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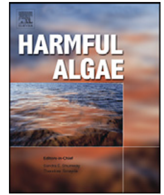

Mesozooplankton and microzooplankton grazing during cyanobacterial blooms in the western basin of Lake Erie

Timothy W. Davis [a,1], Florian Koch [a], Maria Alejandra Marcoval [a], Steven W. Wilhelm [b], Christopher J. Gobler [a,*]

[a] Stony Brook University, School of Marine and Atmospheric Sciences, Stony Brook, NY 11794-5000, USA
[b] Department of Microbiology, University of Tennessee, Knoxville, TN 37996, USA

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ABSTRACT

Lake Erie is the most socioeconomically important and productive of the Laurentian (North American) Great Lakes. Since the mid-1990s cyanobacterial blooms dominated primarily by *Microcystis* have emerged to become annual, late summer events in the western basin of Lake Erie yet the effects of these blooms on food web dynamics and zooplankton grazing are unclear. From 2005 to 2007, grazing rates of cultured (*Daphnia pulex*) and natural assemblages of mesozooplankton and microzooplankton on five autotrophic populations were quantified during cyanobacterial blooms in western Lake Erie. While all groups of zooplankton grazed on all prey groups investigated, the grazing rates of natural and cultured mesozooplankton were inversely correlated with abundances of potentially toxic cyanobacteria (*Microcystis*, *Anabaena*, and *Cylindrospermopsis*; $p < 0.05$) while those of the *in situ* microzooplankton community were not. Microzooplankton grazed more rapidly and consistently on all groups of phytoplankton, including cyanobacteria, compared to both groups of mesozooplankton. Cyanobacteria displayed more rapid intrinsic cellular growth rates than other phytoplankton groups under enhanced nutrient concentrations suggesting that future nutrient loading to Lake Erie could exacerbate cyanobacterial blooms. In sum, while grazing rates of mesozooplankton are slowed by cyanobacterial blooms in the western basin of Lake Erie, microzooplankton are likely to play an important role in the top-down control of these blooms; this control could be weakened by any future increases in nutrient loads to Lake Erie.

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1. Introduction

The Laurentian (North American) Great Lakes are a vital global resource containing roughly 18% of Earth's available freshwater (Fuller et al., 2002). Over the past several decades these systems have been subject to a series of anthropogenic pressures such as the introduction of non-native species (i.e., dreissenid mussels) and eutrophication. Of the Great Lakes, Lake Erie is the most socioeconomically important (Fuller et al., 2002; Munawar et al., 2002) serving the recreational, commercial, and drinking water needs of over ten million people (Fuller et al., 2002). It is divided into the physically, chemically, and biologically distinct eastern, central, and western basins. Lake Erie is also the smallest and shallowest Great Lake, and thus is the most sensitive to nutrient loading.

Anthropogenic nutrient loading has contributed toward enhanced phytoplankton biomass in Lake Erie, often dominated by potentially toxic cyanobacteria, in the central and western basins of Lake Erie since 1960 (Davis, 1964; Rosa and Burns, 1987; Makarewicz, 1993). The intensity and frequency of cyanobacteria blooms waned during the 1970s and 1980s with the establishment of phosphorus (P) loading reduction measures and the introduction of dreissenid mussels (Nicholls and Hopkins, 1993; Madenjian, 1995; Fahnenstiel et al., 1998). This recovery was temporary, however, as by the mid-1990s cyanobacterial blooms dominated by *Microcystis* spp. returned despite relatively constant allochthonous P inputs (Conroy et al., 2005; Rinta-Kanto et al., 2009a,b).

Many factors potentially control the dynamics of cyanobacterial blooms in Lake Erie, including nutrient availability, light, wind strength (Nicholls and Hopkins, 1993; Wilhelm et al., 2003; Porta et al., 2005; Conroy et al., 2005; Millie et al., 2009) and benthic grazing (Vanderploeg et al., 2001; Conroy and Culver, 2005). Differences and dynamics among the genetic strains of cyanobacteria within these blooms may also influence population and bloom dynamics (Rinta-Kanto et al., 2005, 2009a,b). In contrast to

* Corresponding author. Tel.: +1 631 632 5043; fax: +1 631 632 8820.
E-mail address: cgobler@notes.cc.sunysb.edu (C.J. Gobler).
[1] Current address: Australian Rivers Institute, Griffith University, Nathan, Queensland, 4111, Australia.

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these factors, few, if any, studies have investigated grazing by pelagic zooplankton during cyanobacteria blooms in Lake Erie.

Traditionally, large (>200 μm), mesozooplankton such as daphnids have been considered the primary grazers of phytoplankton in freshwater ecosystems (see review by Sommer and Sommer, 2006). However, microzooplankton may also be important grazers of phytoplankton in Lake Erie. The phototrophic picoplankton (0.2–2 μm), which account for a majority of primary production in the Great Lakes (Fahnenstiel et al., 1986; Pick and Caron, 1987; Fahnenstiel and Carrick, 1992), are an ideal prey group for microzooplankton, but not larger zooplankton (Sherr and Sherr, 2002).

Few prior studies have quantified zooplankton grazing rates on Lake Erie phytoplankton. Wu and Culver (1991) reported that grazing rates of two pelagic zooplankton, *Daphnia galeata* and *Daphnia retrocurva*, accounted for roughly 85% of the zooplankton community grazing rate and kept algal biomass in western Lake Erie low. Twiss et al. (1996) reported picoplankton (0.2–2 μm) in central and eastern basins were grazed at rates between 0.13 and 0.14 d^{-1} by microzooplankton. Gobler et al. (2008) found that half of phytoplankton mortality in central Lake Erie was due to microbial herbivory. However, to our knowledge, no study has quantified and compared grazing rates by micro- *and* mesozooplankton during cyanobacterial blooms in the western basin of Lake Erie.

The aim of this study was to quantify mortality rates of phytoplankton communities due to micro- and mesozooplankton grazing during cyanobacterial blooms in the western basin of Lake Erie. During a three-year field study, grazing rates of cultured (*Daphnia pulex*) and natural populations of mesozooplankton were quantified and compared to grazing rates of natural microzooplankton communities. Quantification of phytoplankton community composition via pigment and flow cytometric analysis permitted grazing rates on multiple prey groups to be compared. Quantification of intrinsic cellular algal growth rates with and without nutrients permitted the comparison of grazing and growth for each phytoplankton group.

2. Methods

2.1. Sampling sites

In 2005, 2006, and 2007, 12 stations in the western basin of Lake Erie were sampled either on the RV '*Lake Guardian*' or on the Canadian Coast Guard Vessel (CCCV) '*Limnos*' (Fig. 1 and Table 1) during August and September, the period when cyanobacteria form blooms in western Lake Erie (Rinta-Kanto et al., 2009a,b). During each year, temperature and oxygen profiles were collected from each station via automated water column profilers (Table 1). Water was collected from one meter below the surface via a rosette cast. Chlorophyll *a* (chl *a*) concentrations were determined from triplicate samples collected on glass fiber filters (GF/F; 0.7 μm pore-size; 47 mm diameter; Millipore), after extraction (ca. 24 h, −20 °C) in 90% acetone. Extracted chlorophyll *a* and *in vivo* phycocyanin (as a proxy for total cyanobacteria; 2006 and 2007 only) concentrations were measured in triplicate with a Turner Designs TD-700 fluorometer (Parsons et al., 1984; Watras and Baker, 1988; Lee et al., 1994). Duplicate whole water samples were preserved with Lugol's iodine solution (5% final concentration) to quantify the autotrophic plankton assemblages (cells > 10 μm). Autotrophic nano- and picoplankton communities (<10 μm) were analyzed by flow cytometry in samples preserved in 1% formalin which were flash frozen in liquid nitrogen until analysis. In addition to the quantification of eukayotic algae, two distinct classes of cyanobacteria were quantified by flow cytometry. One group consisted of small, unicellular cyanobacteria that contained phycoerythrin, resembling *Synechococcus* spp., while the second population consisted of coccoid, phycoerythrin-containing cyanobacteria, which were slightly larger (ca. 1 μm.) than *Synechococcus*-like cyanobacteria (Gobler et al., 2008). The degree to which individual biological and environmental variables were correlated was evaluated by a Pearson's correlation matrix.

2.2. Mesozooplankton experiments

During August 2006 and September 2007, the cultured cladoceran, *D. pulex* (Aquatic Research Organisms, New Hampshire, USA), was maintained in separate 40-L aquaria filled with 0.2-μm filtered mineral water and fed a diet of *Selenestrun capricornutum* (∼1×10^5 cells mL^{-1}) and Yeast-Cereal-Trout food at a temperature of 23 °C, under 25 μmol quanta m^{-2} s^{-1} of irradiance (cool-white fluorescence lamp). Zooplankton were bubbled with air and fed every other day and aquaria water was exchanged weekly. For experiments, *D. pulex* was individually added to experimental bottles using a modified transfer pipette at densities which have previously been observed during cyanobacteria blooms (52 L^{-1} and 60 L^{-1}, 2006 and 2007, respectively except for site 1163, 11 August 2006, 104 L^{-1}; Threlkeld, 1979; Camacho and Thacker, 2006; Davis and Gobler, 2011). Natural populations of mesozooplankton which potentially included some larger microzooplankton (>61 μm) were concentrated to 4-times ambient concentrations over a submerged 61-μm sieve preventing desiccation or damage to the zooplankton (Deonarine et al., 2006). To minimize the amount of large cyanobacteria in concentrates, the solution was placed over a light for 30 min after which cyanobacterial colonies, that had either risen to the surface or collected at the bottom of the container, were carefully removed using a modified transfer pipette. Few, if any, zooplankton were removed by this process. The entire plankton assemblage after these manipulations was quantified (see below) and used as a basis for interpreting experimental results.

During August 2006 and September 2007, 7 × 250 mL acid-cleaned polycarbonate bottles were filled with whole lake water. One bottle was immediately processed for the analysis of chlorophyll *a* and phycocyanin concentrations, as well as cell enumeration and flow cytometry as described above. The remaining bottles were established as unamended controls ($n = 3$) and *D. pulex* additions ($n = 3$). Four additional bottles were filled to a total volume of 250 mL with 4 times the natural mesozooplankton concentration (using the concentrate described above). One of these zooplankton enrichment bottles was immediately sacrificed for the quantification analysis of chlorophyll *a* and phycocyanin concentrations, as well as plankton enumeration and flow cytometric analyses. The other three bottles were incubated in parallel with the control and *D. pulex* treatments. To minimize the effects of nutrients from zooplankton excretion during experiments, saturating nutrients (20 μM nitrate, 1.25 μM orthophosphate) were added to all experimental bottles. Bottles were incubated in an environmental control chamber using a 14:10 light:dark cycle for ∼24 h. Light and temperature levels were set to match *in situ* conditions via the addition of screening and manipulation of temperatures. All experimental bottles were gently inverted every 4–6 h during experiments to prevent congregation or settling of plankton. At the end of the experiment, aliquots were removed to quantify zooplankton grazing rates on the total phytoplankton community (chlorophyll *a*), total cyanobacteria (phycocyanin), *Synechococcus* spp., unicellular cyanobacteria, and eukaryotic nano- and picoplankton. Growth rates for all populations were calculated using the equation: $\mu = \ln [N_t/N_o]/t$ where μ is the rate of population growth (d^{-1}), N_o and N_t are initial and final cell densities or pigment levels, and t is the duration of incubation. Grazing rates of cultured and concentrated zooplankton were calculated according to Frost (1972)

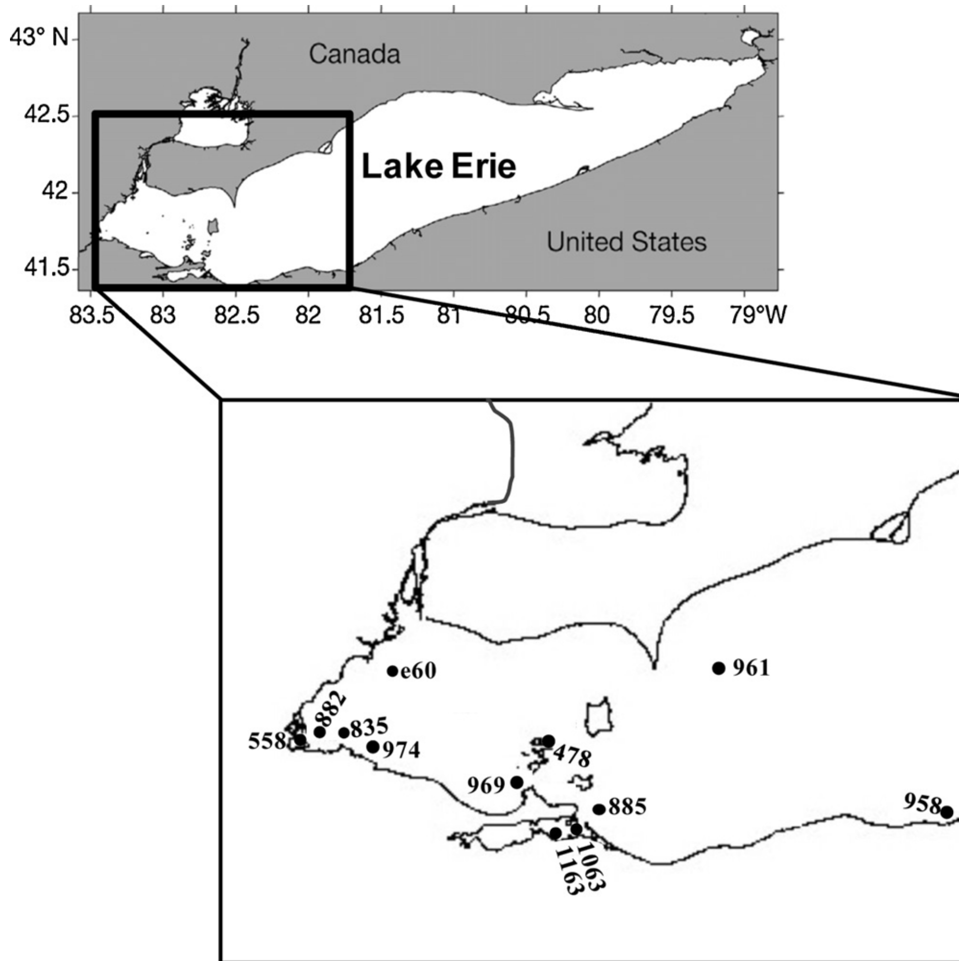

Fig. 1. Stations sampled from 2005 to 2007 in the western basin of Lake Erie.

Table 1
Location and physiochemical parameters recorded for each station from 2005 to 2007. Extracted chlorophyll *a* and *in vivo* phycocyanin concentrations are represented as mean (SE) of triplicate samples. NM indicates the parameter was not measured on that date. Bolded sites represent sites with 'bloom' cyanobacterial densities ($>4\times10^4$ cells mL^{-1}).

Site	Date	Latitude (N)	Longitude (W)	Chlorophyll *a* ($\mu g\,L^{-1}$)	Phycocyanin (RFU)	Surface temperature (°C)	Dissolved oxygen ($mg\,L^{-1}$)
2005							
1163	8-Aug	41°28′26″	82°42′12″	44.6 (6.48)	NM	27	NM
835	8-Aug	41°45′15″	83°20′31″	9.0 (0.53)	NM	27	NM
558	22-Aug	41°41′55″	83°27′40″	27.5 (0.76)	NM	25	6.4
969	23-Aug	41°36′29″	82°55′27″	17.8 (3.4)	NM	25	9.1
1163	23-Aug	41°28′26″	82°42′12″	32.7 (1.5)	NM	24	8.7
882	27-Aug	41°45′59″	83°18′34″	41.7 (3.2)	NM	25	NM
969	27-Aug	41°36′29″	82°55′27″	18.6 (0.14)	NM	25	9.2
1163	27-Aug	41°28′26″	82°42′12″	38.6 (2.3)	NM	25	NM
2006							
1163	11-Aug	41°28′26″	82°42′12″	45.9 (1.6)	25.5 (0.26)	26	9.6
478	11-Aug	41°39′30″	82°49′00″	5.33 (0.22)	1.53 (0.15)	25	8.4
882	11-Aug	41°45′59″	83°18′34″	29.3 (0.32)	2.37 (0.23)	26	8.6
974	13-Aug	41° 43′34″	83° 09′00″	10.6 (0.45)	2.57 (0.46)	26	8.5
885	13-Aug	41°31′09″	82°38′28″	5.11 (0.24)	1.7 (0.1)	25	8.6
961	14-Aug	41°54′33″	82°10′59″	4.25 (0.04)	1.17 (0.06)	23	nd
958	16-Aug	41°31′35″	81°42′33″	6.96 (0.09)	1.87 (0.31)	23	8.6
1063	16-Aug	41°28′40″	82°46′11″	7.77 (0.29)	1.8 (0.1)	25	8.5
2007							
969	13-Sep	41°36′29″	82°55′27″	3.5 (0.01)	1.7 (0.03)	22	8.6
835	13-Sep	41°45′15″	83°20′31″	3.0 (0.06)	1.3 (0)	21	8.0
e60	13-Sep	41°53′30″	83°11′48″	4.8 (0.21)	0.9 (0)	22	8.9
1163	14-Sep	41°28′26″	82°42′12″	51 (3.2)	36 (0.46)	21	9.0

as follows: $g = (\mu_c - \mu_g)$ where g is the grazing rate a prey population, μ_c is the rate of population growth in nutrient control treatments (treatments with N and P addition but no zooplankton) and μ_g is the rate of population growth in zooplankton addition treatments. Using the calculated g value, clearance rate (CR) for the cultured *D. pulex* was determined using the equation: $CR = (g \times (V/(t \times n)))$ where V is the bottle volume, t is the time of incubation (in hours), and n is the number of zooplankton added. However, since the natural mesozooplankton community was comprised of multiple genera with differing clearance rates, a community grazing rate was obtained by dividing the Frost (1972) grazing rates by four to account for experimental enrichment in zooplankton during experiments. Negative grazing rates (increases in algal growth rates upon the addition of the grazers) were used and interpreted as an absence of grazing by the added zooplankton (Richman et al., 1977; Vanderploeg and Scavia, 1979). Clearance rates or grazing rates by each grazer on each algal prey group (total phytoplankton (chlorophyll *a*), total cyanobacteria (phycocyanin), phycoerthrin-containing nano- and picocyanobacteria, and photosynthetic nano- and picoeukaryotes) were compared by means of one-way ANOVAs or a non-parametric Kruskal–Wallis test and *post-hoc* multiple comparison tests (Tukey test) with $p < 0.05$ used as the significance level.

2.3. Microzooplankton grazing experiments

To estimate 'microzooplankton' grazing, the dilution technique described in Landry et al. (1995) was utilized which generally quantifies grazing by all protozoan grazers $< 200\ \mu m$ including micro- (20–200 μm) and nanoplankton (2–20 μm; Calbet and Landry, 2004). To commence experiments, filtered lake water (FLW; 0.2 μm) was combined with whole lake water (WW) to create a dilution series consisting of three dilutions (25%, 50%, 75% FLW; $n = 3$ for each) and a no dilution (100% WW; $n = 3$) in acid-washed, 250 mL acid-cleaned polycarbonate bottles, all with complete nutrient enrichment (20 μM nitrate, 1.25 μM orthophosphate; Landry et al., 1995). Experimental bottles were incubated in an incubator with light and temperatures levels matching *in situ* conditions. All experimental bottles were gently inverted every 6–8 h during the incubation to prevent congregation of algae at either the surface or bottom of incubation bottles. After 24 h, levels of extracted chlorophyll *a*, *in vivo* phycocyanin, densities of phycoerthrin-containing nano- and picocyanobacteria, and photosynthetic nano- and picoeukaryotes in each experimental bottle were quantified. Net growth rates per day of each population at each dilution were calculated from changes in cell densities and pigment using the formula: $\mu = [\ln(Q_t/Q_o)]/t/\%WW$ where μ is the net growth rate per day, Q_t is the quantity (cell density or pigment concentration) present at the end of the experiments, Q_o represents the quantity present at the beginning of experiments, t is the duration of the experiment in days and % WW is the percent of whole water used (%WW = 100 − %FLW). Grazing mortality rates (m) of populations were determined using the slope of a linear regression of the dilution of sample water (x-axis) versus apparent net growth rates (y-axis), while nutrient enriched intrinsic growth rates (μ_e) were determined from the y-intercept of these plots (Landry et al., 1995). Grazing rates based on non-significant linear regressions are not presented; such regressions could occur for a variety of reasons including the absence of grazing by microzooplankton (Landry et al., 1995). The percent of standing stock grazed per day was determined using the equation $\%SS = (1 - (e^{-m})) \times 100$ (Calbet and Landry, 2004). Furthermore, we calculated net growth rates (μ_n) which represented the growth of each community in the nutrient enriched control bottle. We also calculated the unamended intrinsic growth rates $(\mu_u) = \mu_e - (\mu_n - \mu_o)$ where μ_o is the growth of the unamended control bottles and μ_e and μ_n are described above. During experiments when grazing rates on multiple prey populations were quantified, differences in grazing rates (i.e. slopes of regression lines) were determined using an analysis of co-variance (ANCOVA) with a *post-hoc* Tukey-HSD test (Zar, 1999) with $p < 0.05$ used as the significance level. For the entire study, we compared grazing rates among dates and locations with and without elevated densities ('blooms') of potentially toxic cyanobacteria ($> 40{,}000$ cells mL^{-1} of *Microcystis*, *Anabaena*, and *Cylindrospermopsis*; Chorus and Bartram, 1999) using t-tests. Since multiple groups of cyanobacteria were investigated during this study, this group will be referred to as 'toxic cyanobacteria' due to their potential to produce compounds such as microcystin, anatoxin-a, and cylindrospermopsin; Chorus and Bartram, 1999; Hudnell, 2008). Finally, we assessed the extent to which zooplankton grazing rates varied as a function of prey populations by means of linear correlation analyses.

2.4. Microscopic analysis

Densities of cyanobacteria and eukaryotic phytoplankton were quantified using gridded Sedgewick–Rafter counting chambers. For all samples, at least 200 cells, colonies, chains, or trichomes were enumerated. This approach provided reproducibility (<15% relative standard deviation) among samples. The number of cells per colony for *Microcystis* was determined according to Watzin et al. (2006). The size of *Microcystis* colonies within each sample was determined from digital images and SPOT™ Advanced software (Diagnostic Instruments Inc., Sterling Heights, MI, USA). Cell densities for the major microplankton groups were converted to biovolume by measuring the length and width of representative cells and using volumetric equations corresponding to the geometric shape each cell resembled (Smayda, 1978). Biovolumes for each phytoplankton group were converted to biomass using the carbon conversion factor (Smayda, 1978).

3. Results

3.1. Field observations

During the sampling period, water temperatures ranged from 21 to 27 °C, averaging of 24 ± 0.4 °C (mean ± SE), and waters were oxic at all stations (Table 1). Chlorophyll *a* concentrations differed among sites ($p < 0.05$) but not among years ($p > 0.05$) and ranged between 3.0 and 51 μg L^{-1} with an overall mean concentration of 20.4 ± 3.8 μg L^{-1} (Table 1). Mean chlorophyll *a* concentrations over the three years were slightly elevated at 'bloom' sites (24.8 ± 5.1 μg L^{-1}) but were not significantly different than non-bloom sites (17.7 ± 5.8 μg L^{-1}; $p > 0.05$; t-test) Furthermore, phycocyanin concentrations (a proxy for cyanobacteria) were similar among most stations (range 0.9–2.6 RFU (raw fluorescence units), mean 1.7 ± 0.2 RFU; Table 1) except for station 1163 (Sandusky Bay) which had significantly higher phycocyanin concentrations (mean: 30.7 ± 5.3 RFU; $p < 0.05$; Table 1).

Autotrophic microplankton communities were dominated, in terms of both cell density and biomass, primarily by cyanobacteria, and to a lesser extent, diatoms (Table 2). Of the 19 individual samplings over the three-year period, cyanobacteria represented more than half of the total phytoplankton biomass on 13 occasions (Table 2). The cyanobacterial community was dominated by three genera, *Microcystis*, *Anabaena*, and *Cylindrospermopsis* (Table 2). *Microcystis* accounted the majority of cyanobacterial biomass in 63% of the samplings (12 of 19; Table 2). Of the stations where *Microcystis* was not the primary cyanobacterium, cyanobacterial community biomass was dominated by *Anabaena* (5 of 7 sites) or *Cylindrospermopsis* (2 of 7; Table 2). Finally, 7 of the 19 sites had more than 40,000 potentially toxic cyanobacterial cells mL^{-1}, and thus were considered 'bloom' samples (Table 2).

Table 2
Mean (±SE) autotrophic plankton densities quantified via light microscopy as well as biomass for the western basin of Lake Erie from 2005 to 2007. Sites and dates are the same as Table 1. Bolded sites represent sites with 'bloom' cyanobacterial densities (>4 × 10^4 cells mL^−1).

Site	Cyanobacteria					
	Microcystis		*Anabaena*		*Cylindrospermopsis*	
	Cells × 10^3 L^{-1}	Biomass (μg C L^{-1})	Cells × 10^3 L^{-1}	Biomass (μg C L^{-1})	Cells × 10^3 L^{-1}	Biomass (μg C L^{-1})
2005						
1163	4000 (50)	59 (1)	8000 (5000)	305 (176)	2000 (1000)	15 (8)
835	4000 (90)	64 (1)	0 (0)	0 (0)	3000 (300)	18 (2)
558	25,000 (9000)	386 (140)	0 (0)	0 (0)	2000 (500)	13 (3)
969	33,000 (5000)	505 (81)	0 (0)	0 (0)	0 (0)	0 (0)
1163	17,000 (100)	259 (1)	700 (700)	25 (25)	0 (0)	0 (0)
882	120,000 (700)	1828 (11)	0 (0)	0 (0)	0 (0)	0 (0)
969	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
1163	20,000 (1000)	301 (14)	2000 (2000)	81 (61)	500 (500)	4 (4)
2006						
1163	34,000 (1000)	526 (18)	31,000 (2000)	1148 (80)	56,000 (800)	389 (5)
478	3000 (100)	47 (2)	400 (60)	13 (2)	0 (0)	0 (0)
882	140,000 (9000)	2170 (132)	400 (60)	13 (2)	0 (0)	0 (0)
974	42,000 (700)	647 (11)	0 (0)	0 (0)	0 (0)	0 (0)
885	0 (0)	0 (0)	200 (30)	8 (1)	0 (0)	0 (0)
961	0 (0)	0 (0)	20 (20)	1 (1)	0 (0)	0 (0)
958	47,000 (2000)	721 (30)	0 (0)	0 (0)	0 (0)	0 (0)
1063	–	–	–	–	–	–
2007						
969	5000 (300)	73 (4)	0 (0)	0 (0)	0 (0)	0 (0)
835	0 (0)	0 (0)	0 (0)	0(0)	2000 (200)	13 (1)
e60	20,000 (1000)	301 (16)	500 (100)	18 (3)	0 (0)	0 (0)
1163	0 (0)	0 (0)	200 (20)	9 (1)	90,000 (5000)	615 (32)
	Non-cyanobacteria					
	Diatoms		Dinoflagellates		Chlorophytes	
	Cells × 10^3 L^{-1}	Biomass (μg C L^{-1})	Cells × 10^3 L^{-1}	Biomass (μg C L^{-1})	Cells × 10^3 L^{-1}	Biomass (μg C L^{-1})
2005						
1163	1000 (400)	152 (53)	80 (10)	37 (5)	6 (6)	1 (1)
835	1000 (300)	168 (32)	60 (20)	30 (9)	10 (10)	0 (0)
558	1000 (200)	128 (27)	30 (30)	16 (16)	10 (10)	2 (0)
969	400 (30)	52 (3)	20 (6)	8 (3)	5 (5)	0 (0)
1163	300 (30)	31 (3)	300 (300)	161 (146)	3 (3)	2 (2)
882	500 (100)	59 (17)	30 (20)	16 (12)	3 (3)	1 (1)
969	200 (6)	22 (1)	100 (4)	69 (2)	10 (3)	0 (0)
1163	1000 (500)	140 (55)	50 (30)	21 (13)	0 (0)	2 (2)
2006						
1163	900 (100)	106 (14)	0 (0)	0 (0)	30 (5)	1 (0.2)
478	200 (10)	23 (1)	0 (0)	0 (0)	40 (2)	1 (0.1)
882	4000 (100)	527 (15)	20 (3)	12 (1)	35 (2)	1 (0.1)
974	200 (20)	26 (2)	0 (0)	0 (0)	10 (2)	0 (0)
885	130 (20)	16 (0.2)	120 (10)	61 (7)	50 (5)	2 (0.2)
961	180 (1)	22 (0.1)	80 (10)	39 (5)	0 (0)	0 (0)
958	300 (20)	38 (3)	0 (0)	0 (0)	0 (0)	0 (0)
1063	–	–	–	–	–	–
2007						
969	160 (3)	19 (0.4)	0 (0)	0 (0)	0 (0)	0 (0)
835	200 (9)	25 (1)	70 (7)	32 (13)	0 (0)	0 (0)
e60	10,000 (200)	1248 (26)	0 (0)	0 (0)	20 (1)	1 (0)
1163	1000 (100)	165 (12)	70 (8)	35 (4)	0 (0)	0 (0)

Photosynthetic nano- and picoplankton (PNPP) were dominated by prokaryotes on every date sampled representing 56–86% of total cell densities (Table 3). Total PNPP cell densities ranged from 0.45×10^5 to 1.97×10^5 mL^{-1} (Table 3). The non-*Synechococcus* unicellular cyanobacteria dominated the PNPP on all dates ranging from 0.23 to 1.5×10^5 mL^{-1}. *Synechococcus*-like cell densities ranged between 0.095 and 1.4×10^4 cells mL^{-1} accounting for up to 10% of PNPP densities (Table 3). Finally, eukaryote densities ranged between 0.95 and 3.4×10^4 cells mL^{-1} (Table 3).

3.2. Mesozooplankton grazing

The cultured cladoceran *D. pulex* was able to graze the total phytoplankton and cyanobacterial communities at similar frequencies (100% and 90%, respectively; $n = 10$; Table 4). Overall clearance rates (CRs) were 0.22 ± 0.04 mL individual^{-1} h^{-1} and 0.17 ± 0.04 mL individual^{-1} h^{-1} for the phytoplankton and cyanobacterial populations, respectively (Fig. 2). During cyanobacteria blooms (>4.0×10^4 cells mL^{-1}), CRs on the phytoplankton community (0.15 ± 0.07 mL individual^{-1} h^{-1}) and the cyanobacterial population (0.05 ± 0.03 mL individual^{-1} h^{-1}) were 50 and 80% lower than during non-bloom experiments (0.29 ± 0.06 mL individual $^{-1}$ h^{-1} and 0.26 ± 0.05 mL individual^{-1} h^{-1}), respectively, a significant decrease ($p < 0.05$, *t*-test; Fig. 2). Furthermore, grazing rates on the total phytoplankton population were inversely correlated with toxic cyanobacterial densities ($p < 0.05$; $r^2 = 0.54$, Fig. 3) and biomass ($p < 0.05$) as well as chlorophyll *a* concentrations ($p < 0.05$). The negative relationship between cyanobacterial densities and grazing rates on the phytoplankton community was largely driven by *Microcystis* densities as relationships between other cyanobacteria genera and grazing rates were not evident (data not shown). Additionally, grazing rates on the phytoplankton community were

Table 3
Mean (±SE) nano- and picoplankton densities quantified via flow cytometry for the western basin of Lake Erie during 2007. The sites in bold were considered 'bloom' sites.

Group	Site			
	969	835	**e60**	**1163**
	Cells × 10^3 L^{-1}	Cells × 10^3 L^{-1}	Cells × 10^3 L^{-1}	Cells × 10^3 L^{-1}
Synechococcus	14,000 (960)	950 (80)	1800 (1)	6000 (500)
Total cyanobacteria	160,000 (1500)	55,000 (6600)	25,000 (80)	131,000 (13,000)
Total eukaryotes	34,000 (1700)	9500 (110)	20,000 (400)	24,000 (300)
Total	197,000 (2300)	64,000 (6600)	45,000 (400)	154,000 (13,000)

not correlated with any individual planktonic group quantified. *D. pulex* also grazed nano- and picoeukaryotes, *Synechococcus*-like cells, and nano- and picocyanobacteria (0.13 ± 0.13 mL individual^{-1} h^{-1}, 0.28 ± 0.05 mL individual^{-1} h^{-1}, and 0.03 ± 0.03 mL individual^{-1} h^{-1}, respectfully) although rates did not differ between bloom and non-bloom sites (Fig. 4).

Natural communities of mesozooplankton grazed the total phytoplankton community in 90% of experiments conducted (9 of 10; Table 4) at rates ranging between 0.003 ± 0.01 d^{-1} and 0.16 ± 0.02 d^{-1} with a mean grazing rate of 0.06 ± 0.02 d^{-1} (Fig. 2). The total cyanobacterial community was grazed by mesozooplankton in all of the experiments conducted ($n = 10$; Table 4) at an average rate of 0.06 ± 0.02 d^{-1} (Fig. 2). Mesozooplankton grazing rates on the total phytoplankton community were six-fold lower at cyanobacterial bloom sites (0.02 ± 0.02 d^{-1}) compared to non-bloom sites (0.12 ± 0.04 d^{-1}; $p < 0.05$, t-test; Fig. 2). Furthermore there was a significant, inverse, correlation between mesozooplankton grazing rates on phytoplankton and toxic cyanobacterial densities ($p < 0.05$; $r^2 = 0.54$; Fig. 3) as well as biomass ($p < 0.05$). This trend was primarily driven by *Microcystis* densities, as the relationship with other cyanobacterial groups was much weaker (data not shown). In contrast, mesozooplankton grazing varied independently of all other phytoplankton groups ($p > 0.05$). The natural community of mesozooplankton grazed the nano- and picoeukaryotes, *Synechococcus*-like cells, and the nano- and picocyanobacteria, at rates of 0.04 ± 0.07 d^{-1}, 0.13 ± 0.08 d^{-1}, and 0.11 ± 0.05 d^{-1}, respectively. Mean grazing rates on each community did not significantly differ between the bloom and non-blooms sites (Fig. 4).

3.3. Microzooplankton grazing

Over the three field seasons, communities of microzooplankton were able to graze the total phytoplankton community in 75% (15

Table 4
Individual mortality rates, mean ± (SE) for phytoplankton (extracted chlorophyll *a*) and cyanobacteria (*in vivo* phycocyanin) for 2006 and 2007 in the western basin of LE. Mean = overall mean (SE) for all sites and years. The sites in bold represent 'bloom' sites.

Site	Natural mesozooplankton	
	Phytoplankton	Cyanobacteria
2006		
882	−0.04 (0.01)	0.01 (0.003)
974	0.003 (0.01)	0.12 (0.003)
885	0.14 (0.003)	0.15 (0.02)
961	0.01 (0.01)	0.05 (0.02)
958	0.01 (0.01)	0.13 (0.02)
1063	0.02 (0.02)	0.06 (0.05)
2007		
969	0.16 (0.02)	0.02 (0)
835	0.15 (0.002)	0.03 (0.04)
e60	0.11 (0.01)	0.06 (0.01)
1163	0.007 (0.02)	0.02 (0.01)
Mean	0.06 (0.02)	0.06 (0.02)
	Daphnia pulex	
	Phytoplankton	Cyanobacteria
2006		
1163	0.05 (0.01)	−0.01 (0.001)
478	0.30 (0.09)	0.43 (0.02)
974	0.20 (0.03)	0.14 (0.03)
885	0.48 (0.07)	0.22 (0.02)
961	0.33 (0.02)	0.28 (0)
969	0.14 (0.03)	0.17 (0.08)
2007		
969	0.11 (0.10)	0.20 (0)
835	0.22 (0.03)	0.17 (0)
e60	0.31 (0.07)	0.05 (0.02)
1163	0.02 (0.002)	0.04 (0.01)
Mean	0.22 (0.04)	0.17 (0.04)

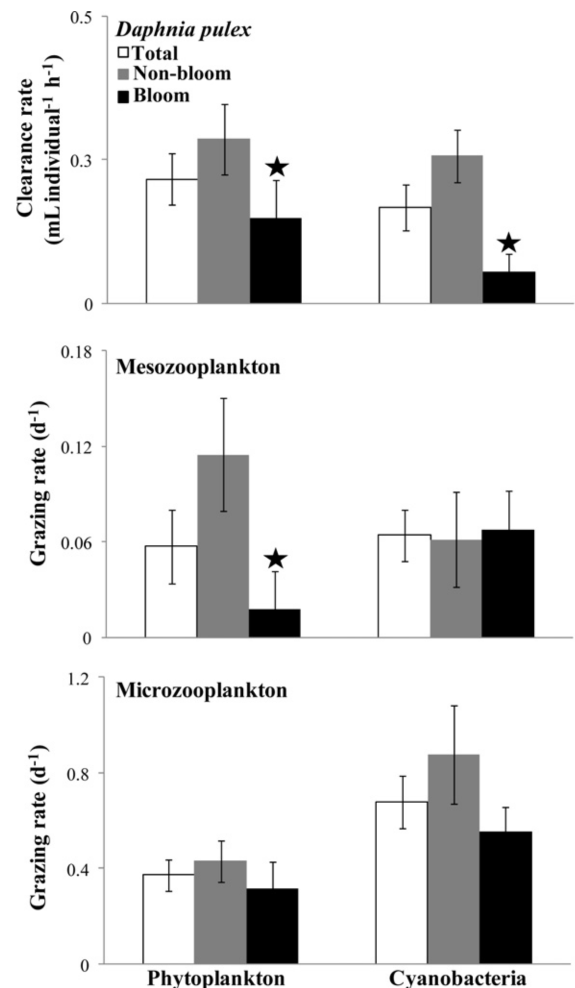

Fig. 2. Grazing rates (mean ± SE) of cultured and natural mesozooplankton in the western basin of Lake Erie from 2005 to 2007. Stars denote instances when grazing rates at 'bloom' sites that were significantly lower ($p < 0.05$, t-test) than grazing rates at 'non-bloom' sites.

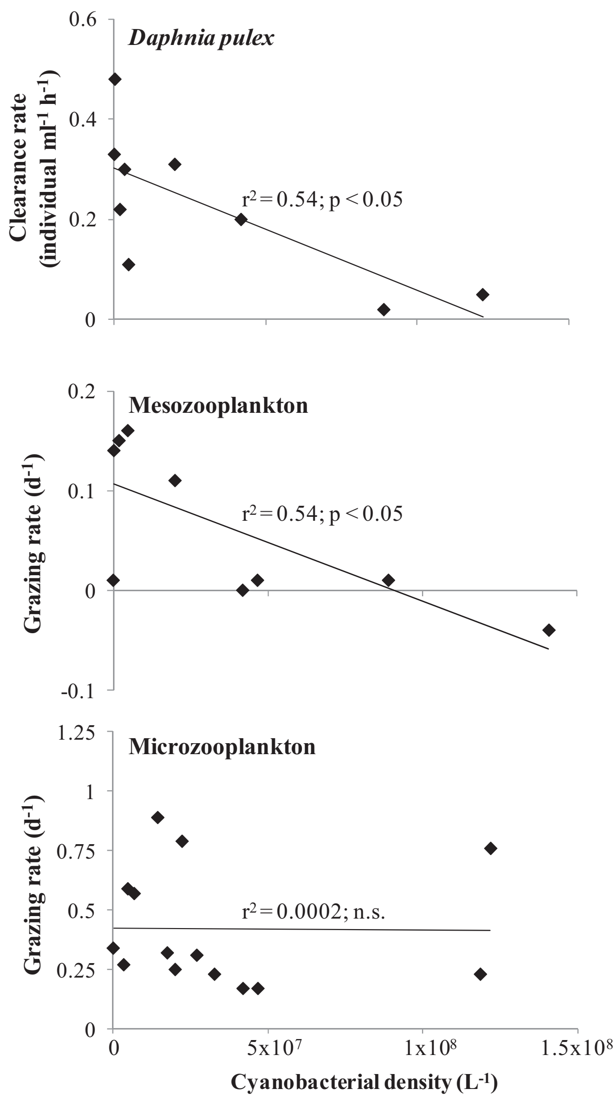

Fig. 3. Correlations between the grazing rates of *Daphnia pulex*, mesozooplankton, and microzooplankton and potentially toxic cyanobacterial (*Microcystis*, *Anabaena*, and *Cylindrospermopsis*) densities in the western basin of Lake Erie from 2005 to 2007. n.s. = not significant.

of 20) of experiments with a mean GR of $0.37 \pm 0.07\ d^{-1}$ (Fig. 2). Microzooplankton grazed, on average, $29 \pm 4\%$ of the phytoplankton standing stock per day (Fig. 5). Microzooplankton grazed the total cyanobacteria population (*in vivo* phycocyanin) at significantly faster rates ($0.68 \pm 0.11\ d^{-1}$) than the total phytoplankton community ($p < 0.01$; *t*-test; Fig. 2). Microzooplankton were responsible for grazing, on average, $46 \pm 5\%\ d^{-1}$ of the cyanobacterial standing stock which is also significantly higher than the portion of phytoplankton standing stock grazed ($p < 0.01$; *t*-test; Fig. 5). Microzooplankton grazing rates on the nano-and picoeukaryotes, *Synechococcus*-like cells, and nano- and picocyanobacteria were $0.30 \pm 0.08\ d^{-1}$, $0.69 \pm 0.17\ d^{-1}$, and $0.38 \pm 0.18\ d^{-1}$, respectively (Fig. 4). Microzooplankton grazed the standing stocks of *Synechococcus*, nano-and picoeukaryotes and nano- and picocyanobacteria similarly (Fig. 5). Unlike mesozooplankton, microzooplankton mean grazing rates of all prey groups did not differ between bloom and non-bloom sites (Fig. 2). Grazing rates of PNPP populations were not correlated with toxic cyanobacterial cell densities ($p > 0.05$) but were positively correlated with chlorophyll *a* and phycocyanin concentrations ($p < 0.05$).

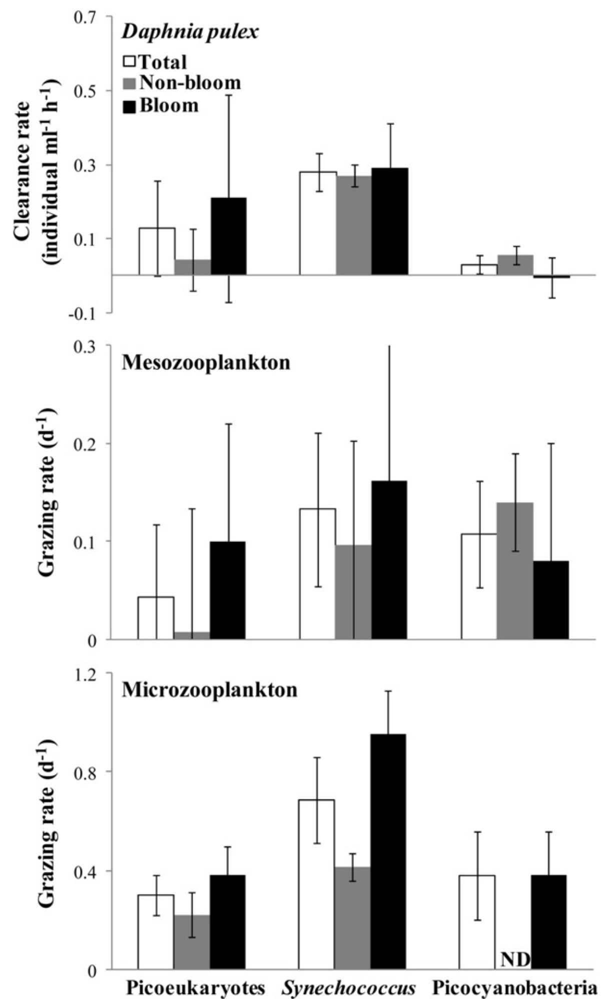

Fig. 4. Grazing rates (mean ± SE) of *D. pulex* and natural communities of micro- and mesozooplankton on photosynthetic nano- and picoplankton by in the western basin of Lake Erie in 2007. ND = grazing not detected.

3.4. Growth rates of algal communities

During 2006 and 2007, intrinsic cellular growth rates of total cyanobacterial communities ($0.48 \pm 0.06\ d^{-1}$, Fig. 6) were significantly faster than those of the total phytoplankton community ($0.25 \pm 0.08\ d^{-1}$; $p < 0.05$; Fig. 6). The addition of inorganic nutrients

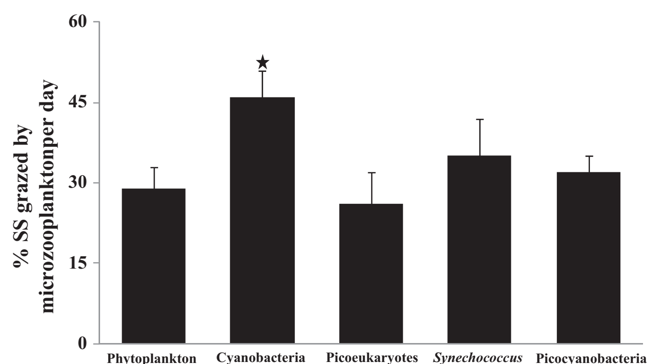

Fig. 5. Standing stocks (SS) of the phytoplankton and cyanobacterial communities as well as the nano- and picoeukaryotes, nano- and picocyanobacteria and *Synechococcus*-like cells grazed per day by microzooplankton in the western basin of Lake Erie from 2005 to 2007. The star indicates that the percent of cyanobacterial standing stocks grazed per day by microzooplankton was higher than the percentages of other phytoplankton groups ($p < 0.05$).

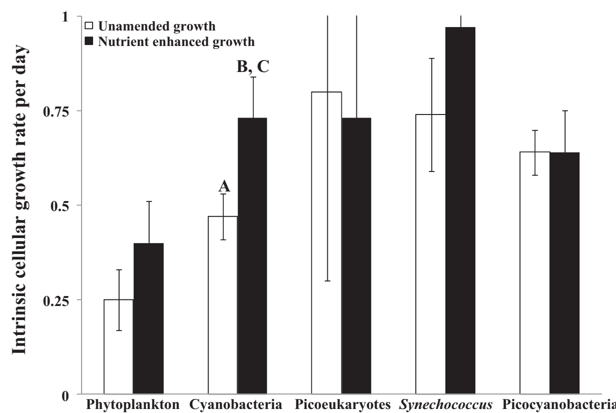

Fig. 6. Intrinsic cellular growth rates, with and without the addition of nutrients, of phytoplankton and cyanobacterial communities as well as the nano- and picoeukaryotes, nano- and picocyanobacteria and *Synechococcus*-like cells in the western basin of Lake Erie from 2005 to 2007. (A) Unamended cyanobacterial growth rates were significantly greater than unamended phytoplankton growth rates ($p < 0.05$), (B) nutrient enhanced cyanobacterial growth rates were significantly faster than phytoplankton growth rates with or without nutrient enrichment ($p < 0.05$), (C) nutrient enhanced cyanobacterial growth rates were significantly higher than unamended cyanobacterial growth rates ($p < 0.05$).

(nitrate and orthophosphate) yielded a higher intrinsic cellular growth in the cyanobacterial community than unamended samples ($0.73 \pm 0.11\ d^{-1}$, $0.47 \pm 0.06\ d^{-1}$, respectively; Fig. 6; $p < 0.05$). Furthermore, nutrient-enhanced cyanobacterial cellular growth rates were significantly higher than nutrient-enriched cellular growth rates for the total phytoplankton community (mean: $0.73 \pm 0.11\ d^{-1}$, $0.40 \pm 0.11\ d^{-1}$, respectively; Fig. 6; $p < 0.05$; *t*-test). Nutrient-enhanced intrinsic cellular growth rates of the nano- and picoeukaryotes, nano- and picocyanobacteria and *Synechococcus*-like cells ($0.73 \pm 0.64\ d^{-1}$, $0.64 \pm 0.11\ d^{-1}$, $0.97 \pm 0.16\ d^{-1}$, respectively) were similar to unamended samples ($0.80 \pm 0.50\ d^{-1}$, $0.64 \pm 0.06\ d^{-1}$, $0.74 \pm 0.15\ d^{-1}$, respectively; Fig. 6).

4. Discussion

To our knowledge, this is the first study to quantify zooplankton grazing rates during cyanobacterial blooms in the western basin of Lake Erie. The interactions between mesozooplankton, microzooplankton, and phytoplankton are complex and natural zooplankton communities consist of a multitude of species that can graze both vertically and horizontally across aquatic food webs (Burns and Schallenberg, 2001). Despite these complexities, we found that mesozooplankton grazing rates within the western basin of Lake Erie varied as a function of putatively toxic cyanobacteria (*Microcystis*, *Anabaena*, and *Cylindrospermopsis*) cell densities while microzooplankton grazing rates did not. Microzooplankton grazed at rates exceeding those of mesozooplankton. Finally, cyanobacterial growth rates consistently outpaced those of eukaryotic algae and were consistently enhanced by nutrient loading. Collectively, these findings provide new insight regarding the dynamics of cyanobacterial blooms and the functioning of microbial food webs during those blooms.

4.1. Mesozooplankton grazing

Mesozooplankton such as *Daphnia* sp. are capable of grazing on a wide range of cell sizes (Jürgens, 1994) including picocyanobacteria (Callieri et al., 2004) and *Synechococcus* (Brendelberger, 1985; Callieri et al., 2004). Consistent with these finding, the cultured cladoceran *D. pulex* and natural communities of mesozooplankton were able to successfully graze on all algal populations, including the phytosynthetic nano- and picoplankton (Figs. 2 and 4), during this study. Grazing rates of both *D. pulex* and mesozooplankton declined significantly when cyanobacterial densities were elevated and their grazing rates were inversely correlated with densities of potentially toxic cyanobacteria (*Microcystis*, *Anabaena*, and *Cylindrospermopsis*; Fig. 3; $p < 0.05$). *Microcystis* was the primary genus driving the negative correlation, likely due in part to its status as the most abundant cyanobacterium in most of our study sites (12 of 19; Table 2). Moreover, a recent meta-analysis of 47 laboratory-based cyanobacteria–zooplankton studies found that *Microcystis* had the largest negative effect on zooplankton population growth of all genera investigated (Tillmanns et al., 2008).

Mesozooplankton and *Daphnia* sp. are often negatively impacted by cyanobacteria blooms. For example, DeMott (1999) found *D. pulex* was the most sensitive *Daphina* species to increasing cyanobacterial proportions of their diet, experiencing sharp declines in growth and reproduction. Furthermore, Tillmanns et al. (2008) found that the growth rates of several mesozooplankton species, including *D. pulex*, were significantly reduced by increasing proportions of cyanobacteria in their diets. In addition to *Daphnia* spp., other genera negatively affected by cyanobacteria were *Bosmina* and *Brachionus*, all of which have been found to be common among the zooplankton communities of Lake Erie (Fahnenstiel et al., 1986; Hwang and Heath, 1999). Furthermore, previous studies have found that grazing by mesozooplankton can be disrupted by larger colonial or filamentous cyanobacteria (Gilwicz and Seidlar, 1980; Fulton and Paerl, 1987; DeMott et al., 1991). The low grazing rates on potentially toxic cyanobacteria found in this study could be partially attributed to the large size of *Microcystis* colonies (71 ± 11 cells) in our experiments which exceeded the threshold size known to inhibit zooplankton grazing (>50 cells colony^{-1}; O'Brian and DeNoyelles, 1974; Nishibe et al., 2002). Also, previous studies found that the grazing of large-bodied *Daphnia* species can be disrupted by filamentous cyanobacteria such as *Cylindrospermopsis* (Davidowicz et al., 1988; Gilwicz, 1990a,b; Gliwicz and Lampert, 1990; DeMott et al., 2001) and thus cannot grow and reproduce rapidly enough to prevent bloom formation (Gilwicz, 1990a). As our bloom sites were comprised of both larger colonial and filamentous cyanobacterial genera it is possible that the physical nature of the cyanobacteria prevented grazing by the mesozooplankton community. Bloom-forming cyanobacteria also produce a suite of protease inhibitors that can negatively affect higher trophic levels (Carmichael, 1992; Codd, 1995; Reshef and Carmeli, 2001) and specifically impair the function of digestive compounds (trypsin and/or chymotrypsin) in *Daphnia* (Rohrlack et al., 2003; Agrawal et al., 2005; Von Elert et al., 2005) and thus may also have partially accounted for the low grazing rates by cultured as well as natural mesozooplankton. Finally, while microcystin has long been hypothesized as a grazing defence, our prior research has demonstrated that *Microcystis* populations able to synthesize microcystin are grazed at a rate similar to *Microcystis* populations that cannot synthesize the toxin (Davis and Gobler, 2011). Similarly, Tillmanns et al. (2008) found no clear effect of putative cyanobacterial toxins on the growth of seven zooplankton species.

4.2. Microzooplankton grazing and food web dynamics

Microzooplankton play important roles in aquatic food webs as primary consumers of autotrophic production (Calbet and Landry, 2004) as well as trophic intermediaries between primary producers and larger zooplankton (i.e. copepods; Gifford, 1991; Calbet and Saiz, 2005; Sherr and Sherr, 2002), and typically dominate zooplankton biomass during cyanobacterial blooms (Leonard and Paerl, 2005; Davis and Gobler, 2011). In agreement with previous field studies (Nishibe et al., 2002; Leonard and Paerl, 2005; Davis and Gobler, 2011) we found that during potentially

toxic cyanobacteria blooms, grazing by mesozooplankton (i.e. large copepods and cladocerans) declined while protozoan grazing persisted at rates significantly higher than those of mesozooplankton ($p < 0.05$). Furthermore, the mean grazing rates on the phytoplankton community ($0.37 \pm 0.07\ d^{-1}$) by microzooplankton were similar to those found in other systems experiencing cyanobacterial blooms (Leonard and Paerl, 2005; Tijdens et al., 2008). Also, microzooplankton grazed at similar rates at bloom and non-bloom sites with grazing rates on the cyanobacterial population being significantly faster rates than those on the total phytoplankton population ($p < 0.01$). While microzooplankton can be consumed by mesozooplankton (Burns and Schallenberg, 2001), any such grazing did not alter microzooplankton grazing rates during blooms, a finding consistent with a study by Leonard and Paerl (2005). Collectively, this evidence suggests, first, that microzooplankton grazing was not affected by increasing toxic cyanobacterial densities and that these grazers may have actually preferred grazing this prey group (Fig. 5). Second, microzooplankton communities are a more important source of mortality to Lake Erie phytoplankton than mesozooplankton and thus have the potential to serve as a top-down control during potentially toxic cyanobacterial blooms. Third, by inhibiting the grazing rates of mesozooplankton cyanobacterial blooms are likely to decrease the efficiency of carbon transfer through the food web and decrease productivity within upper trophic levels in systems with chronic cyanobacterial blooms such as the western basin of Lake Erie.

4.3. Growth rates of autotrophic populations

Throughout this study, intrinsic cellular growth rates of the cyanobacterial community were 80% greater than those of the total phytoplankton community ($p < 0.05$; *t*-test). This could partially account for their dominance during this study and suggests that bloom forming cyanobacteria in Lake Erie must maintain high growth rates to overcome elevated grazing rates by microzooplankton. The difference in growth rates could also be indirectly related to the fact that many mesozooplankton are poor grazers of cyanobacteria (Tillmanns et al., 2008) but graze other phytoplankton species well. This would reduce competition for nutrients allowing cyanobacteria to grow at increased rates and would potentially provide a positive feedback loop facilitating bloom progression. Supporting this notion, nutrients (nitrogen and phosphorus) enhanced the growth rates of all phytoplankton populations except for nano- and picoeukaryotes, nano- and picocyanobacteria and *Synechococcus*-like cells. This finding is consistent with previous studies that have found that summer phytoplankton growth rates in Lake Erie can be strongly limited by nitrogen, phosphorus, and even iron (DeBruyn et al., 2004; North et al., 2007; Moon and Carrick, 2007). In addition, the nutrient enhanced intrinsic cellular growth rates of cyanobacteria exceeded those of the total phytoplankton community, supporting the notion that elevated nutrient concentrations favor the dominance of bloom forming cyanobacteria over eukaryotic algae in Lake Erie (Wilhelm et al., 2003; Millie et al., 2009). Finally, previous studies have shown that along with more intense blooms, increasing inorganic nitrogen and phosphorus concentrations could promote the dominance of toxic strains of cyanobacteria which could lead to blooms of greater toxicity (Davis et al., 2010).

5. Summary

In conclusion, this study demonstrates that the grazing rates of mesozooplankton declined during blooms of putatively toxic cyanobacteria in the western basin of Lake Erie while those of microzooplankton did not. Microzooplankton grazed cyanobacteria at rates greater than mesozooplankton under all conditions thus restricting cyanobacterial net growth rates and evidencing their potential to serve as a top-down control of cyanobacterial blooms in Lake Erie. Finally, cyanobacteria benefited from enhanced nutrient concentrations more than eukaryotic phytoplankton suggesting that future nutrient loading to Lake Erie could exacerbate cyanobacteria blooms in this ecosystem.

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