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Phosphorus Recycling By Profunda Quagga Mussels in Lake Michigan

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PHOSPHORUS RECYCLING BY PROFUNDA QUAGGA MUSSELS IN LAKE

MICHIGAN

by

Caroline Mosley

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ABSTRACT

PHOSPHORUS RECYCLING BY PROFUNDA QUAGGA MUSSELS IN LAKE MICHIGAN

by

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The University of Wisconsin-Milwaukee, 2014
Under the Supervision of Professor Harvey Bootsma

Quagga mussels (*Dreissena rostiformis bugensis)* act as ecosystem engineers in the southern basin of Lake Michigan, altering physical habitats and biogeochemical processes. Adapted to cold and oligotrophic conditions, profunda quagga mussels thrive on the soft substrate of deeper depths. At a 55 m site (10,000 mussels m^{-2}) offshore from Milwaukee, WI, profunda mussel biomass (g m^{-2}) was 1/3 of biomass (g m^{-2}) measured at a 10 m comparison site (5,000 mussels m^{-2}). Higher densities but less biomass is due to profunda mussels having less tissue for a given length and the population per m^2 comprising of mostly small mussels (< 8 mm). Cold temperatures (≤ 6 ℃) and oligotrophy in the hypolimion (≤ 0.10 µmol P L^{-1}) limit profunda quagga mussel grazing, excretion, and egestion. Profunda mussels ≥ 8 mm excrete at similar rates (0.004 to 0.010 µmol SRP $mgDW^{-1}$ d^{-1}) that are nearly a magnitude lower than the nearshore phenotype. Past studies have focused on mussel excretion, but these experiments suggest the excretion : egestion ratio is 3 : 2, and mussel biodeposits could a critical factor in the amount of P sequestered by mussels. Mussel effective clearance rates (0.19 to 3.65 L $mgDW^{-1}$ d^{-1}) increased with decreasing mussel dry tissue weight and were dependent on

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particulate P concentrations above the mussel bed. In one year, nutrient cycling by profunda quagga mussels is 100 times greater than nutrients tied up in biomass, highlighting how the filter feeders increase the cycling rate.

Internal recycling is a critical component of Lake Michigan's P cycle. In the pre-dreissenid period, P was utilized in the hypolimnion by phytoplankton, settled passively to the lake bottom, and largely returned to the system via resuspension. Profunda quagga mussel grazing has altered P fluxes by reducing sediment resuspension and increasing nutrient cycling in the benthos. Mussel grazing rates are higher than passive settling rates due to vertical mixing replenishing the food supply above mussel beds. Dreissenids act as both nutrient recyclers and sinks, but in the deeper depths of Lake Michigan, profunda quagga mussels filtering year-round appear to have altered P residence time in the benthos.

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"When we try to pick out anything by itself, we find it hitched to everything else in

the universe."

-John Muir

1. Introduction

Understanding nutrient cycling in an aquatic system is critical in interpreting energy flow and food web dynamics. Phosphorous (P) is the limiting nutrient in many temperate freshwater systems and a major component in biological metabolism, with around 90 % occurring as organic phosphates, cellular constituents, and P adhered to detrital matter (Wetzel, 2001). P concentrations in aquatic systems rely on both abiotic (water chemistry and climate) and biotic (aquatic organisms) factors. The composition of aquatic food webs affects the distribution of P in a system as well as the partitioning of P between various pools (particulate versus dissolved). Large populations of benthic filter feeders, such as oysters, clams, and mussels, can alter P cycling by efficiently filtering nutrients out of the water column. Linking pelagic and benthic systems, suspension feeders affect energy distribution (Ackerman et al., 2001; Higgins and Vander Zanden, 2010; Kautsky and Evans, 1987; Newell et al., 2005; Padilla et al., 1996). They exert bottom-up forces on aquatic systems by altering the cycling, stoichiometry, and spatial distribution of nutrients (Arnott and Vanni, 1996; Mellina et al., 1995; Naddafi et al., 2009; Stanczykowska and Lewandowski, 1993). At the same time, constant grazing can have a top-down influence, affecting phytoplankton abundance and species composition (Cloern, 1982; Fahnenstiel et al., 2010; Newell, 1988; Vanderploeg et al., 2010). Large populations can act as ecosystem engineers by changing the physical environment and increasing the retention of nutrients in the benthos (Hecky et al., 2004). For example, mussels retain P by excreting at elevated C : P and N : P ratios (Naddafi and Pettersson, 2008), and this sequestration of P in biomass or egested material could constitute a substantial loss of nutrients from a system (Cha et al., 2011; Chapra and Dolan, 2012;

Johengen et al., 1995). Filter feeders are both nutrient recyclers and sinks, and depending on the productivity of an aquatic system, the sequestration of nutrients is either favorable or detrimental to nutrient cycling.

In eutrophic systems, filter feeders are necessary to keep water quality at a tolerable level for other organisms, and their absence can lead to poor water quality, enhanced phytoplankton blooms, and oxygen depletion due to microbial decomposition (Johannessen and Dahl, 1996; Rosenberg, 1985). Poor water quality in the Chesapeake Bay is due to increased anthropogenic N and P loading as well as anoxic conditions, exacerbated by the decline of the native eastern oyster *Crassostrea virginica* (Kemp et al., 2005). Where eastern oyster populations in the early 19th century could filter almost 80 % of the shallow bay, reduced populations now filter less than 1 % (Newell, 1988). The Chesapeake Bay is an example of the disappearance of a vital benthic filter feeder population where a high filtering capacity is needed to control eutrophication. Lake Michigan in the Laurentian Great Lakes region exemplifies the other end of the spectrum, where invasive dreissenid mussels dominate and stress an oligotrophic environment.

The recent invasion of prolific *Dreissena* mussels in North America has caused long-term implications to trophic state as the invasive filter feeders reengineer nutrient cycling in the Great Lakes region (Hecky et al., 2004; Johengen et al., 2014; Mida et al., 2010; Vanderploeg et al., 2010, 2002). Widespread throughout Europe, *Dreissena* are indigenous to the Dnieper River basin in the Ponto-Caspian region and highly adapted to a variety of temperatures and salinities while colonizing a variety a water bodies, from estuaries to rivers and lakes. High genetic diversity and polymorphism within the population, due to invasions attributed to human-mediated actions such as boat traffic

(Therriault et al., 2005), resulted in their rapid success. In North America, two 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 colonized all of the Great Lakes, as well as the Mississippi, Hudson, Ohio, and Colorado River basins. Although both congeners invaded simultaneously, zebra mussels initially proliferated extensively on nearshore rocky habitat and formed a 'belt' around the shoreline (Stanczykowska and Lewandowski, 1993), while quagga mussels were restricted to the offshore (Dermott and Munawar, 1993). Within a decade, zebra mussels were displaced due to K-strategy traits of the quagga mussel (Garton et al., 2014; Naddafi et al., 2009; Stoeckmann, 2003).

By the early 2000s, the quagga mussel in Lake Michigan was largely extirpating the zebra mussel due to earlier spawning at colder temperatures (Roe and MacIsaac, 1997) and lower energetic costs that gives it competitive advantage to withstand stress and low food conditions (Stoeckmann, 2003). In 2004 it was colonizing depths previously uninhabitable by the zebra mussel (Vanderploeg et al., 2002) and by 2010 it was the dominant congener (98 %) with high densities in both nearshore and offshore regions (Nalepa et al., 2010, 2009). Two phenotypically distinct but genetically similar morphs have been identified in the Great Lakes (Claxton and Mackie, 1998; Mills et al., 1999; Vanderploeg et al., 2010) as well as in the Chebosksary Reservoir located along the Volga River in Russia (Pavlova, 2011). The shallow (or epilimnetic) morph has a high flat shell and tolerates warmer temperatures with more wave action, preferring to colonize hard substrate, while the profunda morph has an elongated shell and colonizes soft substrate and deeper depths (Claxton and Mackie, 1998; Claxton et al., 1998). The

profunda morph is highly adapted to extreme oligotrophic conditions in offshore Lake Michigan, with plasticity in shell morphology, infaunal tendencies, and a higher assimilation efficiency allowing it to spread to depths > 90 m (Baldwin et al., 2002; Nalepa et al., 2009; Vanderploeg et al., 2010).

Numerous *in situ* and experimental studies on *Dreissena* in the Laurentian Great Lakes region highlight how extensive populations act both nutrient sources and sinks. The mussels are non-selective filter feeders (Jorgensen et al., 1984; Morton, 1969) that only distinguish food particles following ingestion (Sprung and Rose, 1988), with the rejection of non-food items through pseudofeces (filtered material expelled out of the inhalant siphon) (Lei et al., 1996). Because the freshwater mussels inhabit lakes of varying levels of productivity, the invaded systems are affected differently. In eutrophic systems such as Saginaw Bay and Lake Erie, dreissenid mussels can be a factor in promoting harmful algae blooms (HABs) by selectively rejecting the cyanobacterium *M. aeruginosa* in its pseudofeces (Vanderploeg et al., 2001), while in oligotrophic systems like Lake Michigan, phytoplankton primary production, abundance, and chlorophyll *a* decreased 70 %, 87 %, and 66 %, respectively, in the surface-mixed layer during the mixing period from the early 1980s to 2008 (Fahnenstiel et al., 2010). Focusing on Lake Michigan, *Dreissena* are capable of filtering up to 4 L day^{-1} (Bootsma et al., 2012) 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., 2010, 2009, 2001).

During Lake Michigan's unstratified winter months, dreissenids could potentially access the entire water column (Nalepa et al., 2010). A comparison of phytoplankton

growth rates with mussel clearance rates suggests that quagga mussels have the potential to consume 74 % of phytoplankton production during the winter-spring isothermal mixing period (Fahnenstiel et al., 2000; Vanderploeg et al., 2010). Stratification in the summer and fall limits mussel access to the euphotic zone and could force profunda quagga mussels to increasingly rely on passively settling particles. Understanding the grazing capacity and means of food regulation to profunda mussels is critical in interpreting how dreissenids affect water column nutrients during stratification. Another question linked to mussel food consumption is the fate of grazed material. If a large portion of consumed food is allocated to mussel biomass or permanently buried as egestion, the benthic filter feeders may be an effective channel of nutrient removal. Nutrient sequestration in offshore Lake Michigan could place the oligotrophic system under further duress. The disappearance of the native ampiphod *Diporeia* spp., which used to account for nearly 65 % of benthic biomass in depths > 30 m in southern Lake Michigan (Nalepa, 1989), has already drastically reduced energy cycling between trophic levels, as dreissenid biomass is thought to serve as more an energy sink rather than a pathway (Nalepa et al., 2009). Whether grazed nutrients are recycled or sequestered can impact the spatial and temporal dynamics of nutrient distribution in Lake Michigan.

Nutrient cycling in the offshore region of Lake Michigan is heavily dependent on seasonal dynamics and abiotic factors. Fluxes of nutrients and contaminants are hypothesized to be largely driven by sediment resuspension rather than external inputs (Brooks and Edgington, 1994; Eadie et al., 2002, 1984). A very small portion (< 3 %) of settling P becomes permanently buried, and P is likely made bioavailable from internal recycling and nutrient releases from sediment (Chen et al., 2002; Eadie et al., 1984;

Johengen et al., 1994). In the 1970s and 1980s, offshore sediment trap studies observed increased particle and nutrient fluxes during unstratified winter-spring mixing periods (Eadie et al., 1984), as well as during the summer stratified period (Meyers and Eadie, 1993). High fluxes near the bottom correlated with the presence of a benthic nepheloid layer, a region of turbid bottom water created during the formation of the thermal bar and maintained during the stratified period at depths ≥ 40 m (Chambers and Eadie, 1981). Since the dreissenid invasion, fluxes into and within the profundal benthic region have not been studied. Profunda mussels filtering directly on the sandy substrate could cause alterations to the sediment-water interface. *Dreissena* impact in the offshore is more difficult to monitor than the nearshore, but could provide insight into recent changes in Lake Michigan's productivity.

In the nearshore, *Dreissena* establishment modifies the physical environment, reengineers nutrient recycling, and increases nutrient retention (Hecky et al., 2004). The increased benthos nutrients have been linked to an increase of green filamentous algae *Cladophora glomerata* at shallow depths in the Great Lakes (Auer et al., 2010). The rapid expansion of the profunda phenotype in offshore Lake Michigan waters has often been implicated in changes to phytoplankton structure (Fahnenstiel et al., 2010) and nutrient concentrations (Mida et al., 2010; Vanderploeg et al., 2010). This expansion of mussel habitat has led to the hypothesis of the mid-depth sink (30-50 m) that works in conjunction with the nearshore shunt, intercepting the flow of C and P and effectively starving the offshore (Vanderploeg et al., 2010). Although mussel density and distribution in the offshore has been surveyed, few studies examine the role of the profunda mussel grazing, excretion, and egestion. Dreissenids can efficiently intercept,

sequester, and re-distribute nutrients in the well-mixed nearshore, but the effect of expansive offshore mussel grazing on a nutrient-depleted and thermally-stratified offshore pelagic region is poorly understood.

2. Offshore mussel population and P cycling dynamics

2.1 Background

Since the dreissenid invasion, the nearshore shunt (Hecky et al., 2004) and mid-depth sink (Vanderploeg et al., 2010) support the theory of nutrient draw-down from the pelagic to the benthos and alteration of nutrient exchange between the nearshore and offshore. Dreissenids have been studied in shallow, well-mixed systems such as Lake Erie (Arnott and Vanni, 1996; Conroy et al., 2005) and Oneida Lake (Turner, 2010), but little is known about mussel grazing and nutrient cycling in the deeper waters of a stratified, oligotrophic system such as Lake Michigan. The proportions of P mussels graze, excrete and egest, and assimilate into tissue could affect the apportionment of P in the system if the filter feeding efficiency and population size are extensive enough. Quantifying P cycling by offshore quagga mussels is critical in understanding how these filter feeders act as nutrient recyclers and if they are sequestering a significant amount of nutrients in the profundal benthos.

2.2 Purpose of study

The purpose of this study is to evaluate and quantify the profunda quagga mussel population in offshore Lake Michigan. A recent mass balance model of Lake Michigan P shows a divergence between observed and simulated total P concentrations in the offshore after 1990, providing circumstantial evidence that dreissenids are increasing P assimilation efficiency and sequestering P in either the food web or sediment (Chapra and

Dolan, 2012). However, no studies have quantified profunda quagga mussel P cycling or observed the sequestration of P in mussel biomass, mussel egestion, or sediment.

Observing pelagic nutrient profiles during the stratified season is critical in understanding how quagga mussels graze when they are cut off from the more productive regions of the water column (namely the euphotic zone). Comparisons with nearshore mussels demonstrate how the two *Dreissena* phenotypes cycle nutrients in a shallow, well-mixed region versus a deep, stratified system. Modelling, *in situ* measurements, and monitoring have indicated significant changes to nutrient concentrations and the food web since the dreissenid invasion (Chapra and Dolan, 2012; Fahnenstiel et al., 2010; Mida et al., 2010; Vanderploeg et al., 2010); however, few studies have been conducted to evaluate mussel impact in the offshore.

2.3 Methods

This study integrates field studies and experimental work to examine a 55 m site with a high profunda quagga mussel density site offshore from Milwaukee, WI. The mussel population was evaluated in terms of biomass and size distribution, as well as excretion, egestion, and grazing rates. The profunda morph was compared to the nearshore morph in order to better understand the differences between the two phenotypes.

2.3.1 Study sites

Profunda morph quagga mussels were collected from Lake Michigan at a depth of 55 m, approximately 19 km southeast of Milwaukee, WI (42°58.7853'N, 087°39.9348'W). The 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). A frequently monitored 10 m nearshore site in Atwater Bay near Milwaukee, WI

(43°5'46.1466, 087°51'52.5594) served as a comparison shallow (nearshore) site. Mussel densities were determined with replicate Ponar grabs at both the offshore and nearshore site. For offshore mussel analysis, densities and spatial variability were further assessed using an underwater camera mounted on the top of a 50 cm tall frame with a gridded base, which was lowered to rest on the lake bottom. Samples were collected once a month from April through October 2013, except for September. Mussels for experiments were collected with the Ponar grab, and experiments were conducted either onboard the research vessel or in the laboratory within three hours following collection.

2.3.2 Field sampling

On each sampling cruise to the offshore 55 m station, discrete water samples were taken with 5 L Niskin bottles at 2 m, 10 m, 20 m, 30 m, 40 m, 50 m, 53 m, and 55 m (bottom) for water chemistry (phosphorus, carbon, nitrogen, biogienic silica, and chlorophyll *a*). Water column profiles of temperature, conductivity, photosynthetic available radiation, dissolved oxygen, pH, and chlorophyll fluorescence were measured with a Seabird SBE 25 CTD profiler.

For mussel collection, at least 6 Ponar grabs were taken for one set of experiments. From 3 Ponar grabs, mussels were rinsed and placed in a container with unfiltered lake water during the cleaning process (2-3 hours). Mussels from the remaining Ponar grabs were immediately frozen for counting and length-weight analysis. Two Ponar grabs from June 2012 were used to assess mussel density and size distribution. Mussel density and size distribution was determined by counting and measuring mussels (1 mm resolution from 2 to 30 mm) from the remaining Ponar grabs that were collected

in June 2012, and April-August 2013. Ponar grabs from a 10 m site in Atwater Bay were collected in 2013 and counted for population structure and size density.

2.3.3 Laboratory work

Lake water was filtered onto Whatman pre-ashed GF/F filters for analysis of particulate C and N, particulate phosphorus, and chlorophyll *a*. Filtrate was kept for measurement of soluble reactive phosphorus (SRP) and total dissolved phosphorus (TDP). All phosphorus analysis was conducted using the molybdate-ascorbic acid method (Stainton et al., 1974) with absorbance measured at 885 nm using a 10 cm path length for dissolved P and 1 cm path length for particulate P. Particulate biogenic silica (BSi) was analyzed for the near-bottom (53 m) and bottom (55 m) discrete water samples from each sampling date. Samples for measurement of BSi were filtered onto 0.6 μm membrane filters. Chl *a* was extracted with a 68 : 27 : 5 methanol-acetone-deionized water extraction solvent and measured on a Turner Model 10 Series Fluorometer. Filters for particulate C + N were acidified with 5 % HCl followed by rinsing with distilled, deionized water. These filters were analyzed with a continuous flow isotope ratio mass spectrophotometer interfaced with an elemental analyzer (Delta PlusXP, Thermofinnigan, Bremen).

A length-weight relationship for profunda quagga mussels was established for each month (excluding 2012) by sacrificing 20-25 mussels immediately after the laboratory experiments were conducted. Mussel soft tissue was separated from shells and lyophilized, after which the mussel tissue was weighed for a tissue dry weight (DW). A length-weight relationship was established with the allometric equation $W = aL^b$ where W is the tissue dry weight (DW) and the L is the length of the shell in mm (Nalepa et al., 1993). Size distributions were determined for each month and used in conjunction with

length-weight relationships to estimate total dreissenid biomass density (g m^{-2}) for the 55 m depth. A length-weight relationship calculated for the shallow morph in 2006 was used to compare to 2013 profunda morph length-weight relationships.

2.3.4 Mussel excretion and egestion experiments

Due to depth and location of the offshore 55 m site, laboratory experiments simulating in-lake conditions were performed instead of *in situ* experiments. The morphology of all mussels used in the experiment conformed to that of the profunda morph, according observations made by Nalepa et al. (2010) and Vanderploeg et al. (2010). To quantify mussel excretion, egestion, and effective clearance rate, laboratory incubations were conducted within 3 hours of collection and immediately after a gentle cleaning of the shell. Upon collection and for the duration of the cleaning process, the mussels were placed in cold, unfiltered lake water in the dark to minimize stress and subsequent changes in physiological activity. Mussels were gently scrubbed with an abrasive cloth and then rinsed to remove algae and microbes from their shells. All mussels were carefully examined and only live, undamaged mussels were used in the experiment. For excretion / egestion experiments, mussels were grouped into 3 size classes: small (8-12 mm), medium (13-17 mm), and large (18-22 mm). The length of mussels in each size class was measured to the nearest mm. Temperature (4-6 °C) was held constant at profundal benthos conditions and experiments were conducted in darkness to simulate the low-light environment in the offshore.

Laboratory incubation experiments were conducted in 1 L acid-washed (5 % HCl) polyethylene incubation chambers. Approximately 450 mussels were gently cleaned, and 50 mussels from each size class (8-12 mm, 13-17 mm, 18-22 mm) were placed in each of

3 triplicate chambers containing 1 L of filtered lake water, for a total of 9 incubation chambers. One 1 L incubation chamber with filtered lake water served as a control. The chambers were covered and placed in a dark incubation room at 4-6 ºC. Chambers were incubated undisturbed for 2 hours. Measurements made with an optical (NeoFox Sport micro-optode system) dissolved oxygen (DO) probe indicated that the DO concentration remained above 90 % saturation during incubations. Following chamber incubations, 600–700 mL of water was collected and filtered (ashed, 0.45 µm Whatman GF/F) for dissolved and particulate phosphorus analysis using the method described previously. In October 2013, in order to better determine the excretion and egestion rate relationship to tissue dry weight (mg), an additional smaller scale laboratory experiment using the same methodology was conducted using 60 mL glass syringes with 3 mussels per syringe and 4 size classes (4-6 mm, 8-12 mm, 13-17 mm, and 18-22 mm).

2.3.5 Measurement of mussel effective clearance and grazing rate

Measuring pumping and effective clearance rate is critical in understanding the potential effect of dreissenid grazing on the plankton community. For Lake Michigan, previous observations suggest that this effect can be significant (Fahnenstiel et al., 2010; Vanderploeg et al., 2010). In the present study the pumping rate (PR) is defined as the volume of water passing through mantle cavity per unit time (Yu and Culver, 1999) and the clearance rate (CR) is the volume of water cleared of particulate matter per unit time (Fanslow et al., 1995). Previous laboratory and *in situ* methods examining dreissenid pumping and clearance rates have used lab-grown algae (Ackerman, 1999; Berg et al., 1996; Horgan and Mills, 1997), natural lake seston (Fanslow et al., 1995; Vanderploeg et al., 2009, 2001; Yu and Culver, 1999), mixed cultured and natural algae (Baldwin et al.,

2002; Vanderploeg et al., 2001), dye injection (Bunt et al., 1993), plastic microspheres

(Lei et al., 1996), and inorganic sediment particles (Diggins, 2001; Madon, Schneider,

Stoeckel, & Sparks, 1998). These experiments provide quantifiable rates, but do not

always reflect the *in situ* CR, as they may ignore refiltration (Yu and Culver, 1999) or

any *in situ* fluctuations in temperature, current velocity, and seston abundance or seston

quality. Yu and Culver (1999) applied a method in which the mussel egestion of

inorganic material and the concentration of suspended inorganic material were used to

estimate an *in situ* 'effective clearance rate' (ECR). This method is based on the premise

that, for inorganic material, rates of mussel egestion rate are equal mussel ingestion. Yu

and Culver's approach required an experimental duration of several days for measurable

quantities of egested inorganic material to be collected. Their approach also required a

correction for passively settling inorganic material. We modified Yu and Culver's

method by measuring biogenic silica (BSi) instead of inorganic seston. This allowed us to

determine effective clearance rates using short-term experiments because small amounts

of egested BSi can be measured accurately using the spectrophotometric method. Si is not

assimilated by mussels and unlikely to dissolve at the low pH levels in the mussel

digestive system, so we can assume that BSi egested (as feces and pseudofeces) is equal

to BSi ingested. A similar approach has been used previously to measure assimilation

efficiency in copepods (Tande and Slagstad, 1985).

Using the above method, the ECR of quagga mussels was determined as:

$ECR = E_{BSi}/[BSi]$

where ECR = L mussel^{-1} h^{-1}

E_{BSi} = BSi egestion rate (µmol BSi mussel^{-1} h^{-1})

$[BSi]$ = BSi concentration immediately above the mussel bed (µmol L^{-1})

The phosphorus grazing rate was then determined as:

$G_P = ECR\ [PP]$

where G_P = (µmol P mgDW^{-1} h^{-1})

$[PP]$ = Suspended P concentration 10 m above the mussel bed (µmol L^{-1})

Effective clearance rate and grazing rate experiments were done simultaneously with the mussel excretion and egestion experiments as described above. Following incubations, 100-200 mL of water was filtered (0.6 µm membrane filters) for particulate BSi analysis. Water column particulate BSi was analyzed for the near-bottom samples which were collected with a Niskin from the 55 m site for each experimental date. All BSi filter samples were digested in 1 % Na_2CO_3 for 2 hours in a water bath at 85 °C (Demaster, 1981; Saccone et al., 2006), followed by spectrophotometric analysis of soluble reactive silica (Stainton et al., 1974). A series of preliminary experiments using various combinations of temperature, digestion time, and Na_2CO_3 concentrations with Lake Michigan sediment indicated that this method results in complete digestion of biogenic Si with minimal dissolution of non-biogenic Si.

2.3.6 Statistical analyses

Statistical analyses were performed with the open-sourced statistical programming package R®. An ANCOVA was preformed to look at differences between the length-weight relationships. Mussel excretion and egestion rates were analyzed with ANOVA and pair-wise Tukey's Honest Significant Difference Test (HSD) to determine any significant differences between dates and size classes.

2.4 Results

2.4.1 Ambient conditions during study period

Temperature profiles at the 55 m station indicate that thermal stratification commenced between ~20 m in early June and remained weakly stratified until mid-October, with bottom temperatures remaining relatively constant (3-6 $^{\circ}$C) and not dropping below 3 °C during the entirety of the study period (Figure 1). Thermal profiles also indicate the presence of a deep chlorophyll layer (DCL) below the thermocline during summer stratification (June-October).

Chlorophyll *a* (µg L⁻¹)
Fluorescence (RFU)

June 19

July 16

Chlorophyll *a* (µg L⁻¹)
Fluorescence (RFU)
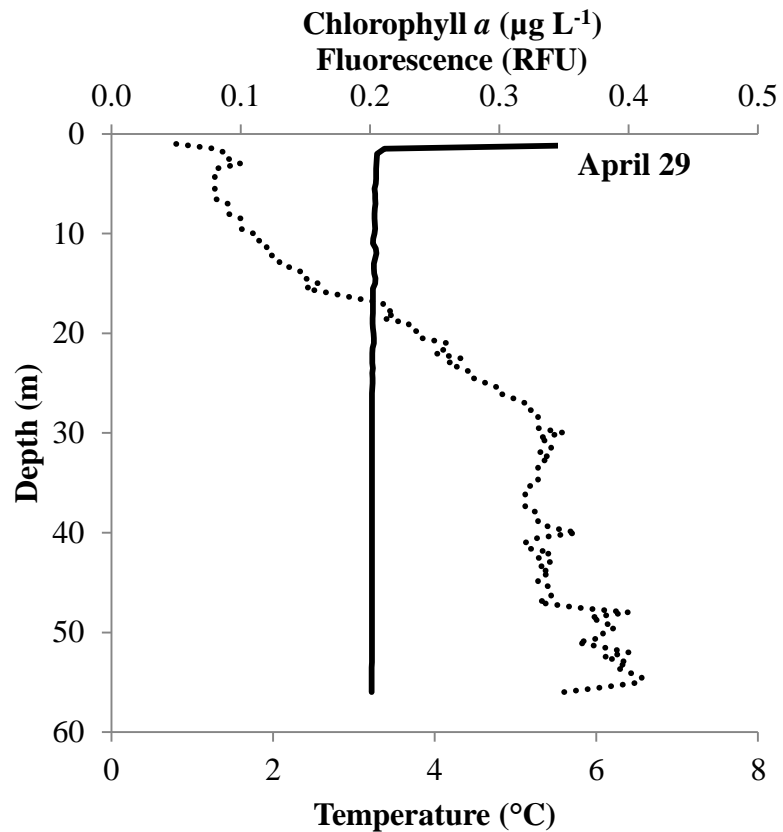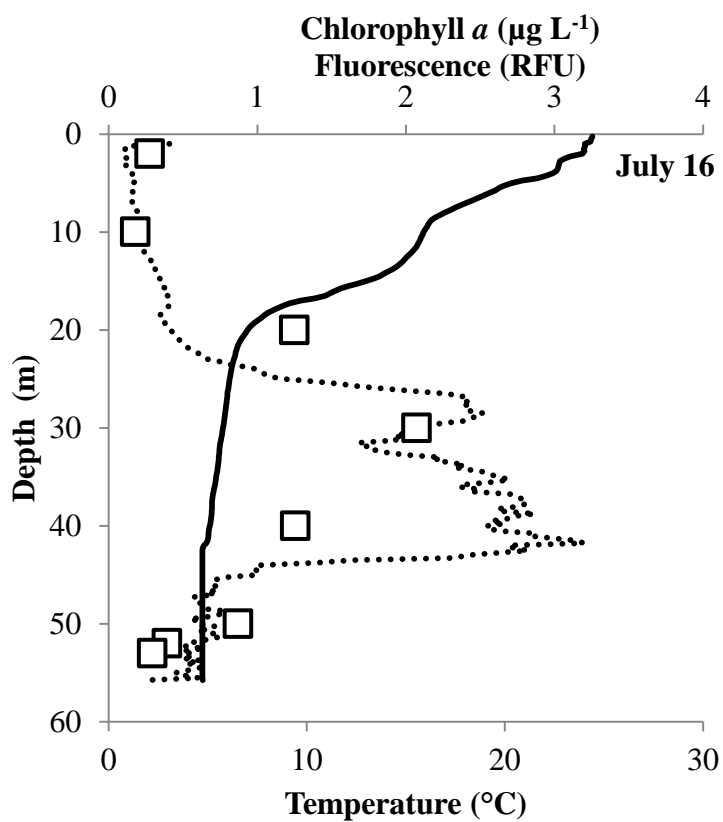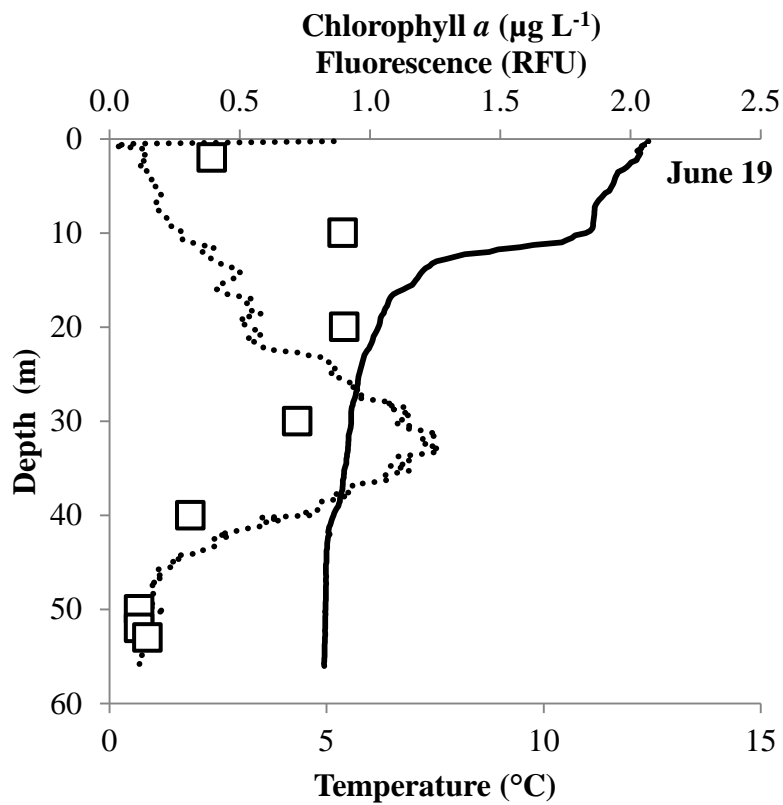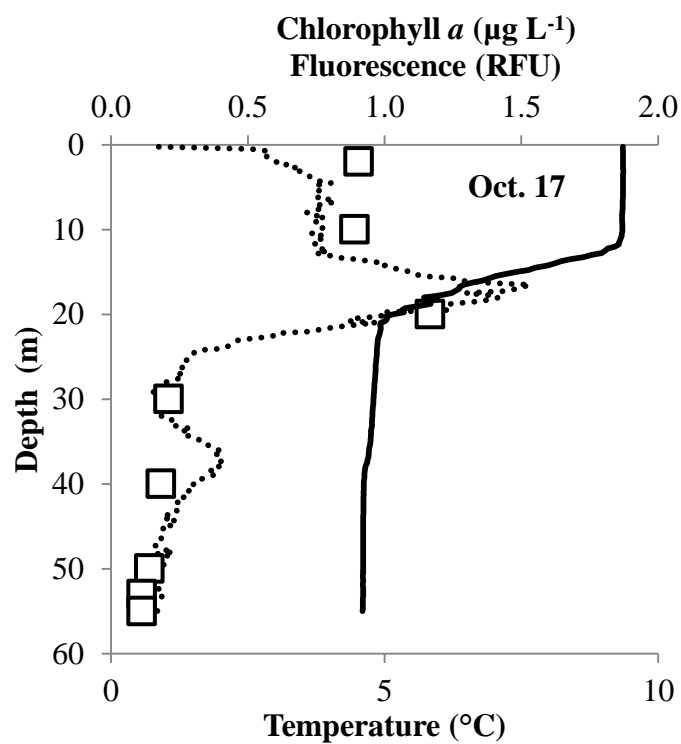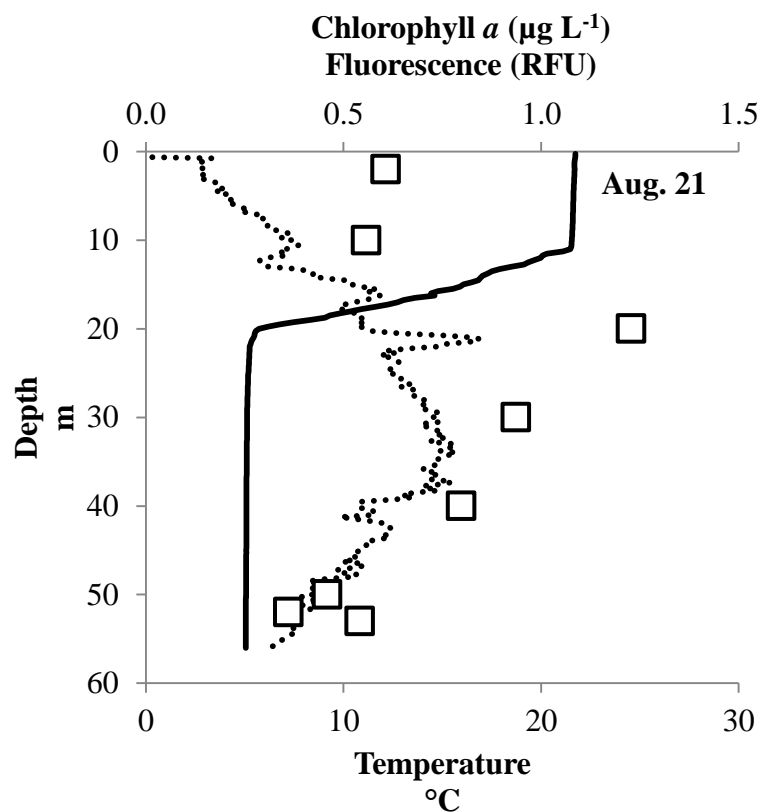
Figure 1: Chlorophyll *a* (μg L^{-1}) (□), *in situ* fluorescence (RFU) (dashed), and temperature (°C) (solid) profiles for the 55 m site in 2013 for April 29, June 19, July 16, Aug. 21 and Oct. 17 (note different scales).

During the stratified period, particulate phosphorus (PP) concentrations tended to decrease with depth below the thermocline, while soluble reactive phosphorus (SRP) and dissolved organic phosphorus (DOP) concentrations tended to increase or stay constant (Figure 2). The highest PP concentrations were in the mid water column (20-30 m), but remained low near the lake bottom. A similar spatio-temporal pattern was observed for chlorophyll *a* (Figure 1). SRP concentrations at the surface (< 20 m) were low (< 0.017 μmol L^{-1}) throughout the study period, but following stratification there was a slight increase in hypolimnetic ($\geq$ 20 m) SRP concentrations, with the highest measured concentration being 0.065 μmol L^{-1}. Examining the partitioning of P in the water column, particulate P constitutes between 35-41 % of water column total P on April 29 (an unstratified date), while from June through October (stratified period), the percentage of particulate P remains high (36-53 %) at depths $\leq$ 40 m, while $\geq$ 50 m particulate P is only 18-27 % of total P.

Epilimnetic seston C : P molar ratios were consistently above 150 : 1 during the study period, suggesting strong P limitation of phytoplankton growth (Healey and Hendzel, 1979). For the epilimnion (< 20 m), the C : P ranged from 112 : 1 to 301 : 1, and the hypolimnion ($\geq$ 20 m) ranged from 124 : 1 to 288 : 1, much higher than the recommended C : P ratio of 106 : 1 (Redfield, 1958). There was no discernible pattern in P-limitation, except that higher ratios were usually found at the surface (2 m) and benthos (52-56 m).

μmol L⁻¹

July 16

Depth (m)

SRP
DOP
PP
Temp

Temperature °C

μmol L⁻¹

Aug. 21

Depth (m)

SRP
DOP
PP
Temp
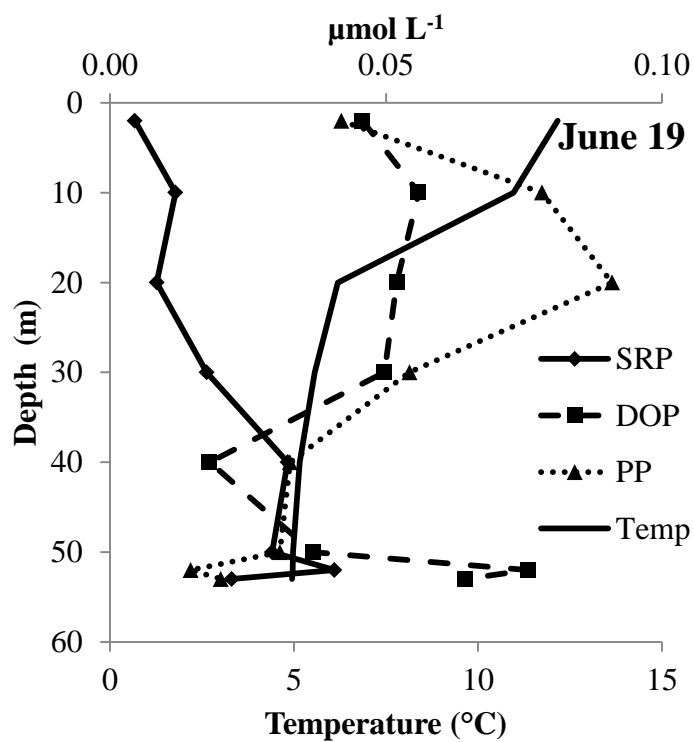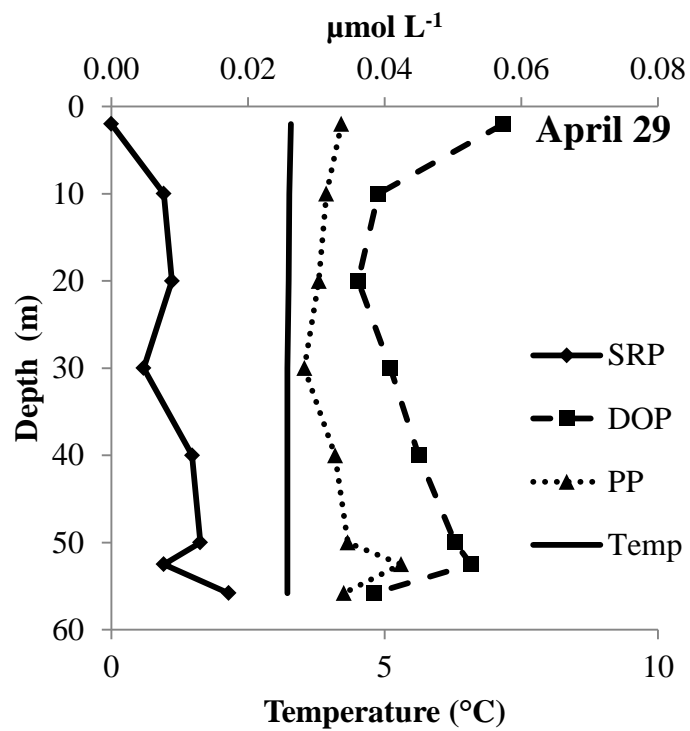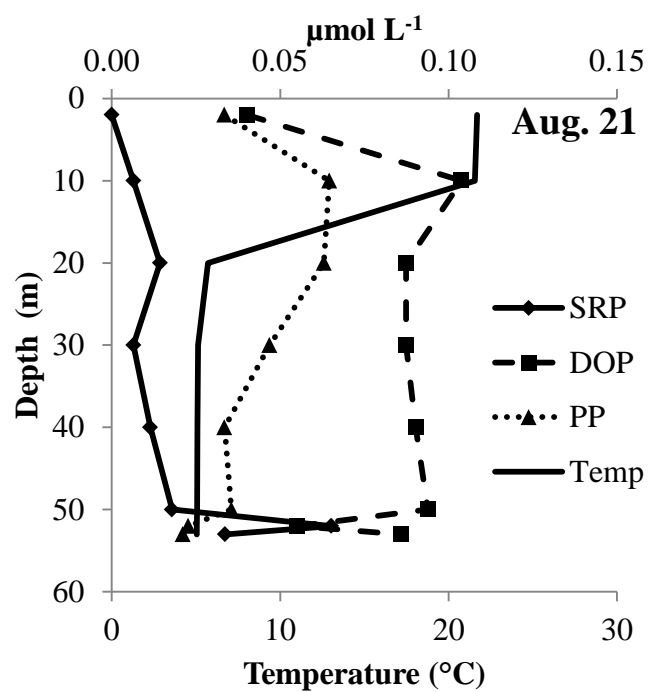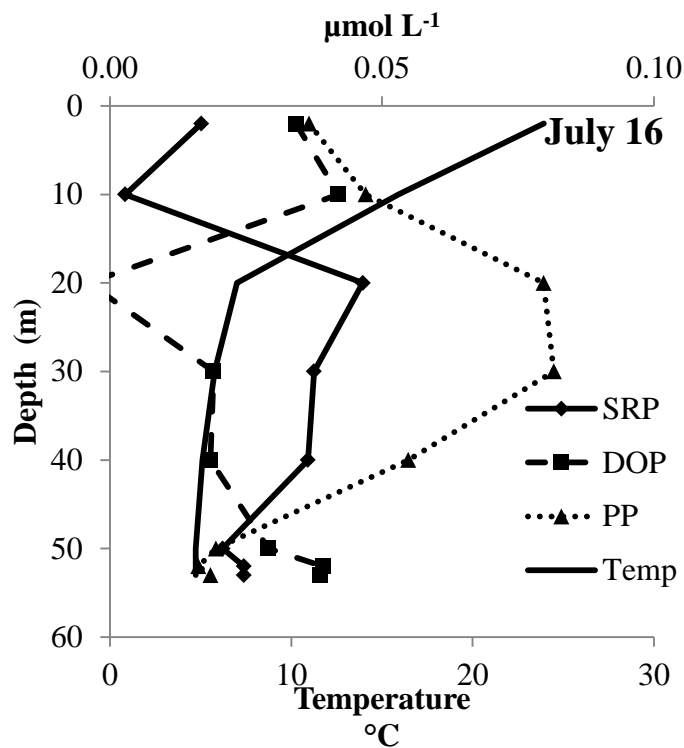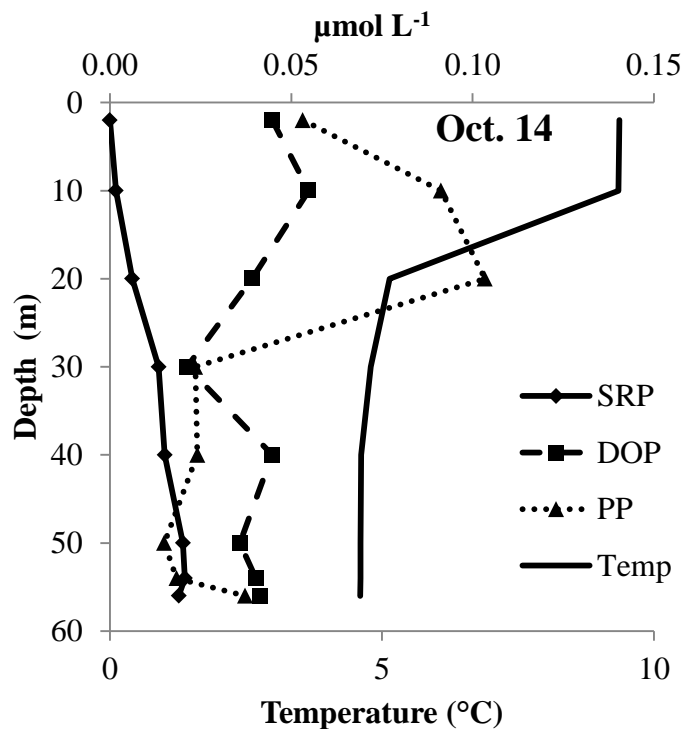
Temperature (°C)

Figure 2: Ambient water column soluble reactive P (SRP), dissolved organic P (DOP), and particulate P (PP) (µmol L^{-1}) plotted against temperature (°C) for the 55 m site in 2013 for April 29, June 19, July 16, Aug. 21, and Oct. 14 (note different scales).

2.4.2 Mussel density and size distribution

Table 1: Percentage of profunda quagga mussel population within various size classes at 55 m based on Ponar grabs collected in 2012 and 2013. The number of Ponar grabs counted is in parentheses.

Length (mm)	June 19 2012 (2)	April 29 2013 (3)	July 16 2013 (3)	Aug. 21 2013 (2)
<8	38.9 ± 19.0	62.2±7.4	51.6±6.6	40.3±23.7
8-12	25.5 ± 8.7	11.2 ± 2.3	17.1 ± 3.0	23.2 ± 7.4
13-17	22.4 ± 11.0	17.6 ± 7.6	24.1±0.4	27.3±10.7
18-22	7.6 ±3.7	6.7±1.5	5.7±1.6	7.2±4.7
>22	5.6±2.7	2.2±0.6	3.5±2.5	2.0±1.0

From Ponar grabs collected from 2012 and 2013, profunda *D.r bugensis* density at the 55

m station was 9968 ± 3232 m^{-2}. An average of 62.2 % at 55 m in 2012-2013 were < 8

mm, with an average of 92.8 % < 17mm (Table 1). Length-weight relationships and

biomass (g m^{-2}) for the 55 m station were calculated from subsampled mussels from

May-October 2013 (Figure 3, Table 2). Profunda quagga mussels gained mass throughout

the summer, with the length-weight relationships of May and October being significantly

different (ANCOVA, p < 0.001). Highest calculated biomass for July and August 2013

is likely associated with gained tissue, since the population structure derived from the

Ponar grabs remained unchanged (Table 2).

Table 2: Length-weight relationships for profunda quagga mussels in 2013. Mussels (n=25) were subsampled for each month from laboratory experiments. Using allometric relationships, mussel dry tissue biomass (g m^{-2}) was derived from Ponar grabs collected each month (except October). Profunda length-weight relationships from each month were compared to a length-weight relationship derived from shallow (10 m) mussels from a comparable nearshore region in the southern basin of Lake Michigan. *2012 Ponar grabs ** not depicted in Fig3*

Month	DW=aL^b, r^2	Biomass (g m^{-2})
Profunda May 2013	$0.0058L^{2.43}$, 0.74	22.4 ± 4.73
Profunda June 2013	$0.022L^{2.86}$, 0.96	21.73 ± 0.74*
Profunda July 2013	$0.0143L^{2.28}$, 0.83	45.9 ± 13.24
Profunda Aug. 2013	$0.0066L^{2.59}$, 0.97	42.4 ± 15.61
Profunda Oct. 2013	$0.0035L^{2.77}$, 0.97	-
Profunda 2013**	$0.005L^{2.61}$, 0.85	-
Shallow 2006	$0.0018L^{3.11}$, 0.95	-

Size distribution and length-weight relationships (log$_{10}$ (x + 1) transformed) of

profunda quagga mussels from the 55 m station were compared with those measured for

shallow quagga mussels collected at a 10 m station in Atwater Bay, WI. There was a

significant difference for length-weight relationships between shallow (W=$0.0018L^{3.11}$,

$r^2= 0.95$) and profunda ($W=0.005L^{2.61}$, $r^2=0.85$) quagga mussels in the southern basin of Lake Michigan (ANCOVA, $p < 0.001$) (Figure 3).
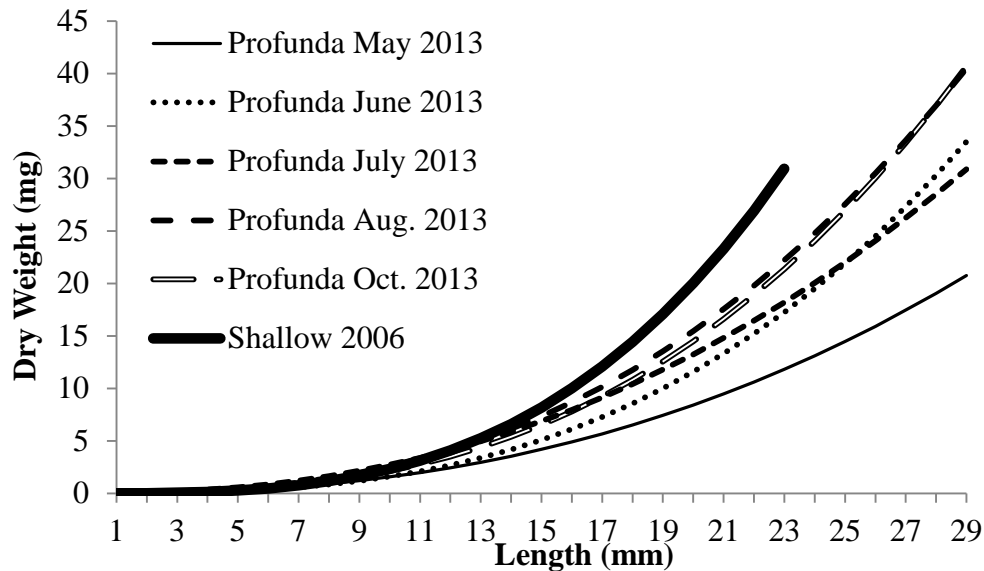
Figure 3: Length-weight relationships ($DW=aL^b$) for subsampled (n=25) profunda quagga mussels from 5 experimental dates from May through October in 2013 compared to a length-weight.

Smaller profunda and shallow mussels have similar weights for a given length, but larger shallow mussels are heavier than their offshore counterparts for a given length. For example, 7 mm shallow and profunda quagga mussels weigh approximately 0.80 mg, while shallow mussels > 10 mm become nearly twice as heavy as profunda mussels. Underwater camera imagery revealed that the 55 m site had some spatial and temporal variability, with most quagga mussels in clumps and aggregates on the sandy bottom (Figure 4).

Mussel size distribution from 2013 Ponar grabs collected from a nearshore (10 m) and offshore (55 m) site near Milwaukee, WI show two very different population structures (Figure 5). In the nearshore, the population structure is dominated predominately by mussels > 15 mm, while in the offshore most mussels are ≤ 15 mm.

Comparing mussel size distributions for these Ponar grabs, the 10 m nearshore site had a lower mussel density (4785 ± 1329 mussels m^{-2}) but higher biomass (93.82 ± 10.65 g m^{-2}) than the offshore site (9358 ± 3464 mussels m^{-2} and 34.95 ± 17.20 g m^{-2}). The mean (±SD) P content of profunda mussel dry tissue is 0.22 ± 0.03 µmol P mgDW^{-1} for 125 mussels subsampled during the 2013 summer. There was no significant different in P tissue content between dates (ANOVA, p=0.09).
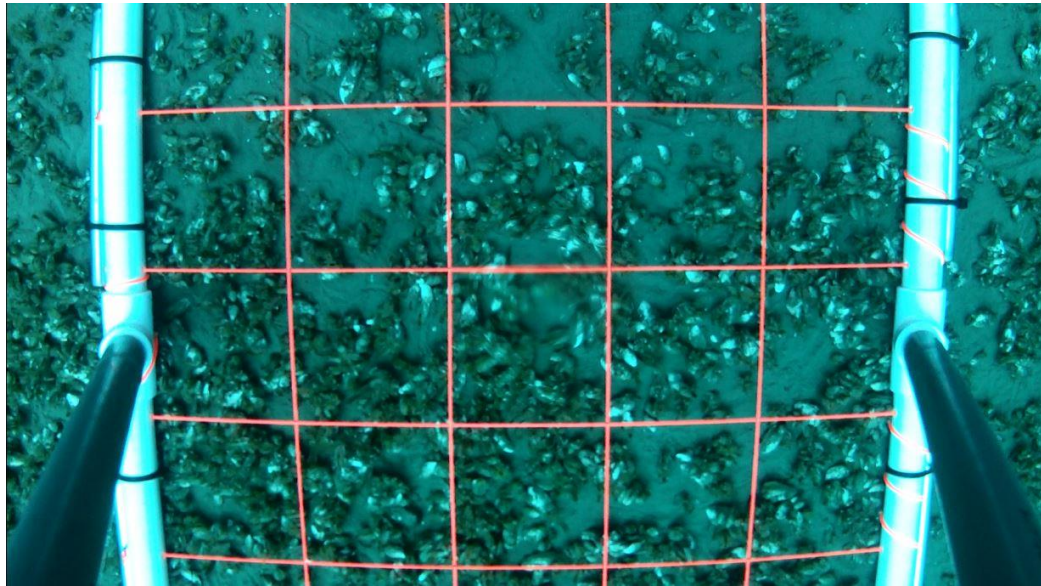
Figure 4: Profunda quagga mussel density at 55 m site taken with an underwater camera that was mounted on a 50 cm tall frame with a gridded base where each individual square is 10 x 10 cm.
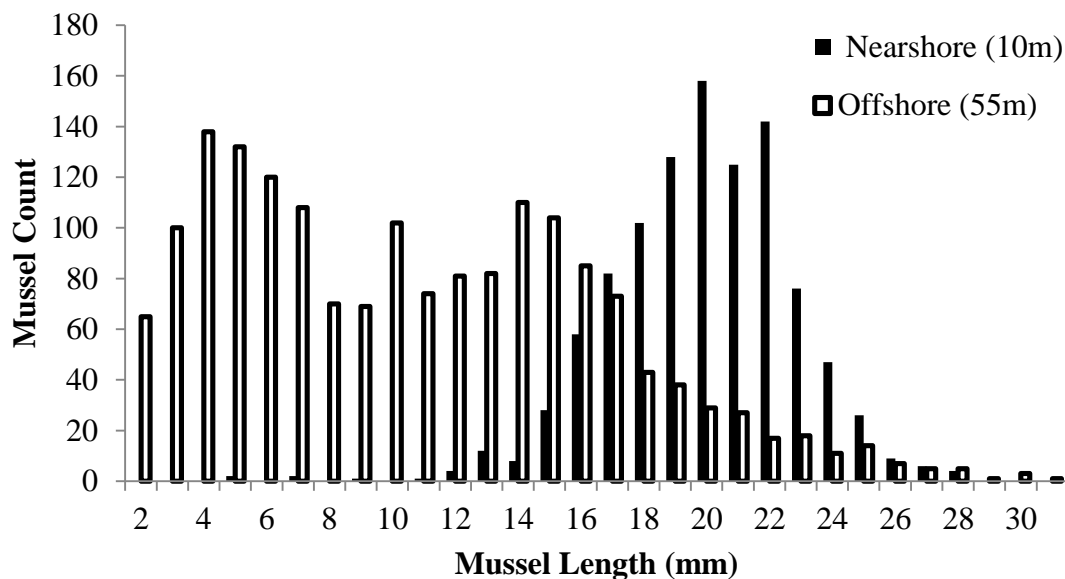
Figure 5: Comparison of length-frequency distributions of nearshore (10 m) and offshore (55 m) quagga mussels collected in 2013. Five Ponar grabs were collected from a 10 m nearshore site (43°5'46.1466 N, 087°51'52.5594 W; n=1021) and 4 Ponar grabs were collected from a 55 m offshore site (42°58.7853 N, 087°39.9348 W; n=1732) in the southern basin of Lake Michigan.

2.4.3 Measurement of mussel excretion and egestion

Profunda quagga mussel phosphorus excretion and egestion rates were normalized to tissue dry weight and compared between 3 size classes of small (8-12 mm), medium (13-17 mm), and large (18-22 mm) on 5 experimental dates (May 1, June 12, July 16, August 21, and October 14) in 2013. A small scale incubation experiment in October observed mass specific excretion (SRP and DOP) and egestion (PP) rates for profunda quagga mussels < 8 mm (Figure 6). Due to the singular nature of the small scale October experiment, the main focus of the study will rely on experiments conducted on the 5 experimental dates with the 3 size classes (8-22 mm).
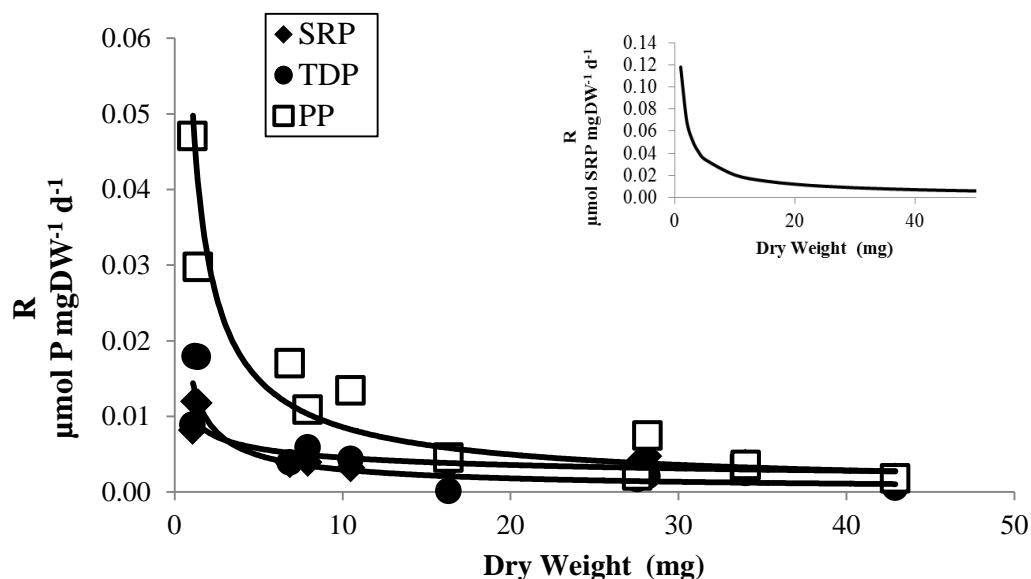
Figure 6: Profunda quagga mussel dry weight-specific excretion rate for SRP (R=0.01DW$^{-0.343}$, r^2=0.75 and TDP (TR=0.0152DW$^{-0.711}$, r^2=0.48) and egestion rate (E=0.0531DW$^{-0.791}$, r^2=0.87) at 5 °C and 0.04 µmol PP L^{-1} derived from October 2013 small-scale phosphorus excretion and egestion experiments. Shallow mussel R (upper left hand) derived from experiments conducted at 23 °C and a food concentration of 0.22µmol PP L^{-1} (R=0.1525DW$^{-0.7617}$, r^2=0.86) (Bootsma, 2009).

Comparing SRP excretion for shallow mussels (Bootsma, 2009) with SRP excretion of profunda mussels in Figure 5, a two-way ANOVA shows a significant difference between the profunda and shallow morph (p = 0.022). The shallow morph excretion ranges from 0.012 to 0.12 µmol SRP mgDW^{-1} d^{-1} (Bootsma, 2009) while the profunda morph ranges from 0.004 to 0.010 µmol SRP mgDW^{-1} d^{-1}. Shallow mussels with a dry tissue weight of 10 mg excrete 4 times more SRP than profunda mussels of similar mass. As tissue dry weight increases, the difference between the shallow and profunda SRP excretion rates decrease, but 100 mg shallow mussels still excrete twice the SRP of profunda mussels.

Figure 7: Profunda quagga mussel morph and shallow quagga mussel morph.

A two-way ANOVA shows no significant difference for profunda quagga mussel SRP excretion (R) between the 5 experimental dates (p = 0.28) or between the 3 size classes (p = 0.20) (Figure 8). For profunda mussel total dissolved phosphorus (TDP) excretion rates (TR), there was no significant difference between size classes (p = 0.20) but a significant difference between experimental dates (p = 0.005) (Figure 6). A pairwise Tukey's Honest Significant Difference test (HSD) showed a significant difference between July and August (p = 0.0035) and between August and October (p = 0.0165). For August, the dissolved organic phosphorus (DOP) (determined as difference between excreted SRP and TDP) was elevated in all three size classes compared to other dates (Figure 8). DOP concentrations in mussel phosphorus excretion experiments were, on average, about half of excreted TDP, with a mean (±SD) of 0.0008 ±0.001 µmol mgDW^{-1} d^{-1} excluding high rates in August (Figure 8). The August water column concentration of DOP immediately above the mussel bed was doubled in comparison to other dates (0.086 µmol L^{-1}) and could be linked to higher excretion on this date. When considering the total

amount of phosphorus excreted by mussels, TDP excretion was used all calculations in

order to account for all phosphorus in mussel excretion (including DOP).
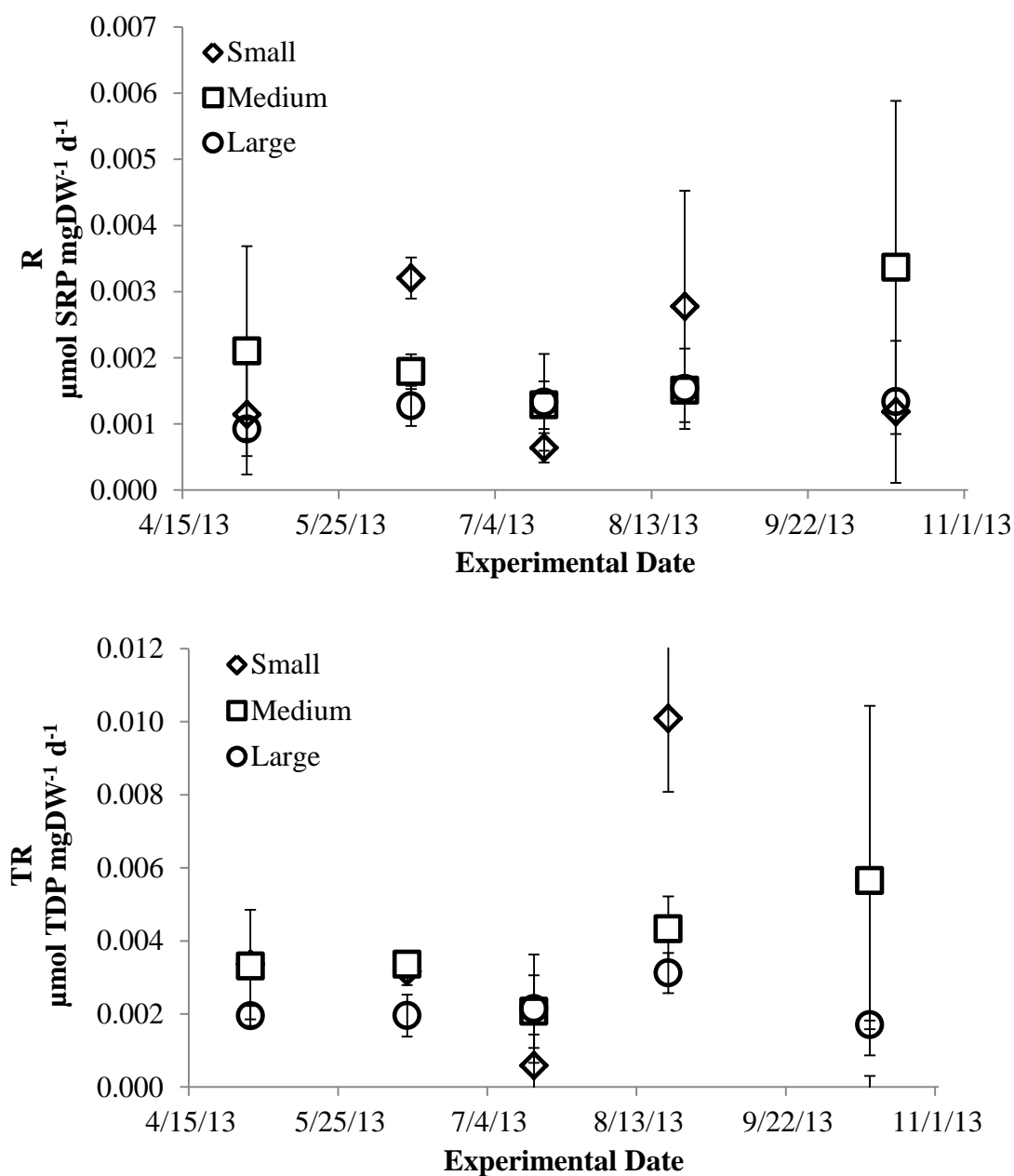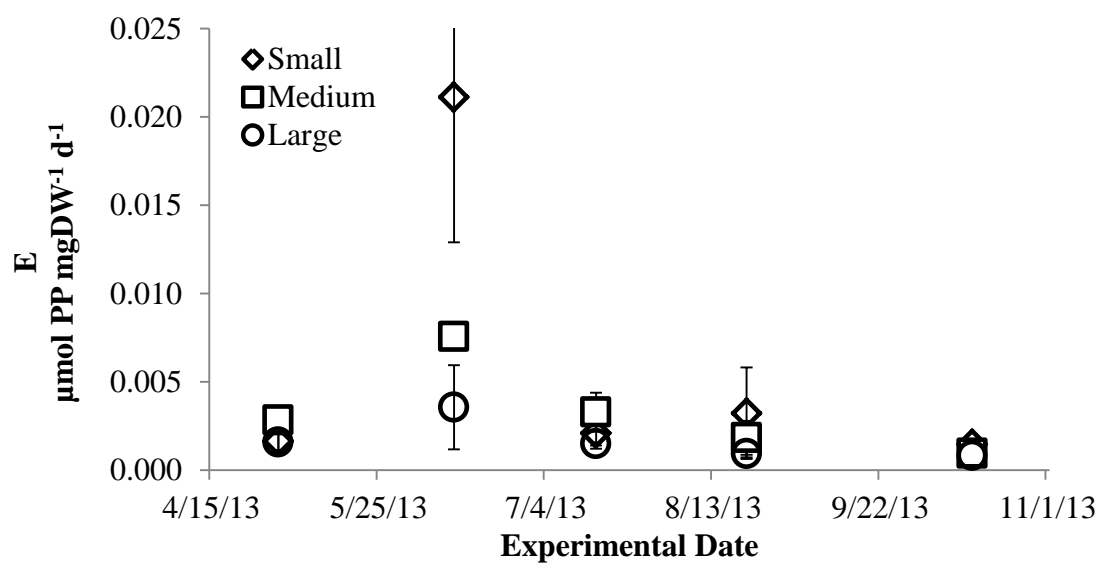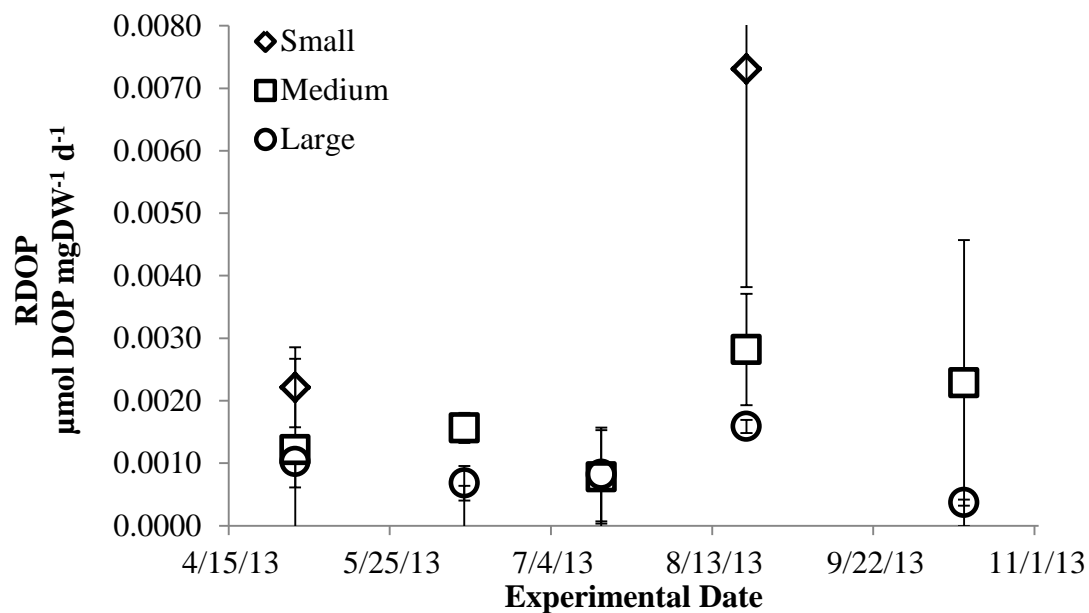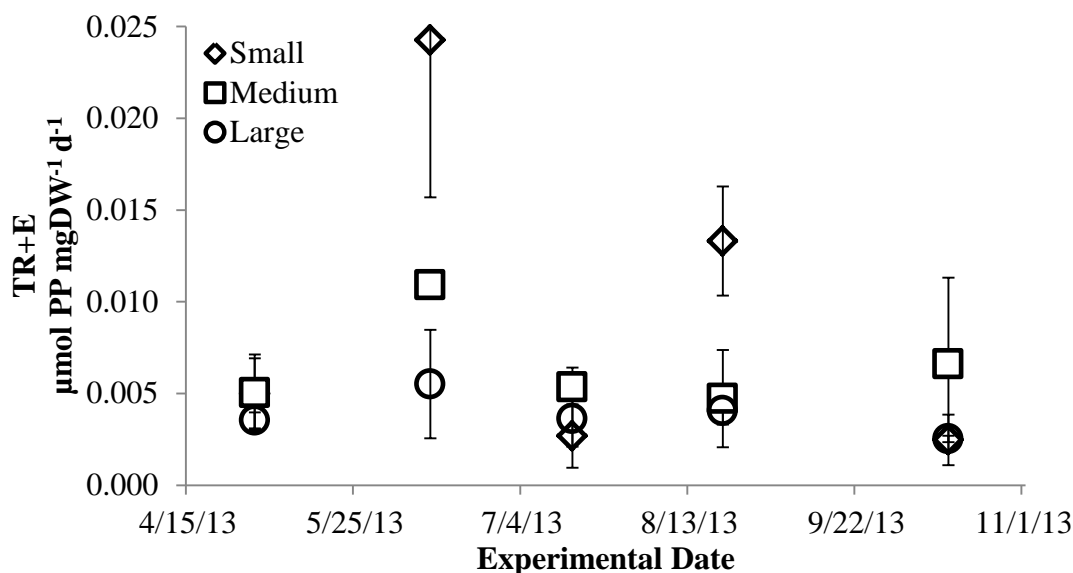
Figure 8: Soluble reactive P (SRP) excretion (R), total dissolved P excretion (TR), dissolved organic P excretion (RDOP), particulate P egestion (E), and total dissolved P excretion + particulate P egestion (TR+E) in μmol P mgDW^{-1} d^{-1} (note different scales) for May through October 2013 incorporating small mussels (8-12 mm), medium mussels (13-17 mm), and large mussels (18-22 mm).

Particulate P egestion rates (E) was similar to excretion rates, showing relatively fixed rates throughout experimental dates, except for June (Figure 8). There was no significant difference between size classes (p = 0.051), and with the exception of high rates in June, no significant difference between experimental dates (p = 0.066). Small mussels (8-12 mm) in June egested at an order of a magnitude higher than the mean of all other dates. Due to the uncertainty in the egestion measurement in June, these rates were excluded from mean egestion calculations. Total phosphorus excretion + egestion by profunda mussels is calculated as total dissolved phosphorus (TDP) excretion (TR) plus egestion (E) and is relatively constant throughout the experimental period (Figure 8). For all size classes, the mean (±SD) total phosphorus excretion + egestion rate is 0.0049 ± 0.0034 μmol P mgDW^{-1} d^{-1} (excluding June). There was no significant difference for total phosphorus profunda mussel excretion + egestion between size classes (Figure 9).
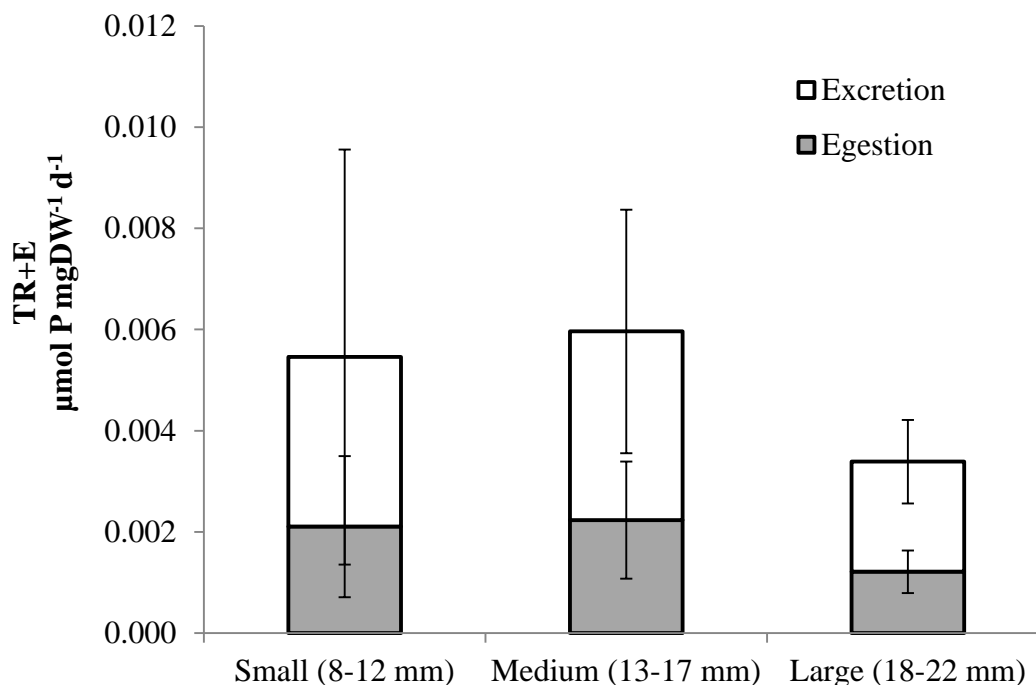
Figure 9: Mean (±SD) total dissolved P excretion (TR) and particulate P egestion (E) for 3 sizes classes of profunda quagga mussels incorporating all 5 experimental days at a 55 m depth in the southern basin offshore Lake Michigan (µmol P mgDW^{-1} d^{-1}).

2.4.4 Measurement of mussel effective clearance and grazing rate

An effective clearance rate (ECR) and P grazing rate were calculated for profunda

quagga mussels on two experimental dates in conjunction with phosphorus excretion and

egestion experiments. ECR was calculated per mussel and per mg DW for each of the 3

mussel size classes in June and October. On each date, ECR calculated per mussel

increased with mussel size while ECR per mg DW decreased (Figure 10). Per mussel,

small and medium mussels (8-17 mm) in June cleared approximately 4 L d^{-1} and large

mussels (18-22 mm) cleared close to 8 L d^{-1}, while in October, small and medium

mussels cleared between 1-2.5 L d^{-1} and large mussels cleared close to 4 L d^{-1}.

Normalized to dry tissue weight, ECR was higher in small mussels compared to larger

mussels. June had a higher ECR than October, with 0.37 to 3.65 L mgDW^{-1} d^{-1} in June compared to 0.19 to 1.09 L mgDW^{-1} d^{-1} in October.
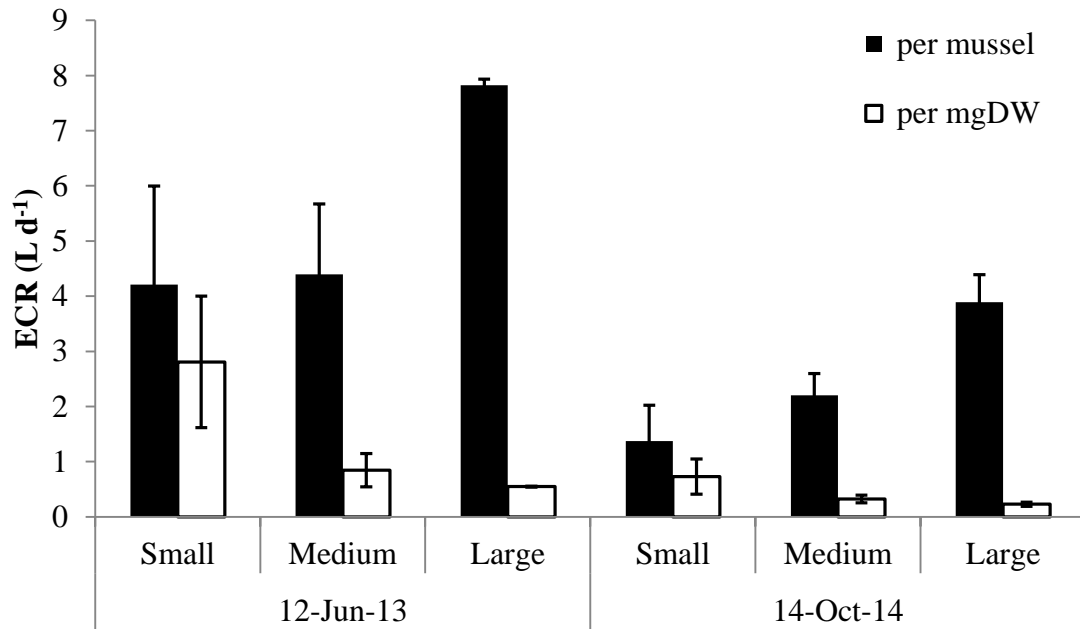
Figure 10: Mean (±SD) Effective Clearance Rate (ECR) for small (8-12 mm), medium (13-17 mm), and large (18-22 mm) mussels for June 12 and October 14. Rates are per mussel (L mussel^{-1} d^{-1}) and per mgDW (L mgDW^{-1} d^{-1}).

A mean (±SD) water column particulate P concentration for the 10 m above the lake bottom was used as the mean food concentration for estimating P grazing rates. The mean food concentration for June and October was similar (0.02 ± 0.01 µmol L^{-1}) and applied to the effective clearance rates calculated for the three size classes on both dates. In June, the mean (±SD) grazing rate for mussels 8-22 mm was 0.027 ± 0.024 µmol PP mgDW^{-1} d^{-1}, while the mean (±SD) grazing rate for October was lower at 0.009 ± 0.006 µmol PP mgDW^{-1} d^{-1}. June grazing rates were overall higher than October grazing rates,

as well having a broader range of values. In attempting to reconcile the two
methodologies used to estimate the P recycling rate of profunda quagga mussels, the P
rates in μmol mgDW^{-1} d^{-1} were compared for mussel grazing and mussel excretion +
egestion (Figure 11). The values above the bars represent the percentage measured P
excretion + egestion constitutes out of estimated P grazing.
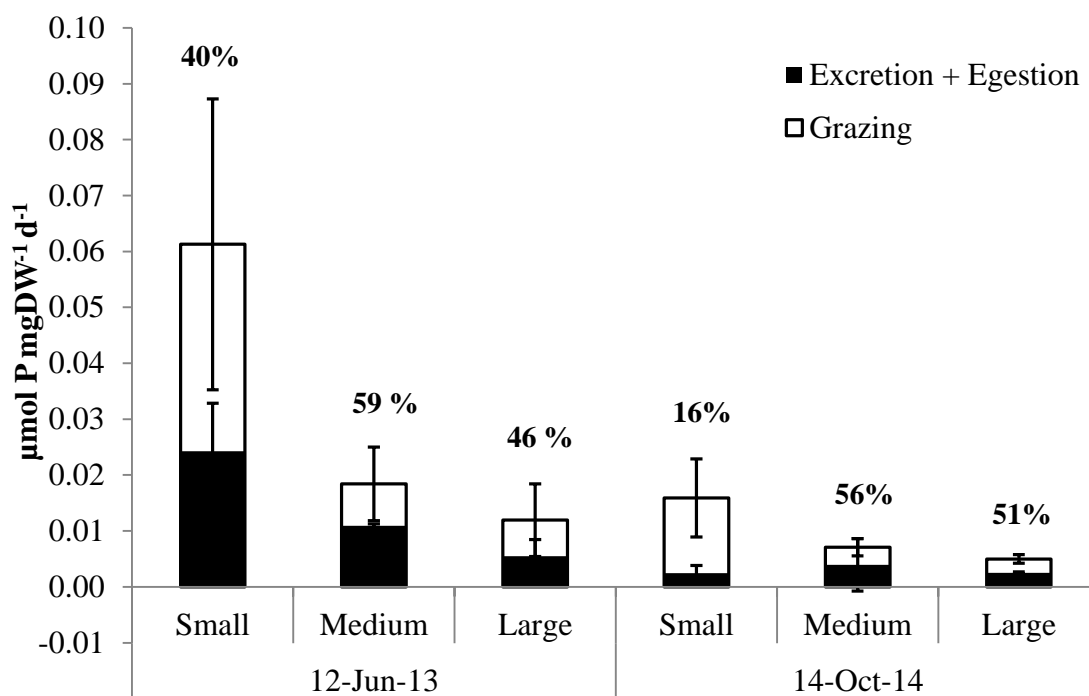
Figure 11: Mean (±SD) Excretion + Egestion and Grazing in μmol P mgDW^{-1}d^{-1} for small (8-12 mm),
medium (13-17 mm), and large (18-22 mm) mussels for June 12 and October 14. The percentage that
Excretion + Egestion constitutes out of Grazing is above each bar.

2.5 Discussion

2.5.1 Mussel phosphorus excretion and egestion in the offshore

Overall, significant differences between size classes or experimental dates for profunda
mussel (8-22 mm) rates of excretion (SRP and TDP) or egestion (PP) were minimal

compared to the nearshore phenotype (Bootsma, 2009). During unstratified (May) and stratified (June, July, August, and October) months, mass specific excretion and egestion rates are low and relatively constant. Temperature has been shown to be a primary driver in mussel respiration and subsequently nutrient excretion, with higher temperatures correlating with higher excretion rates (Bootsma and Liao, 2014; Tyner, 2013). Profundal benthos ambient water conditions (temperature, chlorophyll *a*, particulate C and P) from May through October 2013 are relatively similar. Constant low temperatures ($< 6\ °C$) in the profundal benthos and low food supply in the hypolimnion likely limits quagga mussel metabolism, including grazing and nutrient excretion and egestion. Water column profiles of particulate P and chlorophyll *a* at the 55 m site depict decreasing concentrations near the lake bottom, indicating a high amount of mussel grazing and lowered concentrations of phytoplankton above mussel beds. The uniformity of the profundal environment likely creates little variation in nutrient excretion and egestion, as the deep-water phenotype is adapted to an unchanging cold and oligotrophic environment.

Most previous studies of dreissenid nutrient cycling have focused on dissolved nutrients (Arnott and Vanni, 1996; Conroy et al., 2005; Ozersky et al., 2009; Turner, 2010), with nutrient egestion rates remaining relatively unstudied. From mussel grazed material, assimilation and egestion appears to constitute larger portions than excretion. Excretion has been the focus of mussel impact on nutrient cycling, but with mussels possibly acting as a nutrient sink in the benthos, egestion needs to be more thoroughly investigated. Egestion rates from this study range from 0.0007 to 0.0061 μmol PP mgDW^{-1} d^{-1}, and for all dates (except June), egestion represents up to 1/2 of P cycled by

mussels. Hence, ignoring the egestion of particulates leaves a significant portion of mussel nutrient cycling undocumented. All size classes in June egested at a rate nearly a magnitude higher than the mean, despite similar ambient water conditions. These anomalously high rates highlight the need for better quantification of mussel nutrient egestion and investigation into whether the driving forces for excretion (temperature and food supply) also apply for egestion. Even in a low-food environment, how mussels portion the grazed nutrients between assimilation, excretion, and egestion provides insight to the amount of P mussels sequester versus how much they recycle back into the environment.

Dissolved organic phosphorus (DOP) excretion is determined indirectly by subtracting SRP from TDP excretion and is another relatively understudied component of mussel nutrient cycling. DOP is usually excreted at a lower rate than SRP, but in August DOP constituted ~80 % of dissolved nutrient excretion and was nearly 10 times higher than the mean DOP excretion. This experimental date also had much higher ambient DOP concentrations, and the erraticism in DOP mussel excretion and higher ambient DOP concentrations may be due to immediate water conditions above the mussel bed. Similar to mussel egestion, further investigation is needed to understand the mechanisms influencing DOP excretion.

Methodological variation could account for some differences in measured mussel excretion values. For zebra mussel excretion experiments at comparable temperatures (17-22 °C), Arnott and Vanni (1996) obtained values ranging from 0.020 to 0.053 μmol SRP mgDW^{-1} d^{-1} for experiments conducted immediately after collection using unfed mussels (< 13.5 mm), while Mellina et al. (1995) had a pre-acclimation period of several

months, fed mussels (20 mm) lab-grown algae, and measured excretion at 0.003 to 0.004 µmol SRP mgDW^{-1} d^{-1}. Using different experimental set-ups but the same mussel species, there was a magnitude difference in dreissenid excretion. Any discrepancy in experimental set-ups should be considered when comparing nutrient excretion rates.

2.5.2 Offshore versus nearshore mussels

In order to overcome methodology inconsistencies, the experimental set-up and collection region near Milwaukee, WI was kept consistent. For the 2006 shallow quagga mussel and the 2013 profunda quagga mussel experiments, mass specific mussel excretion is measured using unfed mussels within hours of collection. Mussel excretion and egestion rates decrease quickly after mussels are deprived of their food source due to a mussel gut residence time of several hours (Bootsma, 2009), and conducting experiments as soon as possible allows for the measurement of mock *in situ* rates. Comparing mass specific rates of profunda quagga mussel SRP excretion at 5 °C and shallow quagga mussel SRP excretion at 23 °C, mean (±SD) profunda mussel excretion rates (0.0016 ± 0.001 µmol SRP mgDW^{-1} d^{-1}) are almost 20 times lower than the mean (±SD) mass specific rates for the shallow morph (0.029 ± 0.032 µmol SRP mgDW^{-1} d^{-1}) (Bootsma, 2009). When comparing rates of shallow and profunda quagga mussels, it is important to consider temperature and food supply, as well as physiological differences. For shallow mussel experiments by Bootsma (2009), temperature is nearly 5 times greater and food concentration 6 times greater than experimental conditions for the profunda morph. Some previous studies measure *in situ* rates for nearshore mussels (Bootsma, 2009; Ozersky et al., 2009), but such experiments are more difficult to conduct in the profundal habitat due to SCUBA limitations.

2.5.3 Accounting for mussel population size distribution

The profunda mussel population at deeper depths appears to not have changed in the past five years. In 2008, a 45 m site offshore from Waukegan, WI was estimated to be 9060 ± 2533 mussels m^{-2} with the majority (97.6 %) of the mussel population at depths $\geq$ 50 m to be < 15 mm (Nalepa et al., 2010). Videography of the 55 m station indicates that the few changes in spatial density arise from physical constraint, as the mussels have effectively 'carpeted' the bottom of the study site. The abundance of smaller mussels ($\leq$ 17 mm) in the offshore versus the nearshore could be due to abundance of round gobies (*Neogobius melanostomus*) that have been thought to predate on smaller mussels (< 10 mm) and alter the population size structure (Ray and Corkum, 1997). Comparison of video footage reveals a strong presence of round gobies in the nearshore (Atwater Bay 10 m), while none were spotted in the offshore (55 m). The areal density of mussels in the offshore is nearly double the nearshore (10,000 mussels m^{-2} versus 5,000 mussels m^{-2}), but offshore biomass (g m^{-2}) is only 37 % of nearshore biomass. Higher densities but less biomass is due to profunda mussels having lower length-specific weights and a population dominated by small mussels. Profunda mussels are specifically adapted to an oligotrophic habitat with lower length-specific weights and phenotypic plasticity distinguished by a thinner shell, elongated shape, and infaunal tendencies (Claxton and Mackie, 1998; Nalepa et al., 2009). Looking at the stability of the population structure and length-weight relationships of profunda mussels throughout the summer, the filter feeders appear to gain mass, with an estimated mean ($\pm$SD) biomass in May of 22.4 ± 4.73 g m^{-2} increasing to 42.4 ± 15.61 g m^{-2} in August.

Because of significant differences in excretion rates between shallow and profunda quagga mussels, accurate measurements of nutrient excretion and egestion by both phenotypes are necessary when considering the lake-wide effect of mussels in Lake Michigan. In the nearshore, accurate size distribution is critical, as previous studies have found that nearshore *Dreissena* have high nutrient assimilation and mass specific excretion rates, especially small size classes (Arnott and Vanni, 1996; Bootsma, 2009; Conroy et al., 2005; Naddafi and Pettersson, 2008). For this study, the profunda phenotype (8-22 mm) did not display significantly different mass specific excretion rates. A singular small-scale experiment demonstrates that mussels 4-6 mm have mass specific SRP excretion rates 6.4 times greater, TDP mass specific excretion rates 4.9 times greater, and PP egestion rates 20.7 times greater than the mean excretion and egestion for mussels $\geq$ 8 mm. This indicates that profunda mussel mass normalized P excretion and egestion is likely inversely related to dry tissue weight for mussels < 8 mm. However, more research needs to be conducted on small profunda quagga mussels in order to quantify these rates and better define the mass specific relationship. With a mean offshore population density of 10,000 mussels m^{-2} and ~50 % small mussels < 8 mm, the areal P impact of mussel cycling could be underestimated if all mussels are given a constant rate regardless of size.

In calculating areal P rates (excretion + egestion m^{-2}) for the a high mussel density 55 m site in Lake Michigan, it is assumed that mussels 8-22 mm have a relatively constant rates of excretion and egestion, and mussels < 8 mm are scaled appropriately (TDP excretion ~5 times greater and PP egestion ~21 times greater). A 2013 profunda mussel length-weight relationship ($W=0.005L^{2.61}$) provides approximate mgDW mussel^{-1},

which are applied to mean mussel size class distributions and densities (mussels m^{-2}) from 2012-2013 Ponar grabs. The subsequent mgDW m^{-2} is applied to mean excretion (TDP) and egestion (PP) rates (µmolP mgDW^{-1} d^{-1}) derived from profunda mussel experiments. Using measured values for mussels 8-22 mm and scaled values for mussels < 8 mm, the mean areal P excretion and egestion by profunda quagga mussels at the 55 m site is 215 µmol P m^{-2} d^{-1}. Comparing this to the standing stock of P bound in mussel biomass (calculated using a mean (±SD) mussel dry tissue P content of 0.22 ± 0.03 µmol P mgDW^{-1} and mean (± SD) biomass of 3324 ± 1461 mgDW m^{-2}), P sequestered in mussel biomass at the 55 m site is approximately 745 µmol P m^{-2}. In a year, mussels can cycle over a 100 times more P than is sequestered in biomass at a given point in time. This rough estimate of areal P only applies to a single site with high profunda mussel density, but exemplifies the nutrient cycling efficiency of profunda mussels in comparison to nutrients sequestered in biomass.

2.5.4 Mussel grazing in the offshore

Profunda mussel effective clearance rates (ECR) are inversely related to dry tissue weight, with smaller mussels having increased filtering per mgDW compared to larger mussels. Clearance rates have been found to vary in relation to mussel weight (Lei et al., 1996), with large mussels filtering higher volumes than small mussels. Profunda mussel ECR at 5 °C ranged from 1 to 8 L mussel^{-1} d^{-1}. In comparison, Yu and Culver (1999) measured zebra mussel ECRs in a small inland reservoir from 0.36 to 1.66 L mussel^{-1} d^{-1} at 27 °C using a similar methodology. Looking at mass normalized effective clearance rates of zebra mussels using natural seston in Saginaw Bay, Fanslow et al. (1995) measured a range from 0.1 to 0.98 L mgDW^{-1} d^{-1} with temperatures ranging from 6 to 25

°C. In Lake Michigan, the mass normalized ECR for profunda quagga mussels was comparable with a range of 0.23 to 0.84 L mgDW^{-1} d^{-1} (with an outlier of 2.81 in June) at a temperature of 6 °C. Due to only having two experimental dates, it is difficult to discern the reason for differences in ECR between June and October. Both dates have similar water column particulate P profiles, which are indicative of food availability to mussels and can affect clearance rates, despite June having higher ECR. Studies on mussel clearance rates have found that filtration is highest at low food concentrations (Fanslow et al., 1995; Sprung and Rose, 1988), and low food conditions in Lake Michigan's hypolimnion could potentially result in overall slightly higher effective clearance rates compared to effective clearance rate of zebra mussels or the nearshore phenotype.

The oligotrophic environment of offshore Lake Michigan is unlike other studies, where the incipient limiting threshold is usually reached due to high particulate concentrations (Ackerman et al., 2001; Fanslow et al., 1995; Kryger and Riisgard, 1988; Sprung and Rose, 1988). Although it has been hypothesized that zebra mussels lower their filtering activity during times of low food concentrations as an energy saving measure (Horgan and Mills, 1997), a greater pumping rate by profunda mussels may be necessary to obtain sufficient food to meet basal metabolic requirements. In the only other study examining profunda quagga mussel filtering rates at low temperatures (1-7 °C), Vanderploeg et al. (2010) estimated that profunda quagga mussels (22 mm) in Lake Michigan filter 3.12 L mussel^{-1} d^{-1}. By comparison, profunda mussels from the 55 m site of similar length (18-22 mm) had a higher ECR range (3.89 to 7.83 L mussel^{-1} d^{-1}). Although mussels from the 55 m have higher estimated filtration rates, they are still within a reasonable range, and any differences between the experiments could be because

of immediate environmental conditions, such as particle concentrations and / or currents, above the mussel bed. Based on physiological differences, such as quagga mussels having lower respiration and higher assimilation efficiency than zebra mussels (Baldwin et al., 2002; Stoeckmann, 2003), it is possible profunda mussels have higher effective clearance rates because the incipient limiting threshold is never reached. Even though the measured profunda mussel ECR is slightly higher than previous studies (Fanslow et al., 1995; Vanderploeg et al., 2009; Yu and Culver, 1999), it likely reflects the oligotrophic environment where the deep-water phenotype thrives.

Estimated P grazing rates were twice as large as measured P excretion + egestion rates, except for small mussels in October. For this size class, near zero TDP excretion rates resulted in a low P excretion + egestion value. Overall, these estimated grazing rates calculated from a mean particulate P concentration within 10 m of the lake bottom are higher than expected. Excretion + egestion should constitute a large majority of grazed material, based on a study of the zebra mussel energy budget that hypothesizes that metabolic costs (oxygen consumption and nutrient excretion) comprises > 90 % of energy consumption, while growth and reproduction constitutes 5-10 % (Stoeckmann and Garton, 1997). Quagga mussels are more adapt at surviving low food conditions with a significantly higher assimilation efficiency than zebra mussels (Baldwin et al., 2002), therefore an energy budget for profunda quagga mussels may be slightly different. However, the rates of excretion + egestion suggest that at least half of grazed material is either excreted as dissolved TDP or egested as PP. More research is needed on profunda quagga mussel grazing rates with *in situ* food concentrations in order to accurately

capture the amount of P mussels recycle. In the context of this study, P excretion + egestion is assumed to represent grazing to avoid overestimation.

3. Impact of offshore mussels on Lake Michigan P dynamics

3.1 Background

Before the *Dreissena* invasion, sinking nutrients in offshore Lake Michigan were recycled back in the water column via either biotic (e.g. *Diporeia* spp. and microbes) or abiotic (sediment resuspension, dissolution) mechanisms. As the dominant benthic organism, *Diporeia* spp. had an ecological efficiency of 21 % and provided an effective means for benthic energy to re-enter the food web (Fitzgerald and Gardner, 1993). Nutrient cycling was further supported by sediment resuspension during the winter-spring mixing period (Eadie et al., 1984) which was facilitated in part by the presence of a benthic nepheloid layer during stratification (Chambers and Eadie, 1981). With the recent disappearance of *Diporeia* spp. (Nalepa et al., 2009) and mussel filtering depleting particle concentrations in the hypolimnion, it is reasonable to expect that there have been significant changes in internal P cycling. For example, recent studies near Milwaukee, WI suggest that dreissenid P excretion is 5 times greater than riverine input to the nearshore zone within the Milwaukee region, likely contributing to the rapid growth of the nuisance algae *Cladophora* on coastal rocky substrate (Bootsma, 2009). Recent studies suggest that quagga mussels in deeper parts of the lake may also play a significant role in carbon and nutrient dynamics (Vanderploeg et al., 2010). However, there have been no attempts to directly measure grazing and nutrient recycling by the profunda quagga mussel community.

3.2 Purpose of study

The purpose of this study is to place profunda quagga mussel grazing, excretion, and egestion in context of the Lake Michigan P cycle. Specific questions addressed include: 1) Do these mussels have the capacity to permanently remove nutrients from the system? Evaluating offshore nutrient fluxes and determining the fate of mussel egestion, or biodeposits, provides insight into the extent of dreissenid nutrient sequestration. If biodeposits (feces + pseudofeces) remains sequestered in the sediment, then mussel nutrient egestion may accelerate P removal, thereby maintaining low concentrations of phosphorus in the water column. However, if egested material is re-mineralized, then mussel grazing may result in no net loss of P from the water column. 2) What is the fate of dissolved P excreted by mussels? Does it return to the water column, and if so, does it remain within the hypolimnion? Or is it sequestered by microbial or geochemical processes, such as apatite precipitation (Brooks and Edgington, 1994), within the sediment? 3) How significant is mussel grazing and phosphorus recycling relative to other phosphorus pathways in Lake Michigan? Placing profunda quagga mussel nutrient cycling in a whole-lake context, by comparing mussel-mediated P fluxes with other processes, such phytoplankton production, passive sedimentation, and zooplankton grazing, provides insight into how these organisms may be altering ecosystem structure and function. Nutrient fluxes in the pre- (before 2000) and post-dreissenid (after 2000) offshore environment during summer stratification could reveal if profunda quagga mussels are significant factors in recent Lake Michigan trophic changes.

3.3. Methods

Incubation experiments are used to evaluate the mussel-water-sediment interface as well as the fate of mussel biodeposits (feces + pseudofeces). Sediment trap studies investigate

changes to passive sedimentation since *Dreissena* began grazing the water column and potentially altering Lake Michigan's P cycle. Focusing on the stratified offshore, mussel P recycling is compared to other P fluxes, such as riverine input, passive sedimentation, primary production, and zooplankton grazing. Comparing changes in these fluxes between the pre- (before 2000) and post-dreissenid (after 2000) periods could indicate if mussels are the driving force behind reduced productivity.

3.3.1 Sediment core incubations with live mussels

In October 2013, sediment cores were retrieved at the 55 m station using a box core deployed from the *R/V* Neeskay. Water was siphoned from the top of the box core to be used as replacement water during experiments. Nine cores were manually retrieved from the box core using acid-washed liners, immediately placed on ice, and extruded to produce an overlying water volume of 0.385 L onshore, 2 to 3 hours after collection. After extrusion, specialized stirring caps equipped with syringe sampling ports and metal spinners were placed on top of the cores to create air-tight seals. The metal spinners spin at a slow speed to keep the overlaying water continually mixed without re-suspending sediment. All cores were incubated in a PERCIVAL Scientific Incubator at *in situ* temperature (2-7 °C) in the dark.

After adjusting the overlying water volume, the cores were left undisturbed and any mussels present on top of the sediment were left intact to preserve the *in situ* mussel-water-sediment interface. The eight cores had varying mussel biomass (Table 3). At the mid-point of the experiment (day 25), mussels were collected and counted from all cores to determine core mussel density (mussels m^{-2}), and mussel tissue was lyophilized to determine core mussel dry tissue biomass (g m^{-2}) using the October 2013 profunda

mussel length-weight relationship in Chapter 1 (DW=0.0035L$^{2.78}$). Biomass estimates are representative of mussel tissue biomass at the time of core retrieval, since the mussels were not fed and likely lost mass during the experiment. In analyzing data, cores were classified into two groups based on mussel dry weight biomass (g m^{-2}). The high mussel biomass group (Core 1-4) had biomass ≥ 42.6 g m^{-2} and the low mussel biomass group (Core 5-8) had biomass ≤ 31.6 g m^{-2}. Due to the high density of mussels at the study site, no cores were obtained with zero mussels.

An initial core water sample was taken ~1 hour after set up, after which sampling occurred at lengthening intervals (2, 4, 14, 20, 44, 68 hours…) up to 49 days. For each core water sample, 25 mL was drawn out from the sampling port with a 60 mL acid-washed plastic syringe. After the core sampling, 25 mL of replacement water (water siphoned from the top of the box core) was slowly pushed into the core from a separate port to re-establish core volume. The dilution of core water dissolved P concentrations with replacement water was negligible (≤ 0.03 μmol L^{-1}) and did not alter the trend of the core soluble P concentrations. The 25 mL sample was immediately filtered using a syringe filter (ashed, 0.45 μm Whatman GF/F) and transferred to a 20 mL acid-washed scintillation vial. On day 40 of the experiment, microprofiles of dissolved oxygen (DO) were conducted at 0.8 mm increments using a NeoFox Sport mico-optode system to examine oxygen conditions within the sediment core. At the end of the experiment (day 49), cores were extruded, sliced at 2 mm intervals and weighed. For two cores (one with a high mussel biomass and the other with a low mussel biomass), each slice was lyophilized and weighed for a dry weight. Particulate P analysis of core slices were also conducted using the method mentioned previously. The core slices were not dated.

3.3.2 Chamber incubations with mussel biodeposits

Incubations in May 2014 were used to determine if dreissenid feces and pseudofeces (biodeposits) act as a nutrient sink or source. Ponar grabs were used to collect profunda quagga mussels at the 55 m site, and a gravity core was used to collect 6 sediment cores. Eight liters of lake water was collected from the near-bottom using a 5 L Niskin bottle and placed on ice. The mussels were placed in unfiltered lake water in the dark at *in situ* temperature until cleaning, and all cores were covered and placed on ice until the experimental set-up was complete. All mussels present in the sediment cores were immediately extracted and discarded using acid-washed forceps.

Within 2 hours of collection, approximately 200 mussels of varying lengths (10-25 mm) were gently scrubbed with an abrasive cloth and rinsed to remove algae, microbes, sediment, and particulate detritus from their shells. After cleaning, the mussels were placed in 2 L acid-washed polyethylene containers with filtered later water in the fridge at *in situ* temperature and allowed to egest for ~24 hours. Egested material was visible after 24 hour and the biodeposits were condensed to 100 mL slurry using a separation funnel.

Within 4 hours of collection, the 6 sediment cores were extruded to produce an overlying water volume of 1.8 L. Ten acid-washed, empty core liners were filled with 1.8 L of unfiltered near-bottom lake water. The sediment cores and water cores, which are collectively called 'chambers', were divided into 3 treatments consisting of various conditions with 10 mL of added biodeposits and a set of controls (meaning no added biodeposits) for each treatment. The first treatment was unfiltered lake water, the second treatment was spiked unfiltered lake water with an initial concentration of 1 μmol L^{-1},

and the third treatment was extruded sediment cores. All chambers were placed in a dark walk-in freezer (4 °C), oxygen saturation was maintained with aeration stones placed half-way down the chambers, and chambers were lightly covered with aluminum foil to minimize contamination.

All water samples were collected half-way down the chambers with a 30 cm acid-washed polyethylene tube attached to a 60 mL acid-washed glass syringe. An initial sample (30 mL) was taken 1 hour after the treatments were administered and then every 2 days for the duration of the experiment (26 days). Samples were immediately filtered with a syringe filter (ashed, 0.45 µm Whatman GF/F) and analyzed for dissolved phosphorus using the method described in Chapter 1. If any mussels were sighted in the cores at any point in the experiment, they were immediately removed with acid-washed forceps. After each sample was taken, the water volume height was recorded and taken into account when determining chamber incubation volumes.

3.3.3 Sediment trap deployment

Sediment traps 9.5 cm diameter and 76.2 cm long were deployed in triplicate at 18, 35, and 53 m. To each trap 5 ml of chloroform was added to preserve settling particles. Traps were deployed from June through July for 27 days, July through August for 36 days, and August through October for 57 days. Upon collection, overlaying water was siphoned off, after which contents were lyophilized and weighed to the nearest mg. Trap material was analyzed for particulate carbon, nitrogen and phosphorus using the methods described in Chapter 1.

3.4 Results

3.4.1 Incubation experiments

In sediment core incubations conducted with live profunda quagga mussels at *in situ* temperature (4-6 °C), soluble reactive phosphorus (SRP) concentrations increased over time (Figure 12). Mussels in the cores were monitored daily to ensure that they were actively filtering (Figure 13). In cores with high mussel biomass (Cores 1-4) SRP concentrations increased more rapidly than in cores with low mussel biomass (Cores 5-8). The difference in SRP rates between the high and low mussel biomass cores was significant (paired Student t-test, $p < 0.001$). In the two cores with the lowest densities (Cores 7 and 8), SRP concentrations decreased while mussels were present.
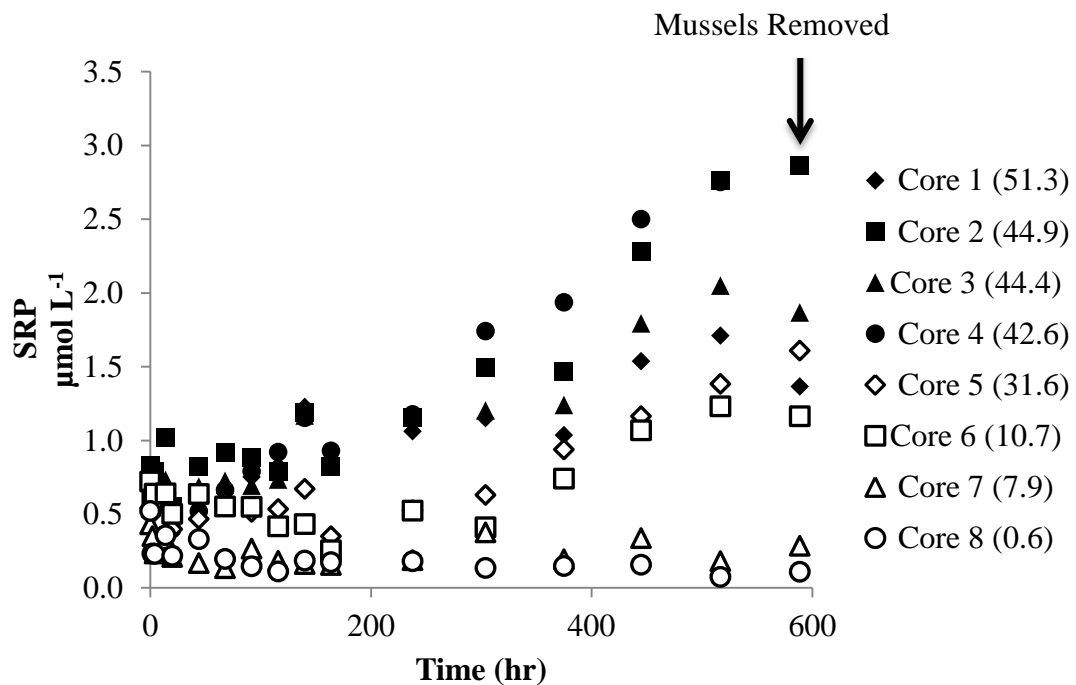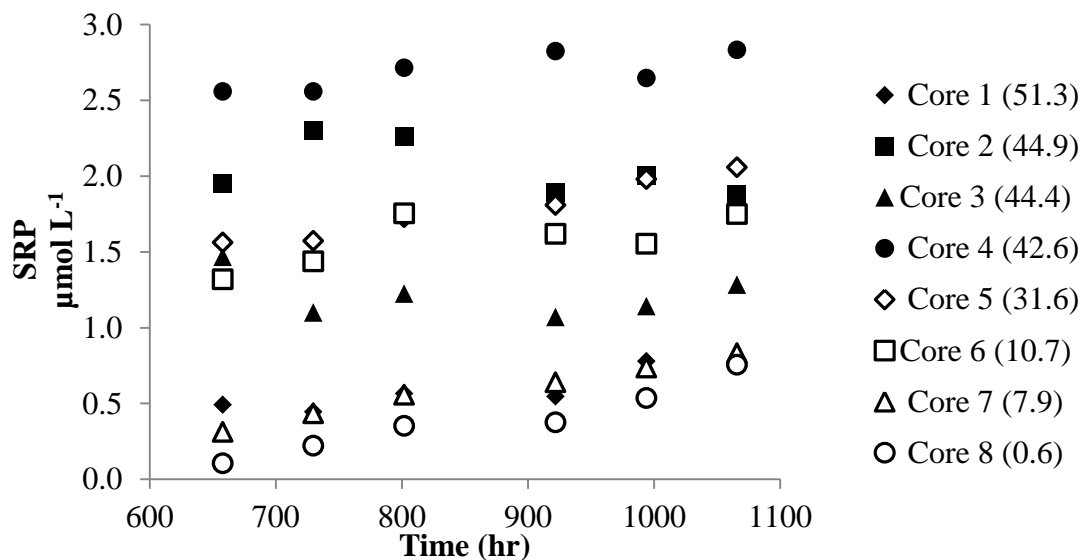
Figure 12: SRP concentrations (µmol L^{-1}) in incubated sediment cores with mussels (top) and mussels removed (bottom) identified by core number with biomass (g m^{-2}) in parantheses and grouped into high mussel density (solid black symbols) and low mussel density (solid white symbols). The black arrow indicates mussel removal.
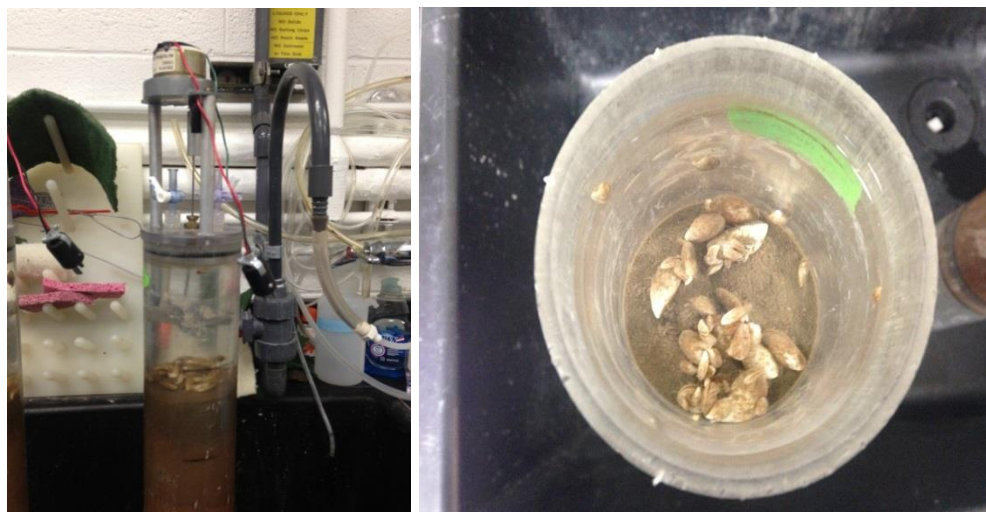
Figure 13: Core incubation set-up with live mussels.

At day 25, mussels were removed from the cores, after which the incubation and regular sampling continued (Figure 12). After mussel removal, SRP concentrations for Cores 1-4 no longer increased, while SRP continued to slowly increase in Cores 5-8. SRP rates for high mussel biomass and low mussel biomass cores are inversely related with

mussel presence (Table 3). During mussel incubation, low mussel biomass Cores 7 and 8 had negative rates, but after mussel removal these rates became positive. High mussel biomass Cores 1-3 had positive rates while mussels were incubated, but these rates became negative after mussel removal.

Table 3: Net SRP production rates (μmol L^{-1} h^{-1}) for cores before and after mussels were removed. Mussel dry biomass (DW) was determined from length (L), using the relationship: $DW=0.0035L^{2.78}$.

		Mussels in Core	Biomass g m^{-2}	With Mussels μmol L^{-1} h^{-1}	Mussels Removed μmol L^{-1} h^{-1}
High	Core 1	83	51.3	0.0017	-0.0004
	Core 2	57	44.9	0.0035	-0.0014
	Core 3	33	44.4	0.0024	-0.001
	Core 4	57	42.6	0.0041	0.0002
Low	Core 5	33	31.6	0.0016	0.0011
	Core 6	10	10.7	0.001	0.001
	Core 7	21	7.9	-0.00001	0.0012
	Core 8	2	0.6	-0.0004	0.0013

A comparison of SRP increase / decrease rate (μmol L^{-1} h^{-1}) with mussel biomass (g m^{-2}) indicates a positive relationship in the presence of mussels, and an inverse relationship after mussel removal (Figure 14). High biomass correlated with the highest SRP production rates during incubation and the lowest SRP production rates after mussel removal. After mussel removal, the mean SRP ($\pm$SD) concentration in high mussel biomass Cores 1-4 decreased from 2.24 ± 0.79 to 1.69 ± 1.35 μmol L^{-1}, while the SRP concentration in low mussel biomass cores continued to increase after mussel removal.
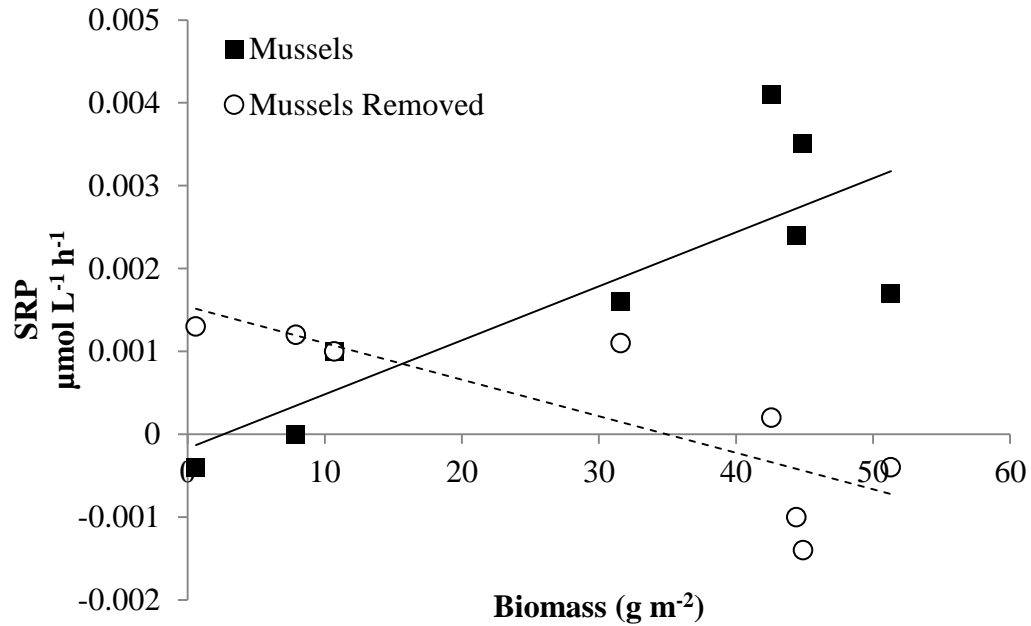
Figure 14: SRP slopes (μmol L^{-1} h^{-1}) with mussels and after mussel removal correlated with each individual core's biomass (g m^{-2}).

Dissolved oxygen microprofiles in the sediment conducted on day 40 depicts decreasing oxygen concentrations with depth in all cores (Figure 15). Surficial sediments had different levels of anoxia, with low mussel biomass cores having higher oxygen concentrations than high mussel biomass cores. Anoxia occurs at shallower depths (< 7 mm) in cores with higher mussel biomass (Cores 1-4).
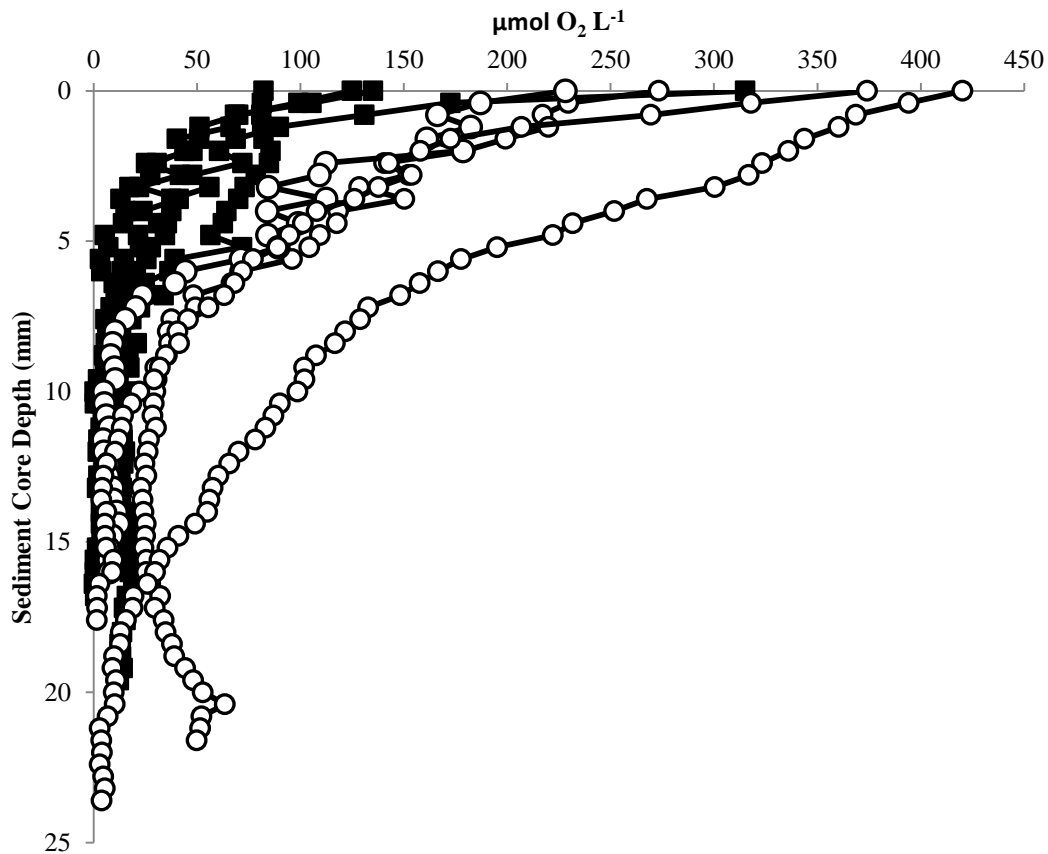
Figure 15: Sediment microprofiles of dissolved oxgyen (μmol O_2 L^{-1}) for high mussel density Cores 1-4 (■) and low mussel density Cores 5-8 (○).

In the experiments designed to determine whether biodeposits serve as a P sink or source, SRP concentrations decreased in all chambers, including controls. Mussel feces + pseudofeces were added to chambers with three different treatments: lake water, phosphate-spiked lake water, and sediment. Two chambers (a lake water replicate and a sediment replicate) showed signs of contamination and were not included in analyses. A small amount of the egestion was measured for P content, and 10 mL of biodeposit slurry has a particulate P concentration of 0.12 μmol L^{-1}. This particulate P content is high relative to Lake Michigan water column particulate P, as well as to mussel egestion rates

(0.0007 to 0.0061 μmol mgDW^{-1} d^{-1}). Although all chambers show decreases in soluble P, chambers treated with biodeposits had greater SRP declines than control chambers, indicating that the biodeposits serve as a net sink for SRP. The biodeposit uptake rate of SRP (BR) was determined as:

$$BR = [B]-[C]/ [Biodeposit\ PP]$$

where $[B]$ = SRP uptake in chamber with biodeposits (μmol SRP)

$[C]$ = SRP uptake in control (μmol SRP)

$[Biodeposit\ PP]$ = PP concentration of Biodeposits (0.12 μmol L^{-1})

Using the above calculations,, mussel egestion has the capacity to adsorb soluble P at a rate between 0.03 to 0.21 μmol SRP μmol biodeposit PP^{-1} d^{-1}, with sediment chambers having much lower uptake rates than lake water and spiked lake water chambers (Figure 16).
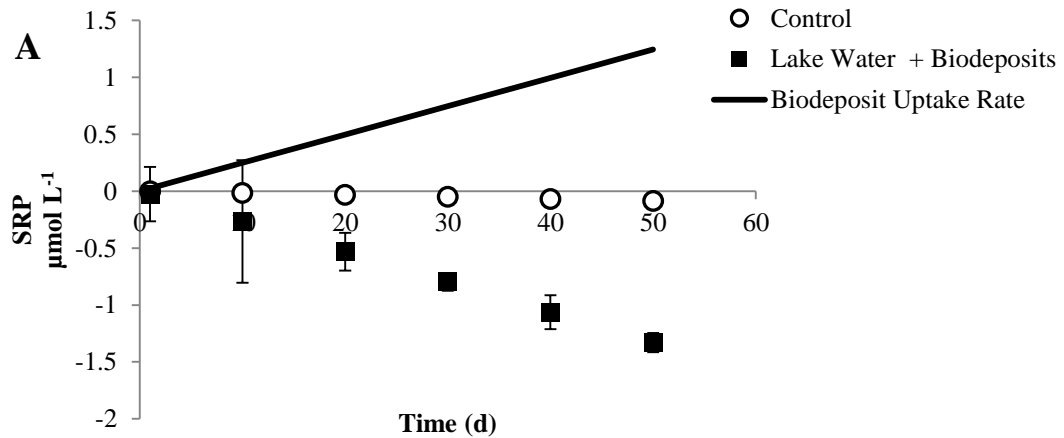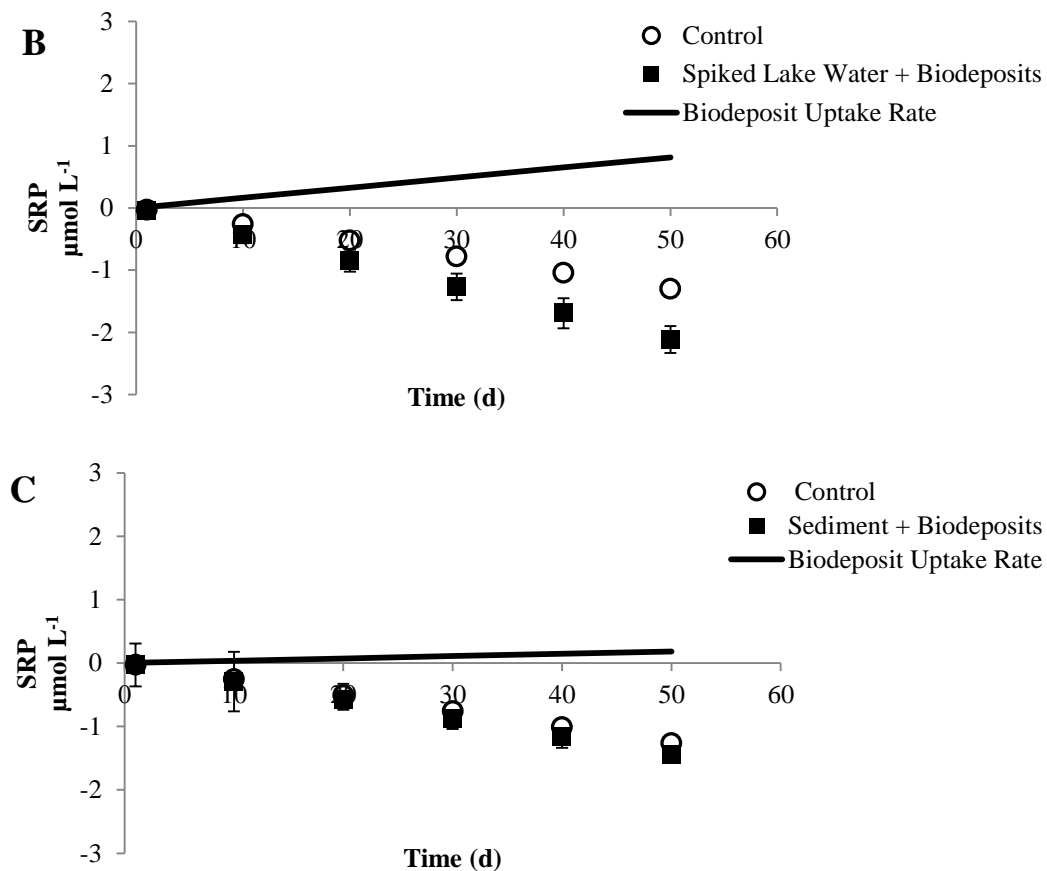
Figure 16: Change of SRP (µmol SRP h^{-1}) in chambers with added biodeposits in lake water (A), biodeposits in phosphate-spiked lake water (B), and biodeposits in sediment cores (C).

3.4.2 Offshore nutrient fluxes versus mussel grazing
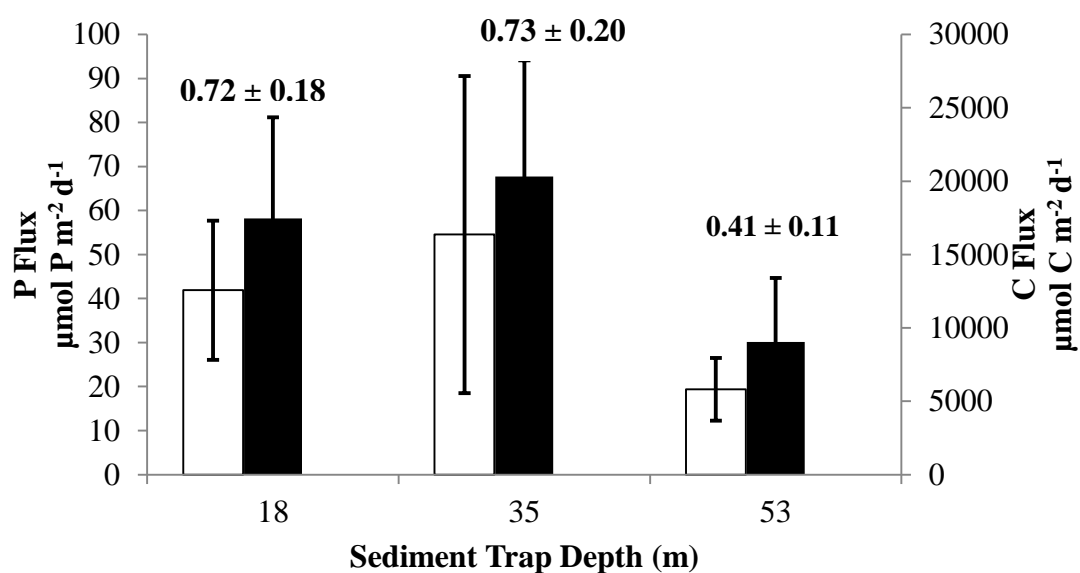
Figure 17: Mean (±SD) P (white) and C (black) flux rates (μmol m^{-2}d^{-1}) for the 3 sediment trap depths (18 m, 35 m, 53 m) inclusive of all deployment periods spanning from June-October 2013 at the 55 m station with mean (±SD) seston sedimentation rates above (g m^{-2}d^{-1}).

Sediment traps were deployed at 3 depths (18 m, 35 m, 53 m) from June to October 2013, and mean (±SD) flux rates for total seston (g m^{-2} d^{-1}), C (μmol m^{-2} d^{-1}), and P (μmol m^{-2} d^{-1}) were calculated for each depth (Figure 17). The epilimnetic trap (18 m) and trap located near the thermocline (35 m) had comparable flux rates that were double the rate of the bottom trap (53 m). The C : P ratio of sediment trap material was ~390 : 1, with no significant difference between depths. In Figure 18, total seston flux rates (g m^{-2} d^{-1}) from June-October 2013 at the 55 m station are compared to sediment trap studies conducted from June-November 1980 at a 140 m station in the southern basin (Meyers and Eadie, 1993). In 1980, sedimentation was inversely related to depth, with increasing sedimentation occurring at deeper depths, while in 2013 higher sedimentation occurs < 35 m.
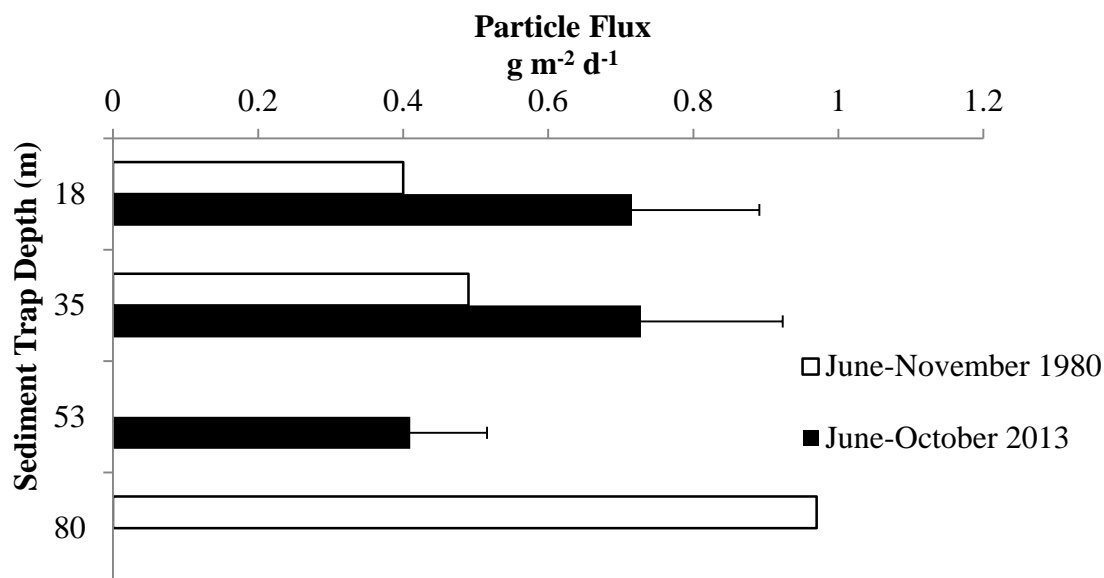
Figure 18: Comparison of mean (±SD) sedimentation rates (g m^{-2}d^{-1}) for June-October 2013 at the 55 m station to sedimentation measured from June-November 1980 at a 140 m station (Meyers and Eadie, 1993).

The mean (±SD) areal sedimentation rates for total seston, C, and P were calculated for each of the three deployment periods for the bottom (53 m) trap at the 55 m station, as measurements at this depth represent conditions in closest proximity to the mussel bed (Figure 19). C and P sedimentation rates increased through the summer, with August through October having the highest rates of C (12418.73 ± 567.52 μmol m^{-2} d^{-1}) and P (27.85 ± 0.94 μmol m^{-2} d^{-1}) sedimentation (Figure 21). The mean rate of P sedimentation during late summer / early fall was 2.3 times greater and C was 2.9 times greater than early / mid-summer measurements.

P sedimentation rates were compared with mussel P excretion + egestion rates in order to estimate the proportion of settling material that may be grazed by mussels. As stated in Chapter 1, the assumption is that grazing is approximately equal to the sum of

excretion + egestion. This will result in a conservative estimate of grazing, as it does not account for assimilation into mussel tissue and shell. Combined mussel P excretion + egestion is 5 to 8 times greater than the measured passive P sedimentation rates, suggesting that mussels are effectively consuming all settling matter in the offshore (Figure 20).
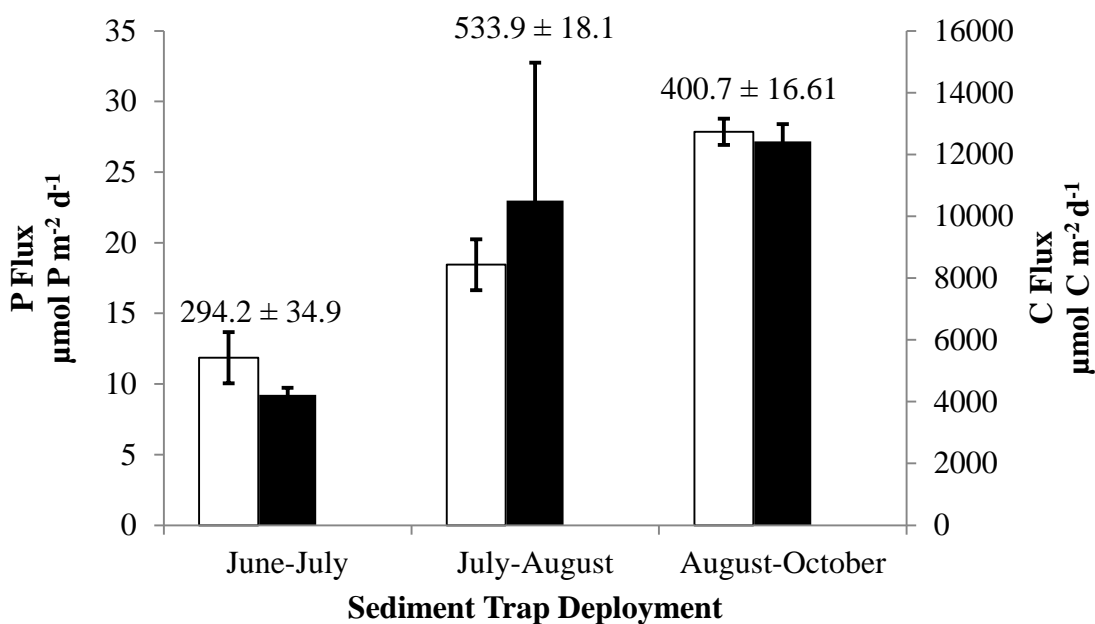
Figure 19: Mean (±SD) sedimentation rates of P (white) and C (dark gray) (μmol m^{-2} d^{-1}) at 53 m for three deployments in the 2013 summer (June 19-July 16, July 16-August 21, August 21-October 17) with areal seston sedimentation rates above each column (g m^{-2} d^{-1}).
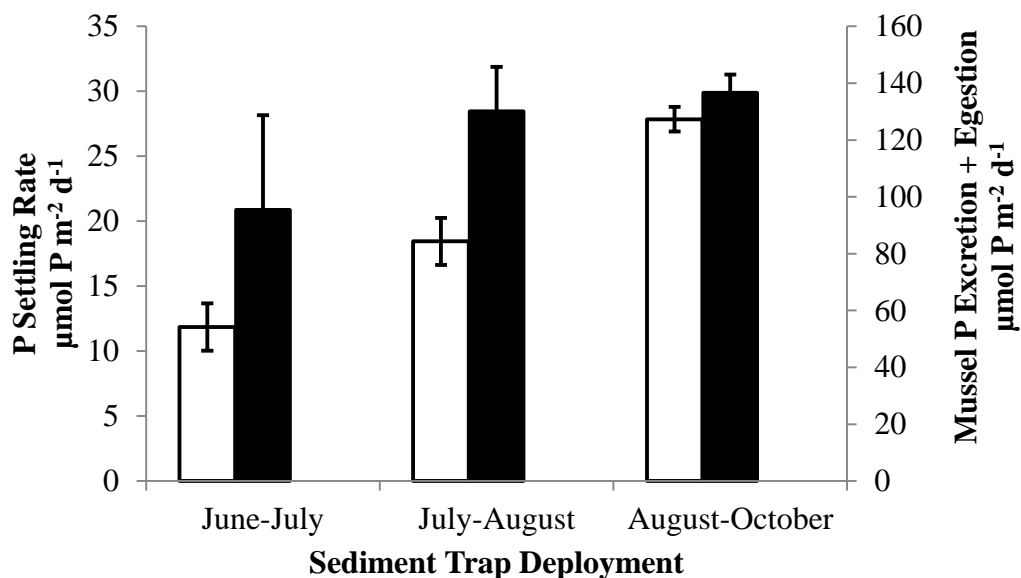
Figure 20: Mean (±SD) P sedimentation rate (µmol P m^{-2} d^{-1}; white) at the 53 m sediment trap compared to mean (±SD) profunda mussel P excretion + egestion rates (µmol P m^{-2} d^{-1}; black).

3.4.3 Changes in water column P concentrations during stratification

If dreissenids create a nutrient shunt to the benthos, this drawdown should be reflected in pelagic concentrations. Using water column P profiles from Chapter 1, the total mass of P (TDP + PP) for the entire 55 m water column was calculated for 2013. Pelagic total P in the spring isothermal mixing period (April 29) to mid-stratification (August 21) increases by 3.1 mol m^{-2} (Figure 21). The increase in the mass of total P in August was due primarily to dissolved P, which increased by 2.5 mol m^{-2}, while particulate P only increased by 0.6 mol m^{-2}. Proportions of dissolved and particulate P remained relatively similar throughout the stratified season, with dissolved P constituting 50-70 % and particulate P 30-50 % of total P. Although particulate P profiles reflect mussel grazing in the lower portion of the hypolimnion (see Chapter 1 Figure 2), this grazing does not

appear to result in a net decrease in total water column P mass during the stratified

period.
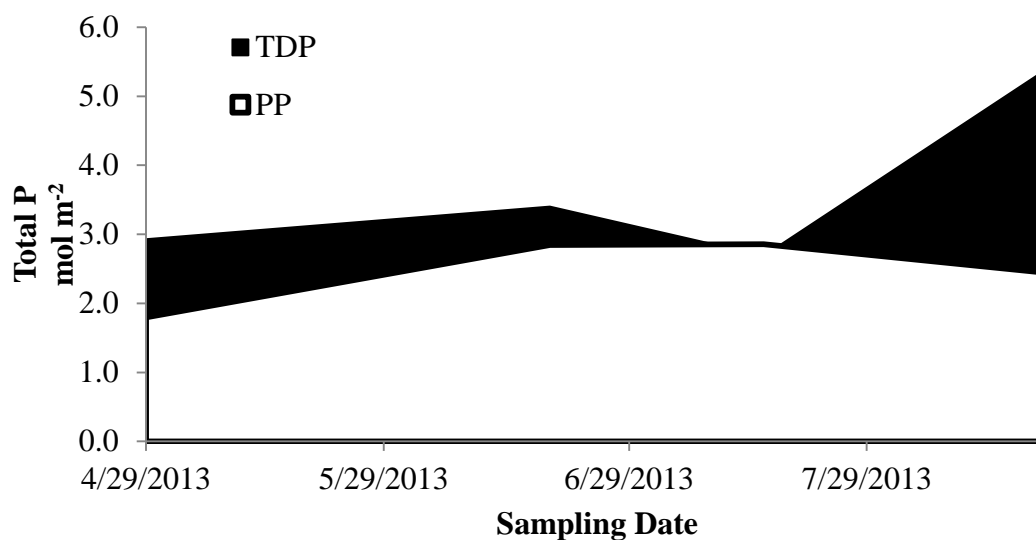
Figure 21: Change in total P mass (mol m^{-2}) partitioned into TDP and PP from April 29 through August 21 2013 for the entire water column at the 55 m station.

3.5 Discussion

3.5.1 Mussels as nutrient sources

The results of sediment core incubations with live mussels support previous *in situ*

observations (Ozersky et al., 2009) and microcosm experiments (Turner, 2010)

highlighting mussels as important nutrient recyclers that increase dissolved nutrient

concentrations directly above mussel beds. Due to the high mussel density at the chosen

site (55 m offshore from Milwaukee, WI), an experimental control core containing no

mussels could not be obtained. The lack of a control makes it difficult to separate the

influence of microbes, bacteria, and other organisms inhabiting the sediment from

profunda quagga mussels. Using mass specific mussel excretion rates and mean mussel

biomass at the 55 m site, areal excretion is expected to be 63 μmol SRP m^{-2} d^{-1}. Applying

these excretion rates to core biomass and area, the expected areal excretion rate for the cores similar in biomass to the 55 m site is 50-70 µmol SRP $m^{-2} d^{-1}$. This suggests that mussels are likely the main factor in influencing changes to SRP concentrations in core incubations.

After mussel removal, the mean SRP concentrations from the high mussel biomass Cores 1-4 stop increasing while the mean from low mussel biomass Cores 5-8 continue to gradually increase. As expected, cores with higher mussel biomass had higher SRP production rates than cores with lower mussel biomass. As demonstrated in Chapter 1, profunda quagga mussels < 8 mm excrete SRP at a much higher mass normalized rate than mussels ≥ 8 mm, similar to findings of other studies (Naddafi and Pettersson, 2008). When examining the size distribution in each of the cores, mussels < 8 mm comprised a similar percentage (37-47 %), and thus size distribution was not a major factor in differences in core SRP concentrations. Although core volume was re-established after sampling by injecting unfiltered lake water to re-establish the volume, the mussels were not fed during the incubation and were likely starved. Despite a starvation state, *Dreissena* continued to excrete SRP over a period of 25 days. It has been thought that quagga mussels are able to depress their metabolic rates at cold temperatures (≤ 5 ℃) without a large impact on their reproductive abilities (Chase and McMahon, 1995; McMahon, 1996). These core experiments support these assumptions that quagga mussels can likely survive in a starved state for an extended period. In the absence of mussels, it is possible that the sediment and overlaying water begin to regain chemical equilibrium, especially in high mussel biomass cores with high mussel excretion..

3.5.2 Fate of egested material

Dreissenid excretion and egestion is thought to be a major source of nutrient regeneration in areas where mussels are abundant in the Great Lakes (Arnott and Vanni, 1996; Bunnell et al., 2009; Heath et al., 1995). However, as mentioned in Chapter 1, there has been almost no research to measure dreissenid egestion rates and determine if biodeposits are a nutrient source or sink. The profunda mussel excretion and egestion rates presented in Chapter 1 indicate that egestion rates are comparable to excretion rates. If this egestion remain sequestered in the sediment, it is possible it represents a net P loss from the system and could contribute to an overall decrease in lake productivity. Biodeposits are the least researched component of the mussel P cycle, and understanding their fate could be important in understanding declining total P concentrations in Lake Michigan (Mida et al., 2010).

In the experiments to quantify phosphate release / uptake by mussel biodeposits, declining phosphates concentrations in control chambers as well as treated chambers could indicate a flaw in the experimental set-up, possibly due to the adsorption of P onto chamber walls (Holdren and Armstrong, 1980). However, chambers with biodeposits had higher rates of phosphate decline than control cores, suggesting that mussel biodeposits were taking up phosphate. A biodeposit P uptake rate (BR) demonstrated that feces and pseudofeces in sediment cores, which are most representative of *in situ* conditions, have the potential uptake rate 0.03 µmol SRP µmol biodeposit PP^{-1} d^{-1}. The uptake rates of lake water and spiked lake water cores were higher than sediment cores, suggesting that the presence of sediment may buffer the uptake rate of soluble P by feces and pseudofeces. Biodeposits contain organic material that may promote the growth of bacteria. The C : P ratio of mussel biodeposits is likely high, reflecting that of Lake

Michigan phytoplankton that serve as the main food source for mussels. This high C : P ratio, and the relatively high P requirements of bacteria (Kirchman, 1994) could result in a P demand by bacteria that may be met through the assimilation of dissolved P. When in contact with the sediment, the P required to support bacterial growth on biodeposits may come from sediment pore water rather than the overlying water column, which would explain the apparent lower rates of uptake in chambers with sediment. At least in the short-term, mussel biodeposits seem to act as a nutrient sink.

P flux between the sediment and water can be regulated by chemical equilibrium between soluble nutrients in the overlaying water column and the mobilization of sediment bound P from reduced ferric oxides (Bostroem, 1981; Mortimer, 1941; Wetzel, 2001) as well as apatite precipitation (Brooks and Edgington, 1994). Mussels could affect nutrient concentrations by lying directly on the sediment and excreting at rates too high for equilibrium. After mussel removal, the decrease in SRP concentrations in high mussel biomass chambers suggests the recovery of this equilibrium. These chamber incubations demonstrate how mussels alter soluble nutrient concentrations; however, these impacts may not be permanent. Although SRP concentrations in sediment cores with live mussels reached levels higher (1.5 μmol L^{-1}) than in chambers with only biodeposits (< 1 μmol L^{-1}), in each experiment the soluble nutrients appeared to reach a steady-state. More research needs to investigate how mussels affect the sediment-water interface and if a nutrient equilibrium re-establishes itself after mussel removal.

3.5.3 Mussel grazing impact in the offshore

Sediment trap studies are invaluable in understanding the origin and amount of settling organic matter reaching the benthos. In the 1970s and 1980s, such studies

evaluated sedimentation rates in the offshore regions of Lake Michigan (Chambers and

Eadie, 1981; Eadie et al., 1984; Meyers and Eadie, 1993). A comparison of sedimentation

rates in the pre- versus post-dreissenid periods reveals stark differences in the flux rates

of particles, carbon, and phosphorus. Before mussels expanded to deeper depths, the

highest particle fluxes were seen in the bottom 10 m, as profiles depict an exponential

increase in particle flux in the near the bottom with a strong presence of a flocculent layer

(Eadie et al., 1984). Sediment traps at 35 m in 1978 revealed a P sedimentation rate of

25.6 μmol m^{-2} d^{-1}, with higher rates in near-bottom traps (Eadie et al., 1984) compared to

a 2013 sedimentation rate at 35 m of 54.5 ± 36 μmol P m^{-2} d^{-1} and a near-bottom rate of

19.4 ± 7.1 μmol m^{-2} d^{-1} . The sediment traps from 2013 depict an inverse trend with

depth, as particle, carbon, and phosphorus fluxes in the bottom trap are ½ of the upper

water column fluxes. The flocculent layer above the lake bottom measured in the pre-

dreissenid period is no longer measurable or even visible with underwater camera

imagery. Time scales of mussel filtration and dissolved P excretion are shorter than those

of mixing within this layer, resulting in a particulate P decline near the lake bottom and

the disappearance of the benthic nepheloid layer. Recent measurements of near-bottom

current structure at the 55 m station suggest only the existence of a weakly stratified

benthic boundary layer ranging from < 2.6 m to 10 m (Cary Troy, personal

communication).

Vertical mixing in the hypolimnion is likely a critical mechanism in food

regulation to profunda quagga mussels in the weakly stratified benthic boundary layer.

Based on P excretion + egestion rates, mussels grazing is up to 8 times greater than the

passive P settling rates. This is a possibility if physical dynamics are replenishing the

food supply to the benthos for the musses. Otherwise dreissenid grazing would likely rapidly deplete particles above the mussel bed, and the filter feeders could have difficultly sustaining a stable population through the stratified season. These findings support previous estimates of *Dreissena* consuming 54 % of annual phytoplankton production and over 100 % of annual settled organic C in the offshore (Tyner et al. 2014, in review). *In situ* fluorescence and chlorophyll *a* profiles depict high chlorophyll *a* concentrations below the thermocline. Whether this is due to phytoplankton sinking out of the epilimnion, growing near the thermocline, or species with high chlorophyll *a* content is uncertain. Regardless, it represents a pool of C and P that is available to quagga mussels within the hypolimnion, and suggests that stratification may not strongly inhibit food supply to mussels.

3.5.4 Oxygen profiles in sediments

Nutrient equilibrium could also be influenced by oxygen concentrations at the sediment-water interface. Oxygen conditions are critical in nutrient exchanges and largely regulated by the metabolism of benthic fauna, including microbes, bacteria, and other organisms. If the cores are air-tight, it is likely mussels would eventually respire all available oxygen and create anoxia. Anoxic conditions in the first few millimeters of the sediment could promote the mobilization of P from reduced ferric oxides, as mentioned previously. Dissolved oxygen microprofiles of sediment cores revealed that cores with higher mussel biomass were anoxic at shallower depths (< 7 mm), and it is possible that the high SRP concentrations in cores with higher mussel biomass were influenced by the release of P from inorganic compounds under anoxic sediment. Passage of material through the anoxic mussel gut could also further promote the release of P bound in

sediment (Hecky et al., 2004), as mussels lying directly on sediment (versus suspended in the water column) were found to have a greater SRP release than could not be accounted for in food consumption (Turner, 2010). Lake Superior cores collected in 1985 and 1986 at depths ranging from 19 to 276 m had oxic conditions up to 25 mm (Carlton et al., 1989). These Lake Superior cores were absent of mussels, and the anoxic conditions at shallower depths in Lake Michigan sediment cores indicates how mussel presence affects sediment chemistry in terms of both nutrients and oxygen.

Dissolved oxygen microprofiles in mussel-impacted, deep-water sediments have never before been closely examined and could reveal indirect effects of invasive dreissenids. Decreased oxygen concentrations directly above mussel beds and in the first few millimeters of sediment not only affect nutrient concentrations and chemical equilibrium, but also the habitability of the profundal benthos. Benthic amphipods such as *Diporeia* spp. survive in deep-water surficial sediments, and populations have rapidly declined since the *Dreissena* invasion and expansion (Nalepa et al., 2009). Proposed reasons for their disappearance include food competition, as mussels filter out settling particles that would normally reach the detritivores, as well as pathogen / toxin transport in mussel egestion (Dermott and Kerec, 1997; Watkins et al., 2007). These microprofiles suggest that *Diporeia* spp. may also have been affected by poor oxygen conditions within the sediment.

3.5.5 Mussel impact on P fluxes in Lake Michigan

A conceptual diagram of P fluxes was created to compare pre-dreissenid (1980-2000) and post-dreissenid (2000-present) P dynamics in the southern basin of Lake Michigan (Figure 22), assuming a stratified water column at a 55 m depth. Published carbon pools

and fluxes were converted to phosphorus using estimated C : P ratios. For > 100 m water column in June-September from 1995-2000 the mean ratio was ~150 ; 1, but by 2007-2011 the mean ratio had increased to ~280 : 1 (Pothoven and Fahnenstiel, 2013). Based on these estimates, any carbon fluxes in the pre-dreissenid period were converted to phosphorus with a ratio range of 150-200 : 1, and any post-dreissenid carbon fluxes were converted using a ratio range of 250-300 : 1. River loading P estimates were calculated using the area of the southern basin (1.9×10^{10} m^2) and estimates from the 1980-1995 and 1995-2000 by Mida et al. (2010). A range of primary productivity was estimated for Lake Michigan's southern basin during mid- and late-stratification from 1983-1987 and 2007-2008 (Fahnenstiel et al., 2010). Passive sedimentation rates for the pre-dreissenid period were calculated from the total organic carbon (TOC) flux in 1980 (Meyers and Eadie, 1993), and the P burial estimate was derived from measurements in 1983-1987 (Shafer and Armstrong, 1994). The dissolved P flux back into the water column for the pre-dreissenid period was considered the difference between the river loading and burial rate. For 2000-present, the P sedimentation was calculated from 2013 sediment trap data described above, and the P burial is unknown.

Zooplankton grazing rates from pre- and post-invasion were calculated using epilimnetic zooplankton clearance rates (Scavia and Fahnenstiel, 1987), total zooplankton biomass (Vanderploeg et al., 2012), and mean water column particulate P concentrations (Pothoven and Fahnenstiel, 2013). The *Diporeia* spp. nutrient uptake rates are based on estimates made in 1990s during the spring diatom bloom (78 days) (Fitzgerald and Gardner, 1993). No grazing rates for *Diporeia* spp. have been calculated since *Dreissena* expansion, and large declines in *Diporeia* populations likely make their current impact on

P cycling negligible. For profunda quagga mussel P fluxes, excretion and egestion rates were calculated as areal rates based on mean mussel biomass, size distribution, and mass normalized nutrient excretion and egestion rates (Chapter 1). Mussel assimilation was assumed to be 10 % of the grazed material (excretion + egestion) (Stoeckmann and Garton, 1997), and 'sequestration', the accelerated sedimentation due to mussel grazing, was determined as mussel excretion + egestion + assimilation.

Pre-Dreissenid Phosphorus Fluxes
μmol P m^{-2} d^{-1}

River Loading
9.3-14

Primary Productivity
170-480

Zooplankton Grazing
170-330

Uptake by *Diporeia spp.*
2.5-3.3

Passive Sedimentation
26-34

Dissolved P
2.3-7

Burial
7

Post-Dreissenid Phosphorus Fluxes
$\mu mol\ P\ m^{-2}\ d^{-1}$

River Loading
7-9.3

Zooplankton Grazing
65-130

Primary Productivity
90-280

Passive
Sedimentation
20

M. Excretion
109

M. Egestion
107

Sequestration
236.5

Mussel
Assimilation
21.5

Burial
?

Figure 22: Conceptual diagram of pre- (top) versus post-dreissenid (bottom) P fluxes ($\mu mol\ m^{-2}\ d^{-1}$).

Comparisons of the two conceptual diagrams (Figure 22) shows shifts in P fluxes and changes in Lake Michigan's offshore productivity since the arrival of dreissenids. Offshore high mussel densities result in more P cycling in the benthos, as mussel grazing utilizes vertical mixing and the advection of particles to the lake bottom to create a P reservoir. Before extensive dreissenid populations carpeted the lake bottom, *Diporeia* spp. were the dominant benthic organism in deep water, consuming nearly 60 % of settling C during the spring diatom bloom (Fitzgerald and Gardner, 1993). But since 2007, the deep-water amphipods have rarely been found at depths < 90 m (Nalepa et al., 2009), and dreissenids are the dominant organism in benthic energy flow. Whereas Diporeia *spp*. were nutrient conduits, dreissenids appear to decrease the turnover of P and

increase sequestration. Nutrient recycling rates are altered, and a P reservoir on the lake bottom has appeared that did not exist previously.

Primary productivity and zooplankton grazing during the stratified period are both estimated to have been up to 1.5 to 2 times greater before *Dreissena* dominated the system. An increase in P-limitation, as suggested by an increase of seston C : P ratios from 150 : 1 to 300 : 1 has resulted in a less productive pelagic zone. Decreases in zooplankton P grazing are due to decreases in whole water column particulate P concentrations, not zooplankton biomass, implying slower zooplankton growth rates. Mean particulate P decreased from 3.5 to 1.8 μmol L^{-1} from 1995-2000 to 2007-2011 (Pothoven and Fahnenstiel, 2013), while zooplankton biomass only decreased from 0.027 to 0.020 mgDW L^{-1} (Vanderploeg et al., 2012). Although pelagic productivity has decreased during the stratified period since the dreissenid invasion, the decreases were not as significant as might be expected, given mussel nutrient recycling and grazing rates.

Passive sedimentation rates are comparable for both periods, but the gross rate of P flux to the benthos post mussel invasion has increased due to mussel grazing. Before 2000, the burial rate was 1/2 to 3/4 of river loading to the southern basin, based on the P content of surficial sediments at a 160 m station dated with ^{210}Pb (Shafer and Armstrong, 1994). Current P burial estimates are unknown, but P burial is likely no greater than pre-dreissenid calculation since total P loading to the lake has continually declined since the 1980s (Mida et al., 2010) and P profiles in undated sediment cores do not depict any increases in P in the top few millimeters of sediment (Appendix A).

Based on the conceptual diagrams presented here, the primary effect of profunda quagga mussels appears to be an accelerated P cycling rate in the benthos. The other P

fluxes (primary productivity, zooplankton grazing, passive sedimentation) have decreased only slightly in the past decade, as mussel impact on the stratified period seems to be limited. This correlates with previous observations of Lake Michigan's stratified period that found no significant change in primary production since the dreissenid invasion (Fahnenstiel et al., 2010). It is likely that mussel filtering activity during the spring isothermal mixing period creates low productivity conditions that are then maintained by the mussels through the stratification. In order to better understand the long-term impact of mussel filtering, it would be necessary to monitor water column nutrient concentrations year-round over the course of several more years and determine the extent of mussel presence creating a reservoir that slows nutrient turn-over.

3.5.6 Implications for dissolved and particulate P concentrations

Dreissena invasion is thought to have shifted nutrient distribution in the water column. Profiles from the late 1970s depicted pelagic SRP concentrations between 0.06-0.10 μmol L^{-1}, pelagic PP comprising 1/3 to 1/2 of total phosphorus in the water column, and high concentrations of both dissolved and particulate P in the clearly defined nepheloid layer (Eadie et al., 1984). In comparison to 2013 water column profiles, mussel grazing has possibly increased the dissolved : particulate ratio of phosphorus in the pelagic zone. The SRP concentrations in the lower hypolimnion are 1/3 of historical concentrations (0.02-0.04 μmol L^{-1}) and PP constitutes only 1/4 of total phosphorus. Water column profiles pre- and post-mussel invasion indicate a general decrease of P in offshore waters (Mida et al., 2010; Pothoven and Fahnenstiel, 2013); however the summer 2013 water column nutrient concentrations show relatively stable PP and even increasing TDP. Even though particulate P concentrations in the hypolimnion have declined since the mussel

invasion, but the mass of particulate P does not change substantially during the stratification, likely due a low initial concentration at the beginning of summer caused by mussel grazing during the spring isothermal mixing period. The increases in P mass at the 55 m site are due to the accumulation of the dissolved P, and since mussel excretion accounts for 40 % of recycled P by mussels, if this portion is mixed back into the water column it could account for the gain in P mass.

For the stratified period, an estimated 'accumulation' of mussel excretion compared to the increase in hypolimnetic dissolved P would indicate if mussel excretion can account for the P mass increase. For the 55 m high mussel density site, an areal mussel excretion rate of 109 μmol TDP $m^{-2} d^{-1}$ was calculated using Chapter 1 profunda quagga mussel biomass and excretion rates. Applying this areal excretion rate to a 30 m hypolimnion and a stratified period of 100 days, a net hypolimnetic 'accumulation' of TDP would be 0.36 μmol L^{-1}, assuming no mixing between the hypolimnion and epilimnion. Based on the water column dissolved P profiles from April 29 through August 16 in Chapter 1, TDP in the hypolimnion increased by only 0.05 μmol L^{-1}. With no vertical or horizontal mixing, areal mussel TDP excretion results in concentrations 7 times greater than the measured increase in the hypolimnion at the 55 m station. However, this calculation is for a high mussel density site and does not take into account nearshore-offshore exchange, dilution due to a large lake volume, or lower mussel densities at deeper sites. Nalepa et al. (2010) estimates that ≥ 65 % of mussels are ≤ 5 mm at deeper depths (> 50 m), and Chapter 1 histograms supports these estimates. Using mussel density and size distribution for mussels > 50 m (Nalepa et al., 2010) and Chapter 1 mussel areal excretion rates, a revised areal TDP excretion rate for the whole lake

ranges between 7.34 to 67.9 µmol L^{-1}. This range of revised areal excretion applied to a

mean whole-lake hypolimnetic depth of 80 m (Bootsma et al., 2003) and a stratified

period of 100 days would result in an expected 'accumulation' between 0.01 to 0.08 µmol

L^{-1}, assuming no mixing. The soluble P increase in the hypolimnion (0.05 µmol L^{-1}) falls

within this range of expected mussel excretion 'accumulation', and suggests that mussel

excretion may play a role in maintaining P mass during the stratified season. The 55 m

site is an example of a high mussel density site, and profunda quagga mussel impact on

the whole lake is less pronounced due to mixing and dilution, which distributes mussel

excretion throughout the lake.

Besides mussel excretion, P from river loading may keep the total P mass in the

water column constant. Based on river loading estimates from 1990-2008 of 1500-2000

MT/year (Mida et al., 2010) and the southern basin area of 1.9 X 10^{10} m^2 (Tyner, 2013),

P loading to the southern basin is 7.3-9 µmol m^{-2}d^{-1}. For the stratified period (~100 d) at a

55 m depth, this would be up to a 0.02 µmol L^{-1} increase. Mussel excretion and riverine

input in the southern basin could contribute 0.03 to 0.1 µmol L^{-1} during the stratified

period. There is no significant decrease in P mass during the stratified period because

diluted mussel excretion and external inputs stabilize any loss from the system.

Mussels are efficient nutrient cyclers, and yet observing the lake as a whole

during the stratified period, profunda mussel filtering does not cause a decrease in water

column P mass. Despite extensive populations, the lower metabolic activity of these

mussels combined with low P concentrations at the onset of stratification appears to

lessen their impact. Considering that greater decreases in primary productivity are seen

during the spring isothermal mixing period (~80 %) in comparison to stratified periods

(~20 %) (Fahnenstiel et al., 2010), the immediate impact of mussel presence is during mixing when the filter feeders have better access to the more productive regions of the water column. For the stratified period, the most noticeable impact of the profunda morph is the increase of P cycling in the benthos and creation of a P reservoir slowing the turnover of nutrients.

4. Conclusion

Profunda quagga mussels have relatively low and constant excretion and egestion rates due to cold temperatures and resultant decreased metabolic rates in offshore Lake Michigan. In the past, studies of *Dreissena* have focused primarily on excretion, but this research indicates that egestion accounts for ~40 % of grazed material for profunda quagga mussels and needs to be evaluated when measuring mussel nutrient recycling rates. The profunda morph has double the densities of the nearshore phenotype, but only 1/3 the biomass due to a lower length : weight ratio. Profunda quagga mussels in offshore Lake Michigan likely have a lower impact on P cycling than their nearshore counterparts per unit area due to lower excretion and egestion rates.

Mussel grazing is greater than passive sedimentation due to vertical mixing increasing the advection of particles to the benthos. Mixing is likely a key mechanism in food regulation to profunda quagga mussels during stratification. This research supports the hypothesis that offshore mussels have altered P cycling and affected phytoplankton structure (Fahnenstiel et al., 2010) and nutrient concentrations (Mida et al., 2010). Decreases in production during summer / fall are not as significant as alterations during the winter / spring (Fahnenstiel et al., 2010) because mussel grazing during the spring isothermal mixing period creates a lowered level of productivity that mussels maintain

during stratification. Looking at a single stratified season, there is no net loss of either dissolved or particulate P due to mussel excretion and riverine input stabilizing P mass in the water column. However, with profunda quagga mussels grazing all settling matter delivered to the benthos (Tyner et al., 2014, in review) and could potentially sequester P over the long term, which is likely responsible for the long-term decrease in pelagic total P concentrations in the lake. Based on *in situ* measurements, experiments, and comparison to other P fluxes, we suggest that mussels have created a nutrient reservoir in the benthos that decreases the turnover time of nutrients in the lake.

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6. Appendices

Appendix A: Phosphorus Profiles in Core Incubations with Live Mussels

**Total Phosphorus
(μg mg^{-1})**
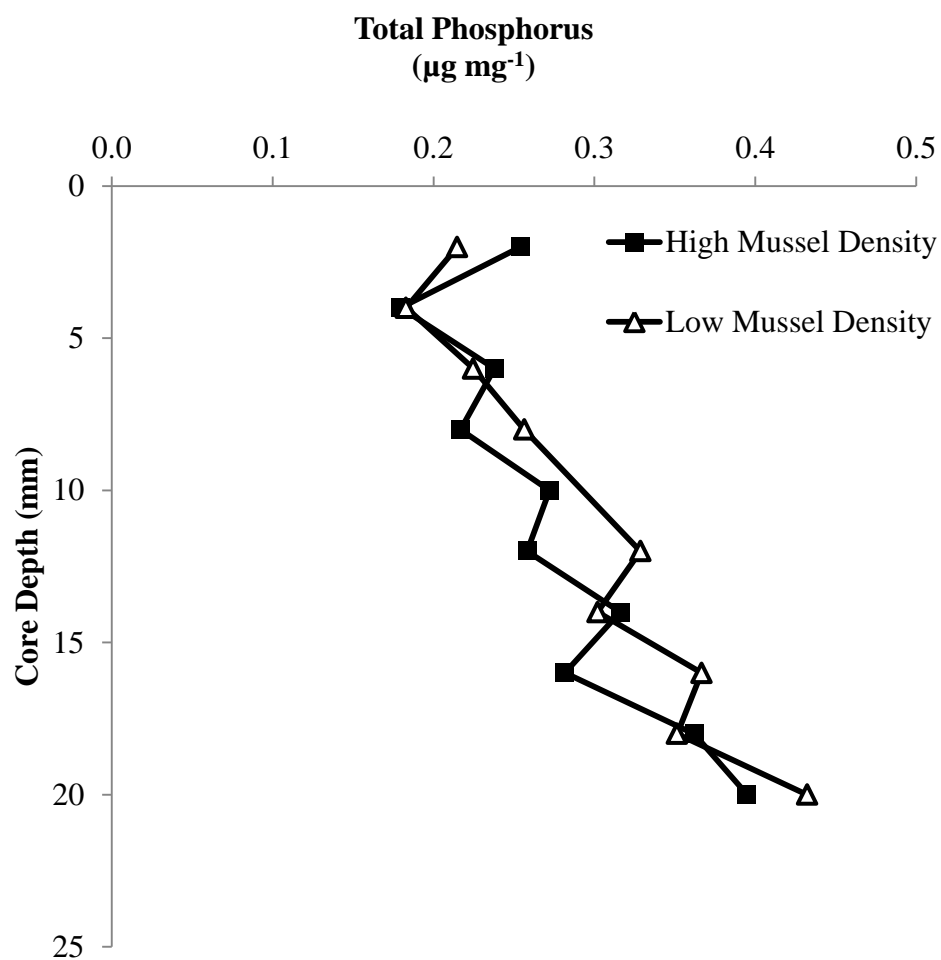
Appendix B: Mussel Phosphorus Excretion and Egestion Experiments

	SRP Excretion μmol mgDW^{-1} d^{-1}				
Mussel Size mm	Sampling Date				
	5/1/2013	6/12/2013	7/16/2013	8/21/2013	10/14/2013
Small 8-12	0.0021	-	0.0008	0.0048	0.0009
	0.0011	0.0034	0.0007	0.0021	0.0003
	0.0003	0.0030	0.0004	0.0015	0.0024
Medium 13-17	0.0010	0.0021	0.0010	0.0015	0.0012
	0.0032	0.0016	0.0012	-	0.0061
	-	0.0017	0.0017	0.0015	0.0028
Large 18-22	0.0010	0.0011	0.0008	0.0012	0.0014
	0.0010	0.0011	0.0022	0.0012	0.0015
	0.0008	0.0016	0.0010	0.0022	0.0011

	TDP Excretion μmol mgDW^{-1} d^{-1}				
Mussel Size mm	Sampling Date				
	5/1/2013	6/12/2013	7/16/2013	8/21/2013	10/14/2013
Small 8-12	0.0050	-	0.0002	0.0087	0.0004
	0.0029	0.0029	0.0016	0.0092	-0.0009
	0.0021	0.0034	0.0000	0.0124	-0.0010
Medium 13-17	0.0032	0.0034	0.0009	0.0037	0.0019
	0.0034	0.0033	0.0025	-	0.0110
	-	0.0034	0.0028	0.0050	0.0040
Large 18-22	0.0019	0.0017	0.0012	0.0027	0.0017
	0.0017	0.0015	0.0039	0.0029	0.0018
	0.0022	0.0026	0.0014	0.0037	0.0016

	PP Egestion μmol mgDW^{-1} d^{-1}				
Mussel Size mm	Sampling Date				
	5/1/2013	6/12/2013	7/16/2013	8/21/2013	10/14/2013
Small 8-12	0.0022	-	0.0017	0.0012	0.0016
	0.0012	0.0153	0.0031	0.0061	0.0011
	0.0015	0.0269	0.0015	0.0023	0.0017

Medium 13-17	0.0035	0.0072	0.0041	0.0007	0.0011
	0.0024	0.0078	0.0020	0.0022	0.0009
	0.0027	0.0078	0.0038	0.0025	0.0009
Large 18-22	0.0021	0.0022	0.0014	0.0008	0.0007
	0.0015	0.0022	0.0016	0.0009	0.0009
	0.0012	0.0063	0.0015	0.0012	0.0008

Appendix C: Mussel Phosphorus Excretion and Egestion Syringe Experiment

Length mm	Replicate	Mussel mgDW	SRP Excretion µmol mgDW^{-1} d^{-1}	TDP Excretion µmol mgDW^{-1} d^{-1}	PP Egestion µmol mgDW^{-1} d^{-1}
4-6	A	1.085	0.008	0.009	0.047
	B	1.209	0.012	0.018	-
	C	1.41	0.012	0.018	0.03
8-12	A	10.495	0.003	0.004	0.013
	B	6.874	0.004	0.004	0.017
	C	7.938	0.004	0.006	0.011
13-17	A	28.183	0.005	0.002	0.007
	B	27.57	0.004	0.002	0.002
	C	16.326	0.003	0.000	0.005
18-22	A	33.983	0.004	0.004	0.003
	B	34.02	0.004	0.002	0.004
	C	42.921	0.002	0.001	0.002

Appendix D: Mussel Effective Clearance Rate and Grazing Rate

		Effective Clearance Rate		Grazing Rate
		L mussel^{-1} d^{-1}	L mgDW^{-1} d^{-1}	μmol P mgDW^{-1} d^{-1}
6/12/2013	Small 8-12	2.95	1.96	0.043
		5.47	3.65	0.080
	Medium 13-17	5.01	0.96	0.021
		2.61	0.50	0.011
		5.56	1.07	0.023
	Large 18-22	5.26	0.37	0.008
		5.48	0.38	0.008
		12.74	0.89	0.019
10/14/2013	Small 8-12	1.53	0.61	0.013
		1.22	0.49	0.011
		2.72	1.09	0.024
	Medium 13-17	2.09	0.31	0.007
		1.79	0.26	0.006
		2.74	0.40	0.009
	Large 18-22	3.20	0.19	0.004
		4.39	0.26	0.006
		4.08	0.24	0.005

Appendix E: Mussel Phosphorus Areal Excretion and Egestion Calculations

Mussel Size mm	Mussel m^{-2}	Biomass		SRP Excretion		TDP Excretion		PP Egestion	
		mgDW mussel^{-1}	mgDW m^{-2}	μmolSRP mgDW^{-1} d^{-1}	μmolSRP m^{-2} d^{-1}	μmolTDP mgDW^{-1} d^{-1}	umolTDP m^{-2} d^{-1}	μmolPP mgDW^{-1} d^{-1}	umolPP m^{-2} d^{-1}
<5	3378.40	0.13	434.8	0.011	4.62	0.015	6.48	0.04	16.69
6	750.84	0.54	403.2	0.011	4.29	0.015	6.01	0.04	15.48
7	680.13	0.80	546.1	0.011	5.81	0.015	8.14	0.04	20.96
8	445.74	1.14	507.1	0.0016	0.84	0.003	1.55	0.0019	0.94
9	403.63	1.55	624.5	0.0016	1.03	0.003	1.90	0.0019	1.16
10	405.22	2.04	825.4	0.0016	1.36	0.003	2.52	0.0019	1.53
11	350.39	2.61	915.3	0.0016	1.51	0.003	2.79	0.0019	1.69
12	425.08	3.28	1393.5	0.0016	2.30	0.003	4.25	0.0019	2.58
13	454.48	4.04	1836.0	0.0016	3.03	0.003	5.60	0.0019	3.40
14	504.54	4.90	2473.2	0.0016	4.08	0.003	7.54	0.0019	4.58
15	479.11	5.87	2811.9	0.0016	4.64	0.003	8.57	0.0019	5.21
16	398.86	6.95	2770.4	0.0016	4.57	0.003	8.44	0.0019	5.13
17	325.76	8.14	2650.6	0.0016	4.37	0.003	8.08	0.0019	4.91
18	205.79	9.45	1943.8	0.0016	3.21	0.003	5.93	0.0019	3.60
19	147.79	10.88	1607.5	0.0016	2.65	0.003	4.90	0.0019	2.98
20	129.51	12.44	1610.5	0.0016	2.66	0.003	4.91	0.0019	2.98
21	96.93	14.12	1369.1	0.0016	2.26	0.003	4.17	0.0019	2.53
22	71.51	15.95	1140.4	0.0016	1.88	0.003	3.48	0.0019	2.11
23-25	219.29	20.06	4399.5	0.0016	7.26	0.003	13.41	0.0019	8.14

Appendix F: Sediment Trap

Deployment	Collection	Trap Diameter cm	Trap Surface Area m^2	Days Deployed	Depth m	Trap Dry Weight g	Sedimentation Rate mg m^{-2}d^{-1}	µgP mgSed^{-1}	Areal P µgP m^{-2}d^{-1}	µgC mgSed^{-1}	Areal C µgC m^{-2}d^{-1}
6/19/2013	7/16/2013	9.53	0.01	27	18A	0.10	527.05	-	-	248.92	131195.92
					18B	0.10	493.79	1.73	27.52	250.88	123879.14
					18C	0.09	457.92	1.61	23.73	252.53	115641.50
					35A	0.10	541.61	2.11	36.92	230.46	124818.45
					35B	0.07	359.17	1.83	21.18	253.23	90953.16
					35C	-	-	-	-	-	-
					53A	0.06	310.83	1.31	13.17	154.13	47906.34
					53B	0.05	254.17	1.19	9.79	198.28	50396.16
					53C	0.06	317.58	1.23	12.62	168.27	53440.03
7/16/2013	8/21/2013			36	18A	0.24	931.70	2.35	70.69	166.04	154699.27
					18B	0.20	777.72	2.23	55.83	296.40	230514.77
					18C	0.19	748.48	2.07	50.04	285.24	213495.79
					35A	0.24	948.07	1.75	53.48	0.00	-
					35B	0.24	932.09	4.66	140.16	335.79	312986.05
					35C	0.20	796.82	1.86	47.89	327.38	260861.92
					53A	0.13	521.99	1.11	18.65	189.18	98749.17
					53B	0.14	554.73	1.13	20.14	338.53	187793.13
					53C	0.13	525.10	0.98	16.55	174.69	91730.40
8/21/2013	10/17/2013			57	18A	0.34	842.78	1.25	-	388.97	327811.99
					18B	0.34	847.21	1.43	34.05	365.72	309844.57
					18C	0.33	813.97	1.31	39.00	342.81	279035.26
					35A	0.29	725.83	1.78	34.35	414.04	300519.53

					35B	0.31	763.74	2.06	41.64	401.83	306892.72
					35C	0.31	753.89	1.82	50.69	410.32	309340.47
					53A	0.16	381.63	2.29	44.30	402.81	153723.81
					53B	0.17	408.22	2.17	28.14	372.68	152135.86
					53C	0.17	412.16	2.02	28.61	342.62	141214.61