Dreissena in Lake Ontario 30 years post-invasion

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Abstract

We examined three decades of changes in dreissenid populations in Lake Ontario and predation by round goby (*Neogobius melanostomus*). Dreissenids (almost exclusively quagga mussels, *Dreissena rostriformis bugensis*) peaked in 2003, 13 years after arrival, and then declined at depths <90 m but continued to increase deeper through 2018. Lake-wide density also increased from 2008 to 2018 along with average mussel lengths and lake-wide biomass, which reached an all-time high in 2018 (25.2 ± 3.3 g AFTDW m^{-2}). Round goby densities were estimated at 4.2 fish m^{-2} using videography at 10 to 35 m depth range in 2018. This density should impact mussel populations based on feeding rates, as indicated in the literature. While the abundance of 0 - 5 mm mussels appears to be high in all three years with measured length distributions (2008, 2013, 2018), the abundance of 5 to 12 mm dreissenids, the size range most commonly consumed by round goby, was low except at >90 m depths. Although the size distributions indicate that round goby is affecting mussel recruitment, we did not find a decline in dreissenid density in the nearshore and mid-depth ranges where goby have been abundant since 2005. The lake-wide densities and biomass of quagga mussels have increased over time, due to both the growth of individual mussels in the shallower depths, and a continuing increase in density at >90 m. Thus, the ecological effects of quagga mussels in Lake Ontario are likely to continue into the foreseeable future.

Introduction

Zebra mussels (*Dreissena polymorpha*) and quagga mussels (*D. rostriformis bugensis*) have free-swimming planktonic larvae and an attached benthic adult stage which together represent a novel ecotype in freshwaters of North America and much of Europe (Karatayev et al., 1997, 2007). Attaining extremely high densities and being effective suspension feeders, they greatly enhance benthic-pelagic coupling and cause profound changes in the entire ecosystem, including increases in water transparency, nearshore macrophyte coverage, decreases in chlorophyll and seston concentrations in the water column, in Karatayev et al., 1997, 2002, 2015; Vanderploeg et al., 2002; Hecky et al., 2004; Higgins and Vander Zanden, 2010; Nakano and Strayer, 2014). In addition, they act as ecosystem engineers, physically modifying bottom substrates by creating 3-D reeflike structures (Mayer et al., 2001; Karatayev et al., 2002; Vanderploeg et al., 2002; Gutierrez et al., 2003; Sousa et al., 2009; Burlakova et al., 2012).

Invasive species often undergo population declines after an initial period of high abundance (Simberloff and Gibbons, 2004), a pattern demonstrated by dreissenid mussels in many systems (Lvova, 1977; Stanczykowska, 1977; Karatayev et al., 2015; Strayer et al., 2017). Populations of invasive species likely decline due to density-dependent processes, including substrate and food limitation (Karatayev et al., 1998, 2015, 2018a; Hunter and Simons, 2004). Invasion dynamics also depend on time since invasion, lake trophic type, and morphometry, make it difficult to form generalizations about which patterns are most common (Burlakova et al., 2006; Strayer et al., 2019). While in shallow polymictic lakes, both zebra and quagga mussel invasion dynamics are more or less synchronized across the whole waterbody; in deep lakes quagga mussels exhibit variable population growth in different depth zones (Karatayev et al., 2015). Therefore, *Dreissena* may have different densities and size distributions across a depth

gradient. As has been shown across all deep Laurentian Great Lakes (Ontario, Michigan, and Huron), it is typical for quagga mussels to reach or exceed carrying capacity in shallow areas 13 - 15 years after the initial invasion and then decline (Nalepa and Baldridge, 2016; Nalepa et al., 2020; Karatayev et al., 2020). The decline in shallow water mussels is usually associated with a shift of the average depth of the dreissenid population to deeper areas as mussel density and biomass is still increasing in deeper areas even though mussel growth is limited by low food and temperature (Karatayev et al., 2018a). Among the deep Great Lakes, Lake Ontario has the longest history of invasion (since 1989 for zebra mussels, Griffiths et al., 1991, and since 1990 for quagga mussels, Mills et al., 1993) and can therefore provide insight into long-term dynamics to be expected in *Dreissena* populations across different depths in deep lakes of North America and Europe.

Another possible cause for population decline is increased predation. Several species of fish, crayfish and diving ducks are known predators of *Dreissena* (Molloy et al., 1997). One of the most effective *Dreissena* predators in North America is the round goby (*Neogobius melanostomus*) (Kornis et al., 2012). Round goby were first found in Lake Ontario in 1998, nine years after the first record of dreissenids in the lake (Owens et al., 2003). By 2005, round goby were abundant in the lake, and the species has remained abundant at least through 2018 (Weidel et al., 2019). During summer months round gobies are most abundant in the nearshore zone, often with the maximum density around the thermocline, but in the fall they migrate deeper and can be found down to 150 m depth during October – April (Walsh et al., 2007; Pothoven, 2018; Andres et al., 2020). There are reports proposing that round goby invasion caused changes in *Dreissena* length-frequency distributions as well as declines in nearshore *Dreissena* populations (Patterson et al., 2005; Barton et al., 2005), however, there is no consensus on whether round

goby can successfully control mussel populations at a lake-wide scale. While several authors suggest that round goby cause declines in quagga mussel density (Lederer et al., 2008; Naddafi and Rudstam, 2014a; Rudstam and Gandino, 2020), others suggest this impact is localized in space and time (Lederer et al., 2006; Pennuto et al., 2012) and have little lake-wide effect at the scale of the Great Lakes (Bunnell et al., 2005; Johnson et al., 2005; Foley et al., 2017).

In this paper we investigate patterns in the lake-wide density and biomass of dreissenids in Lake Ontario in order to evaluate if the population of dreissenids has stabilized or even declined, perhaps as a result of density-dependent processes regulating mussel abundance when close to the carrying capacity. Whole-lake benthic invertebrate surveys have been conducted nine times since the arrival of mussels to the lake (Dermott and Geminiuc, 2003; Lozano et al., 2001; Watkins et al., 2007; Birkett et al., 2015; Nalepa and Baldridge, 2016, this study). In the first lake-wide survey (1990), both *Dreissena* species were still in the initial stage of invasion and present at very low densities (Dermott and Geminiuc, 2003). Initially dreissenids were dominated by zebra mussels; however. by 1999, quagga mussels accounted for over 98% of all dreissenids, and by 2003 zebra mussels had virtually disappeared from depths deeper than 10m sampled in Lake Ontario by these surveys (Watkins et al., 2007). Thus, most of the analysis presented here is about quagga mussels. Based on the review by Karatayev et al. (2015), we expect quagga mussels to reach peak density between 10 and 15 years after arrival (thus either in the 2003 or the 2008 surveys) and then stabilize at a lower density. We are also interested in whether quagga mussels may have declined due to the high abundance of round goby in the lake from 2005 onwards. If round goby are an important predator from 2005 (the year abundant round goby were recorded in the lake, Walsh et al. 2007) onwards, we expect quagga mussels to further decline through 2013 and 2018 and we expect the abundance of mussels in the size range

preferred by gobies to be low (3 to 12 mm, Andraso et al., 2011; Naddafi and Rudstam, 2014b; Foley et al., 2017). Further, we expect that these effects depend on the depth region. A decline in mussels and changes in the size structure should be most prevalent in the shallow and mid-depth regions where we expect round goby to be most abundant. In deeper areas, we expect the population to stabilize at a level representing the carrying capacity of these bottom depths.

To address our research questions, we combined *Dreissena* spp. data from 1990 – 2013 with findings from 2018 (the most recent whole lake survey). We also report the abundance of round goby on bottom depths 11 to 35 m, obtained with a video system deployed along both the north and south shores of the lake. These goby densities, along with observations from elsewhere, are used to evaluate if the goby abundance could be large enough to affect mussel densities.

Methods

Dreissena long-term-dynamics

To compare the pattern of *Dreissena* population dynamics in Lake Ontario, we compiled a dataset of *Dreissena* spp. densities by station and depth for 1990, 1995, 1997, 1998, 1999, 2003, 2008, and 2013 (Dermott and Geminiuc, 2003; Lozano et al., 2001; Watkins et al., 2007; Birkett et al., 2015; Nalepa and Baldridge, 2016) to complement the data from 2018 presented here. To increase the spatial resolution of surveys, we added data from the U.S. EPA Great Lakes National Program Office (GLNPO) long-term monitoring stations to the 2003, 2008, and 2013 surveys (9 - 10 stations per survey, Burlakova et al., 2018). Because different stations were sampled throughout the years, we calculated average *Dreissena* spp. density and biomass (± standard error) in each lake zone (0 - 30 m, >30 - 50 m, >50 - 90 m, and > 90 m), and calculated

lake-wide density and biomass for each year as weighted averages using means of stations located at these four depth zones considering the proportion of the total lake area represented by each zone (21.6, 11.7, 18.5, and 48.2%, respectively) (Manly, 2009).

Over the years different authors reported *Dreissena* biomass in different units. In 1990 – 2003 and in 2008 (GLNPO stations only), *Dreissena* were not weighed, and so the weight was estimated using an average of 3.34 mg tissue dry weight (TDW) per mussel (Birkett et al., 2015). In 2013, total wet biomass (shell and tissue wet weight, STWW) was measured for the GLNPO stations, while mussel biomass was calculated as ash free tissue dry weight (AFTDW) for the Lake Ontario Cooperative Science and Monitoring Initiative (CSMI) stations. Biomass in terms of AFTDW is determined by applying relationships between AFTDW and shell length for different depth zones to size-frequency distributions at each station (see Nalepa et al., 2014, 2020 for more detail). All biomass values reported in this paper were either measured as, or converted to, units of AFTDW.

We made some recalculations and adjustments to the 2008 CSMI data originally reported by Birkett et al. (2015). Because the lengths of the 2008 mussels were measured at each CSMI sampling location, we applied the 2013 AFTDW equations to the length distributions from 2008 to obtain a biomass value for each station. Therefore, our biomass values differ from those in Birkett et al. (2015), as they used a 3.34 mg average TDW per mussel weight to calculate biomass. There were also some discrepancies between mussel densities in the text and in the data appendix in Birkett et al. (2015), which led us to review the original counting sheets. As we corrected a few transcription and calculation errors, our 2008 density values are also not identical to the values published in Birkett et al. (2015).

To convert the 2013 GLNPO station STWW into AFTDW, we used the relationship: AFTDW (g) = 0.0250 × STWW (g). To convert TDW of the 1990-2003 (all) and 2008 (GLNPO only) data into AFTDW, we used the relationship: AFTDW (g) = 0.8538 × TDW (g). Both conversion equations are based on *Dreissena* collected from Lake Ontario in 2018 following the methods described in Glyshaw et al. (2015). In 2018, as described below, biomass of *Dreissena* was determined as STWW as well as AFTDW.

Dreissena 2018 sampling protocol

From August - September 2018, aboard the U.S. Environmental Protection Agency (EPA) R/V *Lake Guardian*, a total of 61 stations were sampled in Lake Ontario to determine *Dreissena* spp. presence, density (number of individuals, m^{-2}), total wet biomass (STWW, gm^{-2}), and length-frequency distribution (Fig. 1). Fifty-two stations were sampled during the Lake Ontario CSMI benthic survey during September 10-18, and 9 GLNPO stations were sampled during the Great Lakes Biological Monitoring Program's Long-Term Monitoring (LTM) summer survey in August 2018. Field and lab operations were conducted as per EPA SOP406 (Revision 12 March 2018) and 407 (Revision 09 April 2015).

Two types of samples were collected: 1) Ponar (sampling area 0.0523 m^2) samples processed for mussel presence, density, size-frequency distribution, and sediment analysis; 2) video images from 34 stations collected using a Benthic Imaging System (BIS) (sampling area 0.215 m^2) and processed for round goby presence and density (Fig. 2).

Three replicate Ponar samples were successfully collected at 55 of the planned 61 stations, excluding 6 stations (##29, 42, 43, 62, 66, and 71B) where samples were not collected due to hard substrate. A total of 165 samples were analyzed for *Dreissena* population

assessment. Similar to our previous study (Karatayev et al., 2014, 2018b), all dreissenids 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. Data from all three replicates collected at each station were used to calculate station averages of density and biomass, and size frequency data were pooled from all replicates. All *Dreissena* collected during this survey were quagga mussels.

To calculate AFTDW we used length-weight relationships (in terms of AFTDW) that were determined from live mussels collected from 12 sites distributed throughout Lake Ontario. Within 48 hours of collection, the soft tissues of 25 individuals per site (target shell length: 10-25 mm) were removed from the shells, placed individually into pre-weighed aluminum planchets, and dried at 60°C for at least 48 hours. After drying, the planchets were stored in a desiccator. Upon completion of the survey cruise and return to the laboratory, soft tissues were weighed, ashed at 550°C for 1 h, and then re-weighed. AFTDW was then calculated as the difference between dry weight and post-ashed weight of the mussel tissue. Corresponding shell length (SL) was measured to the nearest 0.1 mm. Measured AFTDWs and SL were used to develop length-weight relationships according to the allometric equation: $\log_e$AFTDW (mg) = b + a*$\log_e$SL (mm). Relationships were developed for pooled sites within four different depth intervals: 0 - 30 m (b = -5.141, a = 2.72, R^2 = 0.962, P <0.001), >30 - 50 m (b = -6.133, a = 2.884, R^2 = 0.838, P <0.001), >50 - 90 m (b = -5.552, a = 2.656, R^2 = 0.943, P <0.001), and >90 m (b = -5.446, a = 2.658, R^2 = 0.850, P <0.001). To determine AFTDW biomass, the number of individuals in each 1 mm size category was multiplied by AFTDW as calculated from the length-weight regression for an individual with a shell length from the mid-point of that size category. Broken mussels

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(i.e. mussels with shells broken enough to compromise the length measurement) were incorporated into AFTDW estimates by first calculating the biomass ratio of broken to unbroken mussel based on STWW then increasing the AFTDW estimate by that ratio.

We calculated lake-wide *Dreissena* spp. density and biomass (± standard error) as a weighted average using means of stations located at 4 depth zones (0 - 30 m, >30 - 50 m, >50 - 90 m, and > 90 m), considering the proportion of the total lake area represented by each zone (21.6, 11.7, 18.5, and 48.2%, respectively) (Manly, 2009). We used multiple linear regression to explore the changes in $\log_e$-transformed *Dreissena* spp. densities with time and depth, and Kruskal-Wallis non-parametric ANOVA to find differences in densities and biomass of *Dreissena* spp. among years and depth zones, and among the proportions of small *Dreissena* at different depths in 2018. We used two-sided t-tests to compare the average length of *Dreissena* at different depth zones and years. To compare the length-frequency distributions of *Dreissena* spp. >5 mm in length in different depth zones among years (2008, 2013, and 2018), we used Fisher-Freeman-Halton test (a generalization of the Fishers Exact test to r by c contingency table) with a Monte Carlo estimate of the p-value to test for homogeneity in contingency tables. We used distance-weighted least square regression to find the relationship between the proportion of 3 – 12 mm mussels and depth. Tests described above were performed in Statistica (data analysis software system, version 13.5.0.17, TIBCO Software Inc., 2018, http://statistica.io), and effects were considered significant at $P < 0.05$.

Video image analysis

Video images were collected in September 2018 at 34 stations (bottom depths 11 to 35.5 m) using a Benthic Imaging System (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 x 1080 pixels, 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 (Fig. 2; Angradi, 2018). The lens of the down-looking camera was 56 cm above substrate, resulting in a usable field of view (video quadrat area) of 40.8 x 52.8 cm. 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. The BIS remained on the lake bottom for one minute to increase the probability that a clear view of the substrate and scale bars was obtained, as in most cases the resuspended sediment settled or cleared from view within one minute. After the BIS was retrieved from the water, videos from both cameras were downloaded to an external hard drive for onboard analysis. Only one replicate of lake bottom video image for round goby density estimation was collected at 25 of 34 stations. At the remaining 9 stations, 3 replicates were taken: the BIS rested on the bottom for approximately 1 minute (first replicate), then lifted 1-2 m from the bottom for about 30 seconds; lowered again to the lake bottom for another minute (second replicate), then raised; this process was repeated again to collect a third replicate. Round gobies were counted within each image (replicate) and data from all three replicates collected were used to calculate a station average for those 9 stations. The differences between the mean density for each replicate collected at these 9 stations and the average of all replicates ranged from 0 to 25%. For each station and each replicate we used the clearest still image (screen shot) to estimate round goby density from the down-looking camera, and round goby presence/absence from the side-looking camera (Fig. 3). To ensure round goby presence in the still image, we reviewed the whole video segment from the time when the BIS is approaching the lakebed to make sure that

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no round gobies escaped or moved into the frame from outside during carriage landing. Gobies that moved into the frame were excluded from the count whereas gobies moving out of the frame were included.

Results

Dreissena long-term-dynamics

In 1990 during the first lake-wide study of Lake Ontario, densities of both *Dreissena* species were still very low, and quagga mussels were found deeper in the lake (>50 - 90 and >90 m) than zebra mussels (0 - 30 m, Fig. 4). In 1995, six years after being first reported in the lake, zebra mussels reached their lake-wide population density maximum (676 ± 242 ind./m^2, mean ± one standard error here and elsewhere). Although already starting to spread deeper, over 99% of the lake-wide population density of all dreissenids in 1995 was in the shallowest zone where zebra mussels densities averaged 3108 ± 1118 ind./m^2 and quagga mussels averaged 1798 ± 1078 ind./m^2 (Fig. 4). In 1997, the quagga mussel lake-wide average population density exceeded that of zebra mussels (339 ± 111 vs. 283 ± 151 ind./m^2) and in 1998, quagga mussel densities lake-wide were significantly higher than in previous years (all P <0.001, multiple comparison tests after Kruskal-Wallis ANOVA). By 1999, 99% of the combined dreissenid density and biomass consisted of quagga mussels, and no zebra mussels were found during lake-wide surveys in 2008, 2013 or 2018. In 2003, 13 years after being first reported in the lake, quagga mussels reached the maximum lake-wide population density (4638 ± 907 ind./m^2) which was 6.6 times higher than that of zebra mussels during their population maximum in 1995 (Fig. 4). The average lake-wide quagga mussel biomass in 2013 was still growing and was 8.2 times higher than that of zebra mussels maximum in 1995, with the bulk of the population moving into deeper areas

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(Fig. 4). Quagga mussel density at depths 0 - 30 and >30 - 50 m began to decline after 2003, but density was still increasing at >90 m. In contrast to density, population biomass across all depth zones as well as lake-wide was stable or increasing from 2003 to 2018, indicating that individual mussels became larger.

Dreissena lake-wide density and biomass declined from 2003 to 2008 but then increased in 2013 and again in 2018 (Fig. 4, Table 1). Quagga mussel density in 2018 was significantly higher than in 2008 in the deepest zone and lake-wide (P <0.001, Table 1). Biomass increased in 2018 across almost all depth zones, however the difference was significant only in >50 - 90 m and >90 m, (P < 0.001 for both zones) as well as lake-wide (P <0.001, multiple comparison tests after Kruskal-Wallis ANOVA). The resulting lake-wide biomass was the highest ever reported in the lake (25.2 ± 3.3 g AFTDW/m^2).

Length-frequency distribution

Length-frequency distributions of quagga mussels in Lake Ontario (available for 2008, 2013 and 2018) were significantly different among years (P <0.0001, Fisher-Freeman-Halton test, Fig. 5). In the shallowest zone, most of the population was represented by small recently settled individuals <5 mm, especially in 2013 and 2018 (Table 1). Densities did not change significantly in any size group over time, but there were changes in the size distributions. In 0 - 30 m depth, the 5 - 10 mm mussels were rare in 2008 and 5 - 15 mm mussels were rare in 2013, but by 2018 some 5 - 10 mm mussels were again present in this depth zone. Average size of mussels >5 mm in the shallowest zone was larger than in the deeper zones (P < 0.0001 for all years except 2018 (P = 0.66, two-sided *t*-test) and was slightly elevated in 2013 due to the low

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number of mussels <15 mm (Fig. 5, Table 1). In the mid-depth zone (>30 - 50 m) there was a clear bimodal distribution with a moderate proportion (average for the depth zone 43 ± 17%) of mussels <5 mm, fewer mussels in the 5 - 10 mm size class, and a substantial number of large multi-age mussels in the 10 - 30 mm range. The number of 5 - 10 mm mussels declined from 2008 to 2013, and no mussels were found in that size range in 2018 (the difference between 2008 and 2018 were significant, P = 0.042, Table 1). Density of other size groups did not change significantly from 2008 to 2018 in this depth zone (Table 1). Average size of mussels >5 mm in >30 - 50 m depth zone significantly increased from 14.0 ± 0.1 mm in 2008 to 18.7 ± 0.6 mm in 2018 (Fig. 5, P <0.0001, *t*-test). In the >50 - 90 m depth zone the size distribution shifted progressively towards larger quagga mussels from 2008 to 2018 (Fig. 5) with average shell length (mussels > 5 mm) significantly increasing from 11.8 ± 0.1 mm in 2008 to 14.4±0.1 mm in 2013 to 17.3 ± 0.1 mm in 2018 (all years: P <0.0001, *t*-test). Fewer mussels <5 mm were found at this depth zone in 2013 and 2018 (<8%; Fig. 6), suggesting limited recruitment. In this depth zone, the size groups 5 - 10 mm and 10 - 15 mm declined significantly from 2008 to 2018; whereas, the size group >15 mm increased significantly (Table 1). In contrast, around 35 – 45% of the mussels were <5 mm in the deepest zone in all three years although larger mussels were also common in this zone, and there were no gaps in the length distribution for the 5 - 10 mm size groups. As a result, the average *Dreissena* length in the deepest zone was stable across all three years of sampling (Fig. 5). With the exception of a higher proportion of small mussels in 2018, the shape of the size distribution remained fairly constant over time, and density of all size groups increased significantly (Table 1).

Round goby distribution

BIS footage obtained at all 34 stations was of acceptable quality and usable for recording round goby presence and counts. In most cases, the fish remained within the frame without much movement during the entire recording time. Of the total number of 52 down-looking videos analyzed, gobies moved into the frame in 4 videos (1 - 2 gobies) and out of the frame in 6 videos (1 - 3 gobies). In down-looking images, round gobies were found in 16 (44%) of the 34 stations at depths from 11 to 26 m (depths sampled was 11 to 35.5 m, Fig 7). Maximum round goby densities were found between depths of 17 and 24 m. Densities obtained with the down-looking images from the 16 stations with gobies ranged from 1.4 and 21.8 ind./m^2 (Fig. 7). Average goby density from all 34 stations sampled was 4.2 ± 1.1 ind./m^2. Round gobies were more visible on the side-looking camera due to their lighter lateral and ventral sides (Fig. 3). Examination of these side-looking images revealed round gobies on 8 additional stations, bringing all stations with gobies to 24 (70% of sampled stations) and the depth range with gobies to 11 - 34.5 m.

The depth distribution of round goby densities overlaid with the proportion of dreissenid sizes that most commonly consumed by goby (3 - 12 mm, Patterson et al., 2005 Andraso et al., 2011; Naddafi and Rudstam, 2014b; Foley et al., 2017) showed that both were restricted by depth (Fig. 7). The proportion of 3 - 12 mm mussels was 18.3% at 11 - 18 m depth, declined to the lowest (2.9%) at depths from 20 to 56 m, but increased significantly to 36.7% at depths > 57 m ($P < 0.0001$, multiple comparisons after Kruskal-Wallis ANOVA, Fig. 7). The round goby presence from the 11 to 26 m depth zone thus coincided with a relatively low percentage (18%) of edible size mussels at these depths (Fig. 7).

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Discussion

Dreissena long-term-dynamics

Our analysis of *Dreissena* population dynamics over 30 years corroborated the different temporal trends observed previously across depth zones and also revealed the largest lake-wide mussel biomass to date. Previous studies in Lake Ontario have shown that quagga mussels reached population maximum in the shallow (0 - 30 m) to mid (>30 - 50) depth zone by 2003, 13 years after the first detection in Lake Ontario, and then declined (Fig. 4; Birkett et al., 2015; Nalepa and Baldridge, 2016). Such a decline may be expected if quagga mussels in shallow to mid-depth water had increased to densities greater than their carrying capacity. Similar declines in dreissenid densities in the nearshore zone, along with the shift of maximum density to deeper areas, were also observed in lakes Michigan and Huron (Nalepa et al., 2020; Karatayev et al., 2020; Mehler et al., 2020). At depths <50 m, the decline in density occurred mainly from 2003 to 2008 and there were no significant changes from 2008 to 2018. Mussel densities in >50 - 90m steadily declined from 2003 to 2018, but densities in deep water and lake-wide have significantly increased (Fig. 4). Biomass of mussels increased significantly in both the >50 - 90m and >90 m depth zones. (Fig. 4). The observed increases in mussel density and biomass at >90 m have a strong influence on lake-wide values by virtue of 48% of the lake bottom being >90 m deep.

Density and biomass trends did not always match over time and across depths. The largest discrepancy between density and biomass dynamics was found at >50 - 90 m, coincident with an ~45% increase in average shell length (mussels >5 mm) between 2008 and 2018 (Fig 5). If including >5 mm mussels, the average *Dreissena* length in this zone was twice as large as in all other zones due to having the lowest recruitment and increasing size of larger mussels. Similar discrepancy between *Dreissena* density and biomass due to the lack of recruitment was

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also found in the deepest zone of the eastern basin of Lake Erie where the average mussel length was almost two times higher than in the littoral zone (23.01 ± 0.54 mm vs. 12.05 ± 2.78 mm), indicating higher longevity and lower biomass turnover of mussels in deep vs. shallow areas (Karatayev et al., 2018a).

The recent increases in lake-wide density were unexpected considering the substantial population decline recorded from 2003 to 2008 (Fig. 4). Based on observed declines in lake-wide *Dreissena* density in Michigan in 2015, 18 years after the first record of quagga mussels in the lake (Nalepa et al., 2020), we had expected our 2018 data to corroborate further declines in quagga mussel populations in Lake Ontario given that the mussels have been present in Lake Ontario for 30 years. Contrary to our prediction, we found significant increases in *Dreissena* lake-wide density and biomass, suggesting that the mussel population in Lake Ontario is still increasing. The lake-wide average *Dreissena* biomass was the highest observed in Lake Ontario to date at 25.2 ± 3.3 g AFTDW/m^2.

Round goby abundance

In Lake Ontario, round goby were first reported in 1998 (Owens et al., 2003) and two fish were found in annual USGS spring trawl surveys in 2002 (Walsh et al., 2007). Numbers of goby also increased in the USGS fall trawl survey in 2005 and thereafter (Weidel et al., 2019). Although we only sampled 34 sites, the sites were spread across the lake and our survey is the first lake-wide estimate of goby abundance in any depth zone of Lake Ontario using videography. Our estimated goby density on 11 - 26 m deep bottoms (4.2 ind./m^2, September 2018) were similar to other estimates using videography. In Lake Ontario, Pennuto et al. (2012) found 2.2 ind./m^2 and

40 kg/ha in water depth 2 to 10 m in three nearshore areas in 2008, and Taraborelli et al. (2010) estimated goby biomass in Bay of Quinte in 2005 to be 50 - 112 kg/ha in water shallower than 7 m, which may represent ~5 ind./m^2 (densities not given). Densities in Western Lake Erie were ~3 ind./m^2 basin-wide in 2002 (Johnson et al., 2005). In smaller lakes, Andres et al. (2020) found 1.9 ind./m^2 on bottom depths above the thermocline (<18 m) in Cayuga Lake, NY in 2017, and Brooking et al. (2020) reported 0.8 to 3.2 ind./m^2 lake-wide in Oneida Lake, NY in 2017-2019. Estimates based on fall bottom trawls tend to be lower (~0.4 ind./m^2, Weidel et al., 2019) than estimates from video surveys, as trawls likely underestimate goby abundance (Johnson et al., 2005, Brooking et al., 2020). Unfortunately, we could not use the drop-down camera in water deeper than 36 m due to depth limits of the camera housing. However, gobies are primarily found above the thermocline during the summer when their feeding rate is highest at 20 to 25° C (Lee et al., 2005). In Thunder Bay (Lake Huron), round goby densities peaked around 20 m depth in August and around 30 m in October 2017 (USGS data). Although Lake Huron was sampled in 9 - 150 m depth interval, almost no gobies were found >40 m in August – October 2017. Therefore, we expect higher goby impact in shallower water also in Lake Ontario. However, goby predation could be occurring in the fall and winter, when goby can be found deeper, down to 150 m (October – April, observations from Lake Ontario (Walsh et al., 2007), Lake Michigan (Pothoven, 2018) and Cayuga Lake (Andres et al. 2020)), although their metabolic rate will be greatly reduced during fall and winter limiting their impact.

Impact of round goby on Dreissena

If round goby negatively affect quagga mussel densities in Lake Ontario, we expect a decline in density from 2003 to 2018 due to the high goby abundance in the lake since 2005. Further, we expect this decline to be largest in the shallower depth regions, particularly in the 0 - 30 m depth zone where we estimated goby densities to exceed 4 ind./m^2. Such densities are sufficient to have an impact on mussel abundance. As gobies may consume more than 40 mussels per day (Naddafi and Rudstam 2014a), a density of 4 ind./m^2 could deplete a mussel population of 5000 mussels m^{-2} in about 1 month. However, although *Dreissena* densities did decline from the peak values in 2003 in the three depth zones <90 m, we did not observe further declines between 2008 and 2018.

Even though we could not detect a change in density, the changes in the size structure of the quagga mussels between 2008, 2013 and 2018 in different depth zones suggest an effect of round goby at the depth zones <60 m (Fig. 5 - 7). Despite moderate to high proportions of 0 - 5 mm mussels in 2013 and 2018 indicating continued reproduction, those mussels did not appear to survive to the adult sizes as there were frequent gaps in the size distributions for the size groups 5 to 10 mm and even up to 15 mm. These missing size groups are preferred by gobies. Although large round gobies can eat mussels in the 16 - 20 mm size range, they prefer to consume relatively small mussels, 4 – 12 mm (Naddafi and Rudstam, 2014b), 8 - 11 mm (Andraso et al., 2011) and 0.5 - 14.3 mm (average 3.4 mm, Foley et al., 2017). The lack of mussels in the 3 - 12 mm size category in the summer of 2018 at depths from 30 to 60 m (Fig. 7) may also be due to other factors. In particular, food competition with larger mussels (Karatayev et al., 2018a) may be responsible for the decline in 3 - 12 mm mussels at 30 to 60 m depths. At

the depth zones >90 m, the mussel size distributions did not show signs of reduced mussels <15 mm.

The remaining larger mussels (>15 mm) tended to increase in size and decrease in density from 2008 to 2013 to 2018, suggesting growth but limited recruitment to these larger mussels size groups either because of goby predation on smaller mussels or because of starvation. This interpretation suggest that the larger mussels were already present in 2008, and therefore were at least 10 years old by 2018. However, although quagga mussels can live that long in cold deep water (Karatayev et al., 2018a), they are unlikely to live for 10+ years in shallow, warmer water. An alternative explanation is that there could have been successful recruitment to the adult stages in years we did not sample, perhaps when round goby abundance was lower.

In our opinion, whether or not round goby have affected the quagga mussel population lake-wide is still an open question that requires additional, likely multiyear, investigations. In shallower areas, a round goby-mediated decline in mussels may still have several years to play out, and depends on the longevity of the existing mussels and their ability to successfully recruit to the adult population, particularly in times with reduced predation pressure from round goby. Populations that have recruitment bottlenecks associated with juvenile stages and long-lived adult stages are common, such as in molluscs and fish (Paine, 1976; Werner and Gilliam, 1984; Miller et al, 1988; Houde, 2008; Schröder et al., 2014). Annual size distribution would have been preferable to inferences based on size distribution measured every 5 years as annual data would have allowed us to investigate the possibility of small mussels surviving to adult size in other years. We do not know if quagga mussels can survive as long as ten years in warm waters. However, in Oneida Lake, New York, the gap in the quagga mussel size distribution started in 2015, the year following round goby invasion, and there is little indication of much recruitment

since then making the current population at least 6 years old, likely older in the warm water of Oneida Lake (Jackson et al., 2020; Rudstam pers. obs.). Observation of mussel declines in smaller lakes following round goby invasion (20 and 200 km^2 lakes, Rudstam and Gandino 2020, Jackson et al., 2020) and localized observations from the Great Lakes (Barton et al., 2005, Patterson et al., 2005, Wilson et al., 2006) suggest that goby may also affect mussel in Lake Ontario over time. However, small lakes and studies in more limited areas of the Great Lakes may not be applicable to the lake-wide scale and heterogeneity of the Great Lakes.

On the other hand, limited or no goby effect on mussel density and biomass has been reported from other deep Great Lakes. In spite of a long history of round goby and mussels coexisting in Lake Huron, quagga mussel density was still growing as of 2017 across all depth zones 0 - 30 m, as well as lake-wide (Karatayev et al., 2020). In Lake Michigan, although *Dreissena* populations started declining after 2010 at depths less than 90 m (Nalepa et al., 2020; Mehler et al., 2020), it is likely that factors other than round goby predation (e.g. food limitation) have caused this decline. Ecosystems of lakes Michigan and Huron underwent a period of rapid change in the mid-2000s, including reduction in particulate carbon, spring chlorophyll a, increases in spring silica and Secchi depth (Barbiero et al., 2018) indicating a decline in *Dreissena* food resources. This effect was system-wide and should impact the whole *Dreissena* population, in contrast to goby consumption which may be limited to certain depth zones or habitats. However, similar declines in phytoplankton and spring diatom blooms have not been observed in Lake Ontario (Reavie et al., 2014, Rudstam et al., 2017; U.S. EPA, 2019) which may explain the continued increase in the biomass of Lake Ontario mussels.

However, even if round goby are contributing to a decline in mussels in shallower depths, it is clear from our analysis that the lake-wide densities and biomass of quagga mussels have

increased over time, due to both the growth of individual mussels in the shallower depth zones and to a continuing increase in density in the large (48% of lake bottom) depth zone >90 m. We do not expect large effects of round goby on these deeper bottoms, and lake-wide quagga mussel density and biomass may therefore continue to increase gradually in the coming years. These increases, despite the presence of abundant round goby in the lake for 14 years, is a testament to the ability of quagga mussels to colonize deep, cold, and food-depleted lake bottoms. These deep mussels are still capable of causing food-web impacts, particularly during spring and autumn turnover events, and may also provide a source of veligers to colonize shallower depths each year.

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Table 1. Density (average, m^{-2}) of quagga mussels size groups (0 – 5 mm, 5 – 10 mm, 10 – 15 mm, >15 mm, and total) in Lake Ontario in 2008, 2013, and 2018 in different depth zones. Letters indicate significant differences in densities among the three years. (Tukey HSD test, based on 4th root transformed density values). N is number of stations sampled.

Years	N	Size groups				
		0 – 5 mm	5 – 10 mm	10 – 15 mm	>15 mm	Total
0 – 30 m						
2008	12	690±439	189±151	295±226	1386±754	2560±1244
2013	8	2354±1183	21±11	31±19	896±343	3302±1386
2018	13	3622±1813	311±140	133±61	620±196	4685±2098
P value		0.111	0.6970	0.977	0.97	0.5662
30 – 50 m						
2008	4	131±127	619±516 A	2160±1001	1509±528	4419±1936
2013	6	1636±1045	55±27 AB	798±371	2382±772	4871±1612
2018	3	2634±2628	0 B	291±211	1273±481	4198±2096
P value		0.265	0.042	0.381	0.978	0.960
50 – 90 m						
2008	15	1116±391	2424±577 A	2357±511 A	1251±166 B	7149±1177
2013	9	448±278	898±244 A	1825±328 AB	2236±260 A	5407±625
2018	15	233±102	358±152 B	933±263 B	2138±268 A	3661±463
P value		0.162	<.0001	0.0182	0.013	0.067
>90 m						
2008	15	294±168 B	190±115 C	106±68 C	228±173 B	818±451 B
2013	22	859±148 A	382±123 B	376±141 B	383±107 A	1999±437 A
2018	23	1382±218 A	764±119 A	529±98 A	481±103 A	3156±391 A
P value		<.0001	<.0001	<.0001	<.0001	<.0001

Figure legends

Figure 1. Location of stations in Lake Ontario sampled for *Dreissena* during August – September 2018. Ponar stations (black circles), Benthic Imaging System (BIS, white circles), or both Ponar and BIS (grey circles).

Figure 2. Deployment of the Benthic Imaging System (BIS). Left: BIS on deck of R/V *Lake Guardian*; right: BIS being deployed from starboard side of R/V *Lake Guardian*. Position of cameras and lights are indicated.

Figure 3. Round goby in screen shots from down-looking (A) and side-looking (B) cameras at station 37 (24 m depth) in Lake Ontario in 2018. For scale, the yellow and black squares on the BIS feet are each 24x24mm.

Figure 4. Long-term dynamics of zebra (black lines, triangles) and quagga (red lines, circles) mussel density (left graphs) and biomass (right graphs) in Lake Ontario. Vertical bars are standard errors. Lake-wide density and biomass were calculated as weighted averages from four depth zones.

Figure 5. Length-frequency distributions of *Dreissena* spp. >5 mm in length in Lake Ontario in 2008, 2013, and 2018. The average lengths (L) of mussels >5 mm ± standard error for each year are given.

Figure 6. Proportion of *Dreissena* <5 mm in different depth zones of the total density in 2008, 2013, and 2018 in Lake Ontario. Vertical bars are standard errors.

Figure 7. Round goby and mussel distribution with depth in the nearshore of Lake Ontario in September of 2018. Upper panel: round goby densities (fish/m^2) by depth estimated using down-looking camera of the Benthic Imaging System. Note: depths <11 m and >35.5 m were not sampled. Lower panel: change in percentage of mussels 3 – 12 mm in size (grey

triangles) and density of round goby estimated using Benthic Imaging System. Distance-weighted least squares regression (r = 0.64, P <0.001) was used to indicate the trends.
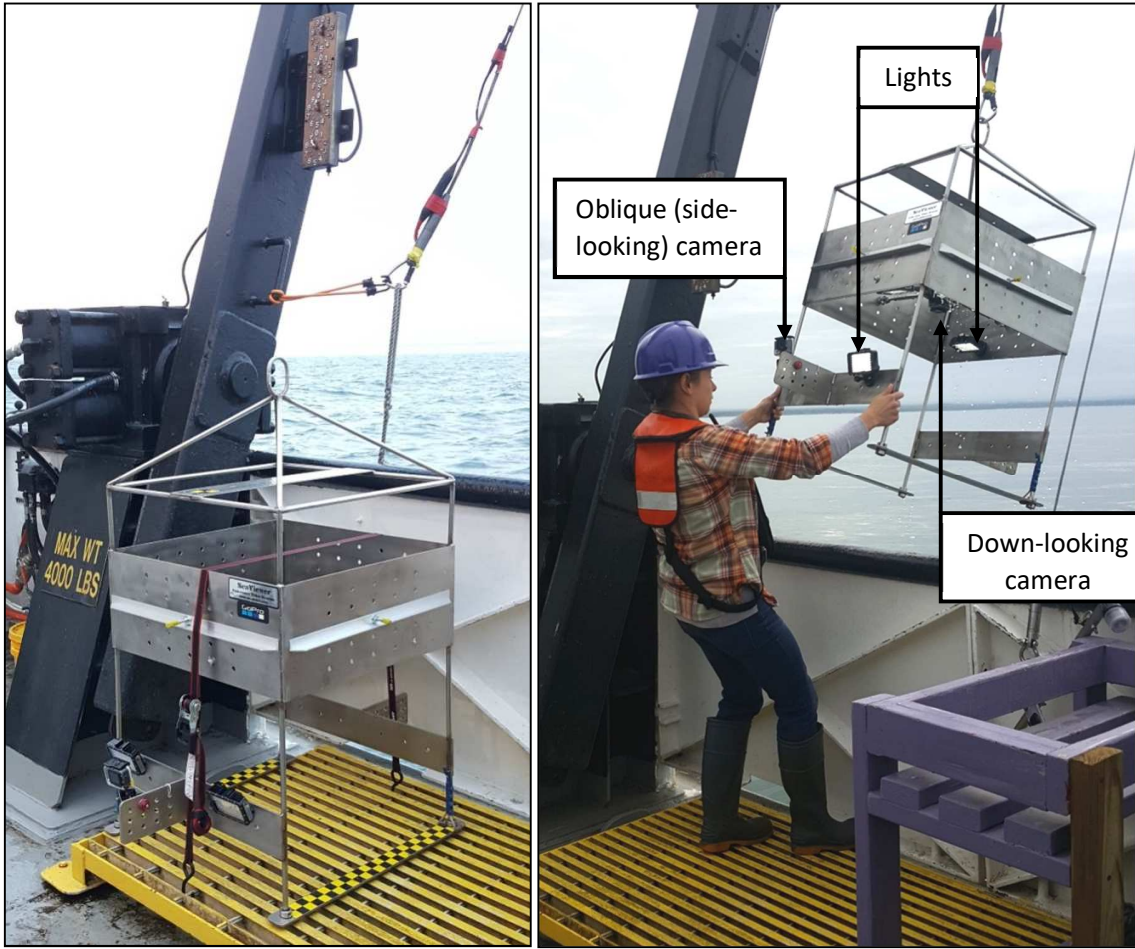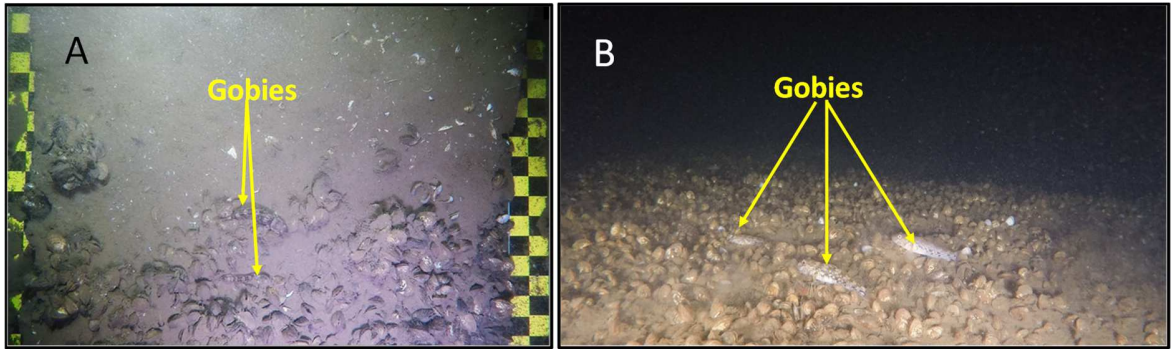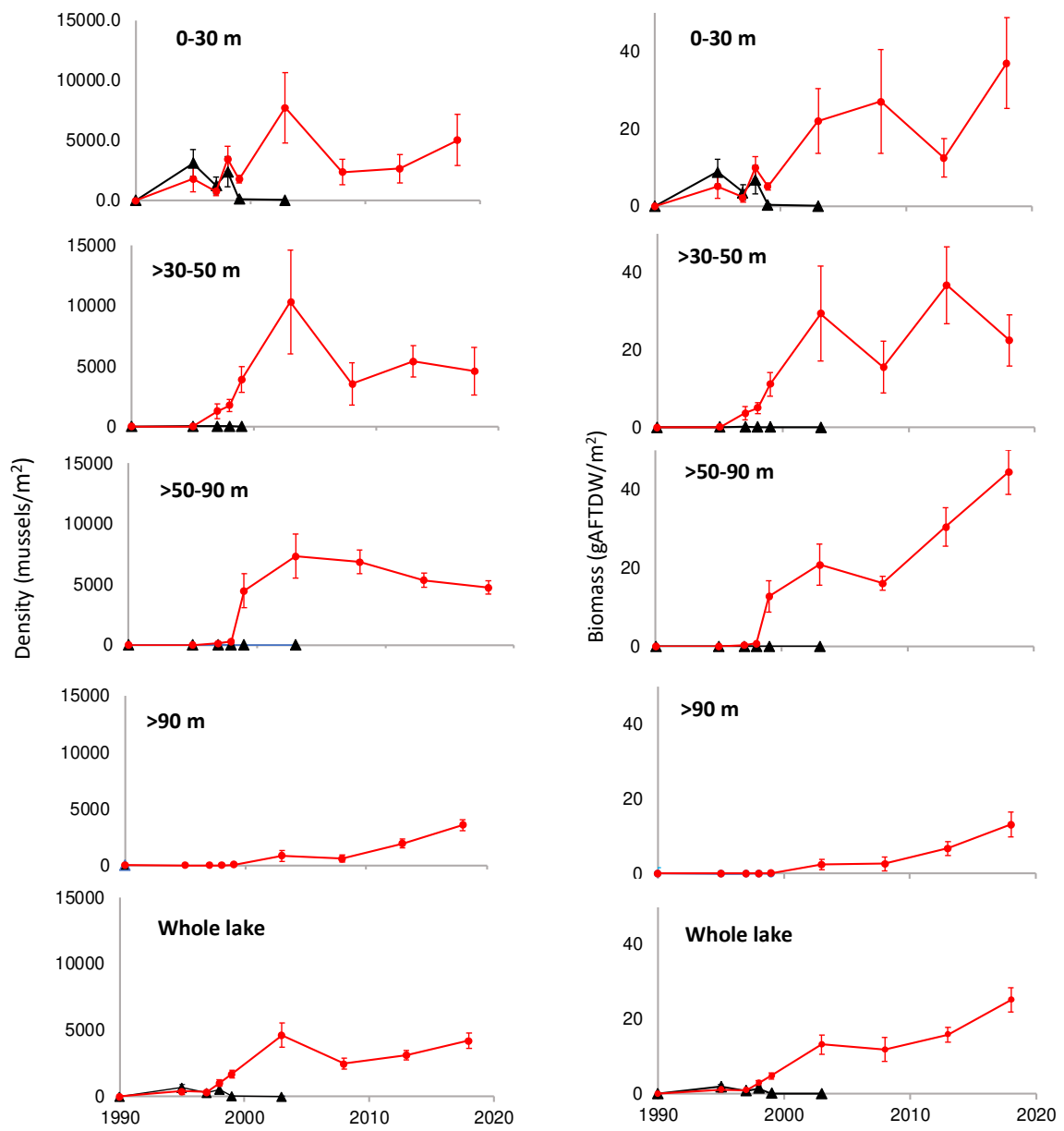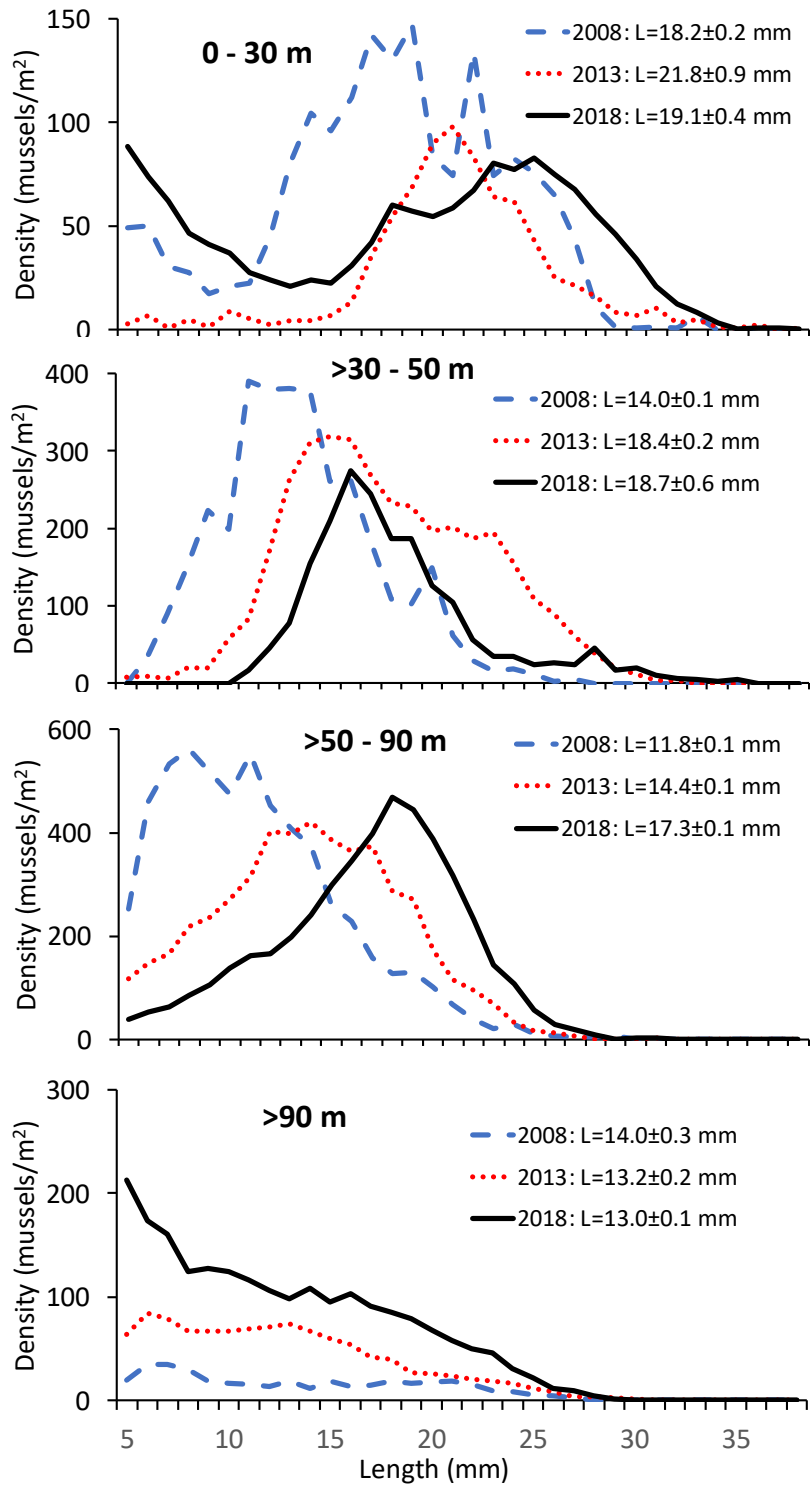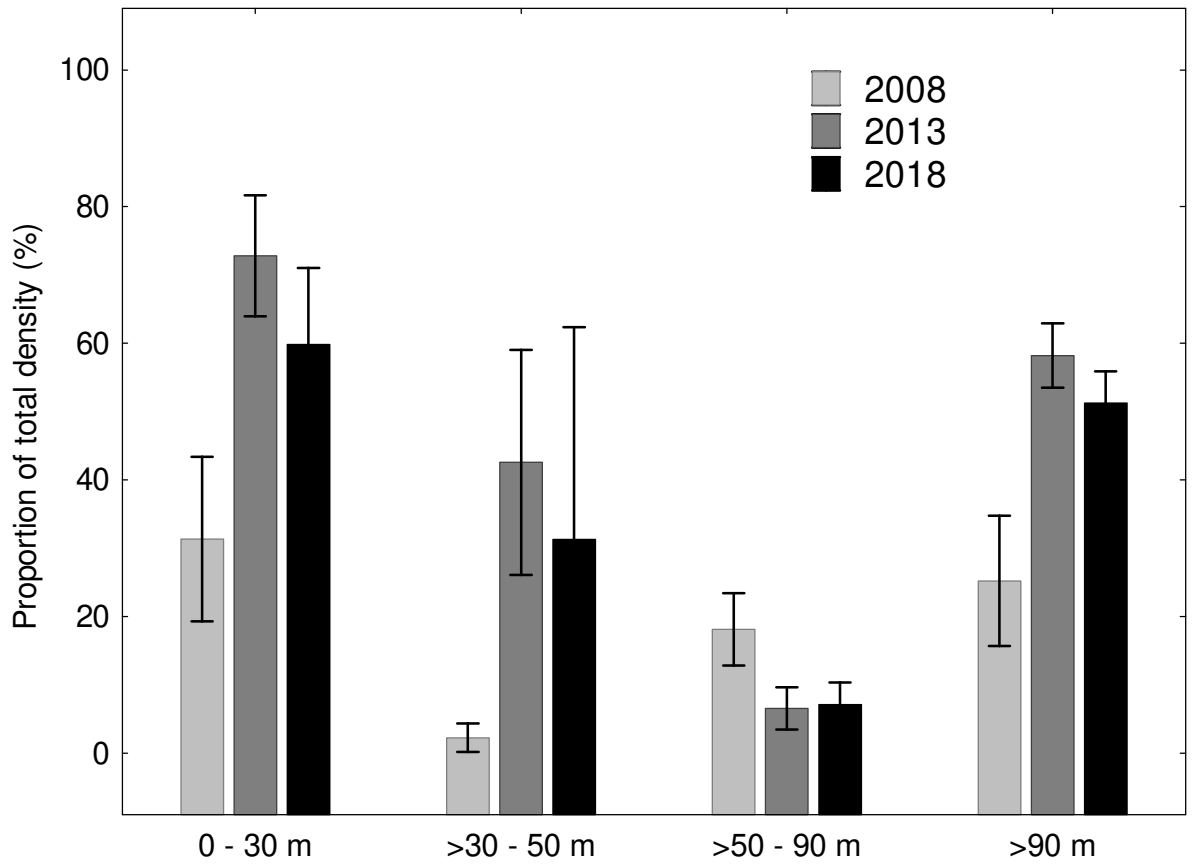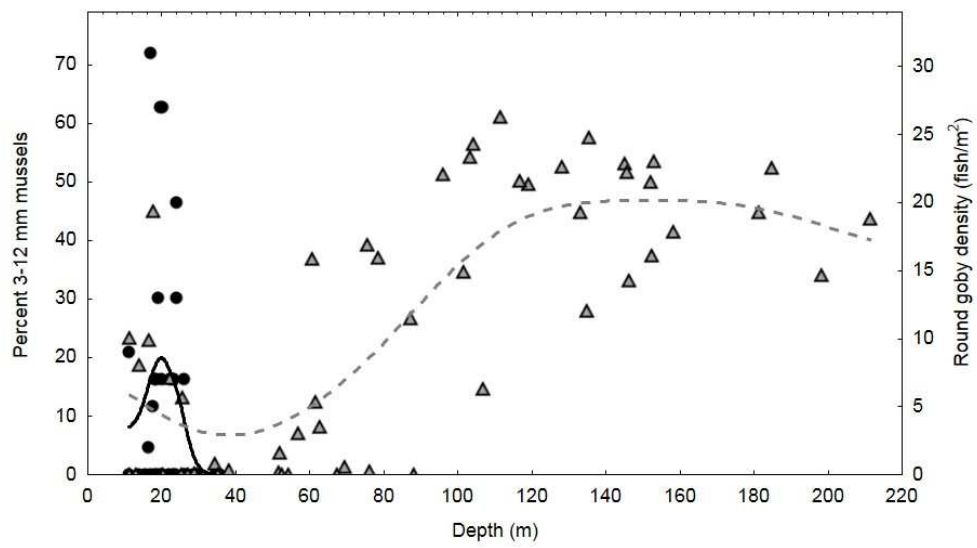
Figure 1.

Figure 2.

Figure 3.

Figure 4.

Figure 5.

Figure 6.

Figure 7.