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Microzooplankton distribution, dynamics, and trophic interactions relative to phytoplankton and quagga mussels in Saginaw Bay, Lake Huron

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ABSTRACT

Invasive quagga mussels have recently replaced zebra mussels as the dominant filter-feeding bivalves in the Great Lakes. This study examined microzooplankton (i.e., grazers <200 μm) and their trophic interactions with phytoplankton, bacteria, and bivalve mussels in Saginaw Bay, Lake Huron, following the zebra to quagga mussel shift. Microzooplankton distribution displayed strong spatial and temporal variability (1.73–28.5 μg C/L) relative to phytoplankton distribution. Ciliates were the dominant component, especially in the spring and early summer. Rotifers and dinoflagellates increased toward late summer/fall in the inner and outer parts of the bay, respectively. Microzooplankton grazing matched bacterial growth rates and removed ca. 30% of the phytoplankton standing stock in the <100 μm size fraction per day. The greatest herbivory occurred at the site dominated by colonial cyanobacteria. Microzooplankton, which comprised <4% of the quagga mussels prey field (i.e. available prey), contributed 77% and 34% to the quagga carbon-based diet during *Microcystis* and diatom blooms, respectively. Feeding on microzooplankton could buffer mussels during lean periods, or supplement other consumed resources, particularly during noxious cyanobacterial blooms. The results of this study demonstrate that microzooplankton are a resilient and critical component of the Saginaw Bay ecosystem.

Introduction

The invasive Ponto–Caspian bivalve zebra mussel (*Dreissena polymorpha*) has had a profound effect on the Laurentian Great Lakes ecosystem since its inadvertent introduction with ship ballast water in the mid-1980s (Vanderploeg et al., 2002). After reaching its peak in the early 2000s, the abundance of the zebra mussel has declined, whereas its congener, the quagga mussel (*Dreissena rostriformis bugensis*), has continued to expand, first in shallow waters (Mills et al., 1999) and then at depths >50 m (Nalepa et al., 2009). The quagga mussel possesses a number of physiological adaptations, including high assimilation efficiency and growth rates (Baldwin et al., 2002; Ram et al., 2012; Stoeckmann, 2003), which have allowed it to displace the well-established and prolific zebra mussel (Ricciardi and Whoriskey, 2004). In Lake Michigan, quagga mussel expansion to mid-depth regions has caused the disappearance of the spring phytoplankton bloom (Vanderploeg et al., 2010) and produced conditions similar to the oligotrophic Lake Superior (Fahnenstiel et al., 2010).

In Saginaw Bay, after an initial decline related to *Dreissena* invasion (Fahnenstiel et al., 1995), phytoplankton biomass rebounded, with increasing dominance by colony-forming cyanobacteria, such as *Microcystis aeruginosa* (Millie et al., 2011; Vanderploeg et al., 2001, 2009). This species includes toxic (microcystin-producing) strains (Dyble et al., 2008; Vanderploeg et al., 2001, 2013) and now comprises a significant proportion of phytoplankton biomass during late summer in Saginaw Bay (Fishman et al., 2009; Vanderploeg et al., 2001, 2002, 2009). The success of *Microcystis* in Saginaw Bay and the ecologically similar western basin of Lake Erie has been linked to alteration of phytoplankton competitive dynamics by invasive mussels through selective grazing (Lavrentyev et al., 1995), rejection of *Microcystis* colonies as pseudo-feces (Vanderploeg et al., 2001, 2013), and to nutrient recycling (Conroy et al., 2005; Gardner et al., 1995; Lavrentyev et al., 2000) with recent evidence pointing to the greater importance of selective rejection rather than immediate recycling of nutrients from mussels (Johengen et al., 2013). The re-engineering of the aquatic environment by non-indigenous bivalves, including altering energy and nutrient fluxes and proliferation of noxious algal blooms and other invasive species, have received much attention in the Great Lakes (Fishman et al., 2010; Hecky et al., 2004; Vanderploeg et al., 2001, 2002). However, our knowledge of pelagic food web structure and dynamics in the Great Lakes after the recent zebra-quagga shift remains incomplete.

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Microzooplankton (*sensu lato* grazers 15–200 μm, including ciliates, rotifers, dinoflagellates, and sarcodines) are a critical component of the Great Lakes ecosystem. They possess biomass comparable to planktonic crustaceans (Fahnenstiel et al., 1998; Gardner, 2004; Vanderploeg et al., 2007) and high growth and herbivory rates (Carrick et al., 1992; Gobler et al., 2008; Lavrentyev et al., 2004). However, little is known about their trophic interactions with the quagga mussel. The impacts of zebra mussels on protists were examined experimentally in 1994–1995 in Saginaw Bay, where mussels preyed selectively on the larger and weak-swimming species of ciliates and flagellates (Lavrentyev et al., 1995, 2000). Zebra mussels have drastically reduced the abundance of planktonic rotifers in the shallow western basin of Lake Erie (MacIsaac et al., 1995) and Lake St. Clair (David et al., 2009).

Rotifers also are the only group of microzooplankton that has been examined post quagga invasion. Barbiero and Warren (2011) found a decline in the abundances of *Polyarthra* and *Keratella*, and a concomitant increase in the colonial *Conochilus unicornis*. To our knowledge, the quagga mussel impact on the entire microzooplankton community, including one of its key components, ciliates, has not been examined so far in the Great Lakes. Based on literature and our previous experiments with the zebra mussel, we hypothesized that the quagga mussel would have a similarly strong and selective impact on microzooplankton in Saginaw Bay. Thus, the objectives of our study were: (1) compare microzooplankton abundance and composition to those before the quagga mussel invasion, (2) examine the spatial distribution and seasonal dynamics of microzooplankton in Saginaw Bay in relation to major environmental factors, (3) measure microzooplankton grazing rates on phytoplankton and bacteria during a *Microcystis* bloom, and (4) determine microzooplankton contribution to the quagga mussel diet during different seasons.

Material and methods

The study sites and field sampling

Saginaw Bay is a large (82 km long and 42 km wide) bay extending from western Lake Huron. It can be divided into the shallow, eutrophic inner bay, which receives inflow from the Saginaw River, and the mesotrophic, deeper outer bay, which is open to Lake Huron (Millie et al., 2011; Nalepa et al., 2005). Sampling was conducted as part of the NOAA-sponsored Multiple Stressors project at established Great Lakes Environmental Research Laboratory (GLERL) sampling locations (Fig. 1), the same sites sampled in the 1990s. Microzooplankton spatial distribution was examined at five sites in May 2008 and at twelve sites in July 2008. Samples were collected at 1-m depth using a 5-L Niskin bottle. In July 2008, samples were also collected from the bottom layer (0.5 m from the bottom). In May–October 2009 and July–October 2010, microzooplankton seasonal dynamics were observed at three master stations: SB5, SB10, and SB20) representing the inner and outer bay (Fig. 1).

Microzooplankton grazing experiments

Phytoplankton and bacterial growth and grazing loss rates were determined in dilution experiments (Landry and Hassett, 1982). The general

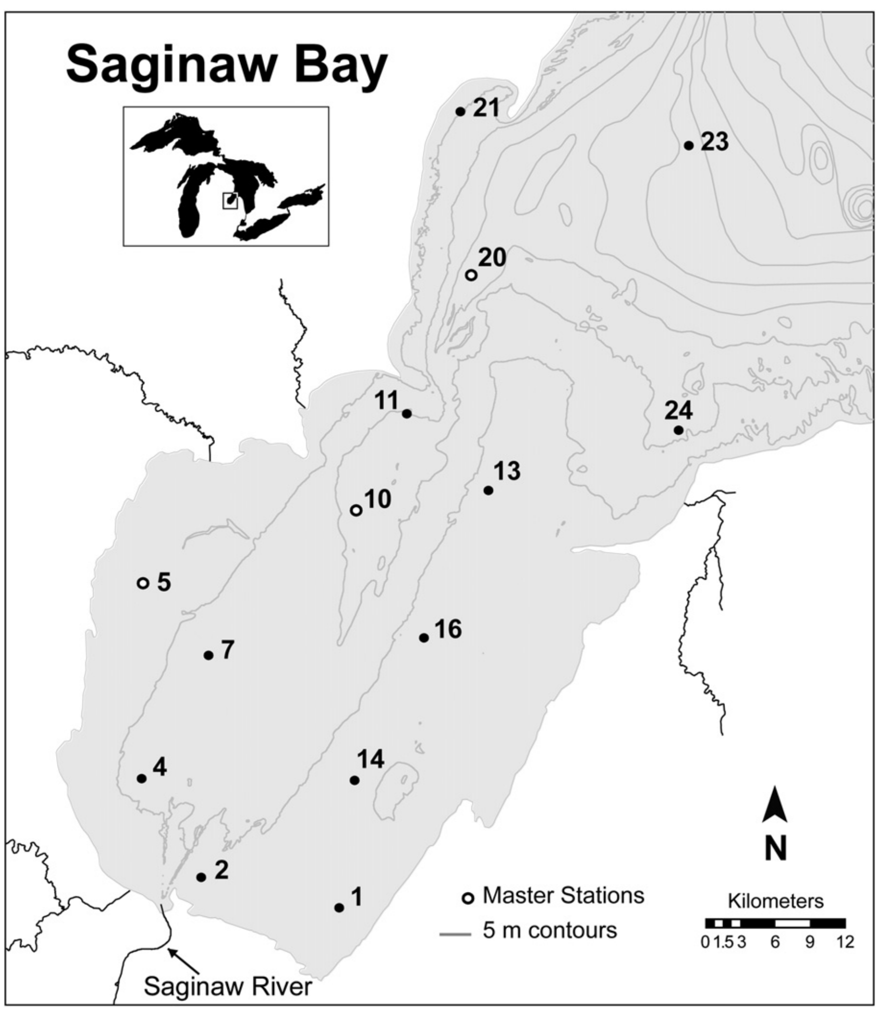

Fig. 1. Sampling locations in Saginaw Bay. Master stations (open circles: SB5, SB10, SB20) were sampled seasonally in 2008–9.

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