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# Phosphorus recycling by profunda quagga mussels (*Dreissena rostriformis bugensis*) in Lake Michigan

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ABSTRACT

The effects of dreissenid mussels on plankton abundance and nutrient cycling in shallow, productive waters of the Great Lakes have been well-documented, but the effects of their more recent expansion into offshore regions have received much less attention. Understanding quagga mussel impact on Lake Michigan's phosphorus (P) fluxes is critical in assessing long-term implications for nutrient cycling and energy flow. In this study, P excretion and egestion rates were determined for mussels in the hypolimnion of Lake Michigan. Constant low temperatures and limited food supply contributed to a lower basal P excretion rate in profunda quagga mussels compared to the shallow phenotype. The P excretion:egestion ratio was approximately 3:2, highlighting the need to consider both of these pathways when assessing the effect of these filter feeders on nutrient dynamics. Total dissolved P (TDP) excretion rates ranged from 0.0002 to 0.0124 μmol $mgDW^{-1}$ $d^{-1}$, soluble reactive P (SRP) excretion rates ranged from 0.0002 to 0.0061 μmol $mgDW^{-1}$ $d^{-1}$, and particulate P (PP) egestion rates (feces + pseudofeces) ranged from 0.0007 to 0.0269 μmol $mgDW^{-1}$ $d^{-1}$. The ability of profunda mussels to alter P cycling dynamics is reflected in an increased hypolimnetic dissolved:particulate P ratio and the disappearance of the benthic nepheloid layer. On an areal basis, mussel P recycling rates are up to 11 times greater than P settling rates as determined by sediment traps, suggesting that mussel grazing has resulted in an increased delivery rate of P to the deep benthos and a shorter P residence time in the water column.


## Introduction

Understanding nutrient cycling in aquatic systems is critical in interpreting energy flow and food web dynamics. Benthic filter feeders can exert bottom-up forces on aquatic systems by altering the rates and stoichiometry of nutrient recycling, as well as the spatial distribution of nutrients (Arnott and Vanni, 1996; Mellina et al., 1995; Naddafi et al., 2009; Stanczykowska and Lewandowski, 1993). At the same time, filter feeders can have a top-down influence through grazing, which can affect both phytoplankton abundance and species composition (Cloern, 1982; Fahnenstiel et al., 2010; Newell, 1988; Vanderploeg et al., 2010). Recent studies have highlighted the potential importance of suspension feeders in coupling pelagic and benthic systems (Ackerman et al., 2001; Higgins and Vander Zanden, 2010; Kautsky and Evans, 1987; Newell et al., 2005; Padilla et al., 1996) and altering the relative importance of pelagic versus nearshore energy flow and nutrient cycling (Bootsma and Liao, 2014; Cha et al., 2011; Hecky et al., 2004; Vanderploeg et al., 2010).

In North America, two *Dreissena* congeners, first the zebra mussel (*Dreissena polymorpha* Pallus) in the late 1980s followed by the quagga mussel (*Dreissena rostiformis bugensis* Andrusov) in the early 2000s, have become abundant in the Great Lakes region. Although both congeners invaded simultaneously, zebra mussels initially proliferated in nearshore rocky habitats, while quagga mussels were predominantly restricted to the offshore (Dermott and Munawar, 1993). Within a couple decades, zebra mussels were displaced by quagga mussels in most parts of the lakes, due to better tolerance of cold conditions (Spidle et al., 1995), lower metabolic costs (Stoeckmann, 2003), and earlier spawning at lower temperatures (<5 °C) (Roe and MacIsaac, 1997). Numerous *in situ* and experimental studies of dreissenids have highlighted the ability of these filter feeders to alter nutrient cycling and food web dynamics in the Laurentian Great Lakes. Dreissenids have been shown to be selective filter feeders, favoring certain phytoplankton taxa, such as cryptophytes and flagellates (Naddafi et al., 2007; Tang et al., 2014). They will ingest particles over a large size range but appear to prefer particles <53 μm (Vanderploeg et al., 2001). Dreissenids are capable of filtering upwards of several liters per day (Bunt et al., 1993; Kryger and Riisgard, 1988; Lei et al., 1996; Yu and Culver, 1999) which, combined with densities of up to 19,000 $m^{-2}$ (Nalepa et al., 2010), can result in shifts in phytoplankton composition, reductions in phytoplankton biomass, and increased water clarity (Fahnenstiel et al., 2010; Vanderploeg et al., 2001, 2009, 2010). In shallow, productive systems such as Saginaw Bay and Lake Erie, dreissenids may be a factor in promoting harmful algae blooms (HABs) by selectively rejecting toxic cyanobacteria in their pseudofeces (Vanderploeg et al., 2001). In less

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productive Lake Michigan, dreissenids appear to be responsible for large decreases in phytoplankton abundance and primary production during the spring isothermal mixing period (Fahnenstiel et al., 2010).

Until ~2005, *Dreissena* populations in Lake Michigan were limited to nearshore regions, as zebra mussels proliferated solely on hard substrate in depths typically less than 50 m. More recently, the zebra mussels have been displaced by quagga mussels, which consist of two phenotypically different morphs (Claxton et al., 1998; Mills et al., 1999). The shallow morph is found primarily on rocky habitat, but the profunda morph can colonize sandy substrate at extreme depths, reaching a mean density of 13,800 mussels $m^{-2}$ at depths of 31–90 m in just 7 years after establishment in 2001 (Nalepa et al., 2009, 2010). A high assimilation efficiency (Baldwin et al., 2002) and low respiration rate (Stoeckmann, 2003) make the profunda morph well adapted to oligotrophic conditions in offshore Lake Michigan (Nalepa et al., 2009, 2010).

The nearshore shunt theory postulates that nearshore dreissenids have modified the physical environment, altered nutrient recycling pathways, and increased nutrient retention in the nearshore (Hecky et al., 2004). With the expansion of dreissenids to deeper regions, these effects may have also expanded away from the shore (Vanderploeg et al., 2010), as the invasive mussels intercept nutrients as they are transported between the nearshore and offshore. However, few direct measurements have been made to quantify the role deep-water dreissenids may have as grazers and nutrient recyclers.

Data presented by Fahnenstiel et al. (2010) suggest that dreissenids may have a significant impact on phytoplankton populations when the lake is unstratified, but their effect is significantly reduced during stratification, presumably due to minimal mixing between the deep benthos and the epilimnion. However, nutrient processing by dreissenids within the hypolimnion during the stratified period may still have significant effects on long-term, whole lake nutrient dynamics by influencing the ultimate fate of settling particulate nutrients. If a large portion of consumed food is allocated to mussel biomass or permanently buried as biodeposits, the invasive mussels may accelerate nutrient removal from the system. However, if the excreted and egested nutrients are returned to the water column, then quagga mussels may have no net effect on the total amount of water column P, although they might alter the distribution of that P among various forms (e.g. dissolved vs. particulate). Discerning this effect from long-term trends is difficult, as Lake Michigan's mussel populations have likely not reached steady state, making it difficult to distinguish the relative roles of mussel population growth versus sediment burial as nutrient loss mechanisms.

A recent Lake Michigan P mass balance model showed a divergence between observed and simulated pelagic total P concentrations in the offshore after 1990, providing evidence that dreissenids are increasing the sequestration of P in the benthos, either in the form of mussel mass, sediment burial, or both (Chapra and Dolan, 2012). However, no studies have quantified profunda quagga mussel P excretion or the sequestration of P in either biomass or biodeposits. In this study, we evaluate (i) profunda quagga mussel density, size distribution, and length–weight relationship; (ii) profunda quagga mussel P excretion and egestion; (iii) differences in P recycling by nearshore versus offshore mussels; and (iv) the effect of profunda quagga mussels on the flux of particulate P from the water column to the benthos.

## Methods

### *Water column profiles and nutrient analysis*

The study site was in Lake Michigan southeast of Milwaukee, Wisconsin (42.979755 °N, 87.6658 °W; depth = 55). This site was chosen because of its high profunda quagga mussel density and the potential capacity of mussels at this depth to be a significant nutrient sink (Vanderploeg et al., 2010). On each sampling cruise to the study site (1 May, 12 June, 16 July, 21 August, and 14 October 2013), water samples were collected with 5 L Niskin bottles at 2 m, 10 m, 20 m, 30 m, 40 m, 50 m, 53 m, and 55 m (near-bottom) for water chemistry. Water samples were filtered through Whatman pre-ashed GF/F filters (nominal pore size = 0.7 μm) for analysis of particulate C + N, particulate phosphorus (PP), and chlorophyll *a*. Filtrate was kept for measurement of soluble reactive phosphorus (SRP) and total dissolved phosphorus (TDP).

SRP analyses were conducted using the molybdate-ascorbic acid method (Stainton et al., 1974) with absorbance measured at 885 nm using a 10 cm path length. TDP samples were digested by addition of 4 N $H_2SO_4$ and $H_2O_2$, followed by exposure to UV light in a photo-oxidizer for 2 hours, after which the resultant SRP was measured as described above. Particulate P filter samples were combusted at 550 °C for 2 hours. After combustion, 1 N HCL and distilled, deionized water were added and the samples were placed in an oven at 105 °C for 1.5 hours. The resultant SRP was measured as described above.

Chl *a* was extracted with a 68:27:5 methanol–acetone–deionized water extraction solvent for 24 hours at −28 °C and measured on a Turner Model 10 Series fluorometer. Filters for particulate C + N were acidified with 5% HCl to remove any inorganic C, followed by rinsing with distilled, deionized water. The mass of C and N on each filter was measured with a continuous flow isotope ratio mass spectrophotometer interfaced with an elemental analyzer (Delta PlusXP, Thermofinnigan, Bremen) using acetanilide standards.

Water column profiles of temperature, conductivity, photosynthetically active radiation (PAR), dissolved oxygen, pH, and chlorophyll *a* fluorescence were measured with a Seabird SBE 25 CTD profiler on each sampling date.

### *Study sites and mussels*

Profunda morph quagga mussels were collected from Lake Michigan at the 55 m study site on each sampling date. Mussel areal densities and size distribution were determined by collecting replicate bottom samples with a Ponar grab (22.5 × 22.5 cm sample area) in May, June, July, and August 2013. The entire contents of each replicate Ponar grab, except June, were counted to determine size distribution. In each of these months, subsamples were used to determine length–weight relationships. A frequently monitored 10 m nearshore rocky site in Atwater Bay near Milwaukee, WI (43.10243 °N, −87.87599 °W, depth = 10) served as a comparison shallow site for mussel densities and biomass in 2013. At this site, SCUBA divers collected triplicate samples by scraping mussels from 20 × 20 cm quadrats on the tops of rocks with upper surface dimensions greater than 40 × 40 cm. Mussel phosphorus excretion and egestion experiments for the offshore site were conducted on 5 dates during 2013: 1 May, 12 June, 16 July, 21 August, and 14 October.

### *Mussel length–weight analysis*

A length–weight relationship for profunda quagga mussels was established for each sampling date (1 May, 12 June, 16 July, 21 August, and 14 October) in 2013. Mussel soft tissue was separated from shells and lyophilized, after which the soft tissue dry weight (DW) was measured. Length–weight relationships were fitted to the allometric model $W = aL^b$, where W is the tissue dry weight (DW, mg) and the L is the length of the shell in mm (Nalepa et al., 1993). Size distributions determined for each month were used in conjunction with length–weight relationships to estimate total dreissenid biomass density (g $m^{-2}$).

### *Measurement of mussel phosphorus excretion and egestion*

Nutrient excretion rates of dreissenids have been extensively studied, and a summary of published rates is presented in Bootsma and Liao (2014). Many previous studies focusing on mussel nutrient excretion (mainly zebra mussels) have measured excretion rates in controlled laboratory experiments with mussels from shallow, well-mixed water bodies (Arnott and Vanni, 1996; Conroy et al., 2005; Mellina et al.,