Rapid assessment of *Dreissena* population in Lake Erie using underwater videography

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Abstract

Dreissenid bivalves (*Dreissena polymorpha* and *D. rostriformis bugensis*) are considered the most aggressive freshwater invaders inflicting profound ecological and economic impacts on the waterbodies that they colonize. Severity of these impacts depends on dreissenid population sizes which vary dramatically across space and time. We developed a novel method that analyzes video recorded using a Benthic Imaging System (BIS) in near real-time to assess dreissenid distribution and density across large waterbodies and tested it on Lake Erie. Lake Erie basins differ dramatically in morphometry, turbidity, and productivity, as well as in *Dreissena* distribution, density, and length-frequency distribution, providing an excellent model to test the applicability of our method across large and dynamic environmental gradients. Results of rapid assessment were subsequently compared with dreissenid density obtained from Ponar grab samples collected at the same sites. In the eastern and central basins, the differences in basin-wide density estimations from BIS and Ponar were 3% and 23%, respectively. In the western basin, this method had limited application due to high turbidity and abundance of small (< 10 mm length) mussels. By substantially reducing the time required to assess dreissenids across large areas, rapid assessment could be a useful and cost-effective addition for monitoring their populations.

Introduction

Dreissenids (*Dreissena polymorpha* Pallas and *D. rostriformis bugensis* Andrusov) are considered the most aggressive freshwater invaders in the Northern Hemisphere (Nalepa & Schloesser, 1993; Karatayev et al., 2007a, b). They can severely modify the physical, chemical, and biological integrity of invaded waterbodies, eliciting profound ecological and economic impacts in much of the European (van der Velde et al., 2010; O go et al., 2020; Pergl et al., 2020) and North American freshwaters (Karatayev et al., 2002, 2007a, b; O'Neill, 2008; Higgins & Vander Zanden, 2010; Nakano & Strayer, 2014). Both the ecological and economic impacts of *Dreissena* spp. in a given waterbody are dependent upon

many factors including *Dreissena* species, their population density, population dynamics, and spatial distribution across the lake bottom, as well as upon morphometry of the invaded ecosystem (Karatayev et al., 1997, 2010, 2015, 2020; Nalepa et al., 2010; Strayer et al., 2019). *Dreissena* spatial distribution may vary by three orders of magnitude at all spatial scales from local (meters) to lake-wide (kilometers) due to various environmental factors such as substrate type, depth gradient, and dissolved oxygen (reviewed in Karatayev et al., 1998, 2015, 2018a, c). In addition, sessile organisms such as marine mussels and, in fresh waters, zebra and quagga mussels develop patchiness due to spatial self-organization (Rietkerk & Koppel, 2008), resulting in heterogenous distribution even on homogeneous substrates (Gascoigne et al., 2005; van de Koppel et al., 2005, 2008; Babarro & Carrington, 2013; Liu et al., 2014) further challenging their population estimations. To quantify their ecological role, timely and reliable estimates of *Dreissena* densities are extremely important both at the local (long-term monitoring station) scale and at the whole waterbody scale. Samples obtained using conventional methods (bottom grabs or diver assessments) require a long time for processing (reviewed in Karatayev et al., 2018a). Typically, results of lake-wide *Dreissena* population assessments became available for stakeholders after the sampling event, usually in 2 years (Nalepa et al., 2010), 3 years (Hunter & Simons, 2004; Patterson et al., 2005; Karatayev et al., 2014), or even 4 years later (Watkins et al., 2007; Karatayev et al., 2018b). An increase in the number of stations and replicates sampled has the potential to lead to even larger delays in reporting of population estimations, thus preventing the results from being used to inform managers and stakeholders and guide management actions in a timely manner.

These challenges in *Dreissena* population assessment could at least be partially overcome by using underwater videography (reviewed in Karatayev et al., 2018a). Although *Dreissena* in the Great Lakes have been studied using underwater video for more than two decades, most of these attempts were concentrated in the nearshore zone (Custer and Custer, 1997; Lietz et al., 2015; Ozersky et al., 2009, 2011; Mehler et al., 2018). Since 2015, in support of the Cooperative Science and Monitoring Initiative (CSMI), the Great Lakes Center at SUNY Buffalo State began conducting lake-wide *Dreissena* population assessments in all Great Lakes, with the exception of Lake Superior where mussels do not form sizable populations (Karatayev et al., 2018a, 2020). These lake-wide *Dreissena* assessments are based on the estimation of mussel coverage from 100 still images randomly distributed along the 500 m video footage from a GoPro camera mounted on a benthic sled towed by the U.S. Environmental Protection Agency (US EPA) R/V *Lake Guardian* (Karatayev et al., 2018a), and ground-truthed with Ponar samples. This method allows us to greatly increase the number of replicates analyzed per station and reduce the cost and time for information processing and data reporting. However, this method does not allow for direct counting of *Dreissena* mussels via video and therefore still requires a substantial amount of time for Ponar sample processing (on the order of months after the sampling event).

In this study, we developed a novel sampling method by using Benthic Imaging System (BIS, a drop frame equipped with a GoPro camera) across all three Lake Erie basins to estimate *Dreissena* populations (presence/absence, coverage, and density) in near real-time (during a typically two-week survey) to allow production of lake-wide maps of mussel distribution and preliminary population estimations. These preliminary data used to generate

the distribution maps were later compared with dreissenid data obtained from traditional Ponar grabs to assess the advantages and disadvantages of both methods. As Lake Erie consists of three basins that differ dramatically in morphometry, turbidity, and productivity, as well as in *Dreissena* distribution, density, and mussel length-frequency distribution (Karatayev et al., 2018c), it provides an excellent model to test the applicability of our rapid assessment method for *Dreissena* long-term monitoring across large and dynamic environmental gradients.

Materials and methods

Study area

Lake Erie's three basins include the shallowest western basin (average depth 7.4 m, maximum depth 19 m) which is polymictic and most productive; the mesotrophic, dimictic central basin of intermediate depth (average depth 18.3 m, maximum depth 25 m); and the deepest (average depth 24.4 m, maximum depth 64 m), dimictic, and most oligotrophic eastern basin (Mortimer, 1987; Barbiero & Tuchman, 2004; Conroy et al., 2005). Although the western basin is usually well mixed, occasionally it may experience short-term severe hypoxic events during extensive periods of calm weather (Ackerman et al., 2001; Bridgeman et al., 2006) that have a strong impact on the survival and distribution of benthic organisms sensitive to hypoxia (Bridgeman et al., 2006; Karatayev et al., 2018c). The central basin is deeper and, although well stratified, has a very thin hypolimnion. Due to the large input of nutrients and sediments from the western basin, the central basin usually becomes hypoxic by the end of the growing season in August–September, before the fall overturn (Mortimer, 1987; Scavia et al., 2014; Kraus et al., 2015; Bocaniov & Scavia, 2016; Karatayev et al., 2018c) and is also susceptible to sediment resuspension. The eastern edge of the central basin, however, receives well-oxygenated water from the eastern basin thermocline that keeps the eastern part of the central basin hypolimnion more oxygenated than other parts of the central basin (Boyce et al., 1980) and supports a stable *Dreissena* population (Karatayev et al., 2018c). The eastern basin also develops stable stratification during summer with a thick hypolimnion that never goes hypoxic due to its large volume and low inputs of suspended solids and nutrients (Kemp et al., 1977; Mortimer, 1987).

Dreissena sampling protocol

In July–August 2019, *Dreissena* spp. presence, density (number of individuals/m^2), total wet biomass (total wet weight, tissue with shell, g/m^2), and length-frequency distribution were measured at 95 stations, including 82 stations sampled aboard R/V *Lake Guardian* during the Lake Erie CSMI benthic survey in July, 10 stations sampled aboard the *Lake Guardian* during the US EPA Great Lakes Biology Monitoring Program Long-Term Monitoring (LTM) summer survey in August, and three shallow stations (973, DO2, ER03) in western basin sampled by a NOAA small vessel on July 11 (Fig. 1). During this survey, two types of samples were collected to study *Dreissena* which included (1) Ponar (sampling area 0.0523 m^2, coefficient used to recalculate density per m^2 = 19.12) samples that were processed for mussel presence, density, size-frequency distribution, and sediment analysis; (2) video images collected using BIS (sampling area 0.2154 m^2, coefficient used to recalculate density per m^2 = 5.16) that were processed for mussel presence, bottom coverage (%), and density

from 92 stations sampled aboard the R/V *Lake Guardian* (Fig. 1). Sampling details are described in Standard Operating Procedure for Benthic Invertebrate Field Sampling SOP LG406 (US EPA, 2019).

Three replicate Ponar samples for *Dreissena* were successfully collected at 93 stations from a total of 95 planned CSMI and LTM stations (samples were not collected at stations 948 and J31 due to hard substrate), and a total of 279 samples were analyzed for *Dreissena* population assessment. Because no video images were collected at stations sampled by NOAA, we did not use Ponar samples from these three shallow western basin stations in our BIS *vs.* Ponar comparison, but we did use these Ponars for calculation of *Dreissena* density and biomass. All *Dreissena* were identified to species, counted, and measured using a digital caliper (0.01 mm). All shell length measurements were rounded to the nearest mm, after which all *Dreissena* in each replicate were combined into 5 mm size groups and weighed to the nearest 0.001 g after being blotted dry on absorbent paper. Details are described in Standard Operating Procedure for Benthic Invertebrate Laboratory Analysis SOP LG407 (US EPA, 2015).

Video image analysis

Video images were collected from 92 stations during LTM and CSMI surveys using a BIS equipped with two GoPro Hero 5 Black cameras (one down-looking camera and one oblique (i.e., side-looking) camera; frame rate: 60 frames/s; screen resolution: 1920×1080 pixels; housing certified to a depth of 60 m) and two underwater lights per camera (Suptig 84-LED dive lights) attached to a custom-built stainless-steel carriage (for details see Angradi, 2018; Wick et al., 2020; Karatayev et al., in press). The down-looking camera was fixed 56 cm above substrate, and the side-looking camera was fixed 30 cm above substrate at an angle of about 45 degrees, resulting in a horizontal distance from the lens to the substrate of 1 m. At each station, the BIS was lowered from the starboard side of R/V *Lake Guardian* down to the lake bottom (SOP LG410; US EPA, 2019). The BIS remained on the lake bottom for 1 min (the first replicate, or RFS). This time duration was enough to increase the probability that a clear view of the area within the marked scale would be obtained, as any resuspended sediment was allowed to settle or clear from view. After 1 min, the BIS was lifted 1–2 m from the bottom for 30 s, then lowered again to remain on the lake bottom for another minute (second replicate-FD1), lifted again for 30 s, and then lowered to remain on the lake bottom for another minute (third replicate-FD2). All replicate BIS and Ponar grab samples were collected within the boundaries of an EPA station, with only one GPS record for each station. An EPA station is defined as "a bottom area of approximately 300 m in diameter. If, due to weather and currents, the *Lake Guardian* drifts far off the station, the boat will be re-positioned and sampling will resume" (SOP LG100; US EPA, 2014). After the frame was retrieved from the water, videos from both cameras were immediately downloaded to an external hard drive for onboard analysis. A total of 552 images were initially collected from both down and side-looking cameras (three replicates of each camera from each of the 92 stations). Of these, 482 images from the down- and/or side-looking cameras were used to record *Dreissena* presence/absence, while 235 and 232 images from the down-looking camera were used to record *Dreissena* coverage and to calculate mussel density, respectively. For each station, we used averaged data from three replicates both for coverage and density.

For each replicate, we used the clearest still image (screen shot) to estimate *Dreissena* coverage and density. Occasionally (at 10 stations with soft sediments) the frame sunk into the sediment; to avoid erroneous estimation of *Dreissena* size and counts, we used the screen shot taken exactly at the moment when the frame hit the lakebed. Mussel druses in each video screen shot were manually highlighted in Photoshop CS6 (Fig. 2). In all digitized images, *Dreissena* were black and the background was white (Fig. 2C). *Dreissena* coverage (%) was calculated by dividing the area covered by mussels (black) by total area of the image. For density estimations, all visible mussels were counted in the entire original clipped still image before digitizing (Fig. 2A) and the counts converted to density (individuals/m^2) using BIS sampling area 0.2154 m^2. In six cases with > 90% coverage, mussels were counted in three subsamples (10×10 cm each) and the subsample average was used to estimate *Dreissena* density. Unusable images were excluded from the analysis and therefore for three stations we used only two images (replicates) per station, and only one replicate image for another five stations.

According to US EPA Standard Operation Procedure (US EPA, 2019; SOP LG410) for quality control purposes at least 10% of randomly selected still images should be recounted by a different analyst. Percent errors in *Dreissena* coverage and counts less than 20% are considered acceptable, and all images with differences > 20% should be re-evaluated (US EPA, 2019; SOP LG410). For this study, we accepted a more rigorous threshold and in general considered images acceptable with < 10% differences in coverage and density. However, even small differences while processing images with a very low coverage (usually < 5%) can lead to a high percentage of error, and for such images we used a 20% threshold. Twelve percent of all samples (28 of the 232 total samples) were 're-digitized' for quality control purposes. Only three samples had > 20% difference in counts and were re-evaluated. On average, differences in *Dreissena* coverage across all other images was 11%, and differences in density were 8% (excluding samples with no mussels but including stations with very low coverage and density).

Environmental parameters used in this study were collected 1 m above the bottom from each of the 92 LTM and CSMI stations for which we have video data using a Rosette sampler equipped with a Seabird CTD, transmissometer (WETlab C-Star) measuring beam attenuation due to particles (660 nm wavelengths) across a 25 cm pathlength, and a dissolved oxygen (DO) sensor (SBE 43) deployed from the R/V *Lake Guardian*. We checked the normality of data using Shapiro–Wilk's test and when the data could not be transformed to meet the normality assumption, we used non-parametric tests. To compare beam attenuation coefficient (used as a proxy for turbidity), DO, and temperature among different Lake Erie basins (western, central, and eastern), we used Kruskal–Wallis ANOVA by ranks. To test the difference in density of *Dreissena* estimated for each station from BIS and Ponar grabs in different basins in Lake Erie, we used Wilcoxon Matched Pairs test. The Wilcoxon Matched Pairs test was also used to compare densities of *Dreissena* at stations sampled in 2014 and in 2019. Analyses were performed using Statistica (data analysis software system), version 13 (TIBCO Software Inc. (2018), http://tibco.com). All test effects were considered significant at $P < 0.05$ and marginally significant at $P < 0.10$.

Results

Dreissena population assessment using BIS *vs.* Ponar samples

Usable images for recording *Dreissena* presence/absence were collected with the BIS (from the down- and/or side-looking cameras) at a total of 86 of the 92 LTM and CSMI stations (93.5% success rate). Images from 82 stations (89.1% success rate) were usable for coverage estimation, and images from 81 stations (88.0% success rate) were used for both mussel counts and coverage. Images from one of the 17 western basin stations sampled with BIS were not usable for assessment of dreissenid presence/absence due to high turbidity. At another station in the western basin, images were too blurry to estimate coverage or to count mussels; however, *Dreissena* were visible and therefore the image was used to determine mussel presence. Similarly, of the 50 central basin stations sampled with BIS, presence/absence of mussels was not assessed at two stations due to high turbidity; at a third central basin station *Dreissena* presence, but not coverage or counts, could be assessed owing to high turbidity. In the eastern basin, algae cover prevented successful BIS sampling at two stations, and rough weather prevented sampling at two other stations. Ponar samples were successfully collected at all but two of the 92 LTM and CSMI stations (97.8% success rate).

From a total of 85 stations sampled with both BIS and Ponars, *Dreissena* spp. occurrence recorded with BIS was the highest in the eastern basin (95%), much lower in the western (44%) and central (32%) basins (Table 1; Fig. 3). Ponar samples revealed the same mussel occurrence (95%) in the eastern basin, 1.5-fold higher occurrence (47%) in the central basin, and 2.1-fold higher occurrence (94%) in the western basin. The discrepancies between BIS and Ponar data in the western basin were most likely due to high turbidity and a large proportion of juvenile mussels (< 10 mm) that were very hard to detect on video images. The average near-bottom beam attenuation coefficient (used as a proxy for turbidity) recorded during the 2019 CSMI study in the western, central, and eastern basins differed significantly among basins ($H = 41.8$, $P < 0.001$, Kruskal–Wallis test) and was, respectively, 1.63 ± 0.15/m, 0.74 ± 0.09/m, and 0.31 ± 0.13/m. In addition, the proportion of large mussels (> 10 mm) was also much smaller in western (23%) and central (33%) basins than in the eastern basin (61%). When mussels < 10 mm were excluded from the analysis, *Dreissena* occurrences estimated using BIS and Ponar became more similar: 32 vs. 36% in the central basin and 44 vs. 63% in the western basin, respectively (Table 1; Fig. 3).

Both coverage and density were the highest in the eastern basin, lower in the western, and the lowest in the profundal zone of central basin, which is a subject to annual hypoxia (Karatayev et al., 2018c). *Dreissena* spatial distribution estimated via BIS and Ponar samples for mussels > 10 mm showed similar patterns in the eastern basin, while in the western basin BIS substantially underestimated mussel coverage, especially when small mussels occurred in the population (Fig. 4).

In the eastern basin, average densities estimated using BIS (1015 ± 230/m^2) and Ponar grabs (1032 ± 179/m^2) were highly similar ($Z = 0.41$, $P = 0.68$, Wilcoxon Matched Pairs test). In the central basin which was dominated by small mussels, basin-wide average density estimated with Ponars (383 ± 196/m^2) was 1.4-fold higher than in BIS images (267 ± 126/m^2), although the difference was not significant ($Z = 1.37$, $P = 0.17$). The largest difference

($Z = 2.92$, $P = 0.0035$) between the two methods was found in the most turbid western basin where the Ponar-generated basin-wide average ($604 \pm 191/m^2$) was over 30-fold higher than BIS estimates ($18 \pm 10/m^2$).

Our rapid assessment of *Dreissena* densities in Lake Erie revealed a strong decline in Lake Erie mussel populations compared to the previous lake-wide survey (2014), which was confirmed by Ponar data. In the eastern basin, both methods revealed a 2.3-fold decline in the average density compared to 2014; however, the changes were not significant due to high variability in the data (Ponar: $Z = 1.57$, $P = 0.12$, BIS: $Z = 1.27$, $P = 0.20$, Wilcoxon Matched Pairs test, Fig. 5). Central basin *Dreissena* densities experienced almost the same decline (2.3-fold estimated with BIS, $Z = 1.82$, $P = 0.07$ and 1.6-fold with Ponar, $Z = 0.51$, $P = 0.61$). The largest significant changes were found in the western basin where BIS estimations suggested > 100-fold decline in *Dreissena* density in 2019 compared to 2014 ($Z = 2.90$, $P = 0.004$), while Ponar data revealed a marginally significant 5-fold decline ($Z = 1.93$, $P = 0.053$).

Dreissena population dynamics

The recent changes in dreissenid populations revealed by both video analysis and traditional grab and sorting methods have advanced our understanding of *Dreissena* spp. population dynamics in Lake Erie (Fig. 6). The largest and most unexpected changes were found in the western basin. The highest average wet biomass (832 ± 132 g/m^2) in the western basin was recorded in 2004, but then declined 18-fold to 48.0 ± 19.6 g/m^2 by 2019 (Fig. 6), the lowest biomass ever recorded in the basin. Due to high variability in the data, the changes in biomass between years were not significant ($H = 9.43$, $P = 0.15$, Kruskal–Wallis test). During the same time period, *Dreissena* density decreased less than 3-fold ($H = 14.33$, $P = 0.026$) due to a dramatic decline in mussel average weight from 0.50 g in 2004 to 0.08 g by 2019. In 2019, the *Dreissena* population in the western basin was dominated by small juvenile mussels: 77% of all mussels were < 10 mm, of which 53% were < 5 mm) (Fig. 7). In addition to higher near-bottom turbidity, the amount of dissolved oxygen in the western basin measured 1 m above the bottom was two times lower (4.86 ± 0.72 vs. 10.38 ± 0.42 mg/L, $H = 36.05$, $P < 0.0001$, Kruskal–Wallis test) than in the eastern basin. Hypoxic conditions at 1 m above the bottom (oxygen < 2 mg/L) were found at three of the 16 western basin stations (19%), and anoxic (0.9 mg/L) at one station. Finally, due to shallow depths, the bottom temperature in the western basin was two times as high than in the eastern and central basins (20.0 ± 0.7°C vs. 9.6 ± 0.4 and 7.9 ± 1.2°C, respectively; $H = 35.75$, $P < 0.0001$).

In the central basin, both density and especially biomass changed significantly among years ($H = 27.68$, $P < 0.001$, Kruskal–Wallis test); both were high during the first 10 years after colonization, and then started to decline after 1998. Initially this decline was more pronounced in density, which dropped 4.7-fold between 1998 and 2002, while biomass declined only < 1.2-fold during same time period. Mussels became larger (average weight increased from 0.13 to 0.5 g from 1998 to 2002), most likely due to the lack of successful recruitment. During the last 15 years, however, both average densities and biomass were very low in the central basin. Similar to the western basin, the *Dreissena* population in the

central basin is now largely dominated by small mussels, especially at depths > 20 m which are subject to seasonal hypoxia (Fig. 7; Karatayev et al., 2018c). The average dissolved oxygen concentration in July and August recorded 1 m above the bottom was 6.00 ± 0.32 mg/L, similar to the western basin ($Z = 1.00$, $P = 0.95$), but significantly lower than in the eastern basin ($Z = 5.41$, $P < 0.0001$, multiple comparisons after Kruskal–Wallis test). Of the 48 central basin stations, only 8.3% (4) had hypoxic bottom waters, and one had anoxic bottom waters.

In the eastern basin, a *Dreissena* population maximum occurred in 2002, followed by declines in both density and biomass (density: H = 37.23, $P < 0.001$, biomass: $H = 18.13$, $P = 0.006$, Kruskal–Wallis test, Fig. 6). The decline in population density, however, was more pronounced/more rapid than in biomass, due to an almost 10-fold increase in mussel average weight (from 0.09 g in 1998 to 0.83 g in 2019). In 2019, *Dreissena* basin-wide average weight in the eastern basin was > 10-fold higher than in the western, and 3.4-fold higher than in the central basin. Also in 2019, the depth zone < 40 m in the eastern basin was the only portion of Lake Erie where the *Dreissena* population was represented by multi-year cohorts (Fig. 7), while at depths > 40 m the population was dominated by mussels > 16 mm. Hypolimnetic waters of the western basin were normoxic. The lowest bottom-water oxygen concentration was 6.7 mg/L, and all deep stations (> 40 m) were saturated with oxygen (> 12 mg/L).

Ninety nine percent of all *Dreissena* collected in the eastern basin in 2019 were quagga mussels, while in the central basin quaggas comprised 79% of combined density and 75% of biomass. The largest proportion of zebra mussels, as in previous years, was found in the western basin where they represented 72% of combined dreissenid density and 59% of biomass.

Sampling and processing time costs

The use of BIS for *Dreissena* population assessment substantially reduced processing time and allowed for production of maps of distribution and density in near real-time. During our first lake-wide BIS survey of Lake Erie in 2019, we were able to complete maps of *Dreissena* abundance and coverage within 12 h after the last station was sampled. The total time on station to collect video images using BIS is comparable to the time it takes to collect three Ponar samples (Table 2). Processing three replicate Ponar samples from one station for *Dreissena* density, size structure, and biomass requires, on average, 21 h for a technician to sort, count and weigh mussels, measure their length-frequency distribution, and enter data into a database (Karatayev et al., 2018a). In contrast, full processing of three video images requires only 0.5 h and can be processed shipboard immediately after sample collection (Table 2). In addition, three replicates from BIS generated a combined sampling area four times greater than three Ponar replicate samples (0.65 m^2 vs. 0.16 m^2). Successful application of BIS, however, is limited to areas of low turbidity and where macrophytes are absent. Therefore, we were able to sample more stations with Ponar (90 stations) than with BIS (82 stations), and BIS largely underestimated *Dreissena* spp. coverage and densities in the most turbid western basin. In addition, BIS cannot be used for *Dreissena* species identification and determination of length-frequency distributions.

Discussion

Systematic approaches for assessing species density using underwater imaging have already been developed in the context of fish monitoring in freshwater (e.g., Egg et al., 2018) as well as fish and invertebrates in marine ecosystems (Diaz et al. 2003; Kannappan et al., 2014; Williams et al., 2015; Ferrari et al., 2018), yet such analyses are still lacking for freshwater mussels. We have developed a novel assessment method using the Benthic Imaging System (BIS) to estimate *Dreissena* spp. distribution and density in near real-time across large waterbodies like the Great Lakes. Comparison of the results of our rapid assessment with Ponar grab data collected at the same stations showed that the agreement depends on near-bottom turbidity and size structure of dreissenids. Despite undersampling of small mussels, the BIS method provided a rapid and reliable estimation of density of ecologically important large mussels. Underestimated by this method, the newly settled small dreissenids have very high mortality, very low biomass, and thus a negligible functional role. Our results showed that by substantially reducing the time to assess dreissenid distribution and population size across large areas, rapid assessment could be a useful and cost-effective addition for monitoring dreissenid populations in the Great Lakes and other freshwater systems where they occur, excluding areas with high turbidity and covered by macrophytes.

Dreissena population assessment using BIS vs. Ponar collection

In the eastern basin of Lake Erie, BIS estimations of *Dreissena* distribution and density were almost identical to estimations from Ponar data. This basin had the highest visibility and supported the largest dreissenid population represented by mussels of various sizes, from recently settled individuals to older mussels up to > 45 mm in length (Figs. 4, 7). The presence of old mussels (> 3 years) across all eastern basin depth zones sampled indicates an environment supportive of stable dreissenid populations characterized by, most importantly, a lack of hypoxia (Karatayev et al., 2018c). However, due to food competition with large mussels, no successful recruitment was recorded since 2009 at depths > 40 m (Karatayev et al., 2018c, d).

In the central basin, there was a small non-significant difference between BIS and Ponar estimations of *Dreissena* distribution and density. Both BIS and Ponar dreissenid count data along with oxygen data confirm previous findings that *Dreissena* spp. occur in the central basin at high densities only at shallow depths. Due to their sensitivity to the lack of oxygen (reviewed in Karatayev et al., 1998, 2007a, 2015; McMahon & Bogan, 2001), *Dreissena* were nearly absent at depths > 20 m, where bottom hypoxia routinely develops in August–September (Figs. 3, 4; Karatayev et al., 2018c). The only exception to this observation was the eastern edge of the central basin which receives well-oxygenated water from the eastern basin (Boyce et al., 1980) and supports stable *Dreissena* populations at > 20 m (Karatayev et al., 2018c, Fig. 4). In most of the hypoxic zone, *Dreissena* were either absent or represented by mussels < 10 mm that likely settled at the beginning of the growing season before the development of hypoxia (Karatayev et al., 2018c). Although these small mussels were largely missed on video images, *Dreissena* distribution obtained via BIS in the central basin corresponded well with Ponar data and thus could be used as a rapid method to map the central basin hypoxic zone (see Karatayev et al. 2018c).

In the western basin, BIS largely underestimated both *Dreissena* occurrence and density (Fig. 3, 4). At least two reasons could be responsible for this discrepancy: high turbidity and high proportion of small mussels (Fig. 7) that are difficult to recognize on the image, especially if visibility is limited. Although the proportion of mussels < 10 mm in the western and central basin were similar (67% vs. 77%), differences in *Dreissena* occurrence and density estimations between BIS and Ponar in the central basin were much smaller than in the western basin (Figs. 3, 4), and became almost identical when mussels < 10 mm were excluded. More reliable data obtained via BIS estimations in the central basin suggest that the discrepancy between Ponar and BIS estimates in the western basin can be attributed to higher turbidity in the western basin since proportions of small mussels in these two basins were very similar (Fig. 7).

Although *Dreissena* density was higher in the western basin compared to the central basin, populations in both basins were dominated by small mussels (Figs. 4, 7). As noted in 2014, over 98% of all *Dreissena* spp. found in the western basin were < 18 mm in length (e.g., < 3 years old), suggesting that populations of *Dreissena* in both basins are subject to periodic mortality events most likely linked with periodic hypoxia (Karatayev et al., 2018c). Although the western basin is shallow and considered a polymictic waterbody, it is prone to episodic severe oxygen depletion events at high water temperatures and calm weather (Ackerman et al., 2001; Bridgeman et al., 2006; Karatayev et al., 2018c). It is likely that periodic massive die-offs in the western basin occur once every 2–3 years, following recolonization from adjacent shallow areas in Lake Erie unaffected by hypoxia, or from upstream tributaries, e.g., in the St. Clair–Detroit River system.

Dreissena population dynamics

Rapid assessment in 2019 revealed *Dreissena* population decline in all three Lake Erie basins compared to 2014 data (Fig. 6). The largest decline in *Dreissena* spp. density was recorded in the western basin. Based on BIS estimations, *Dreissena* densities in 2019 were among the lowest across all three Lake Erie basins for > 25 years record of observations. Ponar data largely confirmed results of the rapid assessment in the central and eastern basins. Although the decline in the western basin estimated via Ponar samples was not as large as the decline estimated via BIS, the patterns were rather similar. In addition to density, we also found an 18-fold decline in *Dreissena* spp. wet biomass from 2004 to 2019, suggesting significant decline in the ecological role of *Dreissena* in the western basin. The ecosystem response to mussel filtration activity in the western basin, however, was the lowest among Lake Erie basins even early in the invasion, when *Dreissena* spp. population densities and biomass were higher (Karatayev et al., 2018b), likely due to high external load of suspended solids and sediment resuspension inhibiting *Dreissena* filtering capacity (Barbiero & Tuchman, 2004).

In the central basin, both *Dreissena* density and especially biomass were high during the first 10 years of colonization, and then started to decline due to an increase in the hypoxic zone extent in the late 1990s and 2000s, which was likely driven by increases in dissolved reactive phosphorus (Richards et al., 2010; Scavia et al., 2014). The increasing DRP trend after the mid-1990s appear to have resulted from recent increases in climate change-driven

storm event frequency and intensity interacting with changes in fertilizer application timing and rate, as well as management practices that increase soil stratification and phosphorus accumulation at the soil surface (Daloˉlu et al., 2012). The increase in hypoxia in the central basin of Lake Erie has had strong impacts on the distribution and migration of a number of aquatic organisms including fish, zooplankton, and phytoplankton communities (Vanderploeg et al., 2009; Scavia et al., 2014; Kraus et al., 2015), has caused severe declines in *Dreissena* density and biomass, and has altered *Dreissena* spatial distribution (Karatayev et al., 2018c). This decline was associated with the decrease in spring dissolved silica concentrations and increases in total phosphorus and near-bottom turbidity not observed in other basins (Karatayev et al., 2018b).

In contrast to populations dominated by small mussels in the western and central basins, the eastern basin *Dreissena* populations are still represented by multi-year cohorts, resulting in much higher average mussel size than in other basins (Fig. 7). Although *Dreissena* density in the eastern basin also declined dramatically after 2002, similar to the western and central basins, population biomass in 2019 was still high. Therefore, the eastern basin is the only Lake Erie basin exhibiting strong ecological impacts of *Dreissena* including increases in water clarity and decreases in phytoplankton, turbidity, and total phosphorus concentrations in the water column (Karatayev et al., 2018b).

Potential applications of BIS

The success rate of BIS application varied among Lake Erie basins and was very effective in the eastern basin where *Dreissena* was dominated by large mussels and near-bottom turbidity was low. In the central and especially western basins, the method was largely limited by high turbidity and dominance of small mussels. Overall success rate of BIS application in the 2019 Lake Erie survey was very similar to a previously conducted video survey at 53 US EPA Great Lakes Biology Monitoring Program LTM stations across all Great Lakes in 2014 where acceptable bottom images were obtained from 87% of the stations sampled using a GoPro installed on a benthic sled towed for 500 m with R/V *Lake Guardian* (Karatayev et al., 2018a). Both the 2014 and 2019 surveys had generally higher success rates compared to the usage of underwater videos in shallow stations with macrophyte coverage and high turbidity (Ozersky et al., 2011; Lietz et al., 2015).

Compared to our earlier method which collected video via a camera towed by a benthic sled (Karatayev et al., 2018a), the BIS produced much clearer images, allowing direct counting of dreissenid mussels. Counting was especially successful in the eastern basin where BIS basin-wide estimation of average density was almost identical to estimates using Ponar data (3% difference). Similarly, application of the BIS camera in Lake Ontario in 2018 produced usable mussel count images of all 33 stations sampled, and average BIS density estimations were not different ($P = 0.24$) from Ponar estimations (authors unpublished data). Most of the CSMI surveys conducted to generate Great Lakes *Dreissena* population assessments occur in areas with low turbidity where BIS video methods could be successfully used for rapid assessment to produce near real-time data on mussel distribution and density.

It should be stressed, however, that despite several advantages of BIS video methods, traditional Ponar samples are still essential as they produce information on species

composition, size-frequency distribution, and density data necessary to calibrate and verify the results of rapid video assessment. Bottom grabs also remain reliable options for sampling areas with high turbidity and macrophyte coverage. Similar to video image analysis from benthic sled tows, BIS should be used in tandem with the conventional Ponar grabs as both methods have their own unique strengths. Our BIS-Ponar combined approach demonstrates advantages for efficient monitoring of *Dreissena* populations in the Great Lakes and other freshwater systems that yield valuable information not obtainable by either method alone.

Benthic video may be the only possible tool to study *Dreissena* coverage over large areas characterized by hard substrates (e.g., bedrock, boulders), where bottom grabs are not efficient (Lietz et al., 2015; Karatayev et al., 2018c) and use of SCUBA divers is prohibitively expensive. In addition, BIS videos could be used to estimate presence and density of round gobies, *Neogobius melanostomus* (Karatayev et al., in press), and, possibly, bottom-dwelling *Mysis*. Furthermore, the oblique-view camera provides useful information on the 3-dimensional structure of *Dreissena* aggregations, substrate characteristics, and spatial distribution of benthic habitats and communities (Burlakova et al., in preparation). By substantially reducing lab processing time, benthic video surveys show promise as effective tools to improve estimates of *Dreissena* population trajectories over time, which is of key interest to Great Lakes scientists and managers considering that dreissenids are now the major drivers of ecological processes in the Great Lakes (Fahnenstiel et al., 2010; Bunnell et al., 2014; Karatayev et al., 2015; Barbiero et al., 2018; Burlakova et al., 2018).

References

Ackerman JD, Loewen MR & Hamblin PF, 2001. Benthic–pelagic coupling over a zebra mussel reef in western Lake Erie. Limnology and Oceanography 46: 892–904.

Angradi TR, 2018. A field observation of rotational feeding by *Neogobius melanostomus*. Fishes. 3(1): 5.

Babarro JMF & Carrington E, 2013. Attachment strength of the mussel *Mytilus galloprovincialis*: effect of habitat and body size. Journal of Experimental Marine Biology and Ecology 443: 188–196.

Barbiero RP & Tuchman ML, 2004. Long-term dreissenid impacts on water clarity in Lake Erie. Journal of Great Lakes Research 30: 557–565.

Barbiero R, Lesht BM, Warren GJ, Rudstam LG, Watkins JM, Reavie ED, Kovalenko KE & Karatayev AY, 2018. A comparative examination of recent changes in nutrients and lower food web structure in Lake Michigan and Lake Huron. Journal of Great Lakes Research 44: 573–589. [PubMed: 31156289]

Bocaniov SA & Scavia D, 2016. Temporal and spatial dynamics of large lake hypoxia: integrating statistical and three-dimensional dynamic models to enhance lake management criteria. Water Resources Research 52: 4247–4263.

Boyce FM, Chiocchio F, Eid B, Penicka F & Rosa F, 1980. Hypolimnion flow between the central and eastern basins of Lake Erie during 1977 (inter-basin hypolimnion flows). Journal of Great Lakes Research 6: 290–306.

Bridgeman TB, Schloesser DW & Krause AE, 2006. Recruitment of *Hexagenia* mayfly nymphs in western Lake Erie linked to environmental variability. Ecological Applications 16: 601–611. [PubMed: 16711047]

Bunnell DB, Barbiero RP, Ludsin SA, Madenjian CP, Warren GJ, Dolan DM, Brenden TO, Briland R, Gorman OT, He Ji X., Johengen TH, Lantry BF, Lesht BM, Nalepa TF, Riley SC, Riseng CM, Treska TJ, Tsehaye I, Walsh MG, Warner DM & Weidel BC, 2014. Changing ecosystem dynamics in the Laurentian Great Lakes: bottom-up and top-down regulation. BioScience 64: 26–39.

Burlakova LE, Barbiero RP, Karatayev AY, Daniel SE, Hinchey EK & Warren GJ, 2018. The benthic community of the Laurentian Great Lakes: analysis of spatial gradients and temporal trends from 1998 to 2014. Journal of Great Lakes Research 44: 600–617. [PubMed: 31031520]

Burlakova LE, Karatayev AY, Hinchey EK, Mehler K, Daniel SE, Hrycik A & Nestlerode J. In preparation. Exploring Great Lakes benthoscapes: can we visually delineate freshwater benthic communities?

Conroy JD, Kane DD, Dolan DM, Edwards WJ, Charlton MN & Culver DA, 2005. Temporal trends in Lake Erie plankton biomass: roles of external phosphorus loading and dreissenid mussels. Journal of Great Lakes Research 31(Suppl. 2): 89–110.

Custer CM & Custer TW, 1997. Occurrence of zebra mussels in nearshore areas of western Lake Erie. Journal of Great Lakes Research 23: 108–115.

Dalo lu I, Cho KH & Scavia D, 2012. Evaluating causes of trends in long-term dissolved reactive phosphorus loads to Lake Erie. Environmental Science & Technology 46(19): 10660–10666. [PubMed: 22962949]

Demott R & Dow J, 2008. Changing benthic fauna of Lake Erie between 1993 and 1998. In Munawar M & Heath R (eds), Checking the Pulse of Lake Erie. Goodwords Books, New Delhi: 409–438.

Diaz RJ, Cutter GR Jr. & Able KW, 2003. The importance of physical and biogenic structure to juvenile fishes on the shallow inner continental shelf. Estuaries 26: 12–20.

Egg L, Pander J, Mueller M & Geist J, 2018. Comparison of sonar-, camera- and net-based methods in detecting riverine fish-movement patterns. Marine and Freshwater Research 69: 1905–1912.

Fahnenstiel G, Pothoven S, Nalepa T, Vanderploeg H, Klarer D & Scavia D, 2010. Recent changes in primary production in the offshore region of southeastern Lake Michigan. Journal of Great Lakes Research 36(Suppl. 3): 20–29.

Ferrari R, Marzinelli EM, Ayroza CR, Jordan A, Figueira WF, Byrne M, Malcolm HA, Williams SB & Steinberg PD, 2018. Large-scale assessment of benthic communities across multiple marine protected areas using an autonomous underwater vehicle. PLoS ONE. 10.1371/journal.pone.0193711.

Gascoigne JC, Beadman HA, Saurel C & Kaiser MJ, 2005. Density dependence, spatial scale and patterning in sessile biota. Oecologia 145: 371–381. [PubMed: 15968539]

Higgins SN & Vander Zanden MJ, 2010. What a difference a species makes: a meta-analysis of dreissenid mussel impacts on freshwater ecosystems. Ecological Monographs 80: 179–196.

Hunter RD & Simons KA, 2004. Dreissenids in Lake St. Clair in 2001: evidence for population regulation. Journal of Great Lakes Research 30: 528–537.

Jarvis P, Dow J, Dermott R & Bonnell R, 2000. Zebra (*Dreissena polymorpha*) and quagga mussel (*Dreissena bugensis*) distribution and density in Lake Erie, 1992–1998. Canadian Technical Report of Fisheries and Aquatic Sciences 2304: 1–46.

Kannappan P, Walker JH, Trembanis A & Tanner HG, 2014. Identifying sea scallops from benthic camera images. Limnology and Oceanography. 10.4319/lom.2014.12.680.

Karatayev AY, Burlakova LE & Padilla DK, 1997. The effects of *Dreissena polymorpha* (Pallas) invasion on aquatic communities in Eastern Europe. Journal of Shellfish Research 16: 187–203.

Karatayev AY, Burlakova LE & Padilla DK, 1998. Physical factors that limit the distribution and abundance of *Dreissena polymorpha* (Pall.). Journal of Shellfish Research 17: 1219–1235.

Karatayev AY, Burlakova LE & Padilla DK, 2002. Impacts of zebra mussels on aquatic communities and their role as ecosystem engineers. In Leppäkoski E, Gollach S & Olenin S (eds), Invasive aquatic species of Europe: distribution, impacts and management. Kluwer Academic Publishers, Dordreicht: 433–446.

Karatayev AY, Padilla DK, Minchin D, Boltovskoy D & Burlakova LE, 2007a. Changes in global economies and trade: the potential spread of exotic freshwater bivalves. Biological Invasions 9: 161–180.

Karatayev AY, Boltovskoy D, Padilla DK & Burlakova LE, 2007b. The invasive bivalves *Dreissena polymorpha* and *Limnoperna fortunei*: parallels, contrasts, potential spread and invasion impacts. Journal of Shellfish Research 26: 205–213.

Karatayev AY, Burlakova LE, Karatayev VA & Boltovskoy D, 2010. *Limnoperna fortunei* vs. *Dreissena polymorpha*: population densities and benthic community impacts of two invasive freshwater bivalves. Journal of Shellfish Research 29: 975–985.

Karatayev AY, Burlakova LE, Pennuto C, Ciborowski J, Karatayev VA, Juette P & Clapsadl M, 2014. Twenty five years of changes in *Dreissena* spp. populations in Lake Erie. Journal of Great Lakes Research 40: 550–559.

Karatayev AY, Burlakova LE & Padilla DK, 2015. Zebra versus quagga mussels: a review of their spread, population dynamics, and ecosystem impacts. Hydrobiologia 746: 97–112.

Karatayev AY, Burlakova LE, Mehler K, Hinchey EK & Warren G, 2018a. Benthic video image analysis facilitates monitoring of *Dreissena* populations across spatial scales. Journal of Great Lakes Research 44: 629–638. [PubMed: 31359906]

Karatayev AY, Burlakova LE, Mehler K, Barbiero RP, Hinchey EK, Collingsworth PD, Kovalenko KE & Warren G, 2018b. Life after *Dreissena*: the decline of exotic suspension feeder may have significant impacts on lake ecosystems. Journal of Great Lakes Research 44: 650–659. [PubMed: 30505066]

Karatayev AY, Burlakova LE, Mehler K, Bocaniov SA, Collingsworth PD, Warren G, Kraus RT & Hinchey EK, 2018c. Biomonitoring using invasive species in a large lake: *Dreissena* distribution maps hypoxic zones. Journal of Great Lakes Research 44: 639–649. [PubMed: 30713364]

Karatayev AY, Karatayev VA, Burlakova LE, Rowe MD, Mehler K & Clapsadl MD, 2018d. Food depletion regulates the demography of invasive dreissenid mussels in a stratified lake. Limnology and Oceanography 63: 2065–2079.

Karatayev AY, Burlakova LE, Mehler K, Daniel SE, Elgin AK & Nalepa TF, 2020. Lake Huron Benthos Survey Cooperative Science and Monitoring Initiative 2017. Technical Report. USEPA-GLRI GL00E02254. Great Lakes Center, SUNY Buffalo State, Buffalo, NY. Available at: https://greatlakescenter.buffalostate.edu/sites/greatlakescenter.buffalostate.edu/files/uploads/Documents/Publications/LakeHuronBenthosSurveyCSMI2017FinalReport.pdf.

Karatayev AY, Burlakova LE, Mehler K, Rudstam LG, Watkins JM & Wick M, in press. *Dreissena* in Lake Ontario 30 years post-invasion. Journal of Great Lakes Research. 10.1016/j.jglr.2020.11.010

Kemp ALW, MacInnis GA & Harper NS, 1977. Sedimentation rates and a revised sediment budget for Lake Erie. Journal of Great Lakes Research 3: 221–233.

Kraus RT, Knight CT, Farmer TM, Gorman AM, Collingsworth PD, Warren GJ, Kocovsky PM & Conroy JD, 2015. Dynamic hypoxic zones in Lake Erie compress fish habitat, altering vulnerability to fishing gears. Canadian Journal of Fisheries and Aquatic Sciences 72: 797–806.

Lietz JE, Kelly JR, Scharold JV & Yurista PM, 2015. Can a rapid underwater video approach enhance the benthic assessment capability of the national coastal condition assessment in the Great Lakes? Environ. Manage 55: 1446–1456. [PubMed: 25832344]

Liu Q-X, Herman PMJ, Mooij WM, Huisman J, Scheffer M, Olff H & van de Koppel J, 2014. Pattern formation at multiple spatial scales drives the resilience of mussel bed ecosystems. Nature Communications. 10.1038/ncomms6234.

Mehler K, Burlakova LE, Karatayev AY, Biesinger Z, Valle-Levinson A, Castiglione C & Gorsky D, 2018. Sonar technology and underwater imagery analysis can enhance invasive *Dreissena* distribution assessment in large rivers. Hydrobiologia 810: 119–131.

McMahon RF & Bogan AF, 2001. Mollusca: bivalvia. In Thorp JH & Covich AP (eds), Ecology and classification of North American freshwater invertebrates. Academic Press, New York: 331–430.

Mortimer CH, 1987. Fifty years of physical investigations and related limnological studies on Lake Erie, 1928–1977. Journal of Great Lakes Research 13: 407–435.

Nakano D & Strayer D, 2014. Biofouling animals in fresh water: ecology, impacts, and ecological engineering. Frontiers in Ecology and the Environment 12: 167–175.

Nalepa TF & Schloesser DW, 1993. Zebra Mussels Biology, Impacts, and Control. Lewis Publishers, Boca Raton.

Nalepa TF, Fanslow DL & Pothoven SA, 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.

O'Neill CR Jr., 2008. The Silent Invasion: Finding Solutions to Minimize the Impacts of Invasive Quagga Mussels on Water Rates, Water Infrastructure and the Environment. Hearing of the U.S. House of Representatives Committee on Natural Resources–Subcommittee on Water and Power, Washington, DC Available at: http://naturalresources.house.gov/uploadedfiles/oneilltestimony06.24.08.pdf.

Ozersky T, Malkin SY, Barton DR & Hecky RE, 2009. Dreissenid phosphorus excretion can sustain *C. glomerata* growth along a portion of Lake Ontario shoreline. Journal of Great Lakes Research 35: 321–328.

Ozersky T, Barton DR, Depew DC, Hecky RE & Guildford SJ, 2011. Effects of water movement on the distribution of invasive dreissenids mussels in Lake Simcoe, Ontario. Journal of Great Lakes Research 37: 46–54.

O go M, Urba ska M, Hoos P, Imhof HK, Kirschenstein M, Mayr J, Michl F, Tobiasz R, von Wesendonk M, Zimmermann S & Geist J, 2020. Invasive zebra mussel (*Dreissena polymorpha*) threatens an exceptionally large population of the depressed river mussel (*Pseudanodonta complanata*) in a postglacial lake. Ecology and Evolution 10: 4918–4927. [PubMed: 32551070]

Patterson MWR, Ciborowski JJH & Barton DR, 2005. The distribution and abundance of *Dreissena* species (Dreissenidae) in Lake Erie, 2002. Journal of Great Lakes Research 31: 223–237.

Pergl J, Pyšek P, Essl F, Jeschke JM, Courchamp F, Geist J, Hejda M, Kowarik I, Mill A, Musseau C, Pipek P, Saul WC, von Schmalensee M & Strayer D, 2020. Need for routine tracking of biological invasions. Conservation Biology 34: 1311–1314. [PubMed: 31773813]

Richards RP, Baker DB, Crumrine JP & Stearns AM, 2010. Unusually large loads in 2007 from the Maumee and Sandusky Rivers, tributaries to Lake Erie. Journal of Soil and Water Conservation 65: 450–462.

Rietkerk M & van de Koppel J, 2008. Regular pattern formation in real ecosystems. Trends in Ecology and Evolution 23: 169–175. [PubMed: 18255188]

Scavia D, Allan JD, Arend KK, Bartell S, Beletsky D, Bosch NS, Brandt SB, Briland RD, Daloglu I, DePinto JV, Dolan DM, Evans MA, Farner TM, Goto D, Han H, Hook TO, Knight R, Ludsin SA, Mason DM, Michalak AM, Richards RP, Roberts JJ, Rucinski DK, Rutherford ES, Schwab DJ, Sesterhenn T, Zhang H & Zhou Y, 2014. Assessing and addressing the re-eutrophication of Lake Erie: central basin hypoxia. Journal of Great Lakes Research 40: 226–246.

Strayer DL, Adamovich BV, Adrian R, Aldridge DC, Balogh C, Burlakova LE, Fried-Petersen H, Tóth LG, Hetherington AL, Jones TS, Karatayev AY, Madill JB, Makarevich OA, Marsden JE, Martel AL, Minchin D, Nalepa TF, Noordhuis R, Robinson TJ, Rudstam LG, Schwalb AN, Smith DR, Steinman AD & Jeschke JM, 2019. Long-term population dynamics of dreissenid mussels (*Dreissena polymorpha* and *D. rostriformis*): a cross-system analysis. Ecosphere. 10.1002/ecs2.2701.

US EPA, 2014. SOP LG100, Standard Operating Procedure for General Shipboard Scientific Operation, Revision 05, March 2014. Great Lakes National Program Office, U.S. Environmental Protection Agency, Chicago, IL.

US EPA, 2015. SOP LG407, Standard Operating Procedure for Benthic Invertebrate Laboratory Analysis, Revision 09, April 2015. Great Lakes National Program Office, U.S. Environmental Protection Agency, Chicago, IL.

US EPA, 2019. SOP LG406, Standard Operating Procedure for Benthic Invertebrate Field Sampling, Revision 13, March 2019. Great Lakes National Program Office, U.S. Environmental Protection Agency, Chicago, IL.

US EPA, 2019. SOP LG410, Standard Operating Procedure for Collection and Processing of Drop-Down Camera Images for *Dreissena* spp. and round goby (*Neogobius melanostomus*) monitoring, Revision 0, July 2019. Great Lakes National Program Office, U.S. Environmental Protection Agency, Chicago, IL.

van de Koppel J, Rietkerk M, Dankers N & Herman PMJ, 2005. Scale-dependent feedback and regular spatial patterns in young mussel beds. The American Naturalist 165: E66–E77.

van de Koppel J, Gascoigne JC, Theraulaz G, Rietkerk M, Mooij WM & Herman PMJ, 2008. Experimental evidence for spatial self-organization and its emergent effects in mussel bed ecosystems. Science 322: 739–742. [PubMed: 18974353]

Vanderploeg HA, Ludsin SA, Ruberg SA, Höök TO, Pothoven SA, Brandt SB, Lang GA, Liebig JR & Cavaletto JF, 2009. Hypoxia affects spatial distributions and overlap of pelagic fish, zooplankton, and phytoplankton in Lake Erie. Journal of Experimental Marine Biology and Ecology 381: 92–107.

van der Velde G, Rajagopal S & bij de Vaate A, 2010. The Zebra Mussel in Europe. Backhaus Publishers, Leiden.

Watkins JM, Dermott R, Lozano SJ, Mills EL, Rudstam LG & Scharold JV, 2007. Evidence for remote effects of dreissenids mussels on the amphipod *Diporea*: analysis of Lake Ontario benthic surveys, 1997-2003. Journal of Great Lakes Research 33: 642–657.

Wick M, Angradi TR, Pawlowski M, Bolgrien D, Debbout R, Launspach J & Nord M, 2020. Deep Lake Explorer: a web application for crowdsourcing the classification of benthic underwater video from the Laurentian Great Lakes. Journal of Great Lakes Research 46: 1469–1478. [PubMed: 33424103]

Williams A, Althaus F & Schlacher TA, 2015. Towed camera imagery and benthic sled catches provide different views of seamount benthic diversity. Limnology and Oceanography 13: 62–73.
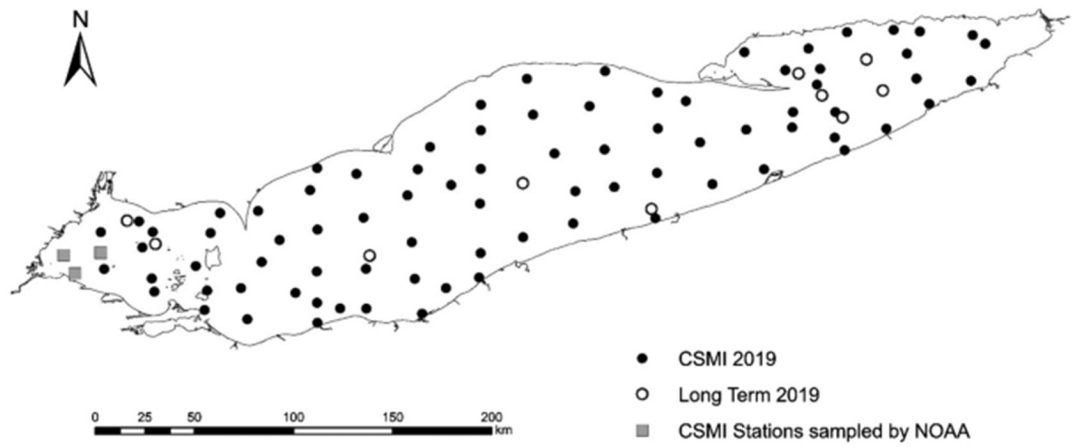
Fig. 1.
Location of stations in Lake Erie in 2019 sampled for *Dreissena* during July CSMI and August LTM cruises aboard the R/V *Lake Guardian* and NOAA research vessel
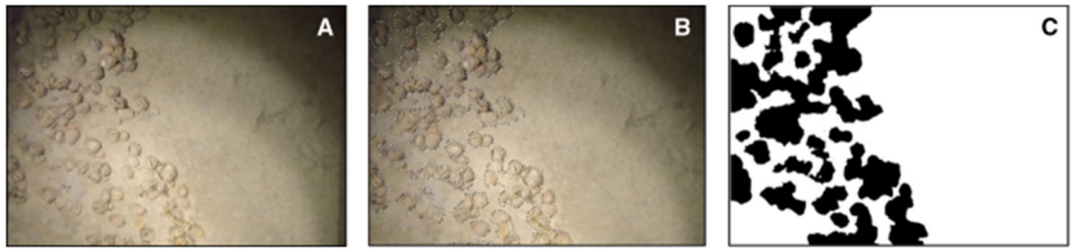
Fig. 2.

Dreissena in original clipped still image before digitizing (A), with *Dreissena* digitized (B), and in black and white image after *Dreissena* digitized (C). In digitized images *Dreissena* appear black and the background appears white. *Dreissena* coverage (%) is calculated by dividing the area covered by mussels (black) by total area of the image
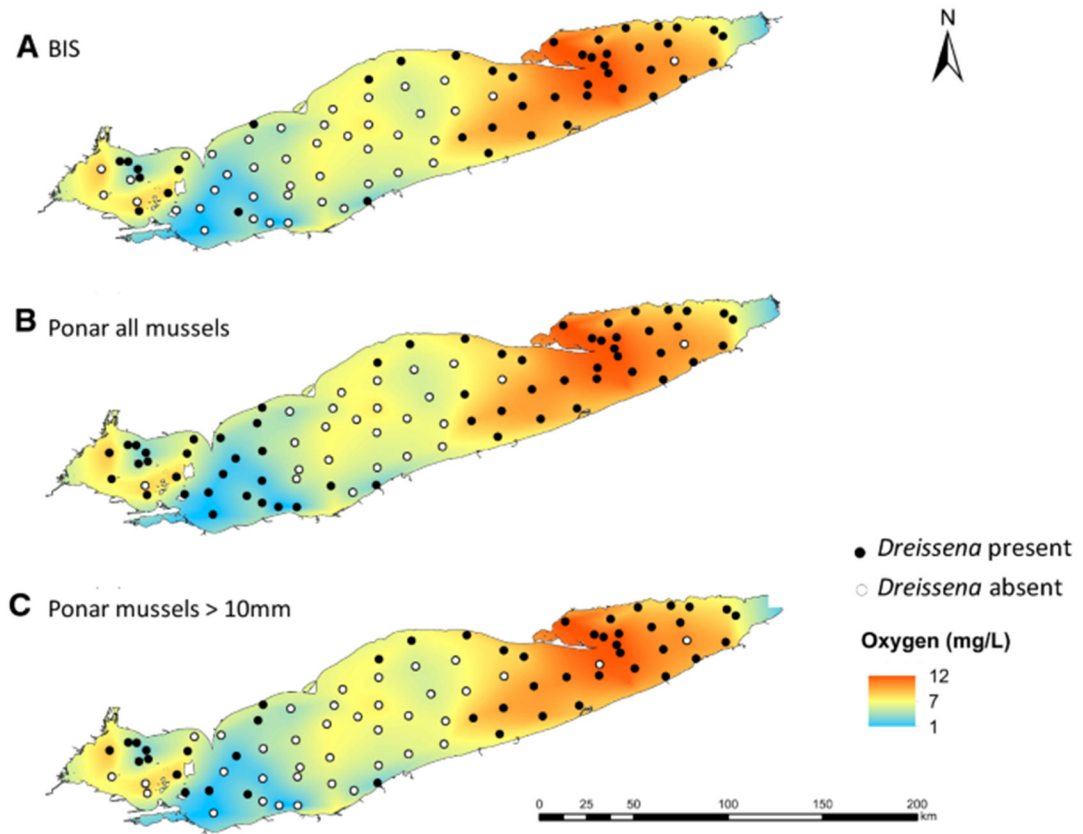
Fig. 3.

Dreissena spp. presence and absence in Lake Erie in 2019 based on BIS (A) and Ponar grabs including all *Dreissena* sizes classes (B), and mussels > 10 mm (C). Only the 85 matching stations where presence/absence data from both BIS and Ponar were available are shown
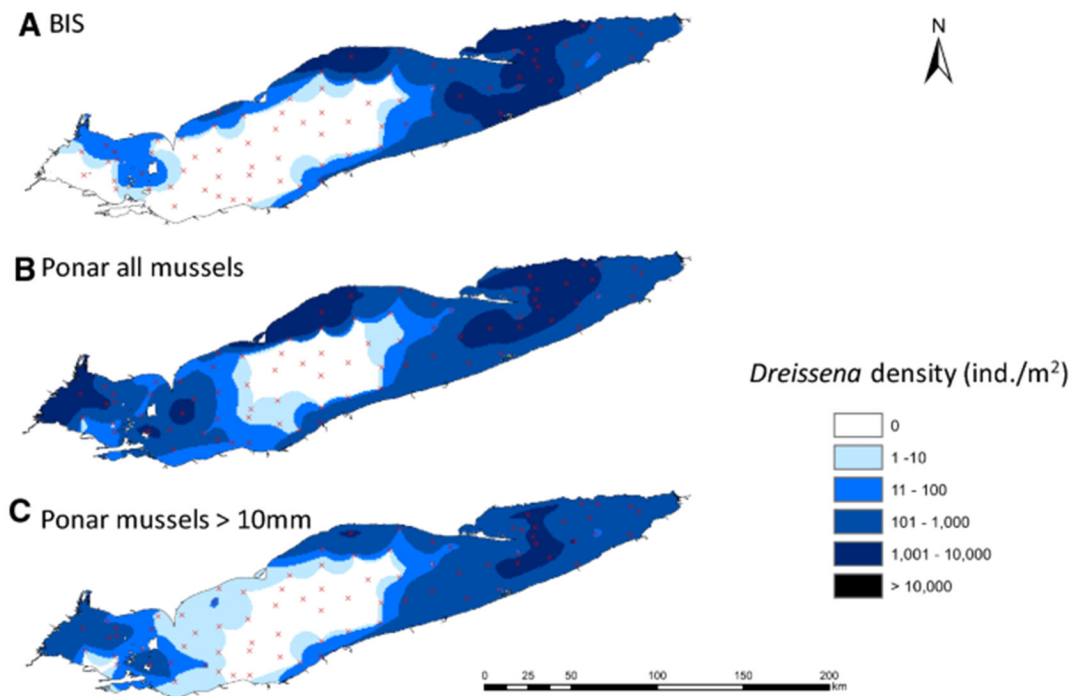
Fig. 4.
Spatial distribution of *Dreissena* spp. in Lake Erie in 2019 expressed as density (ind./m^2) estimated by using BIS video image analysis (A) and Ponar samples including all *Dreissena* size classes (B), and mussels > 10 mm (C). Red crosses indicate sampling stations. Only the 81 matching stations where density data from both BIS and Ponar samples were available are shown
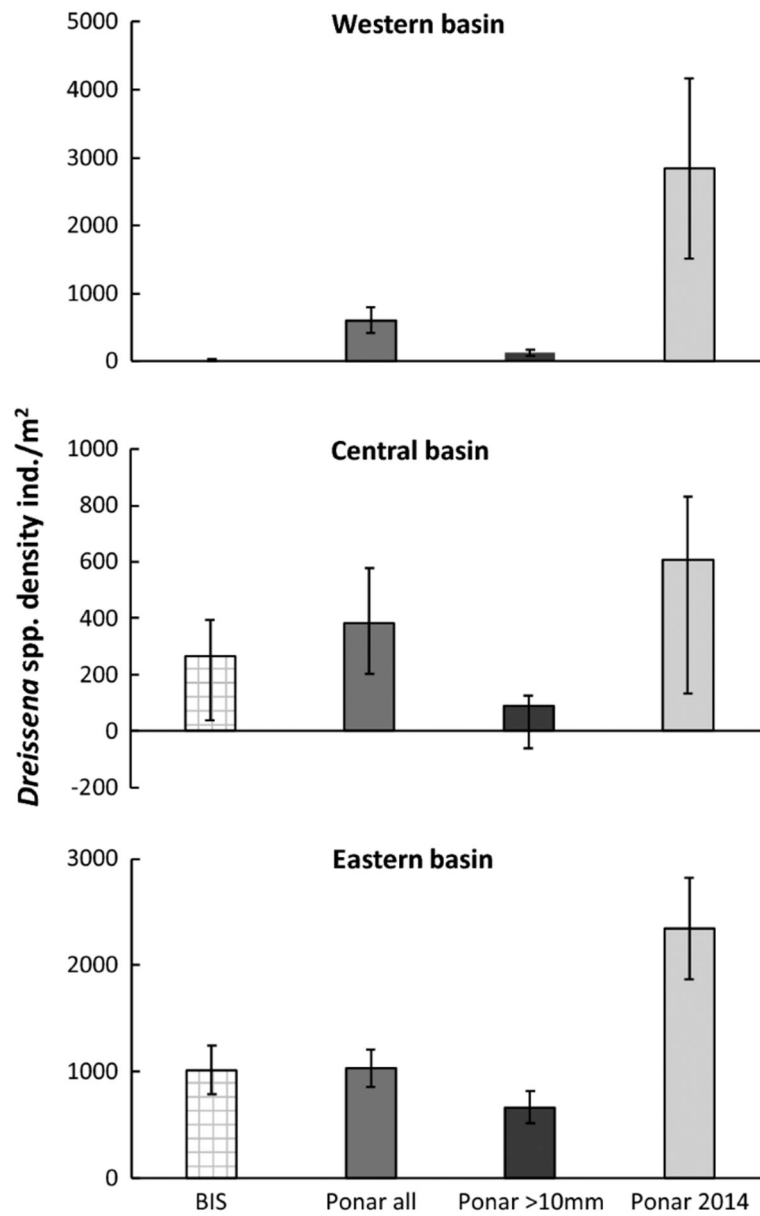
Fig. 5.

Average densities of *Dreissena* spp. estimated from video images in 2019 (BIS), from Ponars in 2019 [all *Dreissena* plotted (Ponar all), only *Dreissena* > 10 mm plotted (Ponar > 10 mm), and from Ponars in 2014 (Ponar 2014)]
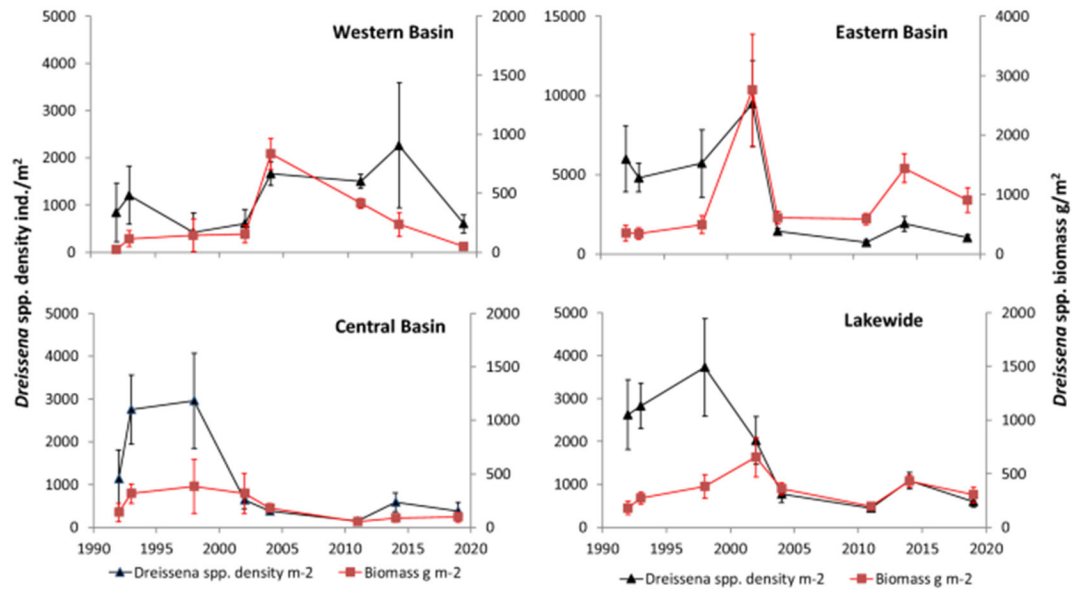
Fig. 6.
Long-term dynamics of *Dreissena* spp. average (± standard error) density (black, left axis) and total wet biomass (red, right axis) estimated using Ponars. Data from Ciborowski et al., in preparation; Jarvis et al., 2000; Patterson et al., 2005; Demott & Dow, 2008; Karatayev et al., 2014, 2018b
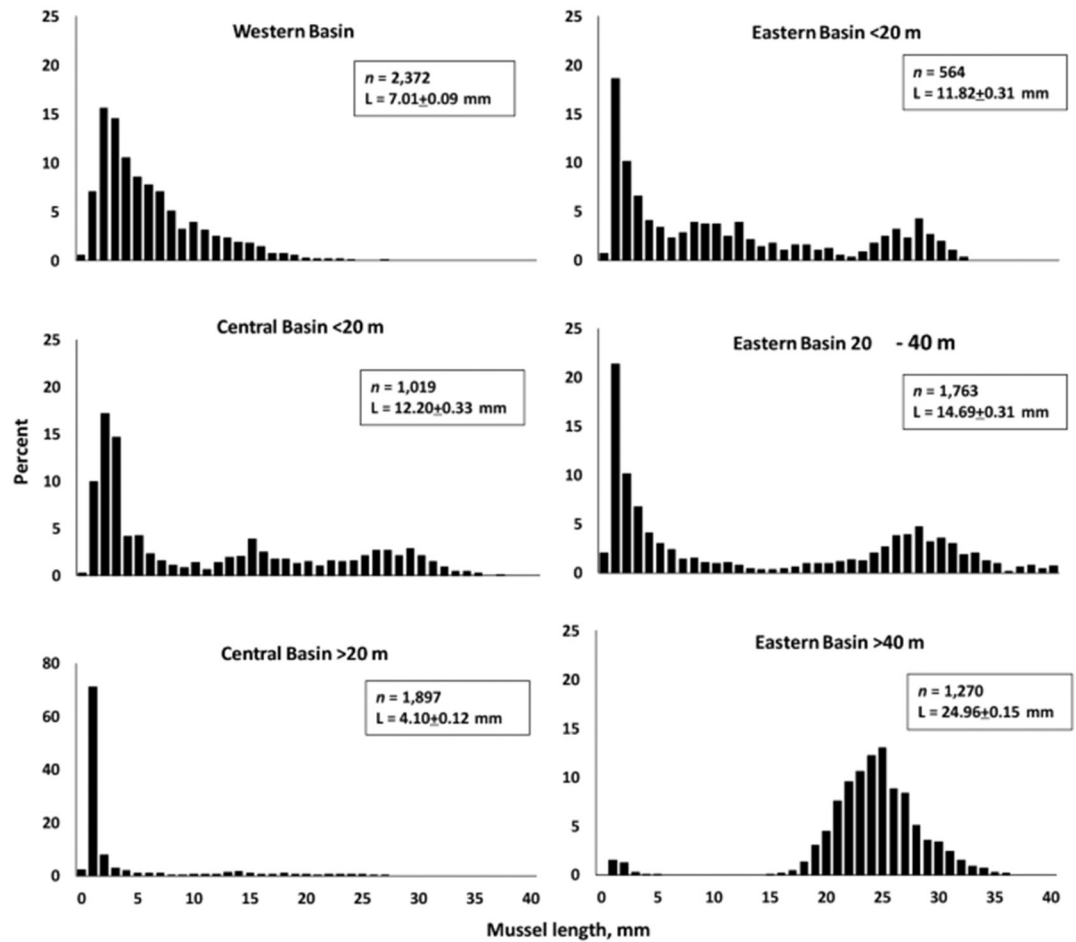
Fig. 7.
Length-frequency distributions of *Dreissena* spp. in Lake Erie in 2019. Sample size and average length (± standard error) for each basin and depth zone are indicated

Table 1

Number of stations where *Dreissena* were recorded (presence/absence and percent of occurrence in parenthesis) from the 85 total stations sampled both with BIS and Ponar grabs in different basins of Lake Erie in 2019

Parameters	Western	Central	Eastern
BIS	7/9 (44%)	15/32 (32%)	21/1 (95%)
Ponar, mussels of all sizes	15/1 (94%)	25/22 (47%)	21/1 (95%)
Ponar, mussels > 10 mm	10/6 (63%)	17/30 (36%)	20/2 (91%)

Table 2

Advantages and disadvantages of the Benthic Imaging System (BIS) and Ponar grabs for *Dreissena* sampling in the Great Lakes

Activity	BIS (3 replicates)	Ponar (3 replicates)
Field sampling time	ca. 20 min (depending on station depth)	ca. 20 min (depending on station depth)
Lab analysis time	Estimating coverage and density—0.5 h	Sorting samples, measuring, counting—21 h
Sampling area, m^2	0.65	0.16
Advantages	Produce data in near real-time; allows large-scale observations of mussel beds structure; successful on hard substrates	Works well on soft substrates, including those covered with macrophytes; not limited by turbidity; can be used for *Dreissena* identification and size determination
Disadvantages	Can overlook small mussels; limited by high turbidity and macrophytes coverage; cannot be used for *Dreissena* identification and size determination	Cannot be used on bedrock and cobble substrates; does not allow observations over large scales