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Twenty five years of changes in *Dreissena* spp. populations in Lake Erie

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ABSTRACT

Lake Erie has the longest history of colonization by both *Dreissena polymorpha* and *Dreissena rostriformis bugensis* in North America and is therefore optimal for the study of long-term dynamics of dreissenid species. In addition, the morphometry of Lake Erie basins varies dramatically from the shallow western to the deep eastern basin, making this waterbody a convenient model to investigate patterns of *Dreissena* distribution, as well as interspecies interactions among dreissenids. We compare our data on the distribution, density and wet biomass of both dreissenid species in Lake Erie collected in 2009 and 2011–2012 with previous data. We found that *Dreissena* spp. distribution in Lake Erie varied depending on the time since the initial invasion, collection depth, and lake basin. In 2009–2012, zebra mussels were smaller than in 1992 and were consistently smaller than quagga mussels. During 2009–2012, quagga mussels were found at all depths and in all basins, while zebra mussels were common in the western basin only, and in the central and eastern basins were limited to shallow depths, resulting in an almost complete replacement of *D. polymorpha* with *D. rostriformis bugensis*. In the shallowest western basin of Lake Erie, zebra mussels represented >30% of the combined dreissenid density even after more than 20 years of coexistence, providing strong evidence that, even in lakes as large as Lake Erie (or at least its western basin), *D. polymorpha* may sustain a significant presence for decades without being displaced by quagga mussels.

Introduction

The introduction of the zebra mussels (*Dreissena polymorpha*) and quagga mussels (*Dreissena rostriformis bugensis*) into North America in the 1980s resulted in significant negative economic and ecological impacts (reviewed in Hecky et al., 2004; Karatayev et al., 1997, 2002, 2007; Nalepa and Schloesser, 1993; O'Neill, 2008; Vanderploeg et al., 2002). The ecological impacts of both species are associated with their role as ecosystem engineers, and the magnitude of their effects is determined by the population density in a given waterbody (Karatayev et al., 2002). However, populations of *Dreissena* species do not stabilize and can vary widely over time (Burlakova et al., 2006; Karatayev et al., 1997, 2002, 2011; Nalepa et al., 2010; Ramcharan et al., 1992; Strayer and Malcom, 2006). In addition, different *Dreissena* species have different spatial distributions in a waterbody. Zebra mussels require hard substrate for their attachment and are usually more abundant in the littoral zones, avoiding silt in deep areas, whereas quagga mussels may effectively colonize soft substrates in the profundal zone (reviewed in Karatayev et al., 2011). When both species colonize the same waterbody, *D. rostriformis bugensis* usually establish high densities and outcompete *D. polymorpha* in deep lakes with large profundal zones while zebra mussels may be abundant and coexist with quagga mussels in shallow lakes and rivers (reviewed in Karatayev et al., 2011; Zhulidov et al., 2010). Moreover, different *Dreissena* species have different population dynamics, and the estimated lag time between initial introduction and maximal population size in a given waterbody is 5 times shorter for *D. polymorpha* than for *D. rostriformis bugensis* (Karatayev et al., 2011). As a result, *Dreissena* species' ecological impacts will depend on their total population density, time since the initial invasion, species composition, and the morphometry of an invaded waterbody. Therefore, up-to-date information on these parameters is critically important for predicting the ecological impacts of *Dreissena*.

Lake Erie has the longest history of colonization by both *Dreissena* species in North America. According to Carlton (2008), the first *D. polymorpha* was found in this lake in 1986, and the first *D. rostriformis*

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bugensis was documented from Lake Erie in 1989 (Mills et al., 1993). Therefore, Lake Erie is optimal for the study of long-term dynamics of dreissenid species in North America. In addition, the morphometry of Lake Erie basins varies dramatically from the shallow western to the deep eastern basin, making it a convenient model for investigating patterns of *Dreissena* distribution and population dynamics, as well as interspecific interactions among dreissenids. The first whole lake study of *Dreissena* species in Lake Erie was conducted in 1992 and then repeated in 1993, 1998, 2002, and 2004 (Ciborowski et al., 2007; Demott and Dow, 2008; Jarvis et al., 2000; Patterson et al., 2005). In 1993, quagga mussels accounted for only 44% of all dreissenids (Demott and Dow, 2008); however, by 2002, their relative abundance had increased to 97% across the entire Canadian shoreline of the lake (Patterson et al., 2005). While the lake-wide density of *Dreissena* in 1992 and 2002 was virtually the same, biomass had increased almost four-fold by 2002 due to the increase in the average mussel size (Barton et al., 2005; Patterson et al., 2005). Up to 90% of whole-lake *Dreissena* biomass in 2002 was located in the eastern basin where no *D. polymorpha* were found. In the central basin, the relative abundance of zebra mussels was only 3.2%. *D. polymorpha* was still common in the western basin, comprising 45% of the total dreissenid density. The authors suggested that *Dreissena* populations in Lake Erie were still changing rapidly in their abundance, biomass, and species composition (Patterson et al., 2005).

The goals of this paper were to determine the current distribution, size structure, abundance, and biomass of *Dreissena* species based on our 2009–2012 collections as well as to analyze the temporal and spatial dynamics of *D. polymorpha* and *D. rostriformis bugensis* in Lake Erie over the last 25 years.

Methods

Sampling protocol

As part of the Nearshore and Offshore Lake Erie Nutrient Study (NOLENS) in 2009 and the Lake Erie Nearshore and Offshore Nutrient Study (LENONS) in 2011–2012, the distribution, density, wet biomass, and length–frequency distribution of *Dreissena* spp. were studied in Lake Erie from nearshore-to-offshore transects with fixed sample stations at 2, 5, 10, and 20 m (15 m in Sandusky River transect in 2009; in western basin in 2011–2012 only 2, 5, and 10 m stations were sampled) (Fig. 1, Electronic Supplementary Material Table S1). In 2009, *Dreissena* samples were collected in June and September along three duplicate transects bracketing three major tributaries of the central and eastern basins. The tributaries represent the largest surface water inputs into the central and eastern basins (Sandusky River, Ohio and Cattaraugus Creek, New York, respectively) and a second major tributary

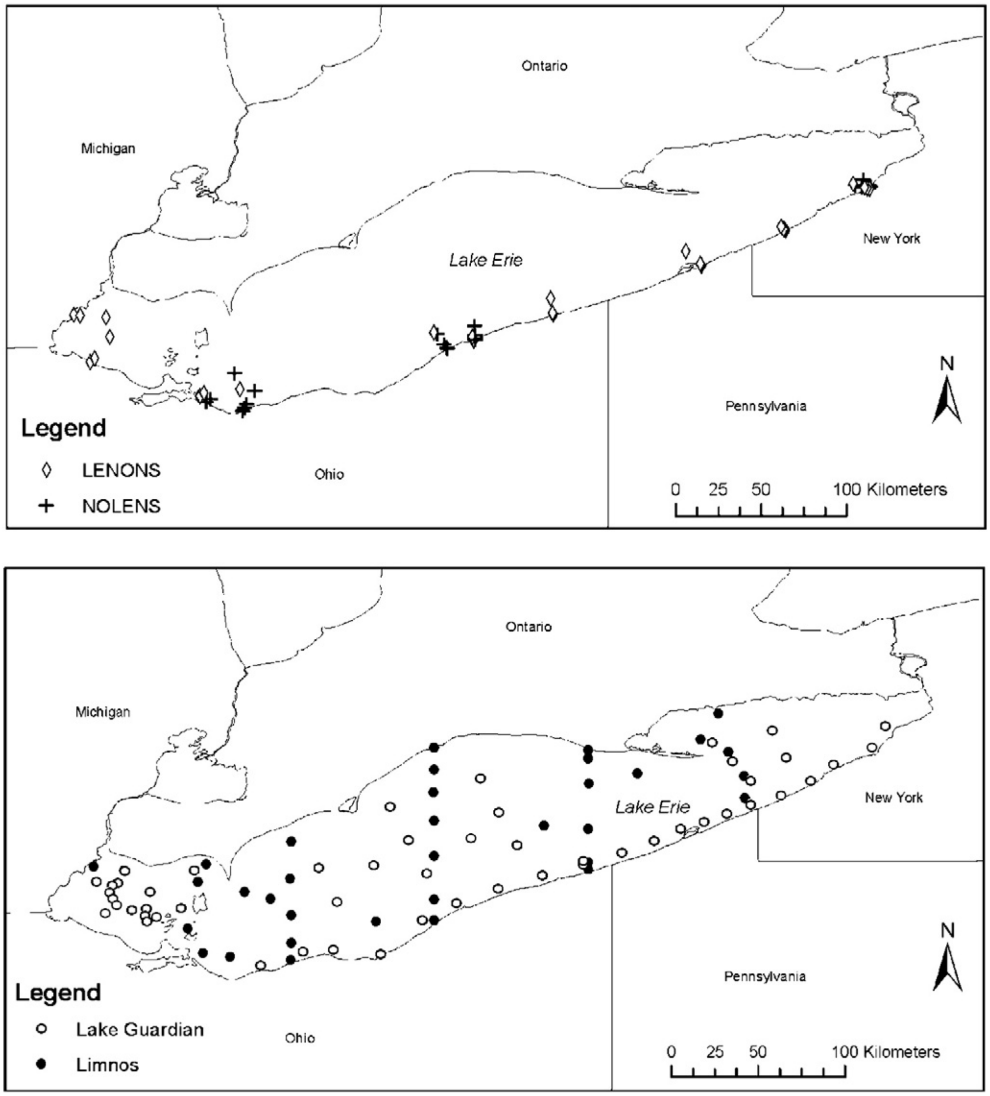

Fig. 1. Locations of sampling sites on Lake Erie collected as part of the Nearshore and Offshore Lake Erie Nutrient Study (2009) and the Lake Erie Nearshore and Offshore Nutrient Study (2011–2012) (upper map), and aboard the R/V *Lake Guardian* (2009) and R/V *Limnos* (2009) (lower map).

in the central basin (Grand River, Ohio). In 2011 and 2012 as part of LENONS, *Dreissena* samples were collected in June and August along 2 transects in the western basin, 4 in the central basin, and 2 in the eastern basin (Fig. 1). Two of these transects also were sampled in 2009. At each depth, three replicate samples were taken on each date using a grab (either petite Ponar or Ekman, with a sampling area of 0.023 m^{-2}) to obtain the sample from soft substrates or by SCUBA divers using an air-lift sampler (0.063 m^2 quadrat, 0.5 mm mesh bag attached) if hard substrates (rock/bedrock) were sampled. The entire sample was placed in a plastic bag, labeled, and placed in a cooler until returning to shore. All replicates for each site were processed separately and then averaged for the analysis.

Additionally, in June and July of 2009, 52 sites from all three lake basins were sampled (2 to 6 replicates per site) aboard the US Environmental Protection Agency R/V *Lake Guardian* using a regular Ponar (sampling area 0.0529 m^2) or Boxcore (0.144 m^2) grabs (Fig. 1, Electronic Supplementary Material Table S1). A further 106 samples were collected by Ciborowski et al. aboard R/V *Limnos* from 37 sites located in all three Lake Erie basins (depths 5–56 m) using a petite Ponar. Samples collected by Ciborowski et al. were kept frozen for 10 months and analyzed in the Great Lakes Center laboratory.

The samples collected during NOLENS, LENONS, and aboard R/V *Lake Guardian* were stored in coolers and processed within 48 h of collection. Sediments were washed through a 500-μm mesh, and all *Dreissena* mussels were identified to species and counted. All mussels from all studies were opened with a scalpel to drain water from the mantle cavity, and the whole sample was weighed to the nearest 0.01 g after being blotted dry on absorbent paper. We report wet weight (soft tissue plus shell minus water from the mantle cavity). We used total weight wet because it can be measured directly in the field, and it avoids inaccuracies associated with measurements derived from length–dry mass or length–AFDM relationships. If the sample was too large to process, it was split into 4 equal parts and one part was randomly selected for analysis. A total of 752 replicate samples from 135 sites were collected in 2009–2012.

To compare our results with previous studies, a dataset was compiled using primary data for 1992, 1993, and 1998 (density and wet biomass by sites and depths from Jarvis et al., 2000), published data for 2002 (density and dry tissue biomass averaged by depths intervals and lake basins from Patterson et al., 2005), and lake-wide average density and dry tissue biomass for 2004 from Ciborowski et al., 2007. To convert the total wet weight, including the weight of water in the mantle cavity (for 1992–1998 data) into wet weight (shell plus tissue minus mantle cavity water), we determined that water in the mantle cavity comprises a mean (± standard error of the mean here and elsewhere unless noted) of 31.4 ± 1.1% of the weight for live *D. rostriformis bugensis*, and 28.4 ± 0.7% of the weight for live *D. polymorpha*. To determine these ratios, 20 mussels of each species were individually weighed (size range of each species 7–21 mm) with and without water; these ratios were not affected by mollusk size. When biomass was reported for both *Dreissena* species together, we used an average (29.9%). To convert dry tissue into wet weight (2002 and 2004 data), we used the relationship from Patterson et al. (2005):

$$\text{Shell-free dry mass (g)} = 0.0265 * \text{whole wet mass (g)} \left(R^2 = 0.96\right).$$

To convert frozen weight into wet weight, we used a ratio between frozen and fresh wet weight of 1:0.699 for quagga mussels and 1:0.636 for zebra mussels (P. Juette, Biology Department, SUNY Buffalo State).

Statistical analysis

For our data (2009–2012), we used each site as a sampling unit, with *Dreissena* density and biomass averaged across all replicates at a given site. For sites along NOLENS and LENONS transects (sampled biannually in 2009, 2011, and 2012), data were also averaged across all sampling events to produce an average *Dreissena* density and biomass for the 2009–2012 period.

To calculate the weighted average (± standard error) of *Dreissena* spp. density and biomass per basin, we calculated the average density and biomass in each depth zone (0–4, 4–8, 8–15, 15–24, and >24 m, Patterson et al., 2005), and then calculated the average density and biomass across the depth zones, weighted by the area of each depth zone relative to the total area of the basin following Manly (1992). The weighted lake-wide average is the sum of the weighted average densities and biomass of *Dreissena* per each basin, multiplied by the proportion of each basin from the total area of the lake. To test if *Dreissena* abundance changed with depth intervals within basins, we performed one-way ANOVA tests on log-transformed density and biomass for each basin. When multiple tests were conducted on the same data, we used a sequential Bonferroni correction to adjust the critical alpha considered for statistical significance (Rice, 1989).

To compare *Dreissena* spp. average length among species, depths, and lake basins, we used a one-way ANOVA with subsequent post-hoc unequal-*n* Tukey's Honestly Significant Difference (HSD) tests, or a Welch's *t*-test (a modification of *t*-test for two samples having possibly unequal variances). When comparing sites where shell length distributions did not satisfy the assumptions of normality and homogeneity of variances, we log-transformed shell lengths for the analysis.

For the long-term data analysis, we used a three-way ANOVA on log-transformed densities and biomass data with year, basin, and depth interval as categorical variables. The period of 2009–2012 was analyzed as a single group of years rather than as individual years. We used only two depth intervals (nearshore, ≤10 m and offshore, >10 m), as these were the only depth categories sampled in all studies in all three basins. Significant differences were then evaluated by post-hoc pairwise tests (HSD test) using sequential Bonferroni-adjusted *p* values. For all statistical tests we used Statistica software (STATISTICA version 10, StatSoft, Inc. 1984–2011). Effects were considered statistically significant at $p < 0.05$.

Results

2009–2012 Dreissena spp. distribution

During the three years of our study, *Dreissena* spp. were found at 78 (58%) of the 135 sampled sites, including 77 sites with quagga mussels (57%), and 31 (23%) sites with zebra mussels. There was only one site (in the western basin) where only *D. polymorpha* and no *D. rostriformis bugensis* were found. The relative proportion of zebra mussels comprised 13% in the lake-wide *Dreissena* spp. density and 2% in lake-wide dreissenid biomass.

Both density and wet biomass of *Dreissena* species varied among basins (Table 1). The highest weighted average *Dreissena* density was found in the western basin and the lowest in the central basin. In contrast to density, the weighted average wet biomass was highest in the eastern basin. Zebra mussels were still common only in the shallowest western basin, where they comprised 33% of the combined weighted *Dreissena* spp. density and 10% of the combined biomass. In the central and eastern basins, zebra mussels comprised only 3% and 1% respectively from the total *Dreissena* spp. density.

Density and biomass of *Dreissena* species in the central and eastern basins differed significantly with depth intervals (central: density $p = 0.0004$, biomass: $p = 0.0015$; eastern: density $p = 0.010$, biomass: $p = 0.001$), but not in the western basin (density $p = 0.35$, biomass $p = 0.08$, one-way ANOVA) (Table 1, Fig. 2). In all three basins maximum *Dreissena* density and biomass were found at the 4–8 m depth interval. However, in the eastern basin, a second peak of *Dreissena* spp. density and biomass was found at depths >24 m, while in the central basin almost no *Dreissena* were found at these depths.

Table 1
Average density (±standard error, m^{-2}), wet biomass (average ± standard error, shell plus tissue g m^{-2}) of *Dreissena polymorpha* and *D. r. bugensis*, and the number of sites (N) sampled in Lake Erie in 2009–2012. Averages for depth zones were calculated using averages from each unique site. Each site had from 2 to 11 replicates, and some were sampled 2 times a year (up to 6 replicates total, see Electronic Supplementary Material Table S1). To calculate the weighted average of *Dreissena* spp. density and biomass per basin, we calculated the average density and biomass in each depth zone (0–4, 4–8, 8–15, 15–24, and >24 m), and then calculated the average density and biomass across the depth zones, weighted by the area of each depth zone relative to the total area of the basin following Manly (1992). The weighted lake-wide average is the sum of the weighted average densities and biomass of *Dreissena* per each basin, multiplied by the proportion of each basin from the total area of the lake.

Basin, depth (m)	N	Density			Biomass		
		All *Dreissena*	*D. rostriformis bugensis*	*D. polymorpha*	All *Dreissena*	*D. rostriformis bugensis*	*D. polymorpha*
Western							
0–4	2	1405 ± 1376	891 ± 869	514 ± 507	17.1 ± 15.3	4.1 ± 2.8	13 ± 12.5
4–8	3	2064 ± 1139	1217 ± 564	847 ± 835	300.2 ± 132.9	281 ± 142.8	22.7 ± 13.2
8–15	22	1069 ± 392	883 ± 355	188 ± 81	65.5 ± 24.1	57.2 ± 22.8	8.5 ± 4.7
Weighted average	27	1501 ± 415	1012 ± 241	490 ± 263	148.1 ± 40.9	134.9 ± 43.7	14.6 ± 4.6
Central							
0–4	7	8 ± 5	7 ± 5	1 ± 1	0.7 ± 0.7	0.4 ± 0.3	0.4 ± 0.4
4–8	7	853 ± 300	742 ± 257	112 ± 95	434.8 ± 179.1	424.8 ± 177.5	10 ± 5.2
8–15	27	427 ± 170	427 ± 170	1 ± 1	136.8 ± 54.1	136.6 ± 54.1	0.1 ± 0.1
15–24	29	37 ± 16	37 ± 16	0 ± 0	18.7 ± 7.6	18.7 ± 7.6	0 ± 0
>24	4	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0
Weighted average	74	141 ± 33	137 ± 33	4 ± 3	55.4 ± 11.8	55.1 ± 11.8	0.4 ± 0.2
Eastern							
0–4	3	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0
4–8	3	1777 ± 1001	1751 ± 987	25 ± 15	742.8 ± 396.2	733.7 ± 391.6	9.1 ± 4.6
8–15	11	645 ± 276	603 ± 245	43 ± 39	407.9 ± 139.4	400.3 ± 138.6	7.6 ± 6.3
15–24	8	189 ± 92	186 ± 91	2 ± 2	29.3 ± 16.4	29.2 ± 16.3	0.1 ± 0.1
>24	9	1050 ± 308	1050 ± 308	0 ± 0	996.7 ± 258.8	996.7 ± 258.8	0 ± 0
Weighted average	34	750 ± 128	742 ± 126	8 ± 5	588.8 ± 94.4	587.2 ± 94.3	1.6 ± 0.8
Weighted lake-wide average	135	442 ± 53	382 ± 39	60 ± 28	193.9 ± 20.7	191.8 ± 20.8	2.3 ± 0.5

Length–frequency distribution

Dreissena spp. length–frequency distributions were different among species, depths, and lake basins. In 2009, the length–frequency distribution of both *Dreissena* species from the western basin (pooled data from 4 sites, all at ~ 10 m depth) showed two distinct size groups (2–12 mm and 14–26 mm), likely corresponding with two age groups — young-of-the-year recruits and >1-year-old adults (Fig. 3). Although the average *D. polymorpha* length (10.5 ± 0.45 mm) was not significantly different from that of *D. rostriformis bugensis* (11.00 ± 0.37 mm, $p = 0.41$, Welch's *t*-test), there was a significant difference when species were analyzed separately by these two size groups (<12 mm: zebra mussel lengths 4.57 ± 0.35 mm vs. quagga mussels 6.66 ± 0.17 mm, $p \ll 0.001$; >14 mm: zebra mussel lengths 15.34 ± 0.25 mm vs. quagga mussels 19.53 ± 0.57 mm, $p \ll 0.001$, Welch's *t*-test on log-transformed data).

In the western basin in 2009, *D. rostriformis bugensis* average lengths at four 10 m sites were significantly different from the average quagga mussel lengths at three sites in the eastern basin (17.8, 35, and 48 m) ($p = 0.024$, one-way ANOVA) (Fig. 3). No mussels smaller than 16 mm were found at deep (35 and 48 m) sites in 2009.

In 2012, *Dreissena* lengths were measured at 10-m sites across all basins (Fig. 4). Zebra mussels were significantly smaller than quagga mussels in the western basin, where the species coexisted ($p = 0.003$; paired *t*-test on mean lengths for each site). Both in June and August, quagga mussel length was significantly different among basins ($p \ll 0.001$, one-way ANOVA), driven mostly by the significantly smaller mussels in the western basin compared to the central and eastern basins ($p \ll 0.001$, post-hoc test after ANOVA). Mean length of quagga mussels did not differ between the central and eastern basins ($p = 0.32$).

1992–2012 dreissenid dynamics

The lake-wide *Dreissena* spp. density varied significantly across years and basins during 1992–2012 (year: $p = 0.001$, basin: $p \ll 0.001$, three-way ANOVA). The year × basin interaction was also significant ($p = 0.0002$, Fig. 5), indicating that changes in density were not consistent across basins. The effects of depth and all other interactions were non-significant (depth: $p = 0.58$; year × depth: $p = 0.45$; basin × depth $p = 0.51$, year × basin × depth $p = 0.89$). Similarly, over this period, significant differences in *Dreissena* spp. wet biomass were seen with years ($p = 0.037$) and basins ($p \ll 0.001$), while the effect of depth and all interaction terms were non-significant (depth $p = 0.62$; year × basin $p = 0.27$; year × depth $p = 0.72$; basin × depth $p = 0.68$, year × basin × depth $p = 0.99$, three-way ANOVA). The lake-wide *Dreissena* spp. density did not change significantly from 1992 to 2002 ($p = 0.23$, HSD tests), but then declined by a factor of seven by 2009–2012 ($p < 0.001$, HSD tests). In contrast, the lake-wide average biomass increased during the first twelve years, reaching a maximum in 2004, and then declined by 2009–2012 (Fig. 5). Unfortunately, because primary data for 2004 were not available, we were unable to calculate the significance of the increase in biomass by 2004; however, the difference was significant between 1992 and 2002 ($p = 0.003$), and 2002 and 2009–2012 ($p = 0.001$, HSD test).

Different basins were characterized by different patterns in *Dreissena* spp. dynamics. While in the western basin dreissenid density did not change significantly during 1992–2012, in the central basin the density was significantly lower in 2009–2012 than in 1993 ($p \ll 0.001$) and in 1998 ($p = 0.01$) (Fig. 5). Dreissenid density in the eastern basin in 2009–2012 was lower compared to all earlier years ($p = 0.015$). Changes in basin-wide biomass were not significant among years.

Each *Dreissena* species had clearly opposite trends in their dynamics, at least during the first 8–10 years of observation (Fig. 6). Due to the high abundance of *D. r. bugensis*, fluctuations in dreissenid populations in the eastern basin are reflected in the lake-wide *Dreissena* dynamics. While the average *D. polymorpha* density in the whole lake declined since 1992 by almost two orders of magnitude by 1998 ($p \ll 0.001$) and has not changed significantly since, the lake-wide density of *D. r. bugensis* had significantly increased by 2002 since 1992 ($p < 0.0004$) (Fig. 6). Although a significant decline in basin-wide *D. polymorpha* density from 1992 to 2002 was found in the central ($p \ll 0.001$) and

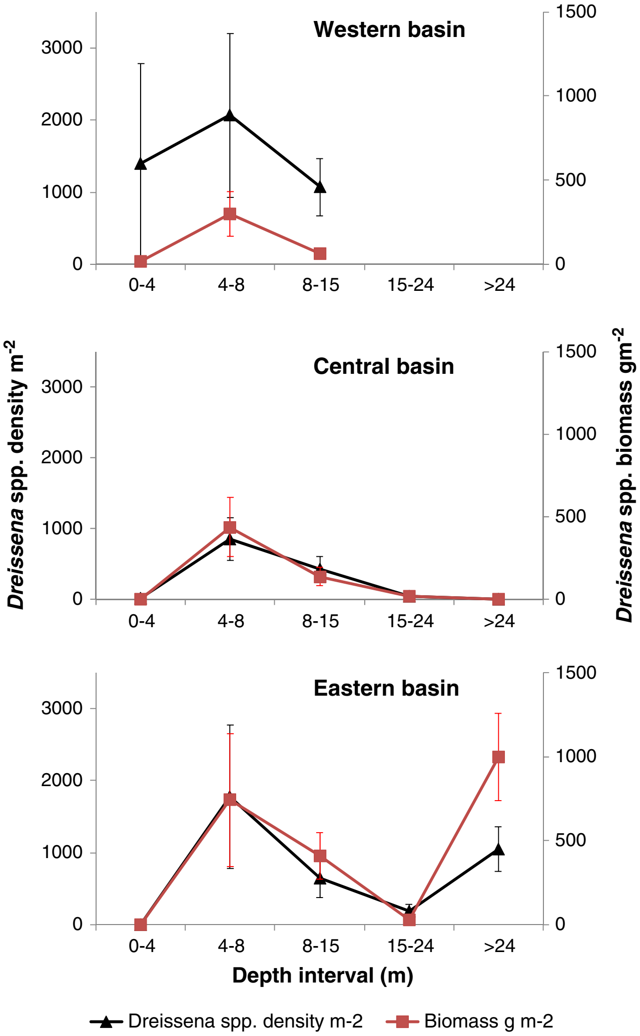

Fig. 2. Density and biomass of *Dreissena* spp. across the depth intervals sampled in the three basins of Lake Erie in 2009, 2011, and 2012. Means ± standard error are provided for each depth interval.

eastern ($p < 0.001$) basins, no decline in *D. polymorpha* density was detected in the shallowest western basin over the 20-year period of observation.

In contrast to *D. polymorpha*, *D. r. bugensis* density had increased during the first 6–10 years of observation, although this was only significant in the central basin ($p = 0.004$). Quagga mussels reached their maximum density in the central basin in 1998 and in the eastern basin in 2002. These peaks in *D. r. bugensis* densities were followed by significant declines in 2009–2012, both in the eastern ($p = 0.04$) and central ($p = 0.006$) basins.

Discussion

2009–2012 Dreissena spp. distribution

In 2009–2012, quagga mussels were dominant among dreissenids in the central and eastern basins, consistent with previous studies of *Dreissena* spp. distribution in Lake Erie (Demott and Dow, 2008; Jarvis et al., 2000; Patterson et al., 2005) and with recent data from other Great Lakes (e.g. Nalepa et al., 2010; Pennuto et al., 2012). There was a large variation in the average *Dreissena* spp. density and biomass among lake basins (Table 1), consistent with previous studies (Demott and Dow, 2008; Jarvis et al., 2000; Patterson et al., 2005). There was also significant variation in *Dreissena* spp. density and biomass across depths within eastern and central basins.

Length–frequency distribution

Zebra mussel size in Lake Erie was much smaller than that of quagga mussels (Figs. 3, 4). Maximum zebra mussel length in western Lake Erie during 2009–2012 (20 mm) was much smaller than early in the invasion in 1992, when both maximum (30 mm) and average *D. polymorpha* length were not different from that of quagga mussels (Dermott and Munawar, 1993). Maximum *D. polymorpha* length in 2009–2012 was also much smaller than in any of 16 European lakes colonized only by zebra mussels (reviewed in Karatayev et al., 2006). This difference is most likely due to the worsened food conditions in Lake Erie associated with the introduction of *Dreissena* species (Barbiero and Tuchman, 2004; Leach, 1993; Macisaac et al., 1992) after which quagga mussels would outperform *D. polymorpha* due to their greater energetic efficiency (Baldwin et al., 2002; Stoeckmann, 2003).

The observed smaller sizes of quagga mussels in the western basin of Lake Erie in 2009 and 2012 compared to the rest of the lake were unexpected. Even after the *Dreissena* spp. invasion, the western basin is still much more eutrophic than the other basins, containing higher phytoplankton and seston concentrations (Barbiero and Tuchman, 2004; Charlton et al., 1999; Conroy et al., 2005), and therefore providing better food conditions for dreissenids. As there is a well-known positive relationship between food conditions and *Dreissena* size and growth rate (reviewed in Karatayev et al., 2006, 2010b), it would be logical to expect larger *D. r. bugensis* lengths in the western basin relative to the other basins. A decline in quagga mussel length with decreasing food availability was observed in Lake Michigan (Nalepa et al., 2010) and in Lake Ontario (Pennuto et al., 2012). Nevertheless, quagga mussels were consistently smaller in the western basin compared to the rest of the lake (Figs. 3, 4), indicating either worse trophic conditions or higher mortality. Although the more eutrophic western basin may have higher food availability, it also has high turbidity (Barbiero and Tuchman, 2004) and strong blue-green algae blooms (Bridgeman et al., 2013), which can negatively affect *Dreissena* filtering abilities and assimilation efficiencies. It is also prone to significant periodic sedimentation following storm events, which can induce high mortality rates by burying mussels in soft sediments (Coakley et al., 2002). In addition, even though the western basin has no seasonal stratification, it is often temporarily stratified due to solar heating (Ackerman et al., 2001), and this stratification suppresses the supply of algae at the bottom layer (MacIsaac et al., 1999). Finally, dissolved oxygen concentrations often decline to <2 mg/L in parts of the western basin (Bridgeman et al., 2006; Krieger et al., 2007). Such hypoxic episodes could cause mass mortality of *Dreissena* spp. of all sizes, but frequent recolonization by veligers between episodes could help explain the smaller size distribution found in the western basin. At this time it is unclear which of the above factors or a combination of factors are responsible for the smaller mussel sizes in the western basin and this question requires further investigation. Most of these adverse conditions may have stronger effects on *D. r. bugensis* than on *D. polymorpha* which is better adapted to the unstable environment of shallow areas of lakes and rivers than quagga mussels (reviewed in Karatayev et al., 2014). No dreissenids were found during our 2009 study in the central basin in areas affected by hypoxia.

In the eastern basin, *D. r. bugensis* collected in 2009 from deep sites (35 and 48 m) below the thermocline were significantly larger than those at the 17.8 m site above the thermocline (Fig. 3). No mussels smaller than 16 mm were found at these deep sites, suggesting a recruitment failure in the previous year. A similar difference in quagga mussel size with depth was observed in Lake Ontario (Pennuto et al., 2012). Several hypotheses have been suggested as potential mechanisms for mussels' greater length in the deep cold profundal zone, including ones involving reduced hydrologic sheer forces and higher

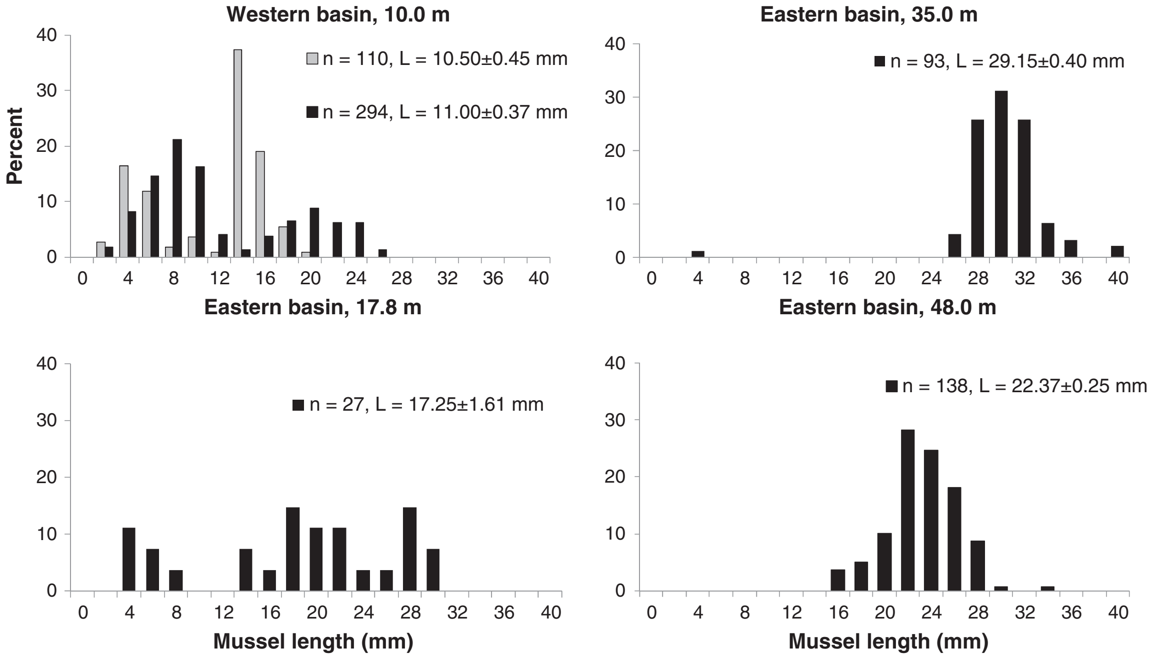

Fig. 3. Length–frequency distribution of *Dreissena polymorpha* (gray bars) and *Dreissena rostriformis bugensis* (black bars) in the western and eastern basins of Lake Erie in June 2009. Sample size (n) and average mussel length (L, mean ± standard error) are provided for each sample site.

food availability associated with deep chlorophyll peaks (Pemberton et al., 2007), which have been reported in eastern Lake Erie (Barbiero and Tuchman, 2001). In addition, the more stable, colder environment of the profundal regions may lead to slower growth of *D. r. bugensis* (Karatayev et al., 2010a) and longer life spans, thus contributing to their larger sizes, relative to shallower areas.

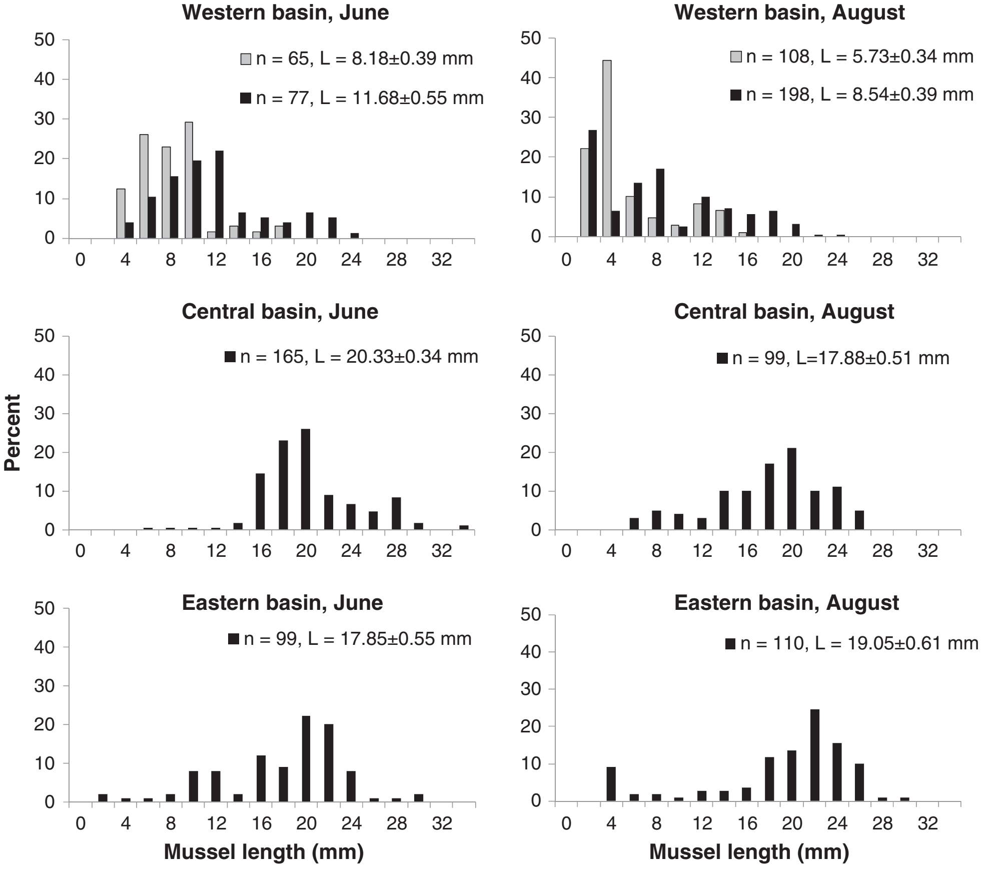

Fig. 4. Length–frequency distribution of *Dreissena polymorpha* (gray bars) and *Dreissena rostriformis bugensis* (black bars) at 10 m sites in Lake Erie in 2012. Sample size (n) and average mussel length (L, mean ± standard error) are provided for each sample site.

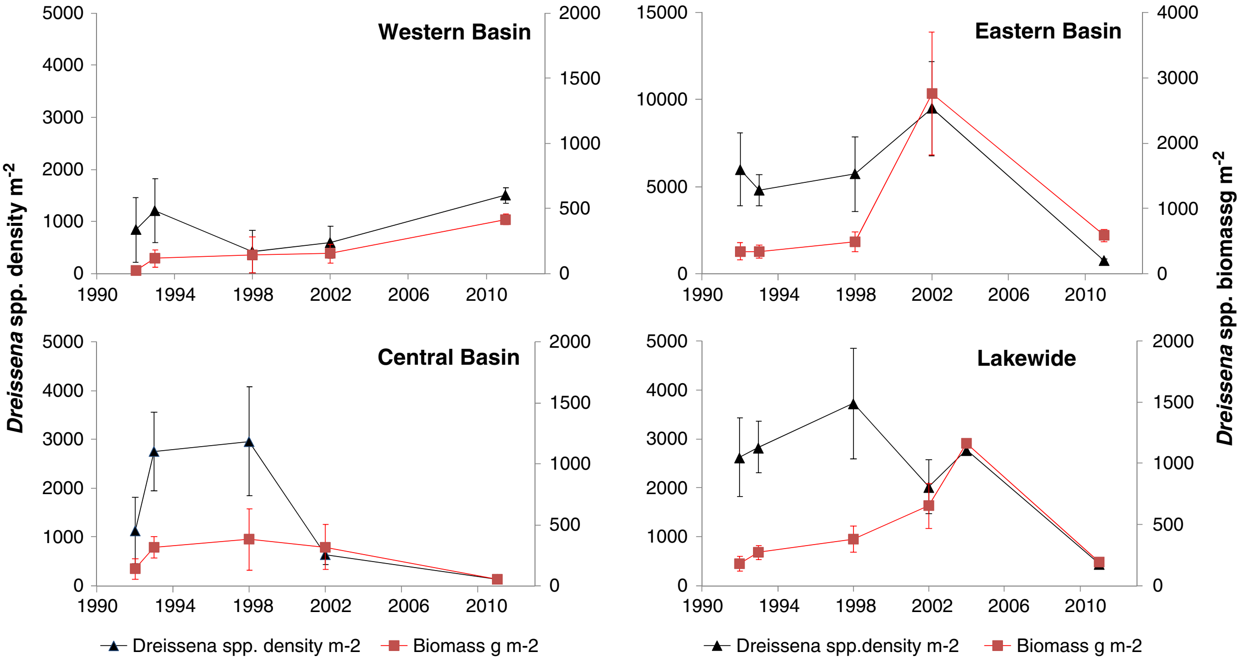

Fig. 5. Long-term dynamics of *Dreissena* spp. density and wet biomass in Lake Erie (vertical bars are standard errors). Data represent a variety of non-randomly selected sampling stations and differing sampling methods over the years. For 1992–1998 (Jarvis et al., 2000), data are presented as averages for all survey sites. Data collected in 2002 (Patterson et al., 2005) and during our study (average for 2009, 2011, and 2012) are presented as weighted averages.

Dreissena spp. dynamics

Typically, *D. polymorpha* reaches its population maximum in about 2–4 years (average 2.5 ± 0.2 y) after it is first detected in an invaded waterbody (reviewed in Karatayev et al., 2011 and references therein). Initially, populations of *D. polymorpha* attain very high densities, but because of density-dependent processes, total sustainable biomass declines as the system is altered by zebra mussel presence, and densities well below the maximum achieved persist (Karatayev et al., 1997, 2002). However, usually populations of zebra mussels do not stabilize, and densities can fluctuate widely (Burlakova et al., 2006; Karatayev et al., 1997, 2002, 2011; Nalepa et al., 2010; Ramcharan et al., 1992;

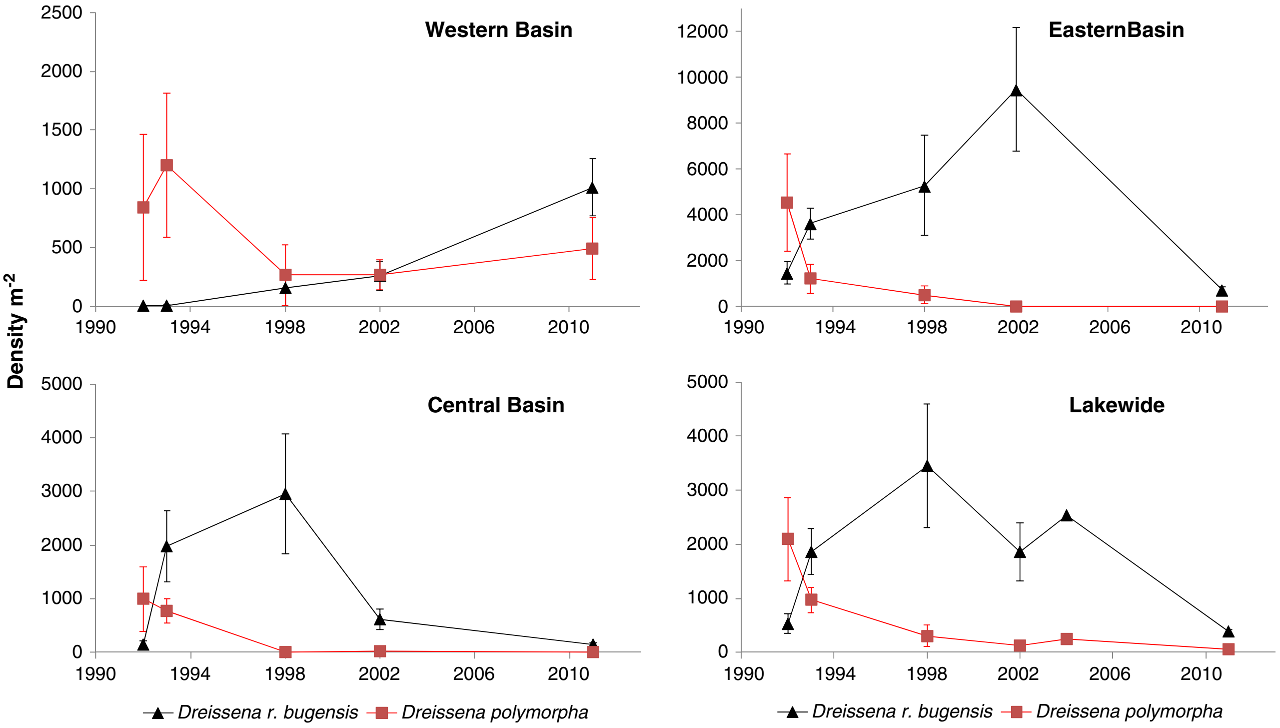

Fig. 6. Long-term dynamics of *Dreissena polymorpha* and *Dreissena rostriformis bugensis* density in Lake Erie (vertical bars are standard errors). Data represent a variety of non-randomly selected sampling stations and differing sampling methods over the years. For 1992–1998 (Jarvis et al., 2000), data are presented as averages for all survey sites. Data collected in 2002 (Patterson et al., 2005) and during our study (average for 2009, 2011, and 2012) are presented as weighted averages.

Strayer and Malcom, 2006). As *D. polymorpha* was first found in Lake Erie in 1986 (Carlton, 2008), zebra mussels likely reached their maximum around 1989, when they colonized most of the hard substrates in the nearshore areas (Griffiths et al., 1991). Therefore, during the first lake-wide study of *Dreissena* spp. distribution in 1992, *D. polymorpha* may have already passed its maximum population density, and had already been in decline (Fig. 6). Although this decline was evident in the central and eastern basins, as well as lake-wide, it was less pronounced and not statistically significant in the western basin.

In contrast to the zebra mussels, quagga mussels are characterized by a much longer lag time between the initial introduction and large population sizes. Usually, the maximum *D. r. bugensis* population density is not achieved until 6 to 19 years (average 12.2 ± 1.5 y) after their first detection in a waterbody (Karatayev et al., 2011). In Lake Erie, quagga mussels were found for the first time in 1989 (Mills et al., 1993), and the population peaked somewhere between 1998 (central basin) and 2002 (eastern basin) (Fig. 6).

Combined dreissenid density in Lake Erie was high during the first 12 years of observation, but then sharply declined by 2009–2012, while the average wet biomass peaked with some delay in 2004, and then declined as well (Fig. 5). In most cases, biomass was less variable than density. The biomass data for the assessment of population dynamics is more important for monitoring mussels than density as it takes into account both number and size, which ultimately impact the filtering role of mussels in the lake (Burlakova et al., 2006; Karatayev et al., 1997; Nalepa et al., 2010).

Zebra and quagga mussels had clearly opposite trends in their dynamics in the central and eastern basins, as well as lake-wide, resulting in an almost complete replacement of *D. polymorpha* with *D. r. bugensis* in the deep parts of the lake (Table 1, Fig. 6). Similar trends in *D. polymorpha* and *D. r. bugensis* dynamics were found in 16–30 m and 31–50 m depth zones in southern Lake Michigan, where the constant increase in quagga mussel population density from 2001 to 2008 was also accompanied by a replacement of zebra mussels (Nalepa et al., 2010). However, in contrast to Lake Erie, where we found a sharp and significant decline in quagga mussel density and biomass in 2009–2012, no decline in mussel density has been reported thus far in southern Michigan. Perhaps this difference reflects the longer presence of quagga mussels in Lake Erie (at least 22 years), while the first quagga mussels in southern Lake Michigan were found only in 2001, and the population is still growing.

The decline in quagga mussel density and biomass in the central and eastern basins of Lake Erie as well as lake-wide by 2009–2012 could be explained by at least two phenomena involving *Dreissena* density-dependent processes and/or predation. *Dreissena* spp. populations could have declined as a result of substrate (Burlakova et al., 2006; Lvova, 1977) or food limitations (Hecky et al., 2004). According to Lvova (1977), the zebra mussel population decline in Uchinskoye Reservoir (Russia) was due to the accumulation of silt, a result of *Dreissena* filtering activity. Hecky et al. (2004) suggested that mussel populations may decline due to the food limitation associated with their filtering activity. Patterson et al. (2005) reported the disappearance of *Dreissena* spp. in the 3 to 12 mm length range in Lake Erie in 2002, and explained this by round goby (*Neogobius melanostomus*) predation on small mussels. However, in 2009–2012, small mussels were present in most of the sites sampled, with the exception of two deep sites in the eastern basin in 2009 (Figs. 3, 4). Likewise, no reduction in the frequency of 4–10 mm mussels was found at US nearshore sites in Lake Ontario (Pennuto et al., 2012). According to Bunnell et al. (2005) and Johnson et al. (2005), round gobies consume a relatively small fraction of *Dreissena* spp. in Lake Erie. Therefore, while it has been shown repeatedly that round gobies prey on dreissenids (reviewed in Kornis et al., 2012 and references therein), additional studies are necessary to understand the extent to which gobies can control *Dreissena* spp. populations in the Great Lakes.

Another potential reason for the difference between 2002 and 2009–2012 *Dreissena* abundance, particularly in the eastern basin of Lake Erie, could be a geographical sampling bias. Patterson et al. (2005) sampled northern littoral zone of the eastern basin with the extensive limestone outcroppings and high *Dreissena* density, while in 2009–2012 we sampled southern littoral zone dominated by sand with low *Dreissena* density. Future surveys should target the northern coast of the eastern basin to determine if abundance has declined.

Although some of the observed changes in *Dreissena* spp. populations in Lake Erie may be in part a consequence of different methods used by different authors, our analysis showed that over the last 25 years, both the density and biomass of *Dreissena* spp. may have changed by as much as an order of magnitude. Both species together constitute >90% of the benthic biomass in Lake Erie (Burlakova et al., 2014–in this issue) and are an important resource supporting at least 14 fish species, including key prey species such as round gobies and endangered lake sturgeon (reviewed in Kornis et al., 2012; Molloy et al., 1997). Inter-annual changes in *Dreissena* biomass can thus drive temporal dynamics in the food webs of these ecosystems.

Interspecific competition

Usually, when *D. r. bugensis* invade a deep waterbody already colonized by *D. polymorpha*, they first colonize soft substrates of the cold profundal zones unsuitable for zebra mussels, and then spread into the littoral zones, where food resources have already been reduced by *Dreissena* spp. filtering activities (reviewed in Karatayev et al., 2011, 2014; Nalepa et al., 2010). Due to their different tolerances to abiotic factors, a greater rate of byssal thread production, and a higher attachment strength than *D. r. bugensis* (Peyer et al., 2009), *D. polymorpha* are likely to be better adapted to the unstable environment of the upper littoral zone, where fluctuations in water currents, temperature, and waves are prominent (reviewed in Karatayev et al., 2011, 2014). In contrast, quagga mussels may colonize silt, have a higher tolerance to low oxygen, and could therefore be better adapted to the stable environment found in the deep profundal zone (Karatayev et al., 1998, 2014; Mills et al., 1996).

Numerous reports from both Europe (Orlova et al., 2004, 2005; Zhulidov et al., 2010; Zhuravel, 1952, 1965) and North America (Demott and Dow, 2008; Mills et al., 1996; Nalepa et al., 2009a, 2009b, 2010; Watkins et al., 2007) show that, in waterbodies where both species co-occur, quagga mussels outcompete zebra mussels after 9 or more years of coexistence (reviewed in Karatayev et al., 2011). However, there was some evidence suggesting that this is a scenario typical only of deep lakes with a large profundal zone, while in rivers and shallow lakes, as well as in their native range in the Dnieper River and the Dnieper–Bug Liman (a large shallow coastal lake with no profundal zone), both *Dreissena* species co-occur and are co-dominant (review in Karatayev et al., 2011; Zhulidov et al., 2010). The fact that in the shallowest, western basin of Lake Erie zebra mussels comprise more than 30% of the total dreissenid density even after more than 20 years of coexistence, provides strong evidence from North America that, even in lakes as large as Lake Erie (or at least in its western basin), *D. polymorpha* may sustain a significant presence for decades without being displaced by quagga mussels.

In the deep central and eastern basins, zebra mussels were largely replaced by the quagga mussel during the first decade of coexistence (Patterson et al., 2005). However, we found that even in the eastern basin, zebra mussels have not completely disappeared, as was previously suggested (Patterson et al., 2005). Moreover, zebra mussels are still common, and sometimes more abundant in tributaries, bays, and shallow areas of the lakes with greater water motion (e.g., breakwaters), which generally are not sampled during routine benthic surveys (Karatayev et al., 2013). Similarly, in Lake Ontario, where quagga mussels represent ~99% of the combined *Dreissena* species density (Pennuto et al., 2012), zebra mussels are often more abundant than quagga mussels in the upper littoral zone (<1 m depth), bays, and tributaries (Karatayev et al., 2013).

Dermott and Munawar (1993) predicted that the two *Dreissena* species would partition Lake Erie's benthic habitat, with zebra mussels colonizing hard substrates in shallow water, and *D. r. bugensis* colonizing soft sediments in the colder profundal zone. Twenty five years of coexistence among dreissenids partially support this prediction. Although expected (Patterson et al., 2005), the complete replacement of zebra mussels has not occurred in any of Lake Erie's basins. The zebra mussel is abundant in the western basin and in certain refugia in shallow parts of the central and eastern basins, which are otherwise dominated by quagga mussels. The overall role of *D. polymorpha* in the total density, and especially biomass, as well as its ecological impacts in these two basins is almost negligible compared to *D. r. bugensis*. Nevertheless, zebra mussel larvae are still sufficiently abundant to colonize buoys, raw water intakes, and boats, on which *D. polymorpha* is often more prevalent than *D. r. bugensis* due to its higher attachment strength. Moreover, despite quagga mussels' dominance in the benthic environment, even the eastern basin of Lake Erie still has the potential of being a source for the spread of zebra mussels (Karatayev et al., 2013).

Generally, quagga mussels are larger and have a weaker shell and attachment strength than zebra mussels (Casper and Johnson, 2010; Peyer et al., 2009, 2010), and may therefore be a more accessible food source for benthivorous fish such as round gobies. The preference of deeper habitats by quagga mussels also means that the effects of the two dreissenid species peak at different depths, leading to an offshore shift in the dreissenid-driven "nutrient shunt" (Hecky et al., 2004). As dreissenids also increase the density and biomass of benthic invertebrates by forming complex 3-D habitat structures, these shifts may also be reflected in the distribution of the overall benthic community. Therefore, monitoring the species makeup and distribution of dreissenids is crucial to understanding the spatial dynamics of the Lake Erie food web.

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