliquot size was varied to insure that at least 300 individuals were enumerated per sample. Individuals were identified to the lowest possible taxon and life history stage.

Grazing experiments

Incubation experiments (Rollwagen-Bollens & Penry, 2003; Gifford et al., 2007) with adult females of the cyclopoid copepod *Diacyclops thomasi* feeding upon the natural assemblage of protist and cyanobacteria prey were conducted three times per year for two years, from March 2008 to February 2010. Experiments were timed to measure copepod grazing rates before, during and following cyanobacteria blooms that occurred in August–September of both 2008 and 2009. Copepods were collected via vertical hauls of a 73-μm plankton net, returned to the laboratory and adult females sorted under dim light into holding beakers containing filtered lake water, where they were held for a minimum of 4 h to acclimate and empty their guts (Dam & Peterson 1988, Irigoien et al. 1998). The number of copepods used in each experiment (80 per l) was selected to insure sufficient consumption of prey to reduce prey abundance by 30–60% over the course of the incubation, but not so high as to completely consume any prey category.

For each incubation experiment, 500-ml incubation bottles were carefully filled with lakewater containing the natural assemblage of planktonic prey obtained from the surface using a clean, acid-washed bucket. Quadruplicate bottles containing only the natural assemblage were established as initial controls. The initial controls were immediately subsampled, preserved in 5% Lugol's solution, and later analyzed microscopically to enumerate and identify the cyanobacteria and protist plankton as described above. Final control (natural assemblage only) and final treatment (assemblage plus copepod predators) bottles were prepared in quadruplicate, topped off with unfiltered

lakewater, and sealed with parafilm and a lid (to prevent air spaces and turbulence-causing bubbles). These bottles were incubated in a temperature-controlled chamber at ambient lake temperatures for 12 h overnight (in the dark) on a slowly rotating (0.5–1 rpm) plankton wheel. At the end of the incubation, all final bottles were subsampled, preserved and analyzed as described above for the initial bottles.

Prey cells enumerated from the experimental samples were identified at least to genus, sized, and then placed into one of six taxonomic categories of potential prey: small (<15 μm) diatoms, large (>15 μm) diatoms, small (<15 μm) dinoflagellates, large (> 15 μm) dinoflagellates, small (<15 μm) ciliates, large (>15 μm) ciliates, cryptophytes, chlorophytes, or cyanobacteria. The 15-μm size cut-off reflected a natural division in the overall size distribution of diatoms, dinoflagellates, and ciliates in Vancouver Lake over the sampling period. Cryptophytes, chlorophytes, and cyanobacteria individuals/filaments were generally <15 μm in size. In order to determine whether copepod predators had exerted a significant grazing impact on planktonic prey in any incubation experiment, *t* tests using equal variances (Zar, 1996) were used to determine if there was a significant difference between the number of prey cells in each taxonomic category in the final controls versus the final treatments. Levene's test was used to test for equality of the variances. Grazing experiments were considered valid if: (1) there was a significant reduction ($P < 0.05$) in at least one prey category or taxon, and (2) the significantly reduced group had five or more cells in the final control.

Copepod feeding rates and selectivity

Copepod clearance (CR; ml copepod^{-1} h^{-1}) and ingestion rates (IR; μg C copepod^{-1} h^{-1}) for each category of prey in each experiment were estimated according to Marin et al. (1986), using the following equations. $IR = CR * B_i$, where B was the biomass (μg C) of prey cells, and *i* represented initial values from the incubation bottles at the beginning of the experiment. $CR = [(V * g)/N]$, where V was the volume (ml) of the incubation bottles, *g* was the grazing mortality rate coefficient (t^{-1}), and *N* was the number of copepod predators in the incubation. The grazing mortality rate coefficient (*g*) was calculated as $g = r - [\ln(C_{fp}/C_i)/t]$, where *r* was the growth rate coefficient of prey in control incubations without predators (t^{-1}), C was the abundance of prey cells (cells/ml), *fp* represented final values from bottles containing predators at the end of the incubation, *i* represented initial values from bottles without predators, and *t* was the incubation time (hr). Finally, growth-rate coefficient of prey without predators was calculated as $r = [\ln(C_{fc}/C_i)/t]$, where *fc* represented final values from control bottles without predators at the end of the incubation.

Feeding selectivity and prey preferences of copepod predators were then assessed in two ways. First, copepod clearance rates on different prey types were compared within each experiment using 1-way ANOVA (Zar, 1996). Significant ($P < 0.05$) differences among clearance rates from a single experiment were interpreted as selective consumption of prey, with the highest clearance rates indicating the prey most preferred in that experiment (see Rollwagen-Bollens & Penry, 2003 for rationale of this selection method). Second, copepod selection for particular prey types was estimated by calculating an electivity index (*E**, Vanderploeg & Scavia, 1979a, b) following the approach and equations described below and in Rollwagen-Bollens & Penry (2003).

Electivity (*E**) ultimately compares the proportion of a particular prey type in the available medium with the proportion of that prey type in the predator's diet. To estimate *E**, several calculations were made. First, the number of individuals of each prey type consumed by the copepods (R_i) in each experiment was determined as $R_i = [(N_{ic} + N_{fc})/2] - N_{ft}$, where *i* was the prey item, N_{ic} was the mean number of individuals present in the initial bottles, N_{fc} was the mean number of individuals present in the control bottles at the end of the incubation, and N_{ft} was the mean number of individuals present in each treatment bottle at the end of the incubation. The proportion of each prey type in the diet (r_i) and in the available medium (n_i) were then further calculated as:

$$n_i = \frac{N_{ic}}{\sum_{j=1}^{m} N_{jc}}$$

and

$$r_i = \frac{R_i}{\sum_{j=1}^{m} Rj},$$

where m was the number of prey types, and R_i and N_{ic} were as described above.

The electivity index (E^*) for each prey type was calculated according to the formula:

$$E_i^* = \frac{W_i - 1/m}{W_i + 1/m},$$

where W_i was defined by the following equation:

$$W_i = \frac{r_i/n_i}{\sum_{j=1}^{m} r_j/n_j}.$$

Neutral preference was indicated by an E^* of 0, with positive values up to +1 representing increasing preference and negative values down to −1 representing increasing avoidance. As reviewed by Lechowicz (1982) and Confer & Moore (1987), E^* is sufficiently stable to accommodate both changes in relative abundance of food types and the presence of rare prey types, and allows for comparison among more than two different prey choices.

Finally, the influence of copepod grazing on cyanobacteria and other prey taxa was assessed by (1) estimating the difference between grazing mortality coefficient (g) and growth rate coefficient (r) for each prey type in each experiment; and (2) through estimation of copepod grazing impact (% of prey biomass consumed per day), calculated by multiplying the observed per capita copepod carbon ingestion rates in each experiment by the standing stock of copepods in the Lake and dividing by the standing stock of prey in the Lake during each experimental period.

Results

Environmental conditions

The most striking differences in overall water quality between 2008 and 2009 were in water clarity (as measured by Secchi depth) in the weeks preceeding each summer's algae bloom, and in wintertime dissolved oxygen concentrations. In May–June of 2008 Secchi depths reached as much as 1.5 m (when lake levels were at a 2-year high), indicating exceptionally clear water during this period. But in summer 2009 Secchi depths averaged ~0.6 m, and were never deeper than 1.0 m. In addition, dissolved O_2 concentrations were substantially higher in winter 2009 as compared to 2008, with a maximum of 23 mg l^{-1} observed in January 2009 (Fig. 2).

Plankton abundance and composition

Filamentous cyanobacteria (dominated by *Aphanizomenon flos-aquae* and *Anabaena flos-aquae*) bloomed in August–September of both 2008 and 2009 in Vancouver Lake, accounting for the large peaks in chlorophyll biomass observed during those periods. However, *Aphanizomenon flos-aquae* abundance remained quite elevated following the decrease in chlorophyll in both years, suggesting these cells

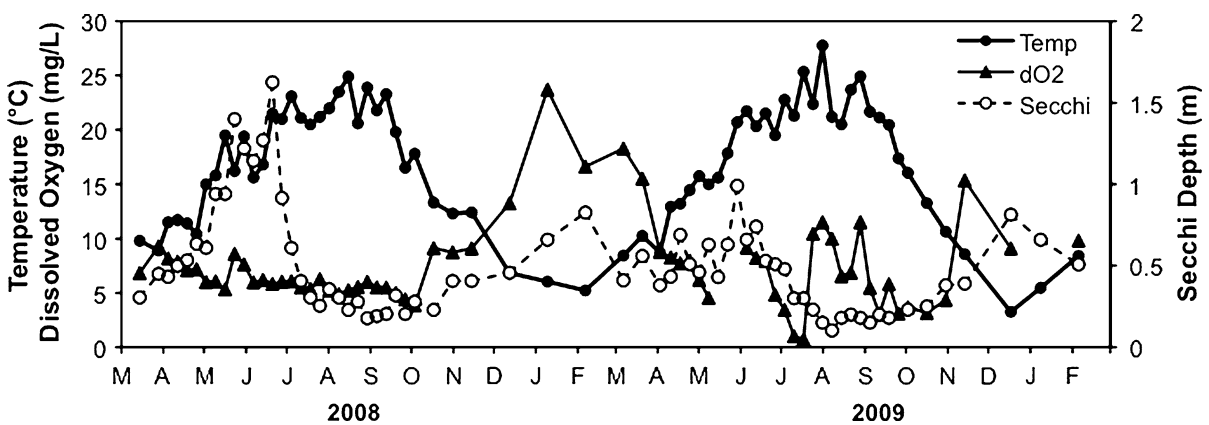

Fig. 2 Surface temperature, dissolved oxygen concentration, and Secchi depth measured from the Vancouver Lake Sailing Club dock between March 2009 and February 2010

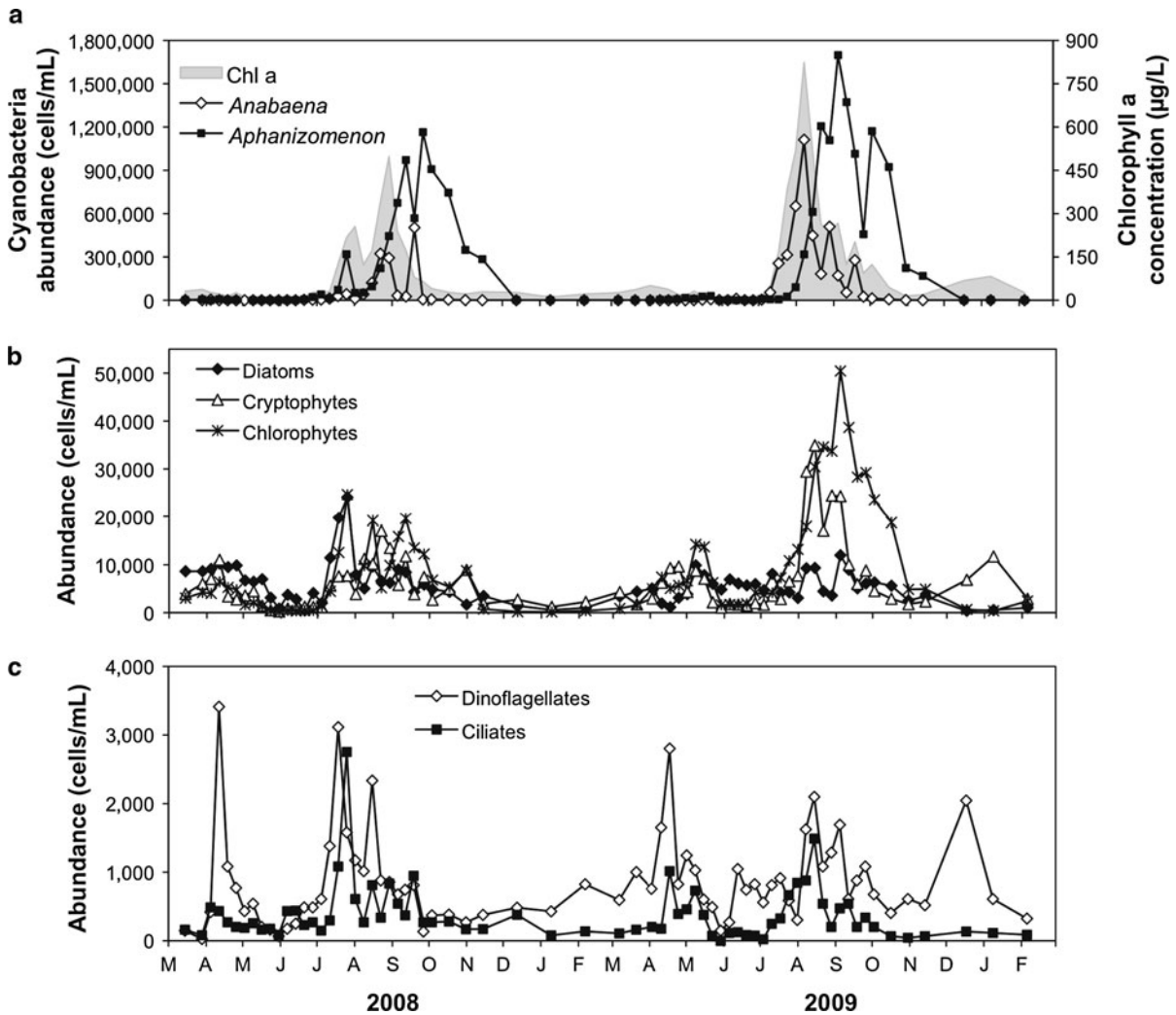

Fig. 3 Mean abundance of major taxonomic groups of protist plankton and cyanobacteria collected from the Vancouver Lake Sailing Club dock between March 2009 and February 2010. **a** Chlorophyll *a* concentration (*shaded region*) and cyanobacteria taxa; **b** diatoms, cryptophytes, and chlorophytes; **c** dinoflagellates and ciliates

were degraded and contained very lowpigment concentrations (Fig. 3a).

Among the protist community (unicellular eukaryotic algae and protozoans), similar patterns were observed between 2008 and 2009. In both years there was a small spring bloom of diatoms, chlorophytes, and cryptophytes (averaging $\sim 0.7 * 10^3$ cells ml^{-1}), followed by a second more substantial bloom in late summer, concurrent with the cyanobacteria. In 2008 the eukaryotic algal community during the second bloom was dominated by diatoms and chlorophytes, reaching $\sim 2.2 * 10^4$ cells ml^{-1}, but in summer 2009 the second algal bloom was larger (up to $5 * 10^4$ cells ml^{-1}) and dominated mostly by chlorophytes and cryptophytes (Fig. 3b). Heterotrophic-mixotrophic dinoflagellates and ciliates showed a similar pattern of separate spring and summer blooms, concurrent with peaks in the algal taxa. Dinoflagellate abundance was comparable between the two seasonal blooms in both 2008 and 2009, while ciliate abundance peaked mostly during the second (late summer) bloom of each year (Fig. 3c).

The pattern of abundance of metazoan zooplankton (cladocerans, copepods, and rotifers, adults only) differed substantially between years, with larger peaks of all three groups occurring during spring and

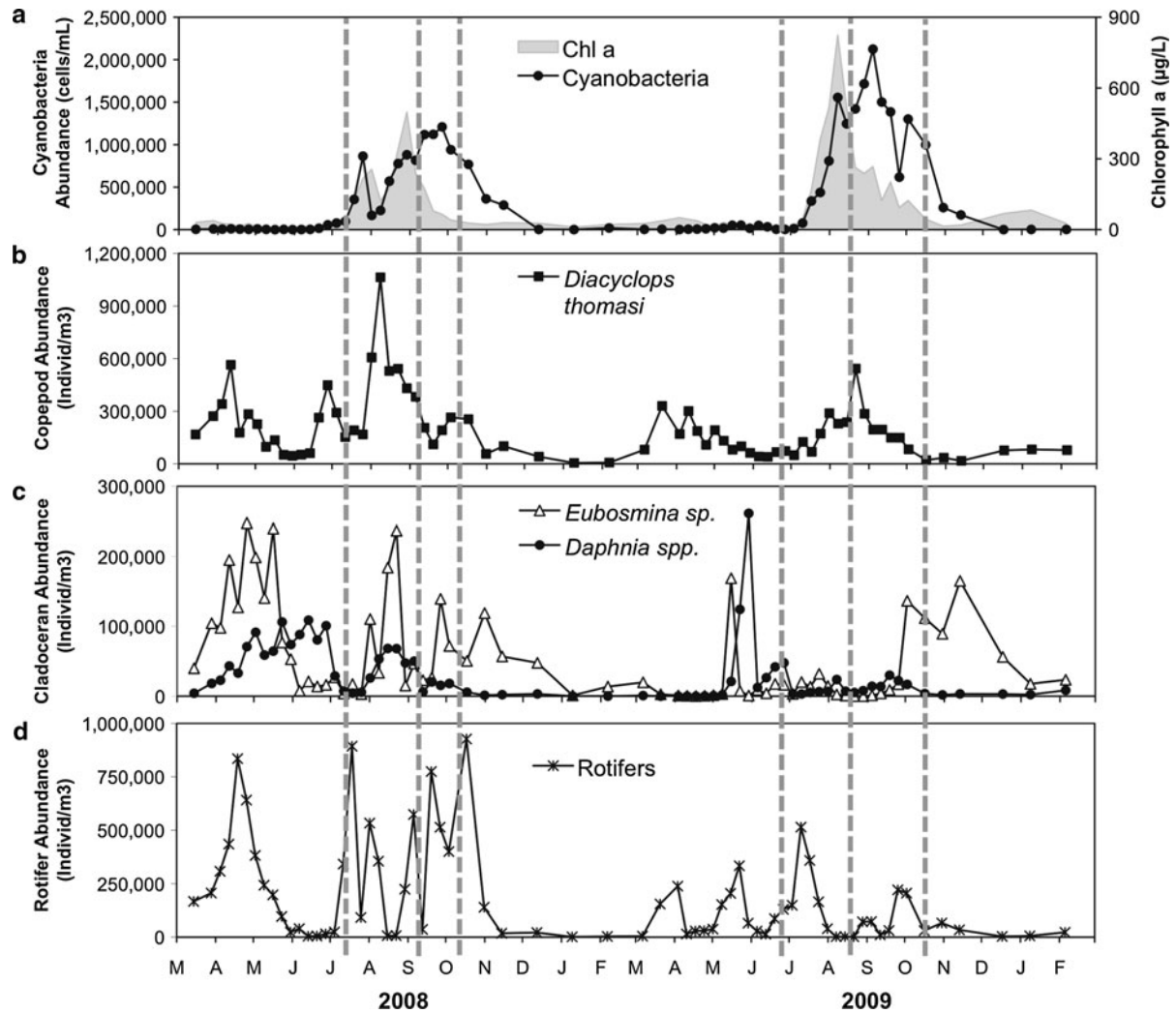

Fig. 4 Mean abundance of major taxonomic groups of metazoan zooplankton collected from Vancouver Lake Sailing Club dock between March 2009 and February 2010. **a** Chlorophyll *a* concentration (*shaded region*) and cyanobacteria; **b** copepods; **c** cladocerans; **d** rotifers. *Vertical dashed lines* indicate dates of grazing experiments

summer of 2008 compared to 2009 (Fig. 4). Copepods were most abundant during the spring and late summer chlorophyll bloom periods of both years (Fig. 4b). Notably, cladoceran abundance was close to zero throughout the summer 2009 peak in chlorophyll *a* concentration (Fig. 4c). Rotifer abundance, while highly variable from month to month, was generally lower during 2009 versus 2008 (Fig. 4d).

Zooplankton community composition showed a consistent seasonal succession during our two-year study, with cyclopoid copepods (exclusively *Diacyclops thomasi*) dominant in spring (March–April), followed by an increase in relative abundance of small cladocerans (mainly *Eubosmina* sp.) in May (Fig. 5). In June-July, a few weeks before each year's cyanobacteria bloom, a short-lived but substantial increase in larger cladocerans (*Daphnia retrocurva* and *Daphnia laevis*) occurred, but then rapidly disappeared. Rotifers (*Keratella* sp., *Polyarthra* sp., *Brachionus* sp., and *Asplanchna* sp.) gained dominance in the days just before cyanobacteria dramatically increased. During the August–September cyanobacteria blooms, cladocerans and rotifers generally became very low in abundance and copepods again dominated the assemblage. Finally, as chlorophyll *a* concentrations rapidly decreased in autumn, but the filamentous cyanobacteria

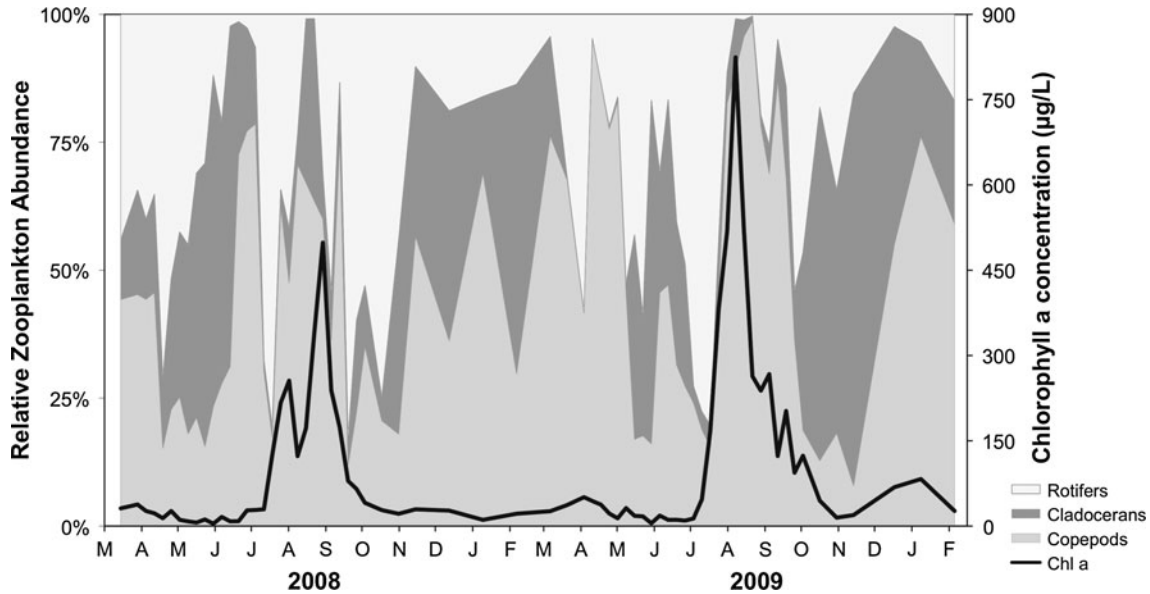

Fig. 5 Relative abundance of major taxonomic groups of metazoan zooplankton collected from Vancouver Lake Sailing Club dock between March 2009 and February 2010

Aphanizomenon flos-aquae was still highly abundant, small cladocerans (*Eubosmina* sp.) regained dominance of the zooplankton community, particularly in 2009 (Fig. 5).

Copepod diet and prey selectivity

All of the incubation experiments conducted over the two-year sampling period met our criteria for validity, and in each experimental period the dominant crustacean zooplankton taxon present was the cyclopoid copepod *Diacyclops thomasi* (except October 2009, when *Eubosmina* sp. cladocerans were most abundant). Therefore, we used *D. thomasi* as the predator in all of our experiments, such that all results of prey selectivity, feeding rates and grazing impact are measures of copepod grazing in Vancouver Lake.

Diacyclops thomasi prey selectivity was determined by comparison of (i) clearance rates and (ii) electivity indices (E^*) on different prey categories. Significant differences among prey clearance rates were observed during the incubation experiments conducted before each year's cyanobacteria bloom, indicative of selective feeding. In July 2008 the highest clearance rate (1.8 ml copepod^{-1} h^{-1}) was observed on ciliates <15 µm in size, and in June 2009 the highest clearance rate (1.1 ml copepod^{-1} h^{-1}) was observed on diatoms >15 µm in size. However, no significant differences in clearance rates between prey taxa were observed during or following the 2008 bloom or following the 2009 bloom (Fig. 6). Similarly, electivity indices calculated from feeding experiments in 2008 and 2009 showed *D. thomasi* preferred small ciliates before each summer's bloom, and were relatively non-selective feeders during and following the blooms (Fig. 7).

Copepod grazing rates and grazing impact

In July 2008, *Diacyclops thomasi* had the highest carbon biomass ingestion rates on heterotrophic-mixotrophic prey, namely large (>15 µm) dinoflagellates and ciliates. During the 2008 bloom in September, the copepods not only maintained a very high-ingestion rate on cyanobacteria (1.4 µg C copepod^{-1} h^{-1}) but also ingested diatoms at relatively moderate rates (Fig. 8a). During the comparable pre-bloom (June) and bloom (August) experiments of 2009, *D. thomasi* ingestion rates were generally quite low, however during the early part of each year's cyanobacteria bloom the copepods consumed cyanobacteria at exceptionally high rates (2.0 µg C copepod^{-1} h^{-1}) (Fig. 8b). By contrast, in October of both 2008 and 2009, while cyanobacteria abundance was still high but chlorophyll levels were lower, *D. thomasi* ingestion rates were extremely low to zero.

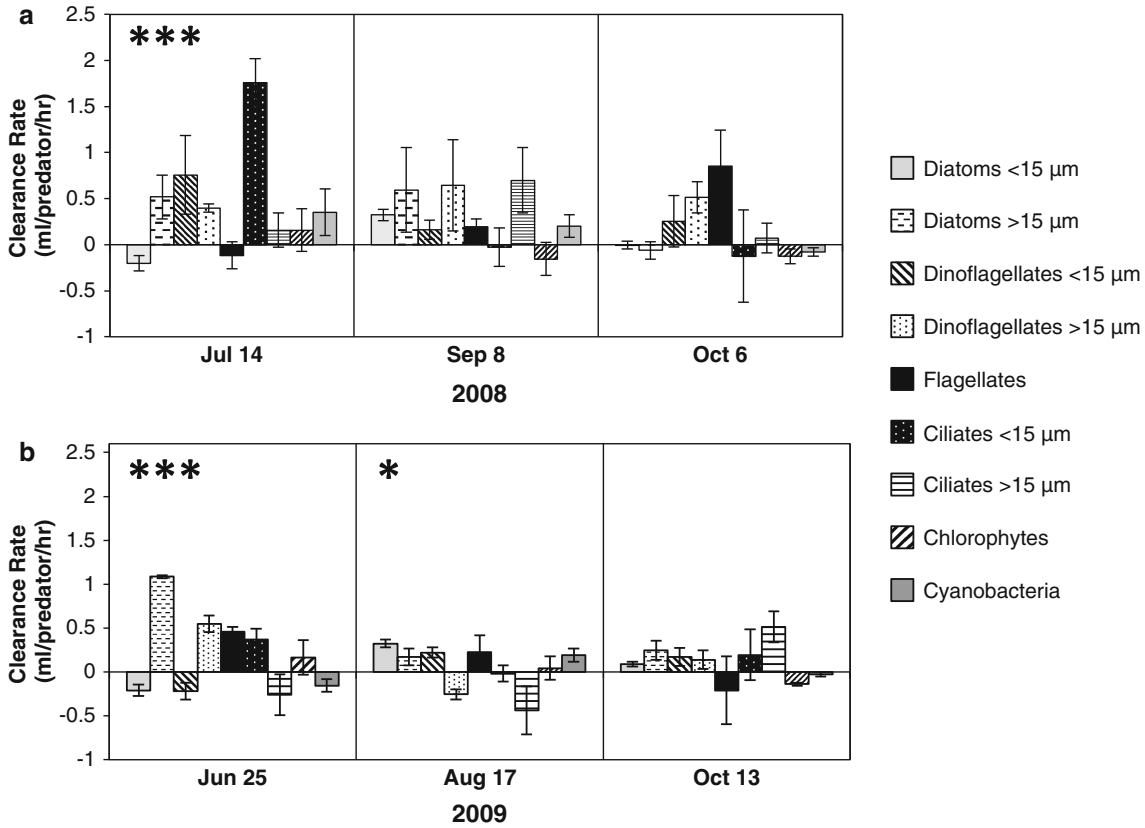

Fig. 6 Mean clearance rates of *Diacyclops thomasi* adult female copepods feeding on natural assemblages of planktonic prey during incubation experiments conducted using organisms collected from Vancouver Lake before, during, and after cyanobacteria blooms in **a** 2008 and **b** 2009. *Error bars* represent one standard error. *Asterisks* indicate experiments in which preference was shown among available prey, based on 1-way ANOVA. $^{*}P < 0.05$, $^{***}P < 0.001$

We calculated the difference between the grazing mortality rate coefficients and growth rate coefficients of each prey category for each incubation experiment with *D. thomasi* in 2008 and 2009 (Table 1). During July 2008, before the cyanobacteria bloom, the difference between grazing mortality and growth rate was most positive for >15 µm dinoflagellates and <15 µm ciliates (0.087 and 0.069, respectively), and was negative for <15 µm diatoms. During the height of the cyanobacteria bloom in September 2008, the difference between mortality and growth continued to be positive for most taxa, except for small (<15 µm) ciliates, chlorophytes, and cyanobacteria. As the bloom was waning, the mortality to growth difference was again high for dinoflagellates, but negative for diatoms. During June 2009, before the bloom, the difference between mortality and growth was again highest for ciliates and large dinoflagellates; however, during August 2009 this difference was most positive for diatoms. In October 2009 after the bloom peak, the growth rates of all prey categories except flagellates were higher than grazing rates (Table 1).

Finally, we estimated the potential grazing impact of copepods on the standing stock of cyanobacteria and protists in Vancouver Lake before, during, and following each year's bloom period. In July 2008, before the bloom, *Diacyclops thomasi* grazing impact was highest on ciliates (~80% of standing biomass consumed per day) and dinoflagellates (~30% of standing biomass consumed per day). The highest grazing impacts occurred in September 2008, at the height of the bloom, when copepods grazed 75–100% of diatom, ciliate, and chlorophyte biomass per day. Following the bloom in October 2008, copepods exhibited substantially lower grazing impact overall, and did not exceed 15% on any prey category (Fig. 9a).

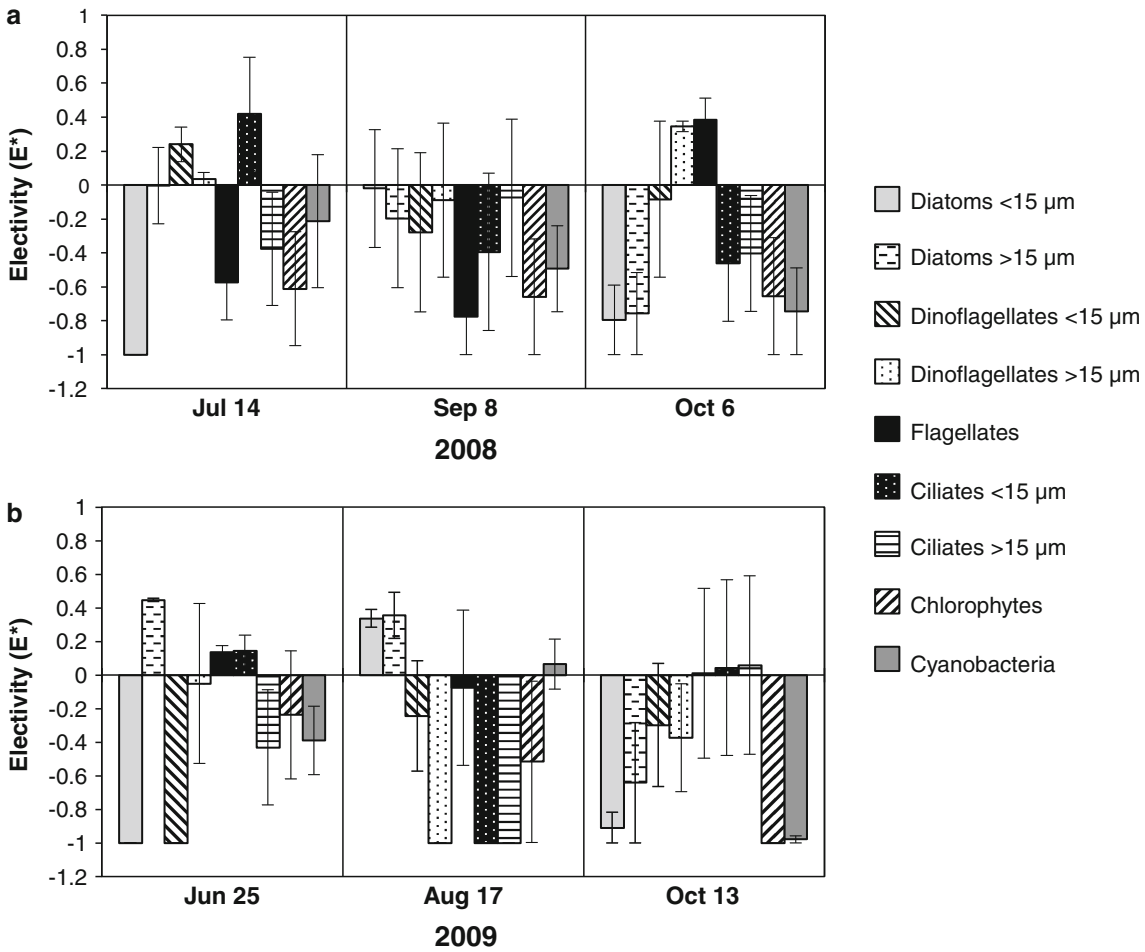

Fig. 7 Electivity indices (E*) of *Diacyclops thomasi* adult female copepods feeding on natural assemblages of planktonic prey during incubation experiments conducted using organisms collected from Vancouver Lake before, during, and after cyanobacteria blooms in **a** 2008 and **b** 2009. *Error bars* represent one standard error

Grazing impact in June 2009, several weeks before that year's bloom, was low to moderate (~15% prey biomass consumed on average per prey type), and focused entirely on non-algal or cyanobacterial prey categories. During the cyanobacteria bloom in August 2009, copepod grazing impact was highest, with comparable impact (~50%) on diatoms, dinoflagellates, and cyanobacteria. In October 2009, when chlorophyll levels were reduced substantially but cyanobacteria biomass was still high, *Diacyclops thomasi* grazing impact remained low on most prey categories (<10% of biomass consumed per day), although grazing impact on large diatoms and ciliates was higher (~20% of biomass consumed per day) (Fig. 9b).

Discussion

In this study we examined the role of metazoan zooplankton grazing before, during and following cyanobacteria blooms in Vancouver Lake, and specifically focused on the influence of copepods, a group of planktonic grazers less studied in freshwater systems than cladocerans (e.g., *Daphnia*), but nevertheless highly abundant in Vancouver Lake.

Zooplankton seasonal succession

Over our two-year project, from March 2008 to February 2010, the metazoan zooplankton community in Vancouver Lake was dominated by small (<1 mm)

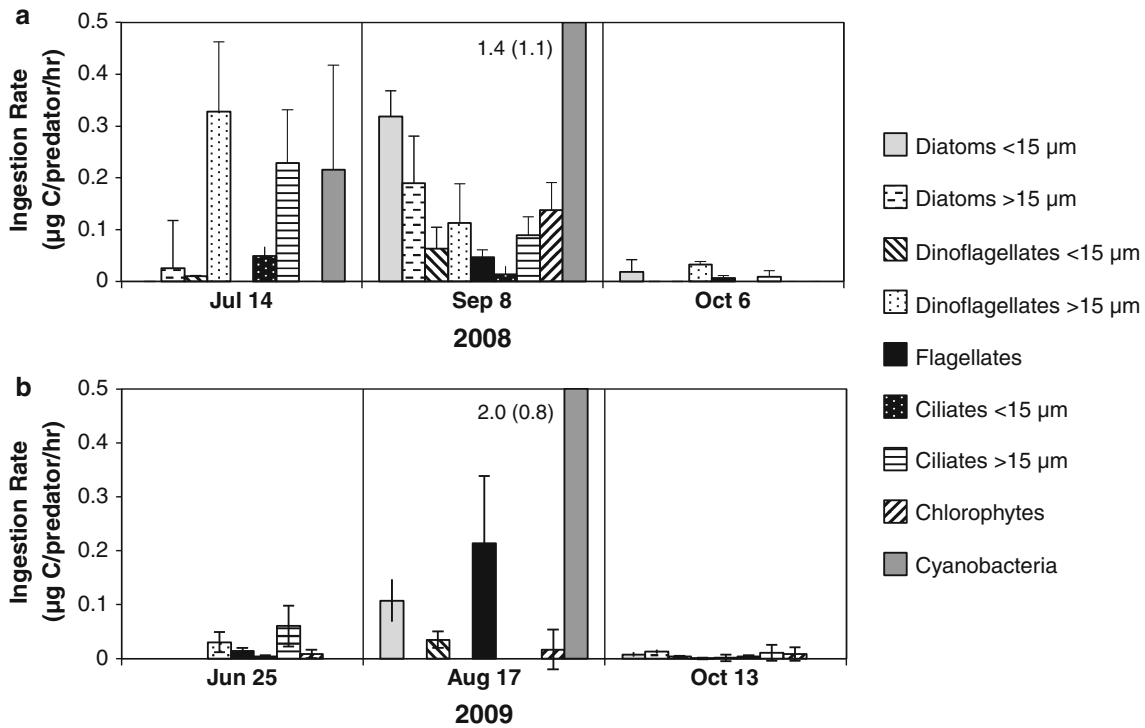

Fig. 8 Mean carbon ingestion rates of *Diacyclops thomasi* adult female copepods feeding on natural assemblages of planktonic prey during incubation experiments conducted using organisms collected from Vancouver Lake before, during, and after cyanobacteria blooms in **a** 2008 and **b** 2009. *Error bars* represent one standard error

cyclopoid copepods, rotifers, and cladocerans, with a general succession pattern over the spring and summer of each year from dominance by copepods to dominance by cladocerans, with copepod relative abundance always highest during algal-cyanobacteria blooms. Large cladocerans (*Daphnia retrocurva* and *D. laevis*), traditionally thought to be the dominant grazers in freshwater lake systems, were abundant only during the spring of 2008 and for a brief period during the summer 2008 cyanobacteria bloom.

This aligns with the typical zooplankton successional pattern observed in temperate lakes, of overall biomass increasing through the spring, with large grazers (e.g. *Daphnia*) attaining maximal abundance in late spring and then declining in summer (Sommer et al., 1986; Vanni & Temte, 1990). More specifically, the pattern of dominance by small sized zooplankton (mainly small copepods) and the loss of large daphnid cladocerans during filamentous cyanobacteria blooms that we observed has been documented in other lakes, such as Steele Lake, Canada (Ghadouani et al., 2003), and the Loostrecht Lakes in the Netherlands (DeMott et al., 2001). In both of these studies, large *Daphnia* spp. were found to be inhibited by feeding interference from cyanobacteria filaments (especially *Aphanizomenon*).

However, the very low abundance of all cladoceran species in Vancouver Lake throughout spring and summer 2009 (except for a very brief, but substantial, peak in May) was not expected and contrasted with the same period in 2008. Secchi depths were deeper (indicating greater water clarity) during spring 2008 compared to spring 2009, but water temperatures were comparable between years. Similarly, the abundance and composition of the algal community (including cyanobacteria taxa) during the spring and early summer were generally comparable between years, suggesting that the low abundance of cladocerans was not likely due to the lack of food resources or potential toxic effects of cyanobacteria before the large summer blooms. One possibility is that the selective fish predation on large cladocerans reduced their abundance, as has been shown in other lake systems (e.g., Brooks & Dodson, 1965; Vijverberg et al., 2005; Iglesias et al., 2011). However, data on the abundance and composition of the fish community in Vancouver

Table 1 Difference between grazing mortality rate (g, h^{-1}) and growth rate (r, h^{-1}) coefficients of prey taxa measured in incubation experiments with *Diacyclops thomasi* conducted before, during, and near the end of cyanobacteria blooms in summer 2008 and summer 2009 in Vancouver Lake, WA

Prey category	July 2008			September 2008			October 2008		
	g	*r*	$(g - r)$	*g*	*r*	$(g - r)$	*g*	*r*	$(g - r)$
Diatoms <15 μm	−0.016	0.014	**−0.030**	0.026	0.022	**0.004**	−0.001	0.000	**−0.001**
Diatoms >15 μm	0.041	−0.005	**0.047**	0.048	0.015	**0.033**	−0.008	−0.001	**−0.006**
Dinoflagellates <15 μm	0.061	−0.022	**0.083**	0.013	0.010	**0.003**	0.030	−0.021	**0.052**
Dinoflagellates >15 μm	0.032	0.002	**0.030**	0.051	0.013	**0.039**	0.062	−0.004	**0.066**
Flagellates	−0.009	−0.021	**0.012**	0.016	0.029	**−0.013**	0.102	−0.016	**0.119**
Ciliates <15 μm	0.141	0.072	**0.069**	−0.002	−0.024	**0.022**	−0.015	−0.021	**0.006**
Ciliates >15 μm	0.013	−0.014	**0.027**	0.056	0.014	**0.042**	0.009	−0.012	**0.020**
Chlorophytes	0.013	0.010	**0.003**	−0.012	−0.008	**−0.005**	−0.015	−0.027	**0.011**
Cyanobacteria	0.028	0.003	**0.025**	0.016	0.023	**−0.007**	−0.009	−0.016	**0.006**
Prey category	June 2009			August 2009			October 2009		
	g	*r*	$(g - r)$	*g*	*r*	$(g - r)$	*g*	*r*	$(g - r)$
Diatoms <15 μm	−0.017	0.011	**−0.028**	0.026	0.008	**0.017**	0.007	0.018	**−0.011**
Diatoms >15 μm	0.087	−0.014	**0.101**	0.014	−0.022	**0.036**	0.020	0.063	**−0.043**
Dinoflagellates <15 μm	−0.018	0.023	**−0.041**	0.018	0.020	**−0.002**	0.014	0.030	**−0.017**
Dinoflagellates >15 μm	0.044	−0.017	**0.061**	−0.020	0.021	**−0.041**	0.011	0.039	**−0.027**
Flagellates	0.037	0.005	**0.032**	0.018	0.013	**0.005**	−0.017	−0.028	**0.011**
Ciliates <15 μm	0.030	−0.015	**0.045**	−0.001	0.021	**−0.023**	0.016	0.017	**−0.001**
Ciliates >15 μm	−0.021	−0.048	**0.027**	−0.035	0.020	**−0.055**	0.041	0.058	**−0.017**
Chlorophytes	0.013	−0.013	**0.026**	0.003	−0.008	**0.011**	−0.011	−0.007	**−0.005**
Cyanobacteria	−0.012	−0.042	**0.030**	0.015	0.003	**0.012**	−0.002	0.003	**−0.005**

Positive values of $(g - r)$ = grazing rates exceeded growth rates; negative values = growth rates exceeded grazing rates

Lake is limited to a brief, three-day survey conducted in September 1998 (Caromile et al., 2000), thus this explanation cannot be confirmed with the data in hand.

Copepod prey selectivity and feeding

Copepods, comprised almost exclusively of the cyclopoid *Diacyclops thomasi*, were the most abundant crustacean zooplankton present in Vancouver Lake immediately before, during and in the two weeks following the cyanobacteria blooms in 2008 and 2009. Like many other copepod taxa, *D. thomasi* was a highly selective feeder, particularly in early summer, before each year's cyanobacteria bloom. Many factors may affect the preferences of copepods feeding on natural prey assemblages, including size and nutritional quality (e.g., DeMott 1995a, b), prey morphology (i.e., filaments, colonies, etc., see Fulton 1988), and the presence of algal toxins (e.g., Teegarden 1999). In Vancouver Lake, *D. thomasi* chiefly targeted ciliates and dinoflagellates, and to a much lesser degree cyanobacteria (in 2008) and diatoms (in 2009).

Diacyclops thomasi is well-known as a carnivore in other lake systems. For instance, in a review by Brandl (2005), *D. thomasi* was found to be a strong predator on rotifers in laboratory experiments conducted using specimens from numerous freshwater, limnetic environments, ranging from large deep lakes (e.g., Lake Michigan) to small shallow lakes (e.g., a Czech carp pond) to ephemeral pools in Australia. *D. thomasi* was also observed to consume large numbers of planktonic ciliates in Castle Lake, California (Wiackowski et al., 1994; Dobberfuhl et al., 1998) and in Lake Ontario (Le Blanc et al., 1997). Indeed, the measured rates of *D. thomasi* grazing on ciliates in Castle Lake were high enough that in 1993, when *D. thomasi* abundance increased dramatically after removal of planktivorous fish, *D. thomasi* likely reduced ciliate abundance

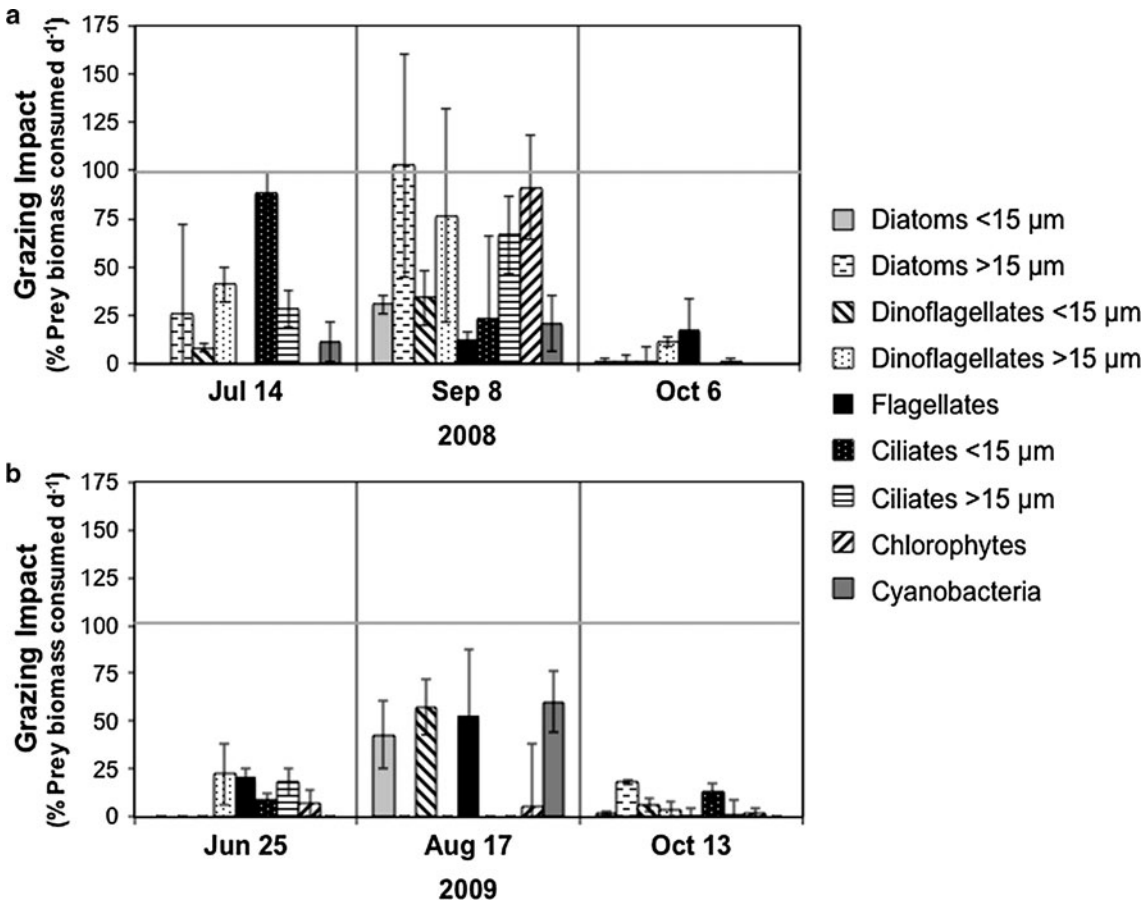

Fig. 9 Grazing impact of *Diacyclops thomasi* adult female copepods on natural assemblages of planktonic prey during incubation experiments conducted using organisms collected from Vancouver Lake before, during, and after cyanobacteria blooms in **a** 2008 and **b** 2009. *Error bars* represent one standard error

enough to result in substantial increases in algal productivity—a "trophic cascade" quite opposite to the expectations of the investigators (Elser et al., 1995).

Because our experiments were designed to test the impact of copepods feeding on protists and cyanobacteria, we did not measure *Diacyclops thomasi* feeding rates on rotifers in Vancouver Lake. However, the preference of *D. thomasi* for ciliates and dinoflagellates in Vancouver Lake is in line with published observations from other temperate lakes shown above, as well as documented preferences of cyclopoid copepods for ciliates (e.g., Wickham 1995) and for small, soft-bodied prey (Brandl 1998, 2005). Moreover, the clearance rates we observed for *D. thomasi* in Vancouver Lake fell within the ranges reported in the few prior studies of grazing by this copepod, in Lake Ontario (Le Blanc et al., 1997) and in laboratory experiments conducted with *D. thomasi* collected from Lake Michigan (Stemberger, 1985). Interestingly, in addition to confirming carnivory in *D. thomasi*, our results also support previous laboratory studies that showed *D. thomasi* can consume algae even in the presence of invertebrate prey (Adrian & Frost, 1993). Thus, *D. thomasi* in Vancouver Lake was an omnivorous feeder, especially during the cyanobacteria blooms.

Diacyclops thomasi selectivity for algal, ciliate, and dinoflagellate prey, when applied to the total biomass of all prey types available, translated into relatively high- ingestion rates of ciliate and dinoflagellate biomass by these copepods in Vancouver Lake, especially before the bloom of 2008. In addition, during each year's cyanobacteria bloom, *D. thomasi*

consumed substantial amounts of filamentous cyanobacteria biomass. This suggests that *D. thomasi* actively sought out more desirable prey when cyanobacteria abundance was low, but when the prey assemblage was heavily dominated by cyanobacteria (both *Aphanizomenon* and *Anabaena*), they were able to consume these cells in addition to their preferred prey. But copepod ingestion rates were extremely low near the end of the blooms of both 2008 and 2009, indicating that either the abundance of cyanobacteria filaments had eventually become so dense that they interfered with the copepods' suspension feeding apparatus, as has been observed for some cladocerans (e.g., Gliwicz 1990; DeMott et al. 2001), or possibly the cyanobacteria may have been producing toxins that over time diminished the copepods' physiological capacity to feed or to survive (e.g., Ger et al. 2010).

Copepod grazing impact and implications for filamentous cyanobacteria blooms

In the winter and spring of both 2008 and 2009, cyanobacteria abundance in Vancouver Lake was relatively constant at $\sim$1–3 * 10^2 cells ml^{-1}. However, over the course of only 5–7 days in late July (2008) and early August (2009), cyanobacteria abundance rapidly and dramatically increased four orders of magnitude to maxima of 1–2 * 10^6 cells ml^{-1}. In the weeks leading up to each year's bloom, *Diacyclops thomasi* copepods were exerting a strong grazing impact on ciliate, and to some degree dinoflagellate, biomass. Similarly, the presence of *D. thomasi* in the experimental incubations also resulted in substantial mortality relative to growth of dinoflagellates before each year's cyanobacteria bloom, and in July 2008 the difference between grazing mortality and growth rate coefficient for cyanobacteria was also relatively high.

It should be noted that in feeding incubation experiments using the natural assemblage of plankton, it can sometimes be difficult to determine the direct consumption of individual prey taxa by the treatment predator, due to the potentially complicated trophic dynamics within the incubation bottles (e.g., Nejstgaard et al., 2001) that can produce either weak (Samuelsson & Andersson, 2003; Jing et al., 2010; Siuda & Dam, 2010) or strong trophic cascading effects (Zollner et al., 2009). In addition, copepod grazing impact determined using the grazing rate coefficient (g) calculated from the feeding incubation experiments may overestimate the effect of copepods in Vancouver Lake. We used constant copepod predator densities (80 per l) in all incubations, which were sufficient to significantly reduce prey abundance but not so high as to completely remove all prey cells. However, these experimental densities were often less than the density of *D. thomasi* present in the field, thus the calculated per capita grazing mortality rates in the incubations could have been higher than would be observed in the Lake due to reduced density-dependent factors (e.g., food limitation). Similarly, our estimation of grazer control on prey growth as measured using difference between grazing rate coefficient (g) and growth rate coefficient (r) may be an overestimation, since the calculation of g is dependent on r, and r could be underestimated from incubation controls that do not contain predators but may still contain other sources of mortality (e.g., micrograzers, viruses).

However, in a companion study to ours, Boyer et al. (2011) used a series of dilution experiments to show that ciliates and dinoflagellates in Vancouver Lake almost exclusively consumed diatoms from May 2008 to July 2008. Thus, in addition to some direct grazing on cyanobacteria by *D. thomasi*, low cyanobacteria abundance in the Lake during the pre-bloom period could have been due to *D. thomasi* selectively consuming ciliates and dinoflagellates, which may have provided diatoms a refuge from grazing and possibly allowed them to out-compete cyanobacteria for nutrients and light. Such a pattern has been observed in laboratory experiments with diatoms and cyanobacteria from a range of mid-latitude lakes (Tilman et al., 1986).

Based on this scenario, copepods may have helped to facilitate the cyanobacteria blooms by shifting their diet toward diatoms as they became more abundant, which could have reduced the competitive pressure on cyanobacteria and contributed to their rapid proliferation. Indeed, at the peak of the cyanobacteria bloom in 2009 *Diacyclops thomasi* were imposing higher overall mortality on diatoms and ingesting diatom biomass at higher rates than they were consuming ciliates or dinoflagellates, sufficient to remove $\sim$100% of large diatom biomass per day. Notably, even though *D. thomasi* were also consuming cyanobacteria at extremely high rates during the height of the blooms, this consumption was not enough to substantially reduce cyanobacteria abundance.

Moreover, in October of both years the difference between mortality and growth rates of cyanobacteria in the experiments was negative or near zero, thus *D. thomasi* likely did not significantly contribute to the eventual decline in cyanobacteria abundance in Vancouver Lake.

We are aware of only three other published studies that have specifically measured *Diacyclops thomasi* grazing on the natural assemblage of lentic plankton, and all were focused in larger, deeper lakes (Castle Lake, California, and Lake Ontario) that do not suffer from nuisance cyanobacteria blooms (Wiackowski et al., 1994; Le Blanc et al., 1997; Dobberfuhl et al., 1998). Thus, we believe our study in Vancouver Lake is the first direct assessment of *D. thomasi* feeding on natural assemblages of co-occurring algal, protozoan and cyanobacterial prey, as well as the first to examine *D. thomasi* feeding in a large, shallow, and highly eutrophic lake.

While still speculative, our results suggest that in Vancouver Lake, grazing by *Diacyclops thomasi* may have indirectly (via consumption of micrograzers, e.g., ciliates and dinoflagellates) delayed the initiation of filamentous cyanobacteria blooms, but that copepod grazing did not prevent the cyanobacteria blooms nor did they substantially control their eventual declines. And while we did not specifically measure the grazing rates of cladoceran zooplankton, given the very low abundance of these grazers before, during, and following the blooms, our results also suggest that copepods were likely the strongest crustacean grazing influence on the cyanobacteria.

Elser (1999) proposed that cyanobacteria blooms in lakes occur as the result of a series of inter-dependent mechanisms, ranging from the quantity and ratio of nutrient inputs into a lake system to the mixing regime acting on the algal community, but that ultimately food web interactions and consumer-driven processes (mainly driven by large daphnid cladoceran zooplankton) may be the last defense against cyanobacteria outbreaks. While our study was not designed to specifically assess the role of abiotic factors (e.g., nutrients, turbulence) or cladoceran grazing on filamentous cyanobacteria blooms, our results suggest that trophic interactions may indeed strongly influence bloom dynamics. More specifically, copepods in Vancouver Lake may have had an indirect effect on cyanobacteria during pre-bloom periods, but probably not a direct effect during and following cyanobacteria blooms. Our study further suggests that efforts to mitigate or eliminate filamentous cyanobacteria blooms in Vancouver Lake and other shallow, turbid lakes through biomanipulation using planktivorous and/or piscivorous fish will necessarily need to consider complex trophodynamics throughout the planktonic food web—especially among lower trophic levels, e.g., both microzooplankton herbivory (Boyer et al., 2011; Rollwagen-Bollens et al., 2011) and mesozooplankton omnivory (Rollwagen-Bollens & Penry, 2003; Gifford et al., 2007).

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