Harmful Algae 15 (2012) 26–35

Contents lists available at SciVerse ScienceDirect

Harmful Algae

journal homepage: www.elsevier.com/locate/hal

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

ARTICLE INFO

Article history:
Received 8 September 2011
Received in revised form 5 November 2011
Accepted 5 November 2011
Available online 18 November 2011

Keywords:
Mesozooplankton
Microzooplankton
Grazing
Lake Erie
Cyanobacteria

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.

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.

1568-9883/$ – see front matter © 2011 Elsevier B.V. All rights reserved.
doi:10.1016/j.hal.2011.11.002

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)