

Zebra and Quagga mussel dynamics in Onondaga Lake, New York, 2005-2013

2013 Annual Report

August 2014

Prepared by

Lars G. Rudstam¹ and Christopher J. Gandino²

1) Department of Natural Resources, Cornell University, Cornell Biological Field Station, 900 Shackelton Point Rd., Bridgeport, NY 13030

2) Onondaga County Department of Water Environment Protection, 650 Hiawatha Boulevard, West Syracuse, NY 13204

Abstract

Quagga mussels (*Dreissena rostriformis bugensis*) have displaced zebra mussels (*Dreissena polymorpha*) in a number of North American lakes, but the mechanism(s) giving quagga mussels an advantage over zebra mussels are not known and may vary across systems. Most North American lakes where quagga mussels have become dominant are deep and oligotrophic with oxygenated hypolimnions suggesting that the ability of quagga mussels to colonize deeper waters or their ability to grow in low productivity systems may be key factors. We analyzed the quagga mussel invasion in a eutrophic lake with summer anoxia in the hypolimnion (Onondaga Lake, NY) where both of these mechanisms should be less important. The mussel population was sampled in 2000, 2002 and annually from 2005 to 2013. In this lake, both mussel species were present in 1992 but remained rare through 1998. Zebra mussels increased in abundance first and dominated collections in 2000, 2002 and 2005-07. Quagga mussels were rare in 2002, increased from 2006 to 2008 and largely replaced zebra mussels in water 3 -6 m (>90% of the biomass) by 2009, indicating that a shift from quagga mussels from a subdominant to a dominant species can occur within three years. However, zebra mussels remained co-dominant with quagga mussels in shallower water. The proportion of quagga mussel by biomass in water shallower than 3 m ranged from 24 to 66% in 0-1.5 m and from 21 to 80% in 1.5-3 m with no time trend between 2008 and 2013. Quagga mussels were larger than zebra mussels at all depths suggesting that faster growth rates of quagga mussels are not limited to oligotrophic systems and contribute to the dominance of quagga mussels also in eutrophic lakes. The continued coexistence of both species in 0-3 m depths may be related to the advantage of greater attachment strength of zebra mussels in areas more affected by wave action. Dreissenid biomass and density in 0-6 m deep water has ranged between 6.9 and 30.9 g ash free dry weight /m² and between 2603 and 23782 m⁻² from 2007 to 2013 with the highest values in 2011 and the lowest in 2013. Low values in 2013 were partly due to dredging at two of the standard locations although the decline was also evident at locations not affected by dredging and may be related to predation by increasing numbers of round goby (*Neogobius melanostomus*) which arrived to the lake in 2010.

Introduction

Dreissenid mussels, both zebra mussel (*Dreissena polymorpha*) and quagga mussel (*Dreissena rostriformis bugensis*), are invasive ecosystem engineers with large effects on the ecosystem through filtering and alteration of the benthic habitat (reviews in Karatayev et al. 1997, 2002, Higgins and VanderZanden 2010, Mayer et al. 2014). Both species arrived to North America and Lake Erie in the mid-1980s (Carlton 2008, Mills et al. 1993, 1996). Zebra mussels then spread rapidly and by 1993 were common across the Great Lakes and in many inland lakes, and had reached the Gulf of Mexico through the Mississippi River and the Atlantic Coast through the Hudson River (Benson 2014). Its congener, the quagga mussel spreads more slowly (Karatayev et al. 2011, Benson 2014). Even so, the quagga mussel did arrive to Lake Ontario in 1990 and

was found in Onondaga Lake in 1992 (Mills et al. 1993). Quagga mussels have displaced zebra mussels in many areas, especially in deeper lakes where quagga mussels are found both in shallow and deep, cold water (Mills et al. 1996, Nalepa et al. 2010, Watkins et al. 2007, 2012). Not a single zebra mussel was found in samples taken deeper than 30 m in Lake Ontario during the last whole lake survey in 2008 (Birkett et al. in press). A similar range expansion of quagga mussels and displacement of zebra mussels have occurred in Europe (Orlova 2014, Matthews et al. 2014). In general, it takes longer time for quagga than for zebra mussels to reach maximum abundance after the initial colonization of a lake (average of 13 years for quagga mussels versus 2.5 years for zebra mussels, Karatayev et al. 2011). However, both species produce large number of veligers suggesting that a fast population increase is possible for both species. The reason for this difference in the time to reach peak abundance after colonization is unknown.

The displacement of zebra mussels by quagga mussels may increase the effects of these ecosystem engineers. As quagga mussels are found in all water depths from nearshore waters to several hundred meters depth and can colonize soft bottoms, they can build up higher lake-wide biomass than zebra mussels (Watkins et al. 2007, Nalepa et al. 2010). Therefore, the displacement of zebra mussels by quagga mussels does not only replace one filter feeder by another with little additional changes to the ecosystem, it increases the ecosystem effects of dreissenid mussels. Deep-living quagga mussels are likely the major cause for the observed decrease in the spring diatom bloom in Lake Michigan with associated negative effects on both the benthic amphipod *Diporeia* and spring zooplankton (Vanderploeg et al. 2010, Kerfoot et al. 2010, Fahnenstiel et al. 2010). Understanding the mechanisms involved in this replacement process is therefore of interest both to population ecologists concerned with species replacement mechanisms and to ecosystem ecologists studying the system-wide effects of dreissenids.

Although less is known about quagga mussels than zebra mussels (Karatayev et al. 2014a), there are several physiological and behavioral differences between the two species that may contribute to the replacement of zebra mussels by quagga mussels. Compared to zebra mussels, quagga mussels have lower metabolic rates, are more resistant to starvation, and can grow and reproduce in lower temperatures (Baldwin et al. 2002, Stoeckmann 2003, Roe and MacIsaac 1997, Karatayev et al. 2014a, Garton et al. 2014). Quagga mussels can therefore build up dense populations in deep, cold water and produce a larger number of veligers giving them an advantage over zebra mussels in the lottery for settling space (Claxton and Mackie 1998, Karatayev et al. 2014a). Results from investigations of filtering rates that directly compared the two species varies, with some finding no differences (Ackerman 1999, Naddafi and Rudstam 2014b) other finding lower weight specific clearance rates for quagga mussels (Baldwin et al. 2002, Zhao 2014). Quagga mussels also grow faster at low food concentrations (Diggins 2001, Baldwin et al. 2002). Therefore, the documented ability of zebra mussels to decrease algal abundance may result in low-food conditions which would favor quagga mussels (Mills et al. 1996, 1999, Negley et al. 2003). Predation has no direct role in the displacement process as quagga mussels are more vulnerable to predation because of their thinner shells, less aggregation

behavior, lower propensity to seek shelter, and lower attachment strength (Kobak and Kakareko 2009, Peyer et al. 2009, Naddafi and Rudstam 2013, 2014a,b, Czarnoleski and Müller 2014). However, this anti-predation adaptation has a cost, and Naddafi and Rudstam (2014a) showed that quagga mussels grew faster than zebra mussels in the presence of predator cues but not when predator cues were absent. Thus, zebra mussels invest more energy in predator defenses, expenditures that may infer too high a growth disadvantage in a new environment with less efficient predators feeding on these mussels (Naddafi and Rudstam 2014c). If true, the relative abundance of zebra mussels may increase in systems invaded by fish adapted to feed on mussels like the round goby (*Neogobius melanostomus*, Kornis et al. 2012, Houghton and Janssen 2014). This species was first observed in Onondaga Lake in 2010 (UFI et al. 2014).

In this paper, we present data from annual surveys of dreissenids in Onondaga Lake, New York, from 2005 to 2013 during a time when quagga mussels increased from a sub-dominant to the dominant dreissenid species in the lake. Annual lake-wide surveys of dreissenids are rare and only available from a handful of lakes (e.g. Burlakova et al. 2006, Karatayev et al. 2014a). Onondaga Lake is particularly interesting because the lake is eutrophic and has an anoxic hypolimnion from late June through fall overturn (UFI et al. 2014), making colonization of deep water impossible for mussels. We use this data set collected by the Onondaga County Department of Water Environment Protection (OCDWEP) to investigate if quagga mussels displace zebra mussels over time in a eutrophic lake with anoxic hypolimnion, the time scale of such a species replacement, if quagga mussels retain a growth advantage over zebra mussels in eutrophic lakes, and if the displacement process is depth dependent. We hypothesize that zebra mussels will remain dominant in shallow water as this species has higher attachment strength and is therefore better able to withstand wave action (V. Karatayev et al. 2013).

Study area

Onondaga Lake has a surface area of 11.7 km² and a maximum length and width of 8 km and 1.5 km, respectively. The mean depth is 10.9 m with a maximum depth of 20 m (Effler 1996). The lake flushes rapidly (4 times/yr) and responds quickly to changes in external loading (Matthews et al. 2001). Onondaga Lake discharges at its north end through the Seneca and Oswego rivers, which flow into Lake Ontario at Oswego, New York. For more than a century the lake has been the recipient of domestic and industrial wastewater from the Syracuse metropolitan area (Effler 1996) and the hypolimnion becomes anoxic from mid to late June through fall overturn. Anoxic conditions at 15 m started between Jun 20 and July 25 in the years 2000-2013 (OCDWEP et al. 2014). However, water quality of the lake has improved substantially during the past 20 years as a result of closures of several industries and improvements to the Metro sewage treatment plant (Effler et al. 2008, UFI et al. 2014). In 2013, anoxic conditions occurred from mid-June through the end of October and reached 6 m depth for a week in July and September (OCDWEP unpubl. data).

Both mussel species were found in Onondaga Lake in 1992, around 5 years after they were documented as present in Lake Erie (Mills et al. 1993). However, dreissenid mussels remained rare in Onondaga Lake up to and including 1997 when reported densities were $< 1 \text{ m}^{-2}$ (Spada et al. 2002). Spada et al. (2002) reported a large increase in zebra mussels in 1999 with densities in 2000 between 1200 and 22,200 m^{-2} in four areas of the lake – quagga mussels were not reported as present by Spada et al. (2002). Most mussels were between 5 and 15 mm shell length. Spada et al. (2002) attributed this increase to improvement in the Metro sewage plants decreasing the ammonia levels in the lake. The lake was surveyed for mussels again in 2002 by OCDWEP and Stantec Consulting Services (OCDWEP 2003), and each year from 2005 to 2013 (this study). In 2002, the lake was first surveyed for mussels using video cameras across depths regions before quantitative samples were collected using quadrants sampled with divers. As few mussels were observed from water depth deeper than 3 m, quantitative samples were only collected from 0 to 3 m. Samples were collected in 8 different regions of the lake and average densities was 1232 in 0-1.5 m and 1584 m^{-2} in 1.5–3 m. A few quagga mussels were found in the 2002 survey.

Methods

Mussel density and size structure was measured at depths from 0 to 4.5 m at 12 transects located around the lake from 2005 to 2013 (Figure 1, Table 1). Samples were collected with a petite ponar (area 0.027 m^2) by the staff of the OCDWEP in October of each year (range of dates October 8 to 25). At each transect site, one sample was collected from each depth range 0 – 1.5 m, 1.5 – 3 m and 3 – 4.5 m. The depths sampled were expanded to include 4.5 – 6 m in 2011 and 6 – 7.5 m in 2013. Samples were sieved in the field and all mussels returned to the laboratory. Up to 100 mussels that were alive at sampling were measured in each sample to the nearest 0.1 mm (longest dimension). Empty shells were not included. If less than 150 mussels for any given transect were measured (because of the lack of mussels in some individual samples), additional randomly selected mussels were measured in those samples within the transect with more than 100 mussels (if such are available), with the goal of at least 150 measurements per transect. When subsampled (samples with > 100 mussels), the weight of the subsample and the total sample were measured to expand the numbers counted in the subsample to the whole sample. Total wet weight of the sample was measured to the nearest 1 g. Ash free dry weight was calculated from the lengths of each mussel measured using the overall species-specific equations in Nalepa et al. (2010):

Quagga mussels: $\log_e \text{AFDW} = -6.535 + 3.143 * \log_e (\text{SL})$

Zebra mussels: $\log_e \text{AFDW} = -5.226 + 2.651 * \log_e (\text{SL})$

Where AFDW is tissue ash free dry weight in mg (shell-free) and SL is maximum shell length in mm. These calculated values were highly correlated with measured wet biomass in the lake with no significant effect of mussel species or significant intercept ($\text{AFDW (g)} = 20.05 \text{ (SE } 0.09) *$

wet biomass (g) + 0.05 (SE 0.145), $R^2=0.991$, $N=429$, $P<0.0001$). Thus, tissue AFDW is on average 5% of the shell-on wet weight. We chose to use the dry weight values because small samples were not always weighed and because of differences among investigators on the method to use for wet weight measurements. Burlakova et al. (2006) recommend opening up each mussel shell to remove water from the mantle cavity - this was not done for the Onondaga data set.

Mussels were identified as quagga and zebra mussels starting in 2007. In 2005 and 2006, quagga mussels were not recorded although some individuals were likely present, especially in 2006 (see discussion). Unfortunately, samples were not archived from those years and could not be revisited for this study.

Statistical analysis were done with Jmp ® Pro 10.0.0 (SAS Institute Inc. 2012). Density and biomass were \log_e transformed after adding half of the smallest value to reduce heteroscedasticity. Length was not transformed. Year, depth region, and transect were considered categorical variables. Analyses for year effects were done after averaging values for the depth regions 0-4.5 m for each transect, thus considering a transect as a sample unit. We also compared depth regions by averaging over transects and using year as a sample unit. This analysis was limited to years after 2008 when quagga mussels were abundant in the lake. If the ANOVA analysis was significant, we tested for pairwise differences using Tukey's HSD test that account for multiple comparisons. Differences in biomass between 2011, 2012 and 2013 were also tested with a non-parametric Wilcoxon's signed rank paired test with transect as the paired value between years. Tests were considered significant at an alpha value < 0.05 .

Results

Density (biomass) of zebra mussels increased rapidly in water depths from 0 – 4.5 m from 1005 m^{-2} (0.9 g afdw/ m^2) in 2005 to 2184 m^{-2} (3.0 g/ m^2) in 2006 and 11013 m^{-2} (27.6 g/ m^2) in 2007. Zebra mussels then declined and average densities ranged between 2722 and 8030 (2.8 – 8.0 g/ m^2) from 2008 through 2012 with no significant difference among these years (Figure 2, Table 2). By 2013, densities declined further to 1683 m^{-2} (2.2 g/ m^2), which were the lowest values recorded since 2005. Densities in 2013 were significantly lower than in 2007 and 2011, biomass was significantly lower than 2007 and 2008 but not significantly different from others years. Average length of zebra mussels ranged from 5.7 to 9.0 mm with the smallest mussels found in 2006 and 2012 and the largest in 2008 and 2009. Quagga mussels in water depths 0-4.5 m were not reported in 2005 and 2006 and reported present in low numbers in 2007 (300 m^{-2} (2.0 g/ m^2)). Densities increased to a peak of 5737 m^{-2} (22.6 g/ m^2) in 2009 and remained between 2283 and 4905 m^{-2} (10.6 – 15.2 g/ m^2) through 2012. Quagga mussels densities declined in 2013 to 800 m^{-2} (2.2 g/ m^2). Only 2005-2007 had densities and biomass of quagga mussels that were significantly lower than most other years. Values in 2013 were not significantly different from any year including 2007 (Table 2). Average length of quagga mussels was longer than for zebra mussels and ranged from 8.1 to 10.8 mm from 2007 to 2013 with only the difference between

2009 (10.8 mm) and 2010 (8.1 mm) significant. The proportion of dreissenid densities represented by quagga mussels increased from 3% to 67 % from 2007 to 2009 and then decreased to 32 - 40% in 2010 – 2013. The proportion of the total dreissenid biomass consisting of quagga mussels increased from 7% in 2007, to 44% in 2008 and to 76 to 84% in 2009 to 2012 and then decreased again to 50% in 2013 in water shallower than 4.5 m (Table 2, Figure 2).

The distribution of mussels was not homogeneous in the lake and transect location was a significant effect in our analysis of year effects. Although density varies among locations and years (Figure 5), most of those effects were due to low number of mussels at location G1. This site located close to the outlet of the Onondaga Creek has mostly muddy substrate and high sediment load that is less conducive to mussel colonization.

Length distributions for quagga mussels showed consistently larger individuals than for zebra mussels (Figure 3). Zebra mussels larger than 12 mm were rare in all years (3-19% of total numbers) whereas the quagga mussel population consisted of 18-75% mussels > 12mm. Mussels larger than 28 mm were very rarely observed (2 individuals out of 25491 individuals measured from 2005 to 2013). In most years, the lengths distributions were unimodal. Two length peaks were evident for quagga mussels in 2007 and to some degree in 2008 and 2009. As the larger peak in 2007 likely represents age-1 or older mussels given observed growth rates elsewhere of 6-8 mm per growing season (Karatayev et al. 2010), we conclude that quagga mussels were present in densities of at least around 200 m⁻² in the lake in 2006 as this is the density of age-1 or older quagga mussels in the lake in 2007. This represents about 10% of the mussels in the lake in 2006. Unfortunately, samples from 2005 and 2006 were not archived and could not be reanalyzed for this study. A few individual quagga mussels were noted in the lake in both 1992 (Mills et al. 1993) and 2002 (OCDEWP 2003).

Sampling depths were limited to bottom depths shallower than 4.5 m from 2005 to 2010. In 2005, dreissenid biomass peaked in 1.5-3 m of water and declined in 3-4.5 m of water (Figure 4) and an extensive survey in 2002 found few mussels below 3 m (OCDEWP 2003). However, from 2008 and onwards, biomass was highest in the 3-4.5 m depth layer (Figure 4, Table 3). In 2011, depths 4.5 - 6 m were added to the surveys and biomass was similar or higher in that depth region than at 3-4.5 m. When sampled, the 4.5 – 6 m layer contributed between 40 and 52% of the total dreissenid biomass (Figure 4). The proportion of quagga mussels in water depths below 3 m was over 90% in 2009 to 2013 with one exception, depth range 3-4.5 m in 2013 when the proportion by biomass was 77% (Figure 4). The 6 – 7.5 m depth region was added in 2013 and showed low density and biomass (3.7 g/m²) of primarily quagga mussels. Limited sampling below 7.5 m in 2012 and 2013 resulted in only a handful of mussels of both species.

We also tested for significant changes in density and biomass by depth regions in the lake for each species and each year (Table 3). Zebra mussels were more abundant and had higher biomass in the 1.5 – 3 m than in the 3-4.5 m depth region in most years. Quagga mussels were more abundant and had higher biomass in 3-4.5 m than in the other two depth regions. Both

mussel species were smaller in 1.5-3 m depths than in 0-1.5 m depths and for quagga also than in 3-4.5 m depth. However, only a limited number of these differences were significant when comparing within years (Tukey's HSD test, Table 3).

Part of the difficulty observing significant differences among depth regions is due to the high variability among transects (Figure 5). To decrease this effect, we averaged catches across all transects by depth region and used year as a sampling unit but limited the analysis of depth regions to years when both mussel species were abundant (2008-2013, Table 4). The main significant difference was that quagga mussel biomass was higher in 3-6 m than in 0-3 m and that the proportion of dreissenid biomass composed of quagga mussels was higher in 3-6 m than in 0-3 m (Table 4).

We tested for declines from 2011 to 2013 in the combined dreissenid biomass and for each species separately. These years all depth regions to 6 m depth were sampled. We averaged depth regions by transect and used transect as a sampling unit in a matched pair analysis among years (Wilcoxon signed rank test). Average biomass (0-6m) declined from 30.9 g afdw/m² in 2011 to 17.2 g/m² in 2012 and 6.9 g/m² in 2013. The difference between 2011 and 2013 was significant for combined dreissenid biomass ($P=0.034$), quagga mussel biomass ($P=0.032$) and zebra mussel biomass ($P=0.027$) as well as for zebra mussel from 2011 to 2012 ($P=0.009$), but not for other differences between 2011 and 2012 and not for any differences between 2012 and 2013. If areas dredged in 2013 were excluded (transects D2, E1, F1 and G1, Figure 1), the decline between 2011 and 2013 was still present but no longer statistically significant ($N=8$, $P=0.148$, 0.148 , 0.109 for combined mussel biomass, quagga mussel biomass and zebra mussel biomass, respectively).

Discussion

Dreissenid density and biomass increased in Onondaga Lake from 2005 to 2007 in depths 0-4.5 m and then remained above 5000 m⁻² (13 g/m²) through 2012. This increase was initially due to an increase in zebra mussels, but quagga mussels started to increase in 2007 and was the dominant species by biomass in the lake from 2009 through 2012, particularly in depths 3-4.5 m. When deeper depths were sampled from 2011 to 2013, quagga mussel dominated also in 4.5 – 7.5 m. Total dreissenid biomass was highest in depth deeper than 3 m after quagga mussels became dominant but higher in 1.5-3 m when zebra mussels dominated (2005, 2007 and 2008). Shallower depths show coexistence of the two species with the proportion of quagga mussels by biomass ranging between 20 and 80% without a time trend from 2008 through 2013. Quagga mussels were consistently larger than zebra mussels at all depths. Thus in Onondaga Lake, quagga mussels have a growth advantage over zebra mussels at all depth. Quagga mussels largely displaced zebra mussels in water deeper than 3 m but both species coexist in shallower water.

Densities and biomass of mussels in Onondaga Lake (0-6 m) are comparable to observations elsewhere in North America (1000 to 100,000 m⁻²) but higher than typically found in Europe (100 – 1,000 m⁻², Ramcharan et al. 1992, Naddafi et al. 2011). Mussel density was positively related to surface area and calcium content and negatively related to total phosphorus content in a comparative study of 55 European and 13 North American lakes (Naddafi et al. 2011). Given the size, calcium content, and phosphorus concentrations in Onondaga Lake, we expect densities of 1000 to 10,000 mussels m⁻², the range of densities observed from 2005 to 2013.

Lake-wide densities are lower because the 70% of the lake bottom below 6 m depth is anoxic during the summer. The decrease of mussel densities in water deeper than 6 m is likely due to anoxia. But even with anoxia sometimes reaching 6 m depth, total dreissenid biomass was higher in 4.5-6 m depth regions in 2011 to 2013 when that depth region was included in the survey in 2011 - 2013. It is likely that mussel densities increased in this depth layer after quagga mussels became abundant. Deep mussels were not present in 2002 and biomass declined between 1.5-3 m and 3-4.5 m in 2005, 2007 and 2008 when zebra mussels dominated. Anoxic conditions shallower than 6 m depth rarely occurred in the lake after 2005 although oxygen content declined to 2-3 ppm at 6 m depth for one - two weeks in most years. Assuming the biomass in 4.5-6 m was similar to biomass in 3-4.5 m for the years 2005-2010 and that there are no mussels in deeper water, we can estimate lake-wide biomass by extrapolating the average biomass in 0-6 m (30% of the lake bottom) to the total lake area. With these assumptions, the peak lake-wide dreissenid density (biomass afdw) was calculated to be 267 m⁻² (0.3 g/m²) in 2005 and increasing to 662 m⁻² (1.1 g/m²) in 2006 and 3562 m⁻² (8.8 g/m²) in 2007. Densities ranged from 1867 to 4160 m⁻² (5.1-9.3 g/m²) between 2009 and 2012 and decreased to 785 m⁻² (2.1 g/m²) in 2013. Using a filtering rate of 0.10 L/hr/g afdw (Diggins et al. 2001), the mussel population in Onondaga Lake would filter between 10 and 20% of the lake volume each day (2007 – 2012), a value that declined to 5% per day in 2013. This estimate will be compared with *Daphnia* filtering rates (Effler et al. submitted) in Onondaga Lake and other nearby lakes in future reports.

Peak density of zebra mussels typically occurs earlier after colonization (2.5 years on average) than peak density of quagga mussels (13 years, Karatayev et al. 2011). Both species were found in 1992 in Onondaga Lake (Mills et al. 1993). However, the abundance of dreissenids remained low in the lake (<1 m⁻²) until 1999, when veliger counts increased and large number of 4-6 mm mussels were found on trap nets (Spada et al. 2002). A nearshore survey in 2000 found average densities between 2000 and 22,000 m⁻² and a size distribution peaking at 5-15 mm. Spada et al. (2002) concluded that improvement to the Metro sewage treatment plant, in particular the reduction of T-NH₃ and free un-ionized NH₃ allowed for survival of early life stages of dreissenids in the lake after 1999. Zebra mussels would then have reached high densities 1 - 2 years after the lake became conducive to dreissenid reproduction, similar to observations elsewhere (Karatayev et al. 2011). Quagga mussels were not reported from the

2000 survey (Spada et al. 2002) or from 2005 and 2006 (this study), but were present in low numbers in a 2002 survey (OCEWDP 2003). It is likely that quagga mussels were overlooked in 2005 and 2006. The size structure of quagga mussels in 2007 suggests that some of those mussels were at least age-1, and would therefore have been present at densities representing about 10% of the mussel population in 2006. In any case, peak quagga mussel abundance occurred in 2009, which would be 11-12 years since 1998 when presumably also quagga mussels could have increased in the lake. This is again similar to observations elsewhere for the time to peak abundance of quagga mussels in lakes initially dominated by zebra mussels. Note that quagga mussels increased from a minor component of the dreissenid population in 2006 to having a higher biomass than zebra mussels in 3 years.

Quagga mussels are displacing zebra mussels in many lakes and several hypotheses have been proposed for the mechanisms behind this process (Karatayev et al. 2011, 2014a, Garton et al. 2014). Because quagga mussels did become dominant in eutrophic Onondaga Lake which lacks colonizable deep bottoms due to oxygen depletion, the better performance of quagga mussels in cold water and at low food concentrations are not necessary for this displacement to occur. Quagga mussels did have a growth advantage in Onondaga Lake indicating that higher growth is not limited to low productivity systems (see also Karatayev et al. 2010). Although growth estimates for zebra mussels are relatively common, comparisons of growth rates of the two species under similar conditions are rare and not consistent; higher growth of quagga mussels was also observed by Baldwin et al. (2002) and Karatayev et al. (2010), but not by MacIsaac (1994). Naddafi and Rudstam (2014c) found lower growth rates of zebra mussels only when the animals were reared with predator cues and not when reared without predators suggesting that some of the differences in the literature could be due to the amount of predator cues present during the experiment. With predator cues present, zebra mussels invest more energy in shell growth and byssal thread production as well as lower their filtering rates resulting in lower overall growth rates (Naddafi and Rudstam 2013, 2014c). These morphological and behavioral responses to predators also resulted in lower vulnerability to predation and higher attachment strength of zebra mussels compared to quagga mussels. Higher attachment strength should allow zebra mussels to be better adapted to persist in high energy environments such as the nearshore shallow water (V. Karatayev et al. 2013). This may be the reason for continued coexistence of both species in the 0-3 m depth range in Onondaga Lake. Elsewhere, the two species coexist in shallow lakes and rivers (Dnieper River -Zhulidov et al. (2010), Mississippi River - Grigorovich et al. (2008), the western basin of Lake Erie - Karatayev et al. (2014b) and Oneida Lake -V. Karatayev et al. (2014)).

Currently, predation on mussels in North America may be too low to give zebra mussels a competitive advantage from their higher anti-predation investments given the cost in reduced growth rates (Naddafi and Rudstam 2014c). This could change with the invasion of a dreissenid specialist, the round goby (Houghton and Janssen 2014, Naddafi and Rudstam 2014a). Round goby arrived to Onondaga Lake in 2010 and has increased in abundance each year (UFI et al.

2014). We do note that mussel densities did decline from 2011 to 2012 and again to 2013, although this is partly due to dredging at several of the stations in 2013 (D2 and E1, Figure 1) in the southern part of the lake. If we limit our analysis to stations north of the dredged area, quagga mussel biomass declined from an average of 21.5 g/m² in 2011 to 12.4 g/m² in 2012 and 3.2 g/m² in 2013 whereas zebra mussel biomass decreased from 6.4 to 3.0 g/m² during the same time period. However, variation among transects is large and the decline was not significant at the 0.05 level when the dredged sites were removed. Even so, the timing of the decline is consistent with the increase in round goby and the decline is larger for quagga mussels than for zebra mussels, both observations that are consistent with a predation effect from round goby. Declines in dreissenids have been observed after round goby invasions elsewhere (Lederer et al. 2008, Barton et al. 2005, Wilson et al. 2006) and fish predation is considered important for dreissenid abundance in both Europe (Stanczykowska 1977, Naddafi et al. 2010) and North America (Thorp et al. 1998, Magoulick and Lewis 2002, Watzin et al. 2008). Additional years of mussel surveys are necessary for evaluating this hypothesis.

Acknowledgement

Support for this study was obtained from Onondaga County Department of Water Environment Protection. This research was supported in part by the Cornell University Agricultural Experiment Station federal formula funds, Project No. NYC 147453 received from the National Institute of Food and Agriculture (NIFA), United States Department of Agriculture (USDA). Any opinions, findings, conclusions, or recommendations expressed in the publication are those of the author(s) and do not necessarily reflect the view of NIFA or USDA. We thank Kristen Holeck for comments on the manuscript.

References

- Ackerman, J. D. 1999. Effect of velocity on the filter feeding of dreissenid mussels (*Dreissena polymorpha* and *Dreissena bugensis*): implications for trophic dynamics. *Canadian Journal of Fisheries and Aquatic Sciences* **56**:1551-1561.
- Baldwin, B. S., M. S. Mayer, J. Dayton, N. Pau, J. Mendilla, M. Sullivan, A. Moore, A. Ma, and E. L. Mills. 2002. Comparative growth and feeding in zebra and quagga mussels (*Dreissena polymorpha* and *Dreissena bugensis*): implications for North American lakes. *Canadian Journal of Fisheries and Aquatic Sciences* **59**:680-694.
- Barton, D. R., R. A. Johnson, L. Campbell, J. Petruniak, and M. Patterson. 2005. Effects of round gobies (*Neogobius melanostomus*) on dreissenid mussels and other invertebrates in eastern Lake Erie, 2002-2004. *Journal of Great Lakes Research* **31**:252-261.
- Benson, A. J. 2014. Chronological history of zebra and quagga mussels (Dreissenidae) in North America, 1988-2010. Pages 9-31 in T. F. Nalepa and D. W. Schloesser, editors. *Quagga and zebra mussels: biology, impacts, and control*, second edition. CRC Press, Boca Raton, FL.
- Birkett, K., S. Lozano, and L. G. Rudstam. in press 2014. Long-term trends in Lake Ontario's benthic macroinvertebrate community from 1994-2008. *Aquatic Ecosystem Health & Management*.

- Burlakova, L. E., A. Y. Karatayev, and D. K. Padilla. 2006. Changes in the distribution and abundance of *Dreissena polymorpha* within lakes through time. *Hydrobiologia* **571**:133-146.
- Carlton, J. T. 2008. The zebra mussel *Dreissena polymorpha* found in North America in 1986 and 1987. *Journal of Great Lakes Research* **34**:770-773.
- Claxton, W. T. and G. L. Mackie. 1998. Seasonal and depth variations in gametogenesis and spawning of *Dreissena polymorpha* and *Dreissena bugensis* in eastern Lake Erie. *Canadian Journal of Zoology* **76**:2010-2019.
- Czarnoleski, M. and T. Müller. 2014. Antipredator strategy of zebra mussels (*Dreissena polymorpha*). From behavior to life history. Pages 345-357 in T. F. Nalepa and D. W. Schloesser, editors. *Quagga and zebra mussels. Biology, impacts and control*. CRC Press, Boca Raton, FL.
- Diggins, T. P. 2001. A seasonal comparison of suspended sediment filtration by quagga (*Dreissena bugensis*) and zebra (*D. polymorpha*) mussels. *Journal of Great Lakes Research* **27**:457-466.
- Effler, A. J. P., R. K. Gelda, S. W. Effler, D. A. Matthews, S. D. Field, and J. M. Hassett. 2008. Decreases in primary production in Onondaga Lake from reductions in point source inputs of phosphorus. *Fundamental and Applied Limnology* **172**:239-253.
- Effler, S. W. 1996. *Limnological and engineering analysis of a polluted urban lake*. Springer Verlag, New York, New York.
- Effler, S. W., M. E. Spada, R. K. Gelda, F. Peng, and D. A. Matthews. 2014 MS. *Daphnia* grazing, the clear water phase, and implications of minerogenic particles, in Onondaga Lake. Manuscript.
- Fahnenstiel, G., S. Pothoven, H. Vanderploeg, D. Klarer, T. Nalepa, and D. Scavia. 2010. Recent changes in primary production and phytoplankton in the offshore region of southeastern Lake Michigan. *Journal of Great Lakes Research* **36**:20-29.
- Garton, D. W., R. McMahon, and A. M. Stoeckmann. 2014. Limiting environmental factors and competitive interactions between zebra and quagga mussels in North America. Pages 383-402 in T. F. Nalepa and D. W. Schloesser, editors. *Quagga and zebra mussels. Biology, impacts and control*. CRC Press, Boca Raton, FL.
- Grigorovich, I. A., T. R. Angradi, and C. A. Stepien. 2008. Occurrence of the quagga mussel (*Dreissena bugensis*) and the zebra mussel (*Dreissena polymorpha*) in the upper Mississippi River system. *Journal of Freshwater Ecology* **23**:429-435.
- Higgins, S. N. and M. J. Vander Zanden. 2010. What a difference a species makes: a meta-analysis of dreissenid mussel impacts on freshwater ecosystems. *Ecological Monographs* **80**:179-196.
- Houghton, C. J. and J. Janssen. 2014. Variation in predator-prey interactions between round gobies and dreissenid mussels. Pages 359-367 in T. F. Nalepa and D. W. Schloesser, editors. *Quagga and zebra mussels. Biology, impacts and control*. CRC Press, Boca Raton, FL.
- Karatayev, A., L. E. Burlakova, and D. K. Padilla. 1997. The effects of *Dreissena polymorpha* (Pallas) invasion on aquatic communities in Eastern Europe. *J. Shellfish Res.* **16**:187-203.
- Karatayev, A. Y., L. E. Burlakova, S. E. Mastitsky, D. K. Padilla, and E. L. Mills. 2011. Contrasting rates of spread of two congeners, *Dreissena polymorpha* and *Dreissena rostriformis bugensis* at different spatial scales. *Journal of Shellfish Research* **30**:923-931.

- Karatayev, A. Y., L. E. Burlakova, and D. K. Padilla. 2002. Impacts of zebra mussels on aquatic communities and their role as ecosystem engineers. Pages 433-447 in E. Leppäkoski, S. Olenin, and S. Gollasch, editors. Invasive aquatic species of Europe. Kluwer Academic Publishers, Netherlands.
- Karatayev, A. Y., L. E. Burlakova, and D. K. Padilla. 2014a. General overview of zebra and quagga mussels: what we do and do not know. Pages 695-704 in T. F. Nalepa and D. W. Schloesser, editors. Quagga and zebra mussels: biology, impacts, and control, second edition. CRC Press, Boca Raton, FL.
- Karatayev, A. Y., L. E. Burlakova, and D. K. Padilla. 2014b. Zebra versus quagga mussels: a review of their spread, population dynamics, and ecosystem impacts. *Hydrobiologia* **on line DOI 10.1007/s10750-014-1901-x**.
- Karatayev, A. Y., S. E. Mastitsky, D. K. Padilla, L. E. Burlakova, and M. M. Hajduk. 2010. Differences in growth and survivorship of zebra and quagga mussels: size matters. *Hydrobiologia* **668**:183-194.
- Karatayev, V. A., A. Y. Karatayev, L. E. Burlakova, and D. K. Padilla. 2013. Lakewide dominance does not predict the potential for spread of dreissenids. *Journal of Great Lakes Research* **39**:622-629.
- Karatayev, V. A., A. Y. Karatayev, L. G. Rudstam, and L. E. Burlakova. 2014c. Eutrophication and *Dreissena* invasion as drivers of biodiversity: a century of change in the mollusc community of Oneida Lake. *PLoS-ONE* **9**:e101388.
- Kerfoot, W. C., F. Yousef, S. A. Green, J. W. Budd, D. J. Schwab, and H. A. Vanderploeg. 2010. Approaching storm: Disappearing winter bloom in Lake Michigan. *Journal of Great Lakes Research* **36**:30-41.
- Kobak, J. and T. Kakareko. 2009. Attachment strength, aggregation and movement of the zebra mussel (*Dreissena polymorpha*, Bivalvia) in the presence of potential predators. *Fundamental and Applied Limnology* **174**:193-204.
- Kornis, M. S., N. Mercado-Silva, and M. J. VanderZanden. 2012. Twenty years of invasion: a review of round goby *Neogobius melanostomus* biology, spread and ecological implications. *Journal of Fish Biology* **80**:235-285.
- Lederer, A. M., J. Janssen, T. Reed, and A. Wolf. 2008. Impacts of the introduced round goby (*Apollonia melanostoma*) on dreissenids (*Dreissena polymorpha* and *Dreissena bugensis*) and on macroinvertebrate community between 2003 and 2006 in the littoral zone of Green Bay, Lake Michigan. *Journal of Great Lakes Research* **34**:690-697.
- MacIsaac, H. J. 1994. Comparative growth and survival of *Dreissena polymorpha* and *Dreissena bugensis*, exotic molluscs introduced to the Great Lakes. *Journal of Great Lakes Research* **20**:783-790.
- Magoulick, D. D. and L. C. Lewis. 2002. Predation on exotic zebra mussels by native fishes: effects on predator and prey. *Freshwater Biology* **47**:1908-1918.

- Matthews, D. A., S. W. Effler, C. M. Brooks Matthews, C. A. Siegfried, and M. E. Spada. 2001. Responses of Onondaga Lake, New York, to early stages of rehabilitation: unanticipated ecosystem feedbacks. *Water Environment Research* **73**:691-703.
- Matthews, J., G. V. d. Velde, A. B. d. Vaate, F. P. L. Collas, K. R. Koopman, and R. S. E. W. Leuven. 2014. Rapid range expansion of the invasive quagga mussel in relation to zebra mussel presence in The Netherlands and Western Europe. *Biological Invasions* **16**:23-42.
- Mayer, C. M., L. E. Burlakova, P. Eklöv, D. Fitzgerald, A. Y. Karatayev, S. A. Ludsins, S. Millard, E. L. Mills, A. P. Ostapenya, L. G. Rudstam, B. Zhu, and T. V. Zhukova. 2014. The benthification of freshwater lakes: exotic mussels turning ecosystems upside down Pages 575-585 in T. F. Nalepa and D. W. Schloesser, editors. *Quagga and zebra mussels: biology, impacts, and control*, second edition. CRC Press, Boca Raton, FL.
- Mills, E. L., J. R. Chrisman, B. Baldwin, R. W. Owens, R. O'Gorman, T. Howell, E. F. Roseman, and M. K. Raths. 1999. Changes in the dreissenid community in the lower Great Lakes with emphasis on southern Lake Ontario. *Journal of Great Lakes Research* **25**:187-197.
- Mills, E. L., R. M. Dermott, E. F. Roseman, D. Dustin, E. Mellina, D. B. Conn, and A. P. Spidle. 1993. Colonization, ecology, and population structure of the quagga mussel (*Bivalvia*, *Dreissenidae*) in the lower Great Lakes. *Canadian Journal of Fisheries and Aquatic Sciences* **50**:2305-2314.
- Mills, E. L., G. Rosenberg, A. P. Spidle, M. Ludyanskiy, Y. Pligin, and B. May. 1996. A review of the biology and ecology of the quagga mussel (*Dreissena bugensis*), a second species of freshwater dreissenid introduced to North America. *American Zoologist* **36**:271-286.
- Naddafi, R., T. Blenckner, P. Eklov, and K. Pettersson. 2011. Physical and chemical properties determine zebra mussel invasion success in lakes. *Hydrobiologia* **669**:227-236.
- Naddafi, R., K. Pettersson, and P. Eklov. 2010. Predation and physical environment structure the density and population size structure of zebra mussels. *Journal of the North American Benthological Society* **29**:444-453.
- Naddafi, R. and L. G. Rudstam. 2013. Predator induced behavioural defence in two competitive invasive species. *Animal Behaviour* **86**:1275-1284.
- Naddafi, R. and L. G. Rudstam. 2014a. Does differential predation explain the replacement of zebra by quagga mussels? *Freshwater Science* **in press**.
- Naddafi, R. and L. G. Rudstam. 2014b. Predation on invasive zebra mussel, *Dreissena polymorpha*, by pumpkinseed sunfish, rusty crayfish, and round goby. *Hydrobiologia* **721**:107-115.
- Naddafi, R. and L. G. Rudstam. 2014c. Predator-induced morphological defences in two invasive dreissenid mussels: implications for species replacement. *Freshwater Biology* **59**:703-713.
- Nalepa, T. F., D. L. Fanslow, and S. A. Pothoven. 2010. Recent changes in density, biomass, recruitment, size structure, and nutritional state of *Dreissena* populations in southern Lake Michigan. *Journal of Great Lakes Research* **36**:5-19.
- Negley, T. L., E. L. Mills, B. Baldwin, R. O. Forman, and R. W. Owens. 2003. The ecology and impact of the invasion of Lake Ontario by the zebra mussel (*Dreissena polymorpha*) and quagga mussel (*D. bugensis*). Pages 559-577 *State of Lake Ontario (SOLO) - Past, Present and Future*.

- Onondaga County Department Water Environment Protection. 2003. 2002 Onondaga Lake and Seneca River zebra mussel (*Dreissena polymorpha*) assessment program. Report.
- Orlova, M. I. 2014. Origina and spread of quagga mussels (*Dreissena rostriformis bugensis*) in Eastern Europe with noters on size structure of populations. Pages 93-102 in T. F. Nalepa and D. W. Schloesser, editors. Quagga and zebra mussels: biology, impacts, and control, second edition. Taylor and Francis, Boca Raton, FL.
- Peyer, S. M., A. J. McCarthy, and C. E. Lee. 2009. Zebra mussels anchor byssal threads faster and tighter than quagga mussels in flow. *Journal of Experimental Biology* **212**:2027-2036.
- Ramcharan, C. W., D. K. Padilla, and S. I. Dodson. 1992. Models to Predict Potential Occurrence and Density of the Zebra Mussel, *Dreissena polymorpha*. *Can J Fisheries Aquat Sci* **49**:2611-2620.
- Roe, S. L. and H. J. Macisaac. 1997. Deepwater population structure and reproductive state of quagga mussels (*dreissena bugensis*) in lake erie. *Canadian Journal of Fisheries and Aquatic Sciences* **54**:2428-2433.
- SAS Institute Inc. 2012. JMP Statistics and Graphics Guide, Version 10. SAS Institute Inc., Cary, NC.
- Spada, M. E. and N. H. Ringler. 2002. Invasion of Onondaga Lake, New York, by the zebra mussel (*Dreissena polymorpha*) following reductions in pollution. *Journal of the North American Benthological Society* **21**:634-650.
- Stanczykowska, A. 1977. Ecology of *Dreissena polymorpha* (Pall.) (Bivalvia) in lakes. *Polskie Archiwum Hydrobiologii* **24**:461-530.
- Stoeckmann, A. 2003. Physiological energetics of Lake Erie dreissenid mussels: a basis for the displacement of *Dreissena polymorpha* by *Dreissena bugensis*. *Canadian Journal of Fisheries and Aquatic Sciences* **60**:126-134.
- Thorp, J. H., J. E. Alexander, B. L. Bukaveckas, G. A. Cobbs, and K. L. Bresko. 1998. Responses of Ohio River and Lake Eie dreissenid molluscs to changes in temperature and turbidity. *Canadian Journal of Fisheries and Aquatic Sciences* **55**:220-229.
- Upstate Freshwater Institute, Anchor QEA LLC, Onondaga County Department of Water Environment Protection, L. Rudstam, and W. W. Walker. 2014. Onondaga 2012 Lake ambient monitoring program. 2012 Annual Report. Onondaga County, NY.
- Vanderploeg, H. A., J. R. Liebig, T. F. Nalepa, G. L. Fahnenstiel, and S. A. Pothoven. 2010. *Dreissena* and the disappearance of the spring phytoplankton bloom in Lake Michigan. *Journal of Great Lakes Research* **36**:50-59.
- Watkins, J. M., R. Dermott, S. J. Lozano, E. L. Mills, L. G. Rudstam, and J. V. Scharold. 2007. Evidence for remote effects of dreissenid mussels on the amphipod *Diporeia*: analysis of Lake Ontario benthic surveys, 1972–2003. *Journal of Great Lakes Research* **33**:642–657.
- Watkins, J. M., L. G. Rudstam, E. L. Mills, and M. A. Teece. 2012. Coexistence of the native benthic amphipod *Diporeia* spp. and exotic dreissenid mussels in the New York Finger Lakes. *Journal of Great Lakes Research* **38**:226-235.

- Watzin, M. C., K. Joppe-Mercure, J. Rowder, B. Lancaster, and L. Bronson. 2008. Significant fish predation on zebra mussels *Dreissena polymorpha* in Lake Champlain, U.S.A. *Journal of Fish Biology* **73**:1585–1599.
- Wilson, K. A., E. T. Howell, and D. A. Jackson. 2006. Replacement of zebra mussels by quagga mussels in the Canadian nearshore of Lake Ontario: The importance of substrate, round goby abundance, and upwelling frequency. *Journal of Great Lakes Research* **32**:11-28.
- Zhao, A. 2014. Investigation of differences in filtration rates between zebra and quagga mussels along an experimental temperature gradient. B.Sc. Honors Thesis. Cornell University, Ithaca NY.
- Zhulidov, A. V., A. V. Kozhara, G. H. Scherbina, T. F. Nalepa, A. Protasov, S. A. Afanasiev, E. G. Pryanichnikova, D. A. Zhulidov, T. Y. Gurtovaya, and D. F. Pavlov. 2010. Invasion history, distribution, and relative abundances of *Dreissena bugensis* in the old world: a synthesis of data. *Biological Invasions* **12**:1923-1940.

Figure 1. Onondaga Lake mussel transects. Three (2005-2010), four (2011-2012) or five (2013) depth regions were sampled at each location each year.

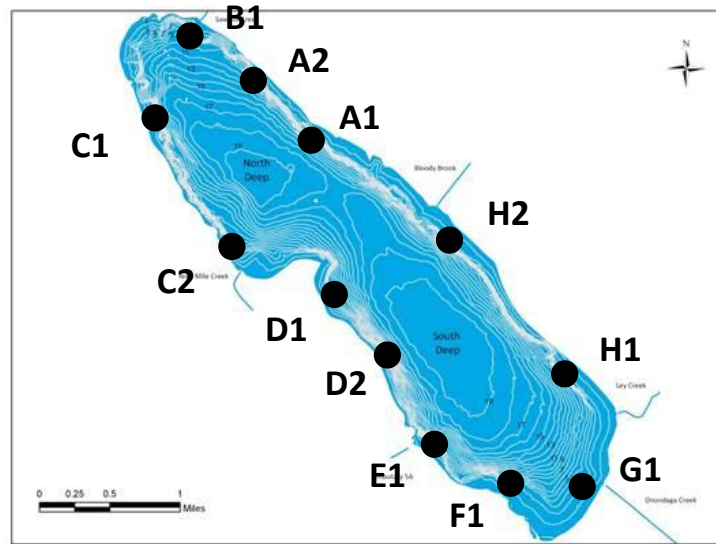


Figure 2. Development of the zebra and quagga mussel population (density and biomass) in Onondaga Lake from 2005 to 2013 in water 0-4.5 m depth. The line represent the proportion of quagga mussel.

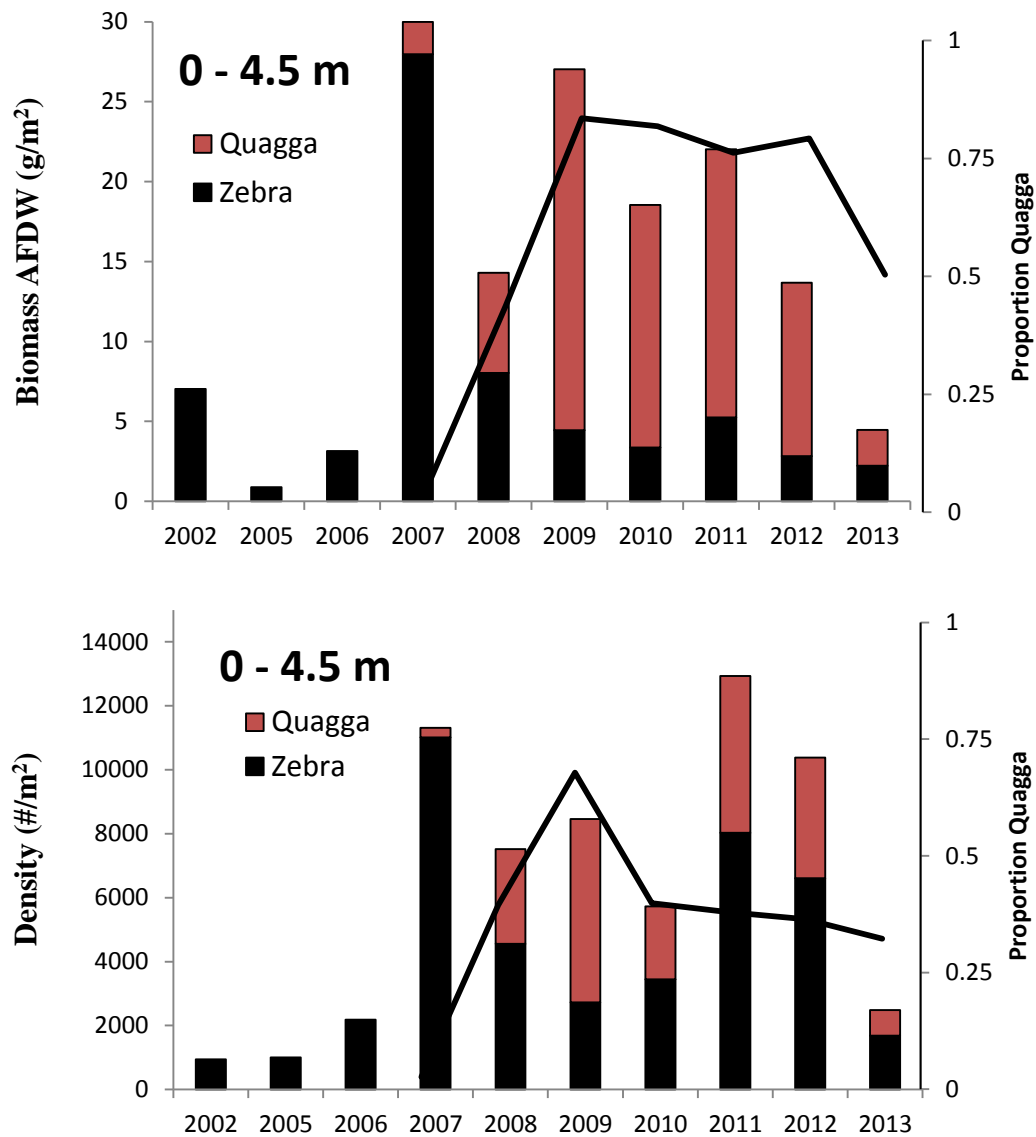


Figure 3. Length distribution of quagga and zebra mussels in Onondaga Lake from 2005 through 2013.

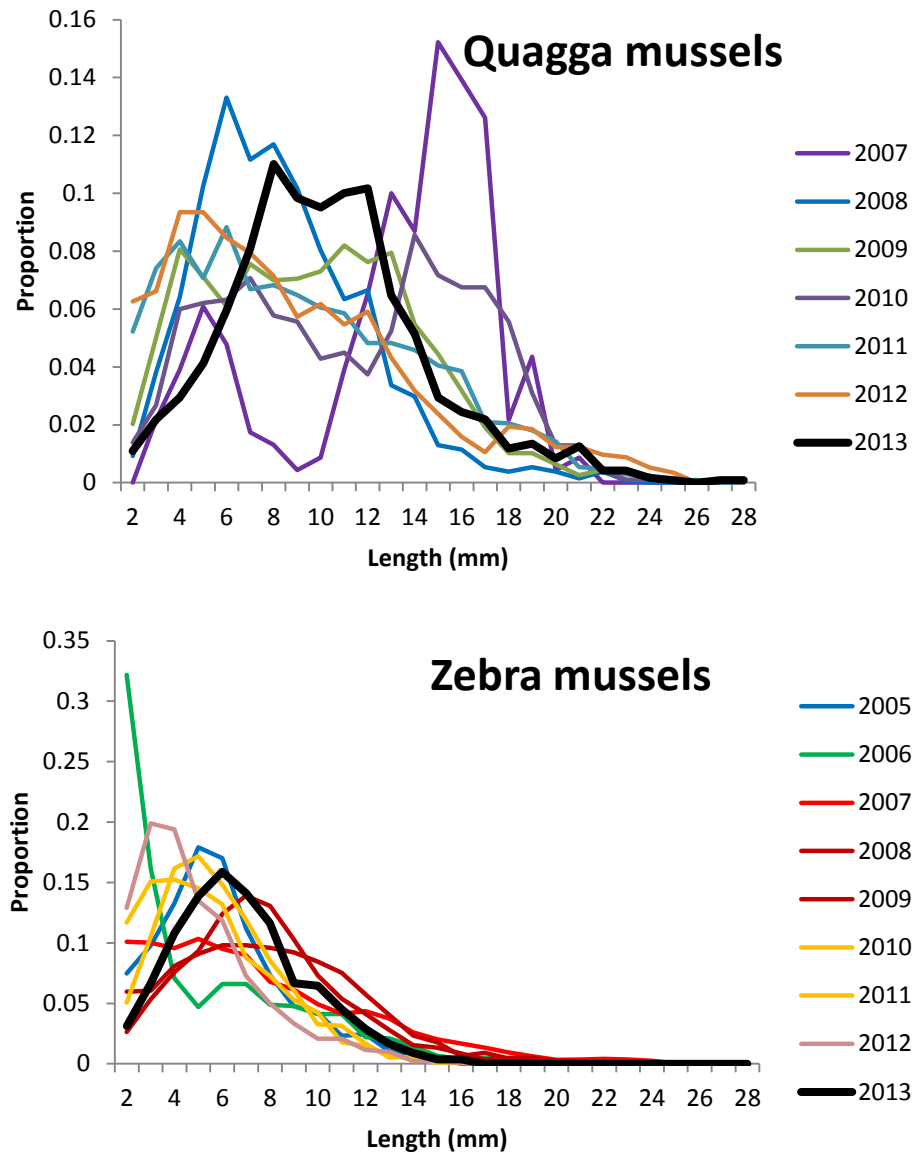
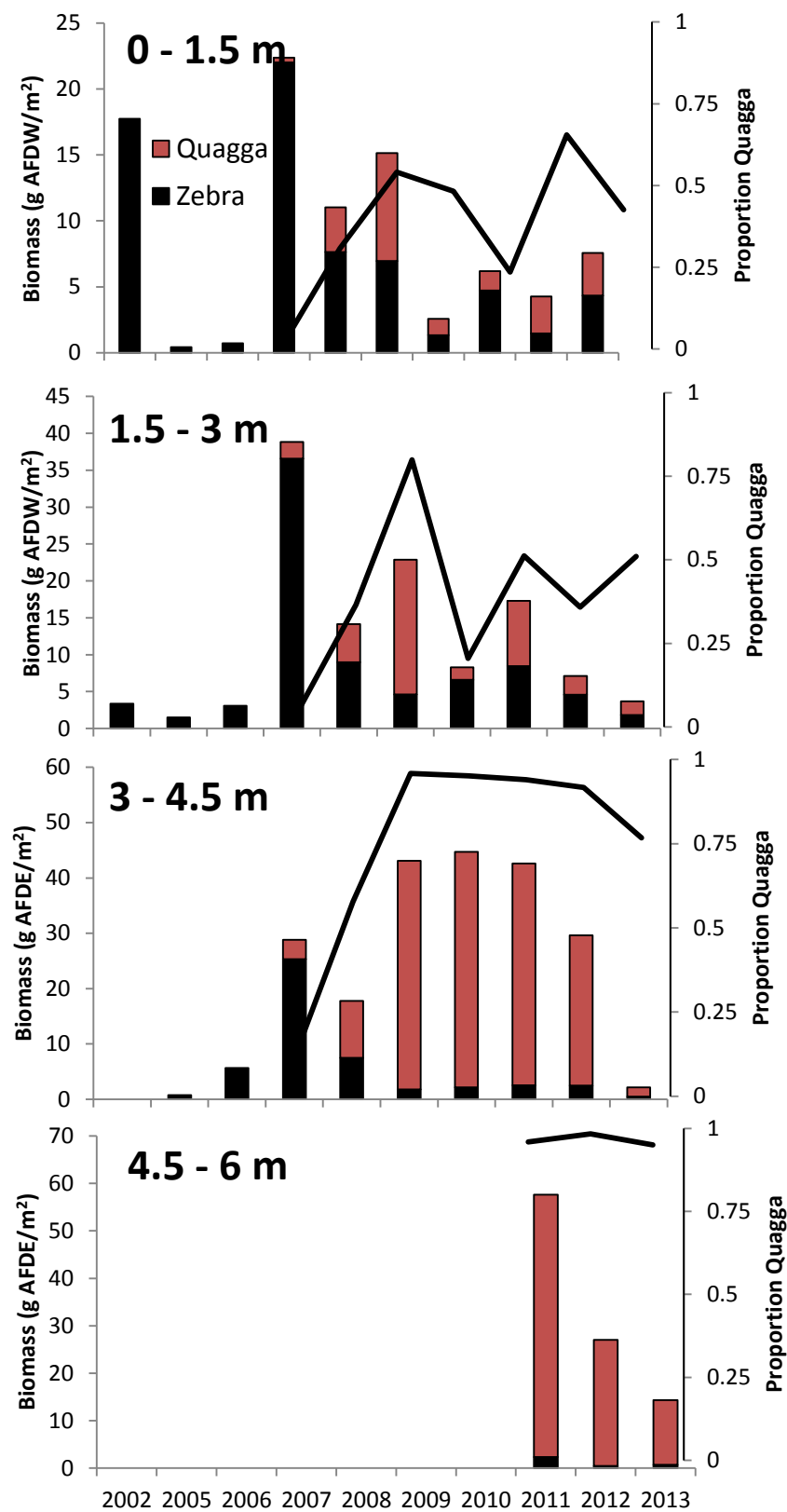


Figure 4. Density and biomass of zebra and quagga mussels in four depth regions: 0-1.5m, 1.5-3 m, 3-4.5 m and 4.5-6 m depths.



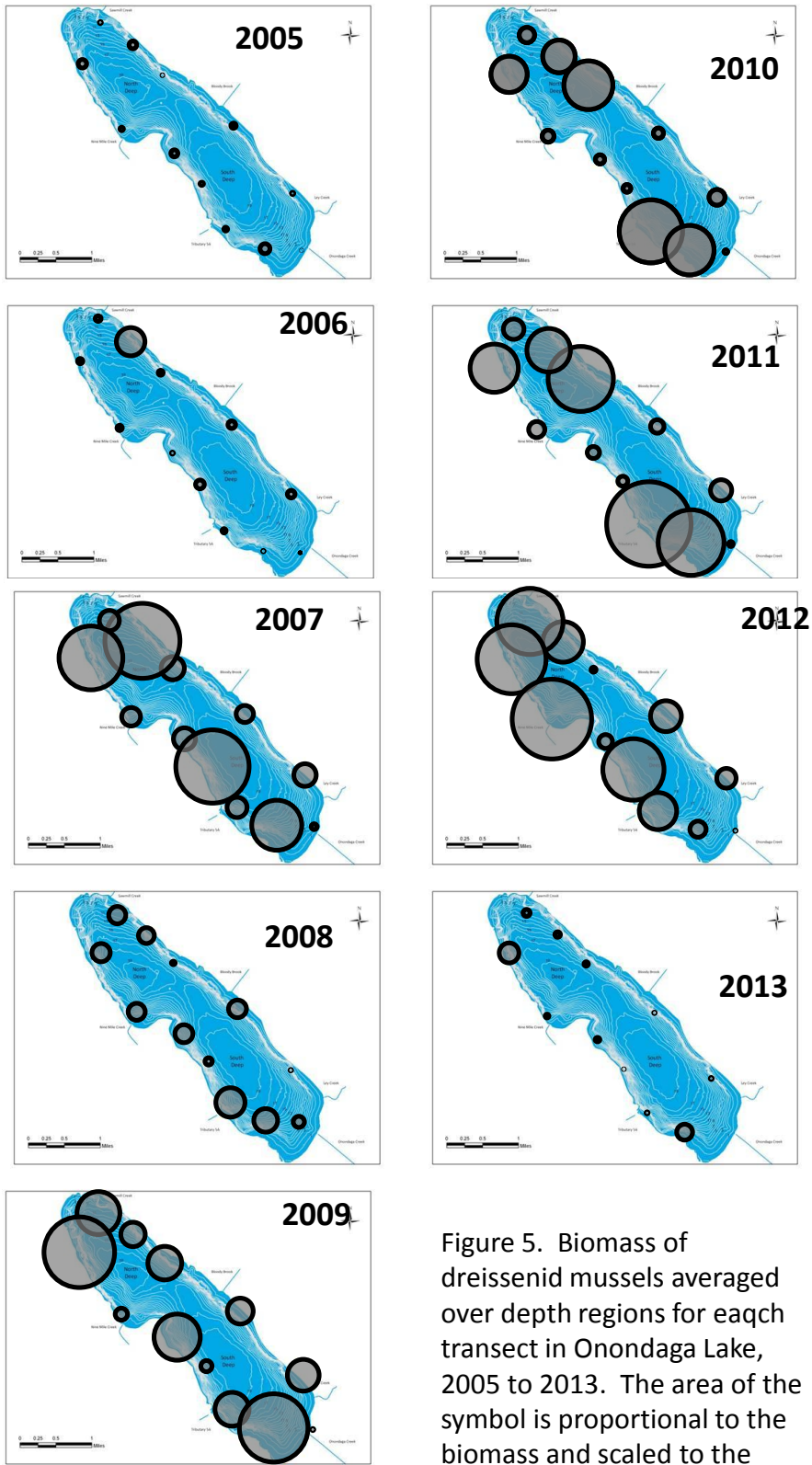


Figure 5. Biomass of dreissenid mussels averaged over depth regions for each transect in Onondaga Lake, 2005 to 2013. The area of the symbol is proportional to the biomass and scaled to the maximum ashfree dry weight in the data set (Station C1 in 2012, 96.8 g afdw/m²).

Table 1. Number of samples taken at difference depth regions and the date of sample collection for the surveys from 2005 to 2013.

Year	Number of samples					Date
Depth	0-1.5m	1.5-3.0m	3.0-4.5m	4.5 – 6.0m	6.0-7.5m	
2002	23	23	0	0	0	Oct 1
2005	12	12	12	0	0	Oct 24
2006	12	12	12	0	0	Oct 16
2007	12	12	12	0	0	Oct 25
2008	12	12	12	0	0	Oct 10
2009	12	12	12	0	0	Oct 12
2010	12	12	12	0	0	Oct 8
2011	12	12	12	12	0	Oct 18
2012	12	12	12	12	0	Oct 12
2013	12	12	12	12	12	Oct 14

Table 2. Average (SE) density, average (SE) ashfree dry biomass and average length (SE, N) of zebra and quagga mussels in Onondaga Lake, New York from 2005 through 2013. Sample size is 12 for all density and biomass. Averages are arithmetic and based on averages of the 0 – 1.5 m, 1.5 – 3 m and 3 – 4.5 m depth regions at each sample location. Groups of years with no significant differences (ANOVA using ln-transformed density and biomass Tukey's HSD test) are connected with the same letter.

Year	Density (m ⁻²)		AFDW (g/m ²)				Average Length (mm)			
	Zebra mussel	Quagga mussel	Zebra mussel	Quagga mussel	Zebra mussel	Quagga mussel	Zebra mussel	Quagga mussel	Zebra mussel	Quagga mussel
2005	1005 (300)	c			0.89 (0.28)	d			6.00 (0.41)	7 bc
2006	2184 (838)	c			3.00 (2.05)	cd			5.75 (0.79)	7 bc
2007	11013 (2391)	a	295 (191)	b	27.60 (9.93)	a	2,02 (1.70)	b	7.55 (0.67)	11 ab
2008	4554 (1250)	abc	2965 (1056)	a	8.03 (1.83)	ab	6.27 (2.65)	a	8.40 (0.28)	9 a
2009	2722 (899)	bc	5737 (1599)	a	4.42 (1.19)	abc	22.56 (8.26)	a	8.96 (0.50)	7 a
2010	3449 (826)	abc	2283 (911)	ab	3.32 (0.82)	abc	15.16 (6.73)	a	6.41 (0.30)	8 bc
2011	8030 (1637)	ab	4905 (1993)	a	5.07 (1.11)	abc	16.66 (7.05)	a	6.46 (0.33)	10 bc
2012	6605 (2466)	abc	3781 (1705)	a	2.77 (0.89)	bcd	10.62 (5.74)	a	5.61 (0.37)	8 c
2013	1683 (435)	c	800 (208)	ab	2.20 (0.61)	cd	2.24 (0.68)	ab	6.45 (0.69)	8 bc

Table 3: Density (m^{-2} , average, SE), biomass (ash-free dry weight in g/m^2 , average, SE), individual length (average, SE, N) and individual ash free dry weight (average, SE, N) of zebra and quagga mussels in Onondaga Lake from 2002 to 2013. Values from each sample taken at a specific depth region is considered one sample for the calculations of averages and SE. Number of samples were 12 in each depth region (2005 -2013), but not all samples contained mussels and therefore the sample size for individual lengths and weights are smaller. Quagga mussels were not identified in the lake prior to 2007. The 2002 individual lengths, weights and biomass are approximated from coarser length distributions. Significant difference between depth regions within a year are noted with letters. When no letters are present, the differences were not significant among depth regions.

Year and Depth Region	Zebra mussel				Quagga mussel			
	Density #/m ²	Biomass g afdw/m ²	Ind length mm	Ind weight mg	Density #/m ²	Biomass g afdw/m ²	Ind length mm	Ind weight mg
2005								
0-1.5m	336 (128)	0.44 (0.23)	6.0 (0.6) 9	0.8 (0.2) 9				
1.5-3m	2154 (832)	1.48 (0.59)	5.9 (0.5) 11	0.8 (0.2) 11				
3-4.5m	527 (195)	0.75 (0.35)	6.2 (0.7) 9	1.1 (0.3) 9				
2006								
0-1.5m	2510 (1139)	0.73 (0.25)	5.5 (1.0) 11	1.2 (0.5) 11				
1.5-3m	1825 (1024)	3.07 (2.18)	5.7 (0.7) 10	1.1 (0.3) 10				
3-4.5m	2216 (1407)	5.66 (4.19)	7.5 (0.9) 8	1.7 (0.4) 8				
2007								
0-1.5m	8554 (2265)	22.00 (7.78)	8.4 (0.9) 12	2.8 (0.9) 12	55 (38)	0.36 (0.24)	14.2 (0.9) 2	6.8 (1.5) 2
1.5-3m	11729 (3923)	36.57 (20.72)	6.9 (0.8) 12	1.7 (0.5) 12	306 (181)	2.24 (1.74)	11.1 (2.5) 4	5.0 (2.0) 4
3-4.5m	12757 (5952)	25.33 (15.21)	7.2 (1.0) 11	1.8 (0.6) 11	524 (402)	3.47 (3.41)	8.3 (2.4) 4	2.5 (2.0) 4
2008								
0-1.5m	3355 (995)	7.63 (2.44)	8.5 (0.4) 11	2.1 (0.3) 11	1184 (689)	3.39 (1.85)	10.3 (1.0) 7	4.0 (1.2) 7
1.5-3m	5844 (2693)	8.97 (2.24)	8.7 (0.7) 10	2.7 (0.9) 10	2544 (851)	5.17 (2.05)	7.8 (0.7) 8	1.6 (0.3) 8
3-4.5m	4462 (1414)	7.50 (3.03)	7.1 (0.7) 12	1.5 (0.3) 12	5166 (2139)	10.26 (5.16)	8.9 (0.5) 10	2.0 (0.3) 10
2009								
0-1.5m	2301 (745)	6.96 (2.26)	10.2 (0.9) 10a	3.3 (0.6) 10 a	2203 (1156))	8.2 (4.6)	10.5 (0.6) 9	3.7 (0.6) 9
1.5-3m	4571 (2613)	4.60 (1.73)	7.7 (0.7) 11ab	2.0 (0.5) 11 ab	5199 (2012)	18.28 (9.5)	9.1 (1.1) 9	2.6 (0.7) 9
3-4.5m	1292 (448)	1.78 (0.68)	7.0 (0.7) 9 b	1.3 (0.4) 9 b	9809 (3734)	41.30 (17.62)	10.2 (0.8) 11	3.4 (0.6) 11
2010								
0-1.5m	1280 (697) b	1.33 (0.60) b	7.0 (0.5) 9	1.2 (0.2) 9	280 (144)	1.25 (0.87)	10.3 (0.9) 7 ab	3.2 (0.8) 7 ab
1.5-3m	7065 (2113) a	6.59 (2.03) a	6.6 (0.3) 12	1.1 (0.1) 12	1025 (421)	1.70 (0.56)	8.6 (0.6) 11 b	1.9 (0.5) 11 b
3-4.5m	2002 (708) ab	2.16 (0.76) ab	6.2 (0.5) 11	1.0 (0.2) 11	5543 (2549)	42.56 (19.69)	12.6 (1.2) 7 a	6.2 (1.3) 7 a
2011								
0-1.5m	7194 (3983) ab	4.73 (2.24)	6.5 (0.6) 10 ab	1.2 (0.3) 10 ab	745 (411)	1.46 (0.71)	7.8 (1.2) 8	1.9 (0.8) 8

1.5-3m	14926 (3553) a	8.45 (2.06)	5.3 (0.3) 12 b	0.6 (0.1) 12 b	4010 (1630)	8.86 (3.53)	7.2 (0.8) 10	1.8 (0.4) 10
3-4.5m	1969 (834) b	2.56 (1.08)	7.8 (0.6) 11 a	1.7 (0.3) 11 a	9961 (5081)	40.04 (19.72)	10.2 (0.8) 9	3.6 (0.5) 9
4.5-6m	2129 (1037) b	2.33 (1.03)	7.2 (0.5) 8 a	1.4 (0.2) 8 ab	14196 (5943)	55.28 (20.70)	9.7 (1.0) 8	4.2 (1.0) 8
2012								
0-1.5m	1412 (489)	1.48 (0.46)	7.1 (0.6) 11 a	1.4 (0.2) 11	575 (282)	2.80 (1.32)	11.7 (1.3) 8 a	5.2 (1.4) 8
1.5-3m	13541 (6810)	4.58 (2.13)	4.6 (0.3) 8 b	0.4 (0.1) 8	3456 (2656)	2.54 (1.60)	6.7 (0.8) 8 b	1.4 (0.6) 8
3-4.5m	4860 (3367)	2.47 (1.22)	5.5 (0.4) 9 ab	0.7 (0.2) 9	7311 (3903)	27.71 (16.15)	8.5 (1.1) 7 ab	2.9 (1.2) 7
4.5-6m	409 (223)	0.44 (0.26)	5.6 (0.8) 9 ab	0.9 (0.4) 9	5568 (3657)	26.58 (17.82)	7.9 (0.9) 10 b	2.0 (0.6) 10
2013								
0-1.5m	3175 (1034) a	4.35 (1.44) a	7.4 (0.4) 10	1.5 (0.2) 10	804 (368)	3.23 (1.60)	10.7 (0.7) 9	3.9 (0.5) 9
1.5-3m	1439 (557) ab	1.81 (0.89) ab	6.1 (0.5) 9	0.9 (0.2) 9	796 (348)	1.89 (0.90)	9.0 (0.5) 9	2.0 (0.4) 9
3-4.5m	435 (197) ab	0.50 (0.24) ab	6.3 (0.6) 8	1.1 (0.4) 8	800 (336)	1.65 (0.82)	8.8 (0.6) 7	2.1 (0.5) 7
4.5-6m	417 (206) b	0.71 (0.34) ab	7.3 (0.9) 7	1.4 (0.4) 7	2544 (1506)	13.65 (8.51)	9.2 (1.2) 9	2.8 (0.8) 9
6-7.5m	177 (96) b	0.33 (0.21) b	7.9 (1.2) 5	1.7 (0.6) 5	616 (292)	3.42 (1.97)	10.9 (0.9) 6	3.7 (1.0) 6

Table 4. Density, biomass and average lengths in different depth regions for the period when both mussel species were abundant (year 2008 - 2013). Data for 3-4.5 m depth region only available for 2011-2013. The analyses were based on year as a sampling unit, and the data was not transformed. Letters connect depth regions that were not significantly different from each other (Tukey HSD post hoc test). No letter indicates no significant differences among depth regions. Test of differences among depth regions do not include 6-7.5 m as this depth region was only sampled in 2013. Values given are the average (range) for the 2008-2013 time period.

Depth	Density (/m2)		AFDW (g/m2)		Average Length(mm)		Proportion Quagga (% by biomass)
	Zebra mussel	Quagga mussel	Zebra mussel	Quagga mussel	Zebra mussel	Quagga mussel	
0-1.5m	3072 (1280-7194)	921 (280-2203)	3.8 (1.3 – 7.0)	3.8 (1.2-8.2) c	7.6 (6.5-10.2)	10.2 (7.8-11.7)	46.9 (23.5-65.8) b
1.5-3m	8308 (1439-14926)	2897 (796-5199)	5.0 (1.8-8.0)	6.6 (1.7-18.3) bc	6.0 (4.5 – 7.7)	8.0 (6.4-9.0)	48.1 (20.7-80.1) b
3-4.5m	2112 (435-4860)	6684 (800-9961)	1.8 (0.5-2.5)	30.3 (7.7-17.3) a	6.5 (5.4-7.8)	10.0 (8.4-12.6)	90.6 (76.5-95.9) a
4.5-6m	985 (409-2129)	7436 (2544-14196)	1.2 (0.4-2.3)	31.6 (13.7-54.8)ab	6.6 (5.5-7.2)	8.8 (7.7-9.7)	96.4 (95.0-98.4) a
6-7.5m	177	616	0.33	3.42	7.89	10.19	91.2