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Dreissenid metabolism and ecosystem-scale effects as revealed by oxygen consumption

Emily H. Tyner [a], Harvey A. Bootsma [a,*], Brenda Moraska Lafrancois [b]

[a] University of Wisconsin-Milwaukee, School of Freshwater Sciences, 600 E. Greenfield Ave., Milwaukee, WI, 53204, USA
[b] National Park Service, 2800 Lake Shore Drive East, Ashland, WI, 54806, USA

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ABSTRACT

Respiration rates of the quagga mussel (*Dreissena rostriformis bugensis*) were determined for the shallow and profunda morph phenotypes from *in situ* and laboratory experiments under a range of temperature (4–20°C), shell size, and food and oxygen availability conditions. Temperature-normalized oxygen consumption was significantly lower for the hypolimnetic profunda phenotype than for the shallow type. Mass-normalized respiration rates were inversely related to mussel size. Mussels adjusted their oxygen consumption in response to food enhancement and deprivation, lowering their respiration to a basal metabolic rate 18 hours after food deprivation. In response to decreasing ambient oxygen, quagga mussels exhibited first-order reaction kinetics, with mass-normalized respiration rate at a dissolved oxygen concentration of 0.002 mol L^{-1} being 1% of that at saturation. Using published data on quagga mussel energy budgets and respiratory quotients, oxygen consumption rates were converted to organic carbon consumption rates. Using these values, along with data on mussel density and size frequency distribution, it is estimated that quagga mussels consume 54% of annual phytoplankton production, from 1.4–4.1 times the offshore annual settled organic carbon in the southern basin of Lake Michigan, and from 2.4–5.5% of offshore areal particulate carbon in the water column. Dreissenids appear to exert significant direct influences on benthic oxygen dynamics, and consume enough organic carbon to have a significant effect on energy flow in the Lake Michigan ecosystem.

Introduction

Following the initial establishment of the zebra mussel (*Dreissena polymorpha*) in nearshore regions of Lake Michigan, the invasive quagga mussel (*Dreissena rostriformis bugensis*) has expanded dreissenid distribution to nearly the entire bottom of the lake (Nalepa et al., 2010). The proliferation of this efficient filter feeder appears to have had a significant effect on nutrient dynamics and the composition and production of plankton (Chapra and Dolan, 2012; Mida et al., 2010; Mosley and Bootsma, in this issue), presumably by accelerating the rate at which particulate material is removed from the water column into the sediment. The resultant large increase in biomass of heterotrophic organisms on the lake bottom is likely to have implications for dissolved oxygen dynamics, which in turn may affect the distribution of benthic organisms, and biogeochemical processes. For example, the recent increase in bird deaths due to avian botulism (Chipault et al., 2015) may be due to a greater prevalence of anoxic conditions in lake sediment, providing conditions for the growth of *Clostridium botulinum* (Lafrancois et al., 2011; Pérez-Fuentetaja et al., 2011).

Since the invasion and colonization of the zebra mussel, a large amount of research has gone into understanding mussel physiology, specifically metabolism and oxygen demands. Mussel metabolism, in addition to affecting processes of nutrient cycling and sequestration (Bootsma and Liao, 2013; Cha et al., 2011; Evans et al., 2011) and bioenergetics (McMahon, 1996), influences mussel feeding (Baldwin et al., 2002; Sprung, 1995), and competitive interactions (Nalepa et al., 2009). Oxygen consumption - one of the most direct measurements of metabolism - has been investigated in zebra mussels (Aldridge et al., 1995; Fanslow et al., 2001; Thorp et al., 1998), but few studies have examined oxygen consumption in quagga mussels, or examined the factors that regulate oxygen consumption. The few laboratory studies that have examined quagga mussel respiration were done under a limited range of environmental conditions (Stoeckmann, 2003; Turner, 2010) and only one study examined the profunda phenotype (Nalepa et al., 2010). In that study, rather than measuring respiration directly, rates were inferred from measurements of electron transport activity, which are a measure of metabolic activity.

Quagga mussels, having almost completely displaced zebra mussels in much of the Great Lakes (Nalepa et al., 2010; Stoeckmann, 2003; Wilson et al., 2006), are currently found at all depths in Lake Michigan. Recent surveys indicate that quagga mussel densities are still increasing at some depth intervals, with almost all quagga mussels collected in

* Corresponding author. Tel.: +414 382 1717; fax: +414 382 1705.
E-mail addresses: ehtyner@uwm.edu (E.H. Tyner), hbootsma@uwm.edu (H.A. Bootsma), brenda_moraska_lafrancois@nps.gov (B.M. Lafrancois).

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these surveys of the profunda morph phenotype (Nalepa et al., 2014), which is found primarily in hypolimnetic waters. This phenotype is particularly suited to living in deep waters, possessing a long incurrent siphon that can be extended vertically upward to overlying water (Dermott and Munawar, 1993; Nalepa et al., 2014) and spawning at 9°C (Claxton and Mackie, 1998), a water temperature characteristic of the hypolimnion. If profundal quagga mussels exhibit grazing and metabolic rates similar to those observed for dreissenids in shallower water, they have the potential to significantly influence particle fluxes, nutrient cycling, and oxygen dynamics in the hypolimnion. A more complete understanding of quagga mussel respiration rates, particularly for the profunda phenotype, will provide insight into how dreissenids may be altering biogeochemical processes and may also be used to estimate dreissenid grazing rates and the role of dreissenids within the larger food web.

The purpose of this study was to determine how four environmental variables – temperature, mussel size, food supply, and dissolved oxygen concentration – influence quagga mussel respiration and determine how oxygen consumption of shallow and profunda morphs may differ. These respiration measurements were used to assess the role of the quagga mussel as an energy conduit in the Lake Michigan food web.

Methods

Experiments investigating respiration response to temperature were conducted both *in situ* and in the laboratory. Respiration responses to all other environmental variables (mussel size, food supply, and dissolved oxygen concentration) were tested in the laboratory. Profunda morph mussels, which are more difficult to collect because of their offshore location and depth, were used only in the temperature experiments. Shallow morph mussels were used in all experiments.

All statistical procedures were performed with R (version 3.1.0; The R Foundation for Statistical Computing 2014). Comparisons were not significant at $p \geq 0.05$. Unless otherwise indicated, all error measurements are standard deviation.

Mussel collection and maintenance

For laboratory experiments, shallow morph mussels were collected from a depth of 10 m at Atwater Bay, Lake Michigan (43° 05.719′ N, 87° 51.875′ W), a rocky, nearshore site 5 km north of the Milwaukee Harbor. Profunda morph mussels were collected at a 55 m site in Atwater Bay in October 2012. Immediately after collection, all mussel shells were gently scrubbed to remove attached algae. Holding time before experimentation ranged from 2–21 days for shallow morph mussels and 7 days for profunda mussels. Approximately 350 mussels were kept in aerated 5 gallon buckets in a dark, refrigerated room at temperatures specific to each experiment. Water in the buckets was exchanged every 1–2 days and replaced with water from the Milwaukee inner harbor, hereafter called harbor water. Sub-samples of harbor water were analyzed once a week for particulate organic carbon content to determine the concentration of food the mussels were receiving. Water was filtered onto pre-ashed Whatman GF/F filters, which were analyzed using an elemental analyzer coupled to a mass spectrometer (Finnigan MAT delta S SIR-MS, with elemental analyzer front end and ConFlo II interface). Between November 2011 and March 2012, during the time period most laboratory experiments were conducted, the mean particulate organic carbon concentration of harbor water was 138 μg ± 22 μg C L^{-1}. This is comparable to in-lake conditions at Atwater Bay, where the mean seston bottom (10 m) concentration between May and November 2012 was 151 ±47 μg C L^{-1} and the mean chlorophyll *a* concentration in the bottom meter of the water column was 0.416 ± 0.15 μg L^{-1} between May and November 2013.

At the conclusion of each experiment, all mussels were counted and their lengths determined to the nearest millimeter. Dry weights (mg) of mussels for all experiments were determined by drying the shell-free tissue at 52°C for 24 hours. Throughout this study, respiration rates were normalized to dry weight, using morphotype-specific length-weight relationships from the most spatially and temporally relevant experimental mussels (Table 1).

All laboratory experiments were 2 hour closed chamber (Nalgene®, gas-permeable polymethylpentene straight-sided jars) incubations conducted in the dark. Mussel-free, pre-aerated control chambers at experimental temperature were used in all experiments to check oxygen loss from use of a gas permeable chamber. Across all experiments, oxygen loss in the control chambers was on average 0.10% ± 0.05% (SE) of total dissolved oxygen change in experimental chambers.

Dissolved oxygen sensor

The initial and final dissolved oxygen (DO) were recorded with a sensor calibrated before each experiment. For the *in situ* experiments, DO was measured with a Clark-type polarographic oxygen electrode (YSI model 600R Sonde) and a YSI 650MDS display data logger. The sonde is designed for *in situ* use and a waterproof housing system for the data logger and the sonde was developed at the School of Freshwater Sciences, University of Wisconsin-Milwaukee. Previous research by the authors demonstrated the sonde's utility for measuring community respiration. The YSI system was also used in the laboratory shallow morph temperature experiments.

Recognizing the difficulty in maneuvering a bulky sonde system in chambers, subsequent experiments used a smaller probe more suited to the lab. A VWR® Traceable® Digital Oxygen Meter (Clark-type polarographic oxygen electrode) was used in the mussel size, food deprivation, and food enhancement experiments. Subsequently, a NeoFox Sport optical oxygen microsensor (optode) system with a finer and highly sensitive optical probe was used for the profunda morph temperature experiment and shallow morph decreasing oxygen experiment. The optode's sensitivity was ideal for the closed chamber experiment, which required a highly sensitive device to track the decreasing changes in DO as the chamber went hypoxic. Because all oxygen systems were calibrated before each use, data between devices are comparable.

Effect of temperature on oxygen consumption

Mussels between 15 and 19 mm were transferred from the aerated containers at maintenance temperature (8°C) to aerated 4 L bottles of harbor water at experimental temperatures: 4, 10, 14, and 19°C, which reflects the range of nearshore bottom water temperatures at Atwater Bay from May-November (4–23°C). Following a three-hour acclimation exposure to the experimental temperature, mussels were transferred into triplicate 175 mL chambers and filled with temperature specific water from the aerated 4 L bottles. While three hours is a relatively short acclimation period, this time scale is similar to observations of swift temperature changes in the Lake Michigan nearshore zone (Troy et al., 2012).

Each chamber contained 23–26 mussels, equivalent to an areal density of 2,170 mussels m^{-2}. Although lower than an estimated nearshore areal density in Lake Michigan of ~5,000 mussels m^{-2}, this experimental density captured changes in DO over 2 hours without completely depleting oxygen in the chamber, which could have confounded respiration rates. A pre-experiment exposure period lasted from 10–15 minutes and was used to ensure that the majority of mussels were opening their shells and extending siphons, at which point the experiment commenced. Replicate temperature experiments were conducted at 2, 8, and 9 days after initial mussel collection. Results of an ANCOVA (factors = temperature and time since collection) indicated no significant difference in respiration among the three dates ($F_{2,32} = 3.073$, $p = 0.06$).

In October 2012, a similar experimental setup was used to measure the effect of temperature on oxygen consumption by profunda morph quagga mussels. Seven days before experimentation, mussels were

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