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A mesocosm investigation of the effects of quagga mussels (*Dreissena rostriformis bugensis*) on Lake Michigan zooplankton assemblages

Andrya L. Whitten ^{*,1}, Jose R. Marin Jarrin ², A. Scott McNaught

Department of Biology, Institute for Great Lakes Research, Central Michigan University, Mount Pleasant, MI 48859, United States

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ABSTRACT

Dreissenid mussels are known to disrupt the base of the food web by filter feeding on phytoplankton; however, they may also directly ingest zooplankton thereby complicating their effects on plankton communities. The objective of this study was to quantify the effects of quagga mussel feeding on the composition and size structure of Lake Michigan zooplankton assemblages. Two mesocosm (six 946 L tanks) experiments were conducted in summer 2013, using quagga mussels and zooplankton collected near Beaver Island, MI, to examine the response of zooplankton communities to the presence and absence of mussels (experiment 1) and varying mussel density (experiment 2). Mesocosms were sampled daily and zooplankton taxa were enumerated and sized using microscopy and FlowCAM® imaging. In experiment 1, the presence of quagga mussels had a rapid negative effect on veliger and copepod nauplii abundance, and a delayed negative effect on rotifer abundance. In experiment 2, mussel density had a negative effect on veliger, nauplii, and copepodite abundance within 24 h. Multivariate analyses revealed a change in zooplankton community composition with increasing mussel density. Ten zooplankton taxa decreased in abundance and frequency as quagga mussel density increased: except for the rotifer *Trichocerca* sp., treatments with higher mussel densities (i.e., 1327, 3585, and 5389 mussels/m²) had the greatest negative effect on small-bodied zooplankton ($\leq 128 \mu\text{m}$). This study confirms results from small-scale (≤ 1 L) experiments and demonstrates that quagga mussels can alter zooplankton communities at mesoscales (~1000 L), possibly through a combination of direct consumption and resource depletion.

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Introduction

Quagga mussels (*Dreissena rostriformis bugensis*) colonized Lake Michigan in 1997, and within ten years, their populations increased and surpassed zebra mussel (*D. polymorpha*) populations (Nalepa et al., 2010), an earlier invader. The expansion of quagga mussels in Lake Michigan coincided with the decrease in zebra mussels from a previous maximum of 2064 live individuals/m² (16–30 m depth contour) in 1999 to zero live individuals/m² in 2008 (Nalepa et al., 2010). Between 1997 and 2007, quagga mussels replaced zebra mussels in near-shore regions, established populations offshore (starting in 2004), and spread to waters >100 m in depth (Nalepa et al., 2010). By 2008, mean density of Lake Michigan quagga mussels at 16–30 m was 19,000 individuals/m² (Nalepa et al., 2010).

* Corresponding author.

E-mail address: awhitten@illinois.edu (A.L. Whitten).

¹ Present address: Illinois Natural History Survey, Prairie Research Institute, University of Illinois, Illinois River Biological Station, 704 North Schrader Avenue Havana, Illinois 62644, USA.

² Present address: Charles Darwin Research Station, Charles Darwin Ave. n/a, Puerto Ayora, Galápagos, Ecuador.

Dreissenid mussels (zebra and quagga) are able to disrupt the base of the food web in aquatic ecosystems by filtering phytoplankton from the water (Hecky et al., 2004; Holland, 1993; Nicholls and Hopkins, 1993; Vanderploeg et al., 2002). A few years after large populations of zebra mussels were established in the nearshore region, of Saginaw Bay, Lake Huron, phytoplankton abundance decreased by 60% (Holland, 1993). More recently, southeastern Lake Michigan experienced an 87% decrease in phytoplankton biomass during the spring isothermal mixing period between 1995 and 1998 and 2007–2008 (Fahnenstiel et al., 2010), coinciding with the establishment of large populations of quagga mussels. Dreissenid mussels can also divert energy and nutrients from the pelagic to benthic zone (Hecky et al., 2004), which enhances benthic organism density and taxonomic richness (Ward and Ricciardi, 2007) and negatively affects the health of zooplankton populations (Hecky et al., 2004; Vanderploeg et al., 2002). In general, the abundance of zooplankton declines in the presence of zebra and quagga mussels (Bridgeman et al., 1995).

In addition to their indirect effect on planktonic animals, dreissenid mussels can also directly ingest zooplankton (Shevtsova et al., 1986; MacIsaac et al., 1991; MacIsaac et al., 1995; Wong and Levinton, 2005). Dreissenids consume zooplankton that fit into their siphon, and

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siphon diameter is directly related to shell size (Wong and Levinton, 2005). The typical size range of particles taken in by zebra mussels is 5–45 μm (Gergs et al., 2009; Sprung and Rose, 1988; Ten Winkel and Davids, 1982; Wong and Levinton, 2005). This particle size range corresponds to the size of algal cells and decaying matter. Adult dreissenid mussels, however, have been reported to filter particles as large as 0.4–1.2 mm (Shevtsova et al., 1986; Horgan and Mills, 1997). Larger particles could include rotifer and microcrustacean zooplankton.

Small-bodied zooplankton have been shown to decrease in abundance in the presence of dreissenids in controlled laboratory experiments (i.e., rotifers and small cladocerans; MacIsaac et al., 1991; Shevtsova et al., 1986; Wong et al., 2003) and monitoring studies in the Hudson River, New York (i.e., rotifers and copepod nauplii; Pace et al., 1998; Strayer et al., 2014). Laboratory observations were made in short-term (2–24 h), small-scale (50–500 mL beaker), high density experiments with up to 10 zebra mussels per vessel (MacIsaac et al., 1991; Shevtsova et al., 1986; Wong et al., 2003). Furthermore, MacIsaac et al. (1991) determined that consumption of specific zooplankton species may depend on zooplankton body shape and mobility. Some zooplankton species have shell spines which deter ingestion or are able to rapidly swim away from predators (Wallace and Snell, 1991). Therefore, zooplankton taxa may respond differently to dreissenid predation.

Over the past ten years, the biomass of zooplankton – especially cladocerans, cyclopoid copepods, and copepod nauplii – has declined in Lake Michigan, and this decline has been attributed to a decrease in phytoplankton availability due to dreissenid feeding (Vanderploeg et al., 2012). However, the results of laboratory experiments and monitoring studies on other systems suggest that the decline might be, in part, caused by direct consumption of zooplankton by dreissenid mussels. With the increase in density and expansion of quagga mussels into deeper water, it is important that we quantify their ability to affect zooplankton assemblages through direct consumption as well as indirect resource competition if we are to fully understand their effects on aquatic food webs.

The goal of this study was to quantify the effects of quagga mussels over time and at a mesoscale (~1000 L) on the composition and size structure of zooplankton assemblages (rotifers and microcrustaceans) collected from Lake Michigan. We conducted a quagga mussel presence/absence experiment and a quagga mussel gradient experiment in mesocosms with natural organism densities. If quagga mussels are able to alter zooplankton assemblages through direct composition at mesoscales, we predict 1) there will be a decrease in the abundance of small, soft-bodied zooplankton with low mobility; 2) changes in zooplankton abundance and composition will occur rapidly due to high mussel filtration rates; and 3) changes will be more pronounced at high relative to low quagga mussel densities.

Methods

Mesocosm experiments

Two six-day mesocosm experiments were conducted in June and July 2013 at Central Michigan University Biological Station on Beaver Island, Michigan, USA. Six 946 L cylindrical mesocosms (surface area = 1.13 m^2) were used to mimic Lake Michigan natural conditions in both experiments. Filtered, epilimnetic, Lake Michigan water was directly pumped into the mesocosms and mixed with 850 gph Hydor Koralia circulation and wave pumps. Overhead high-intensity, full-spectrum lights were available to provide 4 h of artificial light to supplement room lighting for a 15:9 light:dark cycle. Artificial lights heated the water and mean water temperature increased from 18.85 ± 0.13 °C on day three to 20.00 ± 0.10 °C on day six in experiment one. In experiment two, mean water temperature increased from 17.8 ± 0.15 °C on day one to 22.85 ± 0.08 °C on day six. These water temperatures are within the range of values observed for Lake Michigan between

Table 1

Repeated measures ANOVA output for abundance (number per liter) of zooplankton groups (veligers, nauplii, rotifers, cladocerans, and copepods) with *Dreissena rostriformis bugensis* treatment and time as factors. Statistics include degrees of freedom (d.f.), sum of squares (SS), mean squares (MS), and F-statistic (F). Degrees of freedom for time and interaction were adjusted using Greenhouse-Geisser correction. Bonferroni corrected α of 0.01. Significant differences in bold.

Taxa	Source	d.f.	SS	MS	F	p-Value
Veligers	Mussels	1	14,500	14,600	121.6	0.000
	Time	1.65	7620	4620	12.6	0.007
	Interaction	1.65	6740	4090	11.14	0.009
	Error	6.6	2420	367		
Nauplii	Mussels	1	594	594	129.3	0.000
	Time	1.82	313	172	20.59	0.001
	Interaction	1.82	80.4	44.2	5.28	0.040
	Error	7.28	60.8	8.36		
Rotifers	Mussels	1	540	540	30.47	0.005
	Time	1.56	109	69.5	1.63	0.263
	Interaction	1.56	221	141	3.32	0.109
	Error	6.25	267	42.7		
Copepods	Mussels	1	194	194	56.13	0.002
	Time	1.73	29.3	16.9	5.63	0.038
	Interaction	1.73	62.1	35.8	11.93	0.007
	Error	6.93	20.8	3		
Cladocerans	Mussels	1	19.5	19.5	12.12	0.025
	Time	1.47	3.19	2.17	3.28	0.116
	Interaction	1.47	1.81	1.23	1.86	0.233
	Error	5.87	3.89	0.662		

the months of July and August (17–23 °C, NOAA CoastWatch, Great Lakes Node, <http://coastwatch.glerl.noaa.gov>, accessed on 01/12/2016).

For each of the two experiments, quagga mussels and zooplankton were collected from St. James Harbor, Beaver Island, Lake Michigan. Quagga mussels on rocks were collected through snorkeling and transported to the laboratory in plastic crates containing ambient water. A foil weighing method was used to determine the number of mussels colonized per rock for distribution in the mesocosms (Mackie, 2004). We calculated a mean mussel density to foil weight ratio by first covering three 10 × 10 cm areas with foil, counting the number of mussels in each area, and then weighing the 10 × 10 cm piece of foil (Mackie, 2004). Then, mussel colonies on each rock were covered in foil and the weight of the foil was used to estimate mussel abundance per rock. Separate zooplankton assemblages were collected for each experiment using a 0.5 m diameter net with a small enough mesh (64 μm) to collect both rotifers and crustaceans (Barbiero et al., 2012). Fourteen vertical net tows were taken during daylight hours through the entire water column (15 m) and combined into one 18 L bucket and transported back to the laboratory for equal distribution between the six mesocosms after an initial zooplankton sample (1 L) was collected. The initial stocking density was approximately 7 times the estimated zooplankton density in St. James Harbor from a single 15 m net tow.

Experiment 1

Quagga mussel effects on zooplankton community composition were first tested using a presence/absence experiment. In a systematic design, three mesocosms were stocked with 5319 ± 364 (mean \pm 1SD) mussels/ m^2 and three mesocosms were stocked with rocks having no mussels. We diluted the zooplankton assemblage collected from St. James Harbor to 21 L then equally stocked each mesocosm with 3.5 L of concentrated mixed zooplankton. The experiment lasted six days with one zooplankton sample collected daily (2000 h) from each mesocosm. Prior to sampling, water circulators were removed and each mesocosm was thoroughly mixed using a meter stick. Samples were collected using a 10 cm diameter, 64 μm mesh net. The net was submerged and set on the bottom of the mesocosm for 20 s before collecting each sample. All samples were preserved with 10% sugar formalin in 250 mL plastic bottles.

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