Journal of Great Lakes Research 48 (2022) 289–299

Contents lists available at ScienceDirect

Journal of Great Lakes Research

journal homepage: www.elsevier.com/locate/ijglr

Depth drives growth dynamics of dreissenid mussels in Lake Ontario ☆

Ashley K. Elgin [a],*, Paul W. Glyshaw [b], Brian C. Weidel [c]

[a] National Oceanic and Atmospheric Administration Great Lakes Environmental Research Laboratory, Lake Michigan Field Station, 1431 Beach St., Muskegon, MI 49441, USA
[b] National Oceanic and Atmospheric Administration Great Lakes Environmental Research Laboratory, 4840 S. State Rd., Ann Arbor, MI, USA
[c] U. S. Geological Survey, Great Lakes Science Center, 17 Lake St., Oswego, NY, USA

ARTICLE INFO

Article history:
Received 13 April 2021
Accepted 4 August 2021
Available online 25 August 2021
Communicated by: Alexander Y. Karatayev

Keywords:
Dreissena rostriformis bugensis
Dreissena polymorpha
Growth rate
Shell morphometry
Recruitment
Population dynamics

ABSTRACT

Understanding dreissenid mussel population dynamics and their impacts on lake ecosystems requires quantifying individual growth across a range of habitats. Most dreissenid mussel growth rates have been estimated in nutrient rich or nearshore environments, but mussels have continued to expand into deep, cold, low-nutrient habitats of the Great Lakes. We measured annual quagga mussel (*Dreissena rostriformis bugensis)* growth at 15 m, 45 m, and 90 m in Lake Ontario using caged mussels near Oswego, New York, USA from June 2018 to May 2019. Quagga mussel growth (starting size 12 mm) was greatest at 15 m (mean shell length increase = 10.2 mm), and was lower at 45 m (5.9 mm) and 90 m (0.7 mm). Caged mussels were obtained from near the 90-m site and those reared at 15 and 45 m developed thicker shells than those that were caged at 90 m. We observed relatively high colonization by quagga and, to a lesser degree, zebra mussels (*Dreissena polymorpha*) at 15 m, very few colonizers at 45 m, and none at 90 m. Higher growth potential, but low natural mussel densities observed at 15 m and 45 m suggest factors other than growth limit dreissenid abundance at these depths. The relatively slow dreissenid growth rates observed in offshore habitats are consistent with the gradual abundance increases documented in these zones across the Great Lakes and suggest new mussels that become established in these habitats may contribute to ecosystem effects for decades.

Introduction

Dreissenid mussels (zebra mussels, *Dreissena polymorpha*, and quagga mussels, *Dreissena rostriformis bugensis*) are a major driver of ecosystem change across water bodies of North America and Europe. They are rated as one of the top stressors within the Laurentian Great Lakes, having a high potential for impacts (Smith et al., 2015). In Lake Ontario, *Dreissena* introduction has been associated with water clarity and fish habitat use change (O'Gorman et al., 2000), benthic invertebrate community changes (Burlakova et al., this issue), increased phosphorus sedimentation velocity (Chapra et al., 2016), and increased occurrence of cyanobacteria and nuisance *Cladophora* (Estepp and Reavie, 2015). *Dreissena* abundance has been depth-specific, with rapid increases in density followed by declines after 2003 in the <90 m depth zones (maximum densities exceeded 10,000 individuals/m^2 at 31-50 m), and steady increases in deeper zones >90 m, where density now approaches 5,000 individuals/m^2 (Birkett et al., 2015; Karatayev et al., this issue, Watkins et al., 2007). Despite extensive study of these species in Lake Ontario and elsewhere, several aspects of their population dynamics remain poorly understood, including if measures of population performance follow the same patterns through time and how body size changes over time (Strayer et al., 2019).

Individual body size has implications for the success of an organism and its population, as well as its impacts on the ecosystem. The ability to attain larger sizes has clear advantages for dreissenid mussel success in terms of refuge from predation (Andraso et al., 2011; Foley et al., 2017) and reproductive output (Sprung, 1991). Larger mussels in soft sediments or in tight clusters may gain advantage over other mussels by intercepting food before it reaches other smaller individuals. Attaining a larger size also has negative implications. Wacker and von Elert (2008) found that smaller zebra mussels were better competitors than larger mussels when food concentrations were low because smaller individuals had a much lower food threshold for basic metabolic demands compared to larger individuals. These competitive advantages and disadvantages illustrate the balance needed between fast

---

☆ Given their role as Associate Editor, Brian C. Weidel had no involvement in the peer-review of this article and has no access to information regarding its peer-review. Full responsibility for the editorial process for this article was delegated to Alexander Y. Karatayev.

* Corresponding author.

E-mail address: ashley.elgin@noaa.gov (A.K. Elgin).

https://doi.org/10.1016/j.jglr.2021.08.006
0380-1330/Published by Elsevier B.V. on behalf of International Association for Great Lakes Research.

and slow growth in dreissenids. Mussel size is also an important factor in individual filtering (Horgan and Mills, 1997) and nutrient excretion capacities (Arnott and Vanni, 1996), which scale up to determine broader impacts of dreissenids on aquatic ecosystems.

Much of the research on dreissenid mussel growth focused on zebra mussels in Europe and the former Soviet Union (reviewed in Karatayev et al., 2006), however quagga mussel growth has been measured in several laboratory studies (Karatayev et al., 2011; Link, 2010; MacIsaac, 1994; Peyer et al., 2010). Field studies of quagga mussel growth are more limited and have been primarily set in Lake Erie (Karatayev et al., 2018; MacIsaac, 1994) and Lake Mead, Nevada (Wong et al., 2012). Common factors investigated in dreissenid growth studies include temperature, food, and water movement (Karatayev et al., 2018, 2011, 2006; MacIsaac, 1994; Peyer et al., 2010). Other factors that are particularly relevant to productive, nearshore environments including inter- and intraspecific competition (Karatayev et al., 2011) and turbidity (Madon et al., 1998) have been investigated. Dreissenid mussel growth can be sensitive to even subtle variations encountered within lakes (Garton and Johnson, 2000), so it is important to produce estimates that encompass different lakes, regions, and depths.

Understanding the dynamics of deep-water dreissenid mussel populations is important because a large proportion of the Great Lakes is deeper than 90 m and these habitats are being colonized by quagga mussels. Among the lakes with widespread dreissenid populations, Lake Ontario has the highest proportion of the lake bed >90 m (51%; Birkett et al., 2015), followed by Lake Michigan (42%; Nalepa et al., 2009), and Lake Huron (30% of the main basins; Karatayev et al., 2020). The Lake Ontario 2018–2022 Lakewide Action and Management Plan identified several research priorities for Lake Ontario 2018 Cooperative Science and Monitoring Initiative (CSMI) field activities (Environment and Climate Change Canada and the U.S. Environmental Protection Agency, 2018). One CSMI research priority was to evaluate the aquatic food web status, stating that "a better understanding of dreissenid growth and reproductive rates in deeper, colder waters is needed in order to fully understand the impacts this benthic species is having on the Lake Ontario aquatic food web".

The goal of this study was to determine how quagga mussel growth rates varied under a range of environmental conditions and depths. We tracked growth dynamics of mussels caged at the lake bottom over 11 months at depths ranging from 15 to 90 m. We hypothesized that growth would decrease with depth but had no specific expectations with regards to the magnitude of growth differences among depths. In addition to dreissenid shell growth and weight changes, our study design provided observations on mussel morphometry, mortality, and colonization across depths. This is the first study to estimate quagga mussel growth rates within Lake Ontario, and the first published study within the Great Lakes to span all seasons over nearly a year and encompass a broad range of depths extending as deep as 90 m.

Methods

Experiment details

Moorings that held dreissenid cages were deployed at three sites in south eastern Lake Ontario: LO15 (15 m depth, 43.532°N, 76.374°W); LO45 (45 m depth, 43.535°N, 76.447°W); and LO90 (90 m depth, 43.563°N, 76.468°W; Fig. 1). We used two types of dreissenid cages, each with a specific approach for measuring mussel growth. The "Group" cages contained 10 quagga mussels within a consistent size range (11.0–13.0 mm shell length) to produce a robust growth estimate for comparison across sites and to control for the effect of mussel size on growth. We chose this size range based on the assumption that smaller mussels had higher growth potential and because they were the smallest mussels available in sufficient numbers for the experiment. For each Group cage, we measured initial shell length (maximum anterior-posterior dimension) to the nearest 0.1 mm for each mussel using digital calipers and total whole mussel wet weight to the nearest 0.1 mg on a four decimal place analytical balance for all 10 mussels combined. To assess seasonal growth, there were six replicate Group cages per site at LO15 and LO45 to be retrieved in the autumn and another six replicates to be retrieved the following spring. Due to a limited number of mussels available, LO90 only had five replicates of the Group cages for each timepoint. The other, "Individual" cages contained 10 individually labeled quagga mussels per cage so that we could track individual, size-specific growth rates across a broad initial size range (8.5–21.9 mm shell length). The mussels were labeled with numbers printed on waterproof paper (Rite in the Rain DuraRite) attached to one valve of the shell using a drop of cyanoacrylate glue. We recorded initial shell length and whole mussel wet weight for each mussel in the Individual cages. Each site had six replicate Individual cages that were deployed for the 11-month duration of the experiment. Due to the scarcity of mussels near LO45 and LO15, all mussels used to populate the cages were collected on June 11–12, 2018 by Ponar grab in the vicinity of LO90 (depth range: 90–150 m). This transplant created the opportunity to observe changes in growth and morphometry for mussels from a common starting point. The mussels were held in a 4 °C incubator between the time of collection and redeployment, with the exception of when they were handled to be measured and assigned to cages.

A total of 18 cages (16 in the case of LO90) were attached to one mooring at each site. Each mooring frame was constructed of angle aluminum and had two 125.7 cm × 93.5 cm molded fiberglass grate platforms (Fig. 2A). The lower platform, which was elevated 7.6 cm from the lakebed, contained the mussel cages. The cages were constructed from black polyethylene plastic mesh (1.5 mm × 1.5 mm mesh size) that was formed into a tube and then secured with rivets at each end, with the ends perpendicular to each other, to form a tetrahedron (Fig. 2B). Internal dimensions of the Group cages were 8 cm wide × 12.5 cm long (surface area ~ 200 cm^2) and the Individual cages were 8 cm wide × 20 cm long (surface area ~ 320 cm^2). The moorings were deployed on June 13, 2018 and retrieved on May 7, 2019 (328 d). We serviced the moorings on November 15, 2018 to switch out instruments and collect the first batch of Group mussel cages, but these samples were compromised.

We quantified how temperature and chlorophyll *a* varied at the three sites using logging instruments attached to the underside of the upper platform on each mooring. Two thermistors (Onset HOBO TidbiT v2) logged temperature hourly while a fluorometer (Seabird Scientific ECO-FL) logged chlorophyll *a* every 6 h. We summarized the temperature and chlorophyll *a* data as daily means from June 2018-May 2019. To illustrate aggregated differences among the sites over time, we also calculated daily cumulative values for both temperature and chlorophyll *a* using thresholds of 0 °C and 0 μg/L, respectively. We incorporated temperature data from additional sources between June-November 2018 to complete our time series because thermistor readings for all sites from that period were lost. We used water intake temperature (~12 m depth) from the Monroe County water treatment plant as a surrogate for LO15 between the dates of June 13 and November 4, 2018. For LO45 and LO90 we used bottom temperatures from trawls conducted by USGS adjacent to the experimental sites on July 10 and 11 and October 2, 2018. Also for LO45 and LO90, we used temperature profile data collected from nearby Station 72 (107 m depth, 43.550°N, 76.439°W) on September 11, 2018 during the Lake Ontario Cooperative Science and Monitoring Initia-

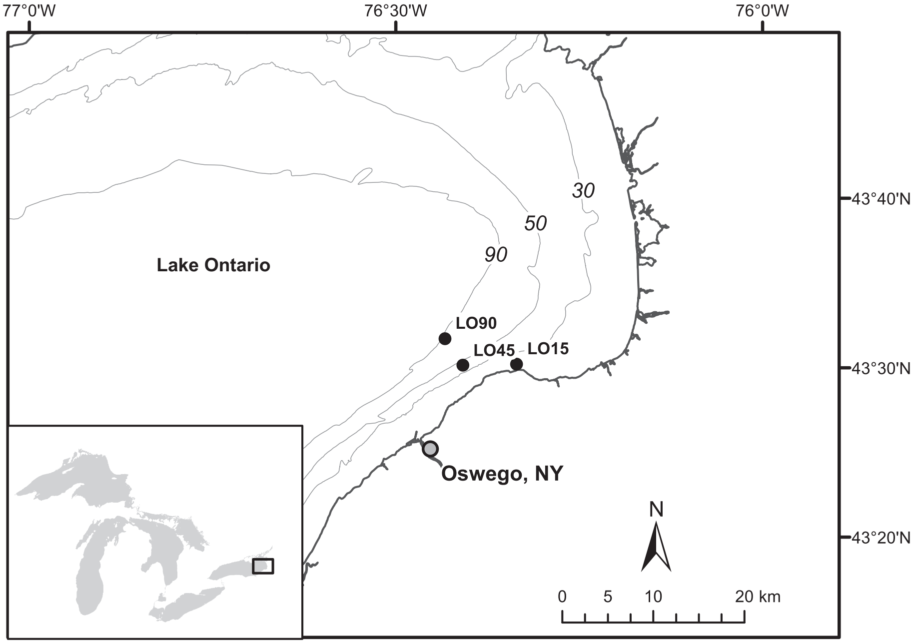

Fig. 1. Large map designates the study sites in eastern Lake Ontario while the smaller inset maps shows the location within the Great Lakes region. The 30, 50, and 90 m depth isoclines are delineated by thin black lines. Approximate distances between sites: 5.9 km between LO15 and LO45 and 3.4 km between LO45 and LO90.

tive benthic survey to determine hypolimnetic temperature, which was applied to both stations. We then used linear interpolation to fill in the values in-between the dates for which we had point data.

To describe the natural densities of mussels we collected three replicate Ponar grabs (area = 0.0467 m^2) at each site in May 2019. Ponar samples were rinsed through a 500-µm sieve and preserved using 10% formalin. Mussels were sorted from the sediments in the laboratory, identified to species, enumerated, and measured for shell length. We used a flattened ventral edge, which was clearly visible even on smaller mussels (shell length < 5 mm), as our primary feature to identify zebra mussels. We also collected additional mussels at LO90 to measure body condition metrics as described below.

We assessed mussel body condition, expressed as tissue biomass (ash-free dry weight, AFDW) relative to shell length, at both the initial and final stages of the experiment, as well as shell length, shell height (maximum dorsal–ventral dimension), and shell weight. These body metrics were measured for a subset of the initial mussels collected near LO90 in June 2018 that were used to populate the cages, as well as background mussels collected near LO90 at the conclusion of the experiment in May 2019. We also assessed a subset of mussels from each cage at the conclusion (3 mussels per Group cage and 5 mussels per Individual cage). For the initial stock of mussels and background mussels from 90 m collected at the conclusion of the study, we selected at least 25 individuals with intact, undamaged shells (target shell length: 10 mm–25 mm). We followed the methods of Glyshaw et al. (2015) to process the mussels. In summary, shells were cleaned of debris and measured for length and height to the nearest 0.1 mm. Whole mussel blotted wet weight was measured before all soft tissue was dissected out and placed into pre-weighed aluminum capsules. The capsules were dried at 60 °C for a minimum of 48 h. The capsules were weighed (for dry weight), ashed at 550 °C for 1 h, and then weighed again (post-ashed weight). AFDW was calculated as the difference between dry weight and post-ashed weight. Shells were dried at room temperature for a minimum of 2 days and then weighed to the nearest 0.1 mg.

We observed that a substantial number of mussels had colonized areas on the mooring grate platforms as well as the internal portions of the LO15 cages. We identified and quantified the length distributions of colonizing zebra and quagga mussels found within the Group cages. We also measured size distributions from a subset of mussels that fouled the grate from the upper platform grate of the mooring.

Data analysis

One way ANOVA and Tukey HSD post-hoc tests were used to quantify differences in depth for growth among the Group cages, shell weight:shell length ratios, and shell height:shell length ratios.

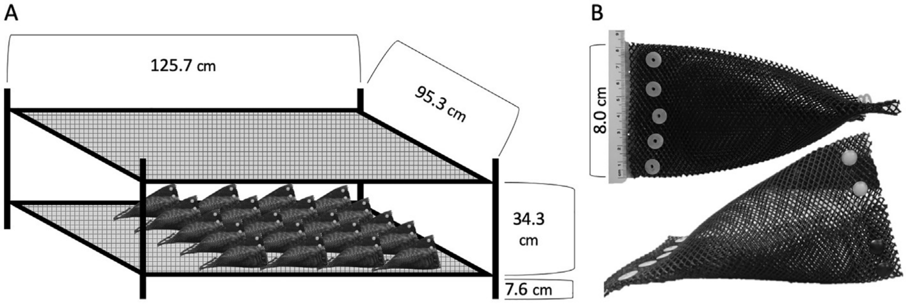

Fig. 2. (A) Mooring design showing overall dimensions and placement of cages on the lower platform grate. (B) Top and side detail views of the 1.5 mm opening mesh cages.

The relationships between change in shell length and initial shell length, tissue AFDW and shell length, and effects of cages were examined using ANCOVA and mixed-effects models. Normality for all statistical tests was assessed using Shapiro-Wilk normality tests, residuals vs fitted plots, and Normal Q-Q plots. All statistical analysis was conducted using the R statistical package (R Core Team, 2019); post-hoc tests were calculated with the lsmeans package (Lenth, 2016). Variation around means is expressed as ± SD.

Dead mussels were not included in the growth estimates. In the Group cages, for each dead mussel we removed a mussel at random from the probable starting pool (i.e., any mussel that was of equal or lesser shell length to the dead mussel). This ensured that the same number of mussels were used to determine the initial and final shell lengths within each cage. Further, we dropped any Group cages from analysis that had more than 50% mortality. Because each mussel in the Individual cages had a unique label, we analyzed the data from all live mussels, regardless of mortality rate for that cage.

For the relationship between change in shell length and initial shell length, we addressed violations of normality by removing values with high Cook's D values, but the results of the statistics did not change. Herein, we report using the full range of values. The data for change in wet weight vs. initial wet weight also violated the assumptions of normality, but neither removing a large number of outlier variables nor performing log transformations was sufficient to correct this violation. As a result, we do not present statistics for change in wet weight.

To investigate for differences between mussels among the replicate Individual cages, we added cage as a random variable in linear mixed effects models using LMER from the lme4 package (Bates et al., 2015) and compared model fits using AICc, which did not reveal any improvement in fit (caged included: AIC = 477.97; excluded = AIC 476.25). Thus, we did not include cage effect in the final models for shell length change by initial shell length. In the case of weight change by initial weight, because the full model violated multiple assumptions, we ran separate models for each depth to investigate for cage effects and did not find any.

We calculated regression coefficients separately for each depth to describe changes in both shell length and whole mussel wet weight for mussels from the Individual cages. Based upon earlier analyses there was no cage effect on growth rates (length or weight), so we pooled all mussels together into a single regression for each depth. We also calculated regression coefficients for tissue AFDW-shell length relationships at each depth for mussels in Individual cages, as well as the initial starting stock of mussels collected from $\geq$ 90 m that were used for the study. We removed one mussel from 90 m (shell length = 8.5 mm, AFDW = 0.44 mg) for tissue AFDW-shell length analysis and presentation because its tissue AFDW was well outside of the 99% confidence interval.

Results

Quagga mussel growth was strongly depth-dependent. There was a significant depth difference among the Group cages (ANOVA: $F_{2,12}$ = 417.2, p < 0.001), with LO15 exhibiting the greatest mean increase in shell length (10.2 mm ± 0.8, 0.031 mm/d), followed by LO45 (5.9 mm ± 0.2, 0.018 mm/d), and LO90 (0.7 mm ± 0.4, 0.002 mm/d; Fig. 3). See Table 1 for mean initial shell length and mean length change for each cage. Whole mussel wet weight followed a similar pattern of a significant overall depth difference (ANOVA: $F_{2,12}$ = 20.6, p < 0.001), with the highest mean weight gain by far observed at LO15 (6.27 g ± 2.42). However, LO45 and LO90 were not significantly different from each other (LO45 = 2.45 g ± 0. 79, LO90 = 0.09 g ± 0.13).

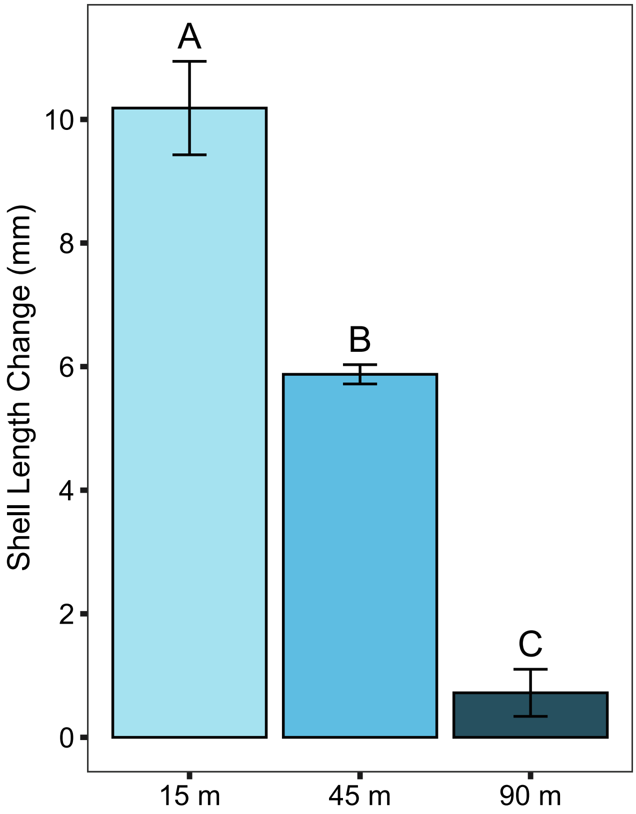

Fig. 3. Mean growth (± SD) of quagga mussels (*Dreissena rostriformis bugensis*) grown in Group cages at three depths in Lake Ontario from June 13, 2018 until May 7, 2019. Growth was measured by the mean change in shell length per cage. Mean starting shell length per cage was ~12 mm. Categories with different letters differ significantly (α = 0.05), according to pairwise comparisons.

Change in shell length was also significant among depths for mussels in the Individual cages (ANCOVA: $F_{2,120}$ = 60.2, p < 0.001), where initial shell length covaried with length change ($F_{1,120}$ = 33.3, p < 0.001). Further, a significant interaction between depth and initial shell length ($F_{2,120}$ = 10.8, p < 0.001) highlights that shell growth was most strongly size-dependent at LO15 (Fig. 4A), where there was a decrease in shell growth as size increased.

Change in whole mussel wet weight for the Individual mussels also differed among depths, but the relationships between initial wet weight and change in weight followed a different pattern than for length, where the magnitude of change increased with initial wet weight at LO15 and LO45 (Fig. 4B). Mussels from 90 m expressed low levels of weight change across all initial values, which corresponds with the low level of shell length change observed.

Seasonal and cumulative patterns in temperature and chlorophyll *a* differed at the three depths (Fig. 5). The cumulative degree day values at the 15, 45, and 90 m stations were 2982, 1544, and 1373, respectively (Fig. 5B) while cumulative chlorophyll *a* concentrations were 718, 339, and 166, respectively (Fig. 5D). We intended to evaluate the relative importance of temperature, chlorophyll *a* concentration, and mussel size in explaining variability in observed mussel growth, but high collinearity (Pearson's correlation > 0.99) between the cumulative temperature and chlorophyll *a* values over the three sites prevented such analyses.

Analysis of relative body tissue mass at the conclusion of the experiment showed significant differences among depths (ANCOVA: $F_{3,108}$ = 48.88, p < 0.001; Fig. 6) and that there was no interaction between shell length (the covariate) and depth

Table 1
Growth and mortality metrics for *Dreissena rostriformis bugensis* deployed for 328 d in replicate cages at three sites in Lake Ontario. Each cage contained 10 mussels at the beginning of the experiment. Asterisks in the Cage # column indicate Group cages with >50% mortality that were excluded from analysis.

Cage type	Site (Depth)	Cage #	Mortality (%)	Mean initial length (mm ± SD)	Mean length change (mm ± SD)
Group	LO15	11	0	11.9 (±0.6)	10.3
	(15 m)	12	50	12.0 (±0.8)	10.3
		13	10	12.0 (±0.7)	10.4
		14	40	12.0 (±0.6)	9.6
		15	50	11.8 (±0.6)	9.2
		16	50	12.0 (±0.8)	11.4
	LO45	41*	60	–	–
	(45 m)	42*	100	–	–
		43	20	11.9 (±0.7)	6.1
		44	40	12.0 (±0.7)	5.8
		45	30	11.9 (±0.5)	6.0
		46	0	12.1 (±0.6)	5.7
	LO90	71	0	12.1 (±0.6)	0.6
	(90 m)	72	0	12.1 (±0.6)	1.1
		73	0	12.1 (±0.6)	0.3
		74	0	12.1 (±0.6)	1.1
		75	20	12.2 (±0.5)	0.5
Individual	LO15	21	30	15.8 (±4.3)	9.3 (±2.2)
	(15 m)	22	40	15.4 (±4.2)	8.1 (±2.5)
		23	0	14.7 (±4.2)	8.1 (±2.9)
		24	20	14.1 (±4.4)	10.3 (±2.5)
		25	30	15.7 (±3.5)	7.6 (±2.6)
		26	40	13.9 (±4.2)	9.0 (±2.8)
	LO45	51	90	9.0 (±NA)	−0.1 (±NA)
	(45 m)	52	0	14.7 (±4.1)	5.3 (±1.0)
		53	60	12.0 (±2.1)	5.9 (±1.2)
		54	80	19.7 (±3.1)	4.6 (±0.7)
		55	80	15.9 (±2.5)	5.2 (±0.6)
		56	30	14.1 (±3.7)	5.2 (±1.5)
	LO90	81	0	14.7 (±4.2)	1.1 (±0.5)
	(90 m)	82	0	14.7 (±4.2)	0.4 (±0.5)
		83	30	13.8 (±3.1)	0.0 (±0.2)
		84	0	14.7 (±4.2)	0.4 (±0.6)
		85	0	14.6 (±4.1)	0.6 (±0.5)
		86	10	14.8 (±4.4)	0.6 (±0.4)

(p = 0.64). Statistical paired comparisons of least-square means revealed significant differences between all pairs (p < 0.01). At a given shell length, mussels from 15 m had the highest tissue AFDW, followed by 45 m. Unexpectedly, mussels from 90 m at the conclusion of the experiment had lower tissue AFDW than the initial stock of mussels from 90 m that were used to populate all cages at the beginning of the experiment. Put into terms of the tissue AFDW of a 15-mm shell length mussel, the initial stock mussels weighed 5.8 mg at the beginning of the study. After 11 months in the field, mussels from 15 m, 45 m, and 90 m weighed 9.5 mg, 7.3 mg, 4.8 mg, respectively, which illustrates substantial tissue weight gain at the 15-m and 45-m sites, holding shell length constant.

Shell morphology of Individual mussels was also strongly influenced by depth (Fig. 7). Shell weight:shell length ratio was significantly different between all depths (ANOVA: $F_{2,75}$ = 101.5, p < 0.001), with the 15-m site having the highest shell weight:shell length ratio (15.9 ± 3.2), followed by 45 m (9.7 ± 3.4), and 90 m (4.9 ± 2.3). Shell height:shell length ratios also varied by depth (ANOVA: $F_{2,75}$ = 7.65, p < 0.001). The mean shell height:shell length ratio was highest at 15 m (0.58 ± 0.04), followed by 45 m (0.57 ± 0.06) and 90 m (0.53 ± 0.04). Post-hoc tests revealed that shell height:shell length differences were only significant between 15 m and 90 m (p = 0.001) and 45 m and 90 m (p = 0.023). There was no significant difference in the shell height:shell length between 15 m and 45 m (p = 0.823).

Mussel mortality was notably higher at the 15 m (30%) and 45 m (49%) sites, compared to 90 m where only 5% of the caged mussels died over the course of 11 months (Table 1). According to the final shell lengths of the dead mussels, they grew a modest amount before dying. Based on data from the Group cages and assuming a starting shell length of 12 mm, these mussels grew, on average, 4.3 mm at 15 m, 4.3 mm at 45 m, and 0.2 mm at 90 m before dying. These levels of growth represent 42%, 73%,

Table 2
Linear regression parameters and statistics for length and weight relationships presented in Figs. 4 and 6. Slopes marked with an asterisk indicate significance at α = 0.05.

Regression	Related Figure	Site (Depth)	Slope	Intercept	R^2	n
Length Change vs. Initial Length	4A	LO15 (15 m)	−0.34*	13.80	0.27	44
		LO45 (45 m)	−0.01	5.20	0.00	26
		LO90 (90 m)	0.00	0.47	0.00	56
Weight Change vs. Initial Length	4B	LO15 (15 m)	0.28	859.29	0.05	44
		LO45 (45 m)	0.78*	161.92	0.62	26
		LO90 (90 m)	0.03	39.69	0.01	56
Tissue AFDW (ln) vs. Shell Length (ln)	6	Initial Stock (≥90 m)	2.80*	−5.83	0.96	35
		LO15 Final (15 m)	2.60*	−4.80	0.91	30
		LO45 Final (45 m)	2.88*	−5.81	0.94	19
		LO90 Final (90 m)	2.75*	−5.88	0.96	29

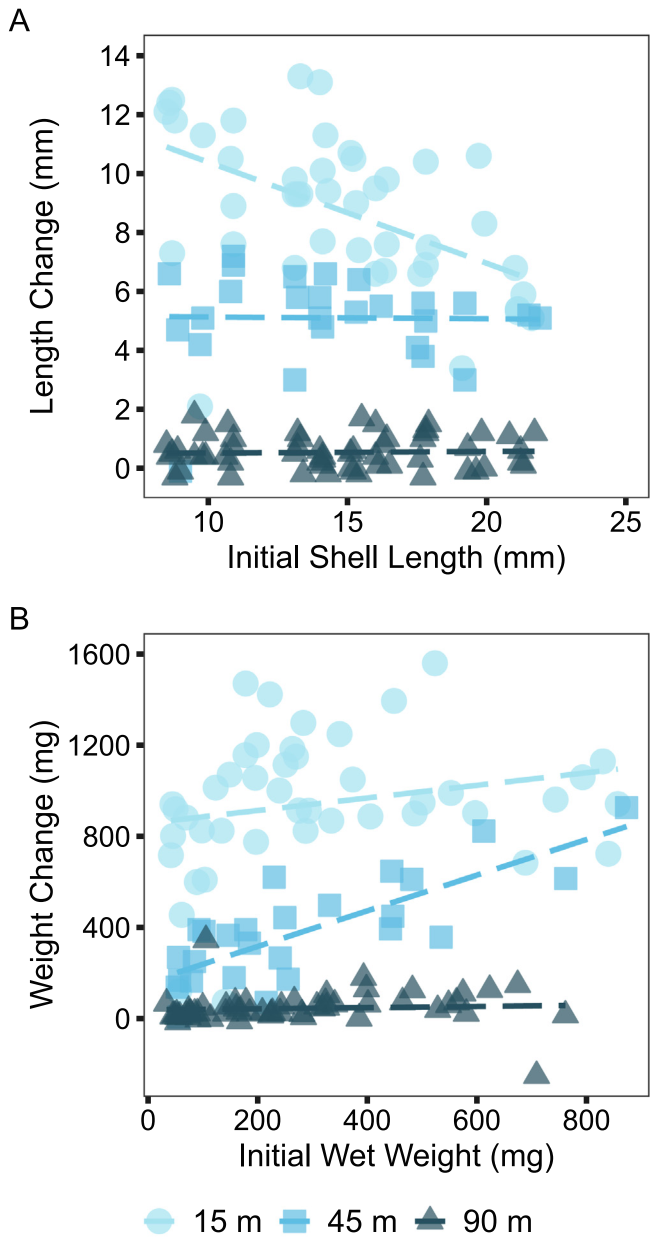

Fig. 4. Change in shell length and mussel wet weight relative to starting conditions, from all quagga mussels (*Dreissena rostriformis bugensis*) in Individual cages at three depths in Lake Ontario, from June 13, 2018 until May 7, 2019. Panel (A) illustrates shell length change in mm as a function of initial shell length and (B) illustrates whole mussel wet weight change in mg as a function of initial wet weight. Trendlines are shown for all relationships, even if not significant. See Table 2 for regression parameters and statistics.

and 29% of the total growth achieved by the live mussels at the three depths, respectively.

To determine if cages had any effect on mussel condition, we compared length-weight regressions of caged mussels from 90 m to background mussels collected by Ponar grab in the vicinity of LO90 at the conclusion of the experiment. There was a significant difference between the two groups (ANCOVA: $F_{1,68}$ = 6.17, $p = 0.02$), with tissue AFDW of caged mussels being approximately 10% higher than that of background mussels. A 15-mm shell length caged mussel had an AFDW of 4.8 mg while a 15-mm shell length background mussel collected at the conclusion of the study weighed 4.4 mg. Comparisons could not be made at the other sites as we were not able to collect a sufficient number of background mussels across the target size range.

Abundant colonizing mussels were found within the cages and on the supporting grate at the 15-m site, just a few were detected at 45 m, and none at 90 m. On average, 84.7 (± 32.7) quagga mussels and 5.0 (± 1.7) zebra mussels were found in each Group cage at LO15 (n = 6). The length of colonizing quagga and zebra mussels ranged from 1 to 14 mm (Fig. 8) and were distinct from the larger experimental mussels which had final lengths ranging from 16.1 mm to 25.2 mm at the end of the experiment. It was clear they were colonizers based on size, and therefore they did not get confused with the unlabeled mussels in the Group cages. The length of colonizing mussels found attached to the mooring grate (quagga range: 1–12 mm; zebra range: 2–8 mm) were comparable to the size distributions of the internal colonizers.

Triplicate Ponar grabs collected from the vicinity of the moorings at the conclusion of the study revealed large differences in quagga mussel density among sites. Many fewer mussels were found at 15 m (121.4/m^2 ± 32.7) and 45 m (71.4/m^2 ± 89.2) than at 90 m (7011.5/m^2 ± 2939.8). Further, the mussels present at 15 m and 45 m were generally smaller (mean length = 2.3 mm, range = 1–5 mm at both sites) than mussels at 90 m (mean length = 17.6 mm, range = 9–25 mm).

Discussion

Growth potential for quagga mussels is strongly influenced by depth. We observed a 10-fold higher growth rate in quagga mussels from 15 m compared to 90 m in eastern Lake Ontario. This is the first published study to produce a growth estimate for quagga mussels as deep as 90 m (0.002 mm/d) and that rate is among the lowest reported for this species. Our estimated daily growth rates at the 15-m and 45-m sites are bracketed by rates reported from quagga mussel field growth studies conducted at comparable depths in other systems. Here, we report all growth rates in terms of mm/d to adjust for different experiment durations across studies, which ranged from 55 d (MacIsaac, 1994) to 205 d (Karatayev et al., 2018) to 328 d (this study). Quagga mussels (15-mm starting shell length) tethered 1.5 m from the lake bed on the northwestern shore of Lake Erie from June to August grew 0.04 mm/d (MacIsaac, 1994), which is slightly higher than our estimate of 0.031 mm/d for mussels at our 15-m site. MacIsaac (1994) also reported negligible growth by quagga mussels in the eastern basin of Lake Erie, from July-September, which likely experienced temperatures more similar to our 45-m site, where we measured growth to be 0.018 mm/d. Another eastern Lake Erie study measured growth rates from May to November/December to be 0.019 mm/d at 13–14 m and 0.005 mm/d at 50–55 m (Karatayev et al., 2018), both of which are lower than the rates we estimated at similar depths in Lake Ontario. Our study confirms previous conclusions that dreissenid growth rates decrease with depth, but we also captured depth-specific conditions across all seasons to produce more representative annual growth rate estimates.

While depth clearly influences shell growth rate, depth-associated conditions and resource availability appear to also alter dreissenid mussel energy allocation. We observed tissue loss coupled with low but positive shell growth among mussels reared at 90 m, which contrasts sharply with the substantial gains in both tissue and shell mass by the mussels at 15 m and 45 m. Stoeckmann and Garton (2001) demonstrated that zebra mussels are flexible with how they allocate energy, particularly when under stressful temperature and food conditions. Our results suggest that resources or environmental conditions at 90 m are limiting enough to force mussels to decide between tissue and shell growth. A similar phenomenon was observed in Lake Constance, Germany,

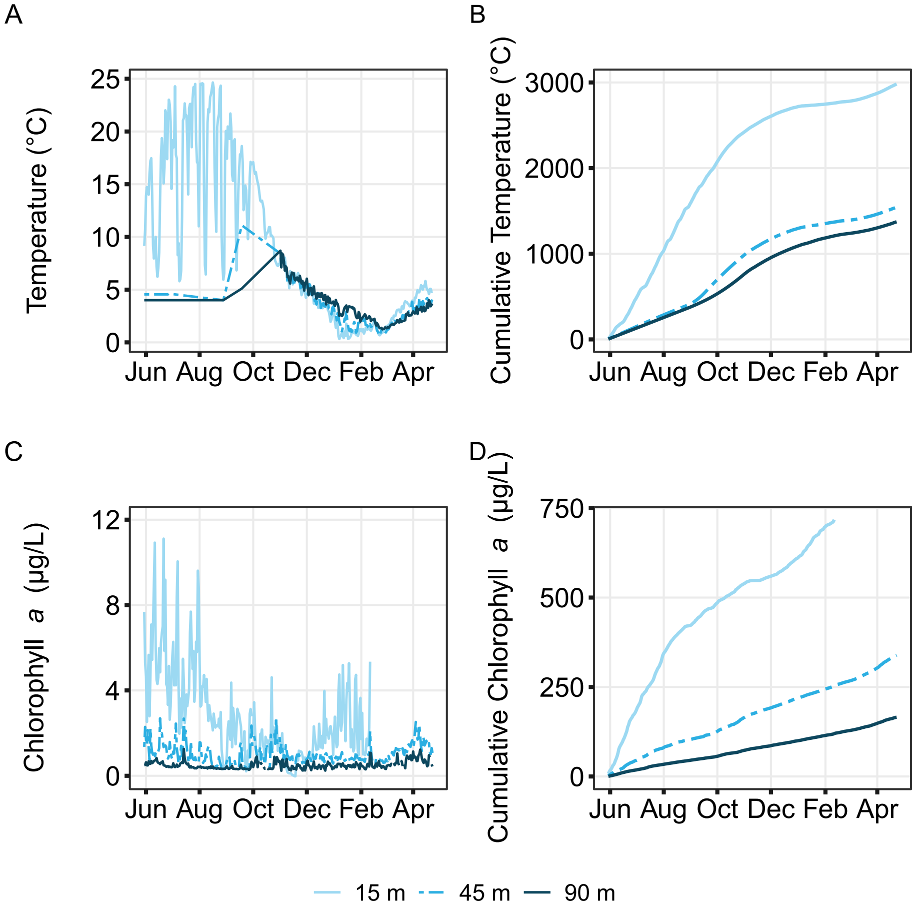

Fig. 5. Daily means of (A) temperature in °C and (C) chlorophyll *a* in µg/L, as measured by instruments mounted < 0.5 m from the lake bed from June 13, 2018 until May 7, 2019. Cumulative values (B, D) are shown through May 7, 2019, except for chlorophyll *a* at 15 m, which truncates on February 25, 2018 due to instrument failure.

where body mass of zebra mussels declined over two years at 60 m, but shell size remained consistent (Walz, 1978). Borrero and Hilbish (1988) found that the marine ribbed mussel (*Geukensia demissa*) lost tissue mass, even though shell growth continued. For blue mussels (*Mytilus edulis*) in eastern Long Island Sound, tissue growth was reported to occur after a period of shell growth (Hilbish, 1986). Counter to these findings, MacIsaac (1994) found that 15-mm dreissenid mussels held in the lab at 6 °C exhibited shell degrowth coupled with overall weight gain. Our results highlight the value of measuring changes in tissue mass and shell mass, in addition to shell length change. A rich area for future research is to quantify how quagga mussels allocate energy towards shell growth, somatic tissue maintenance and growth, and reproductive output under a wide range of conditions.

Our experimental design exposed mussels from a single source to new environmental conditions, and the phenotypic responses we observed were consistent with expected gradients of predation risk and temperature. Not only did the mussels collected from $\geq$ 90 m and reared at 15 m exhibit the largest shell length increase, they also produced relatively thicker shells than at the other depths. Similarly, in eastern Lake Erie, shallow-collected dreissenid mussels had much more robust shells than the more fragile quagga mussels collected from 37 m and 55 m (Roe and MacIsaac, 1997). Quagga mussels have been shown to increase shell thickness when exposed to predator cues (Naddafi and Rudstam, 2014). There is likely a gradient of such cues in Lake Ontario with depth, as the density of fish and avian predators is mostly likely highest at shallow depths, however round goby (*Neogobius melanostomus*) seasonally migrate to depths greater than 130 m (Pennuto et al., 2021; Walsh et al., 2007). Mussels at 15 m and 45 m developed shells with significantly higher shell height:length ratios than at 90 m, indicating an induced change to a shell form associated with shallow mussel populations (Nalepa et al., 2013). Peyer et al. (2010) demonstrated that temperature had a strong impact on shell morphology, where mussels in colder conditions (~6-8 °C) produced the deepwater "profunda" morphotype. Further, *Dreissena* siphon length increases in profunda morphs, presumably to improve access to recently settled material at the sediment water interface (Nalepa et al., 2013). We also speculate that lighter, more elongate shells may benefit quagga mussels in the less-consolidated substrates that are frequently observed at 90 m by reducing sinking and potentially improving their ability to access settling food.

Our results suggest mussel growth is not linearly related to temperature or food levels. For example, cumulative temperature and chlorophyll *a* were slightly different between 45 m and 90 m and shell length growth differed by 5.2 mm between these two sites, whereas temperature and chlorophyll were more disparate between 15 m and 45 m but shell growth only differed by 4.3 mm between these sites. Unfortunately, we did not encounter the combination of conditions necessary to distinguish the relative impacts of temperature and food. We looked to laboratory studies to provide additional insights into the effects of temperature and food on quagga mussel growth, but encountered some differences and limitations among studies. In a 34-d study, temperature and mussel size influenced growth, but food concentration dropped out as not significant in preliminary analyses (MacIsaac, 1994). Similarly, a 289-d study showed that temperature and mussel size

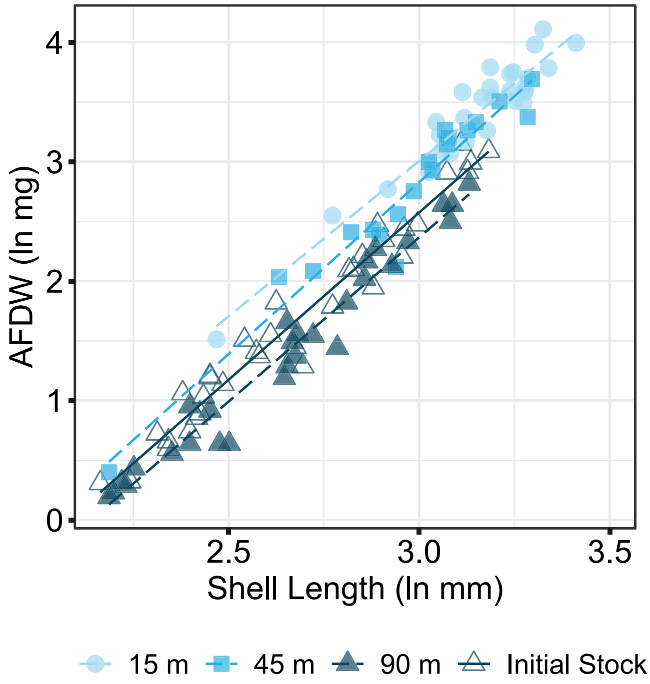

Fig. 6. Tissue ash-free dry weight (ln mg AFDW) as a function of shell length (ln mm) for the quagga mussels (*Dreissena rostriformis bugensis*) from the Individual cages at the conclusion of the experiment. Mussels reared at the three depths in Lake Ontario and retrieved on May 7, 2019 are compared against the initial stock collected on June 11–12, 2018 from ≥ 90 m that was used to populate all cages at the beginning of the experiment. All regressions are significant; see Table 2 for regression parameters and statistics.

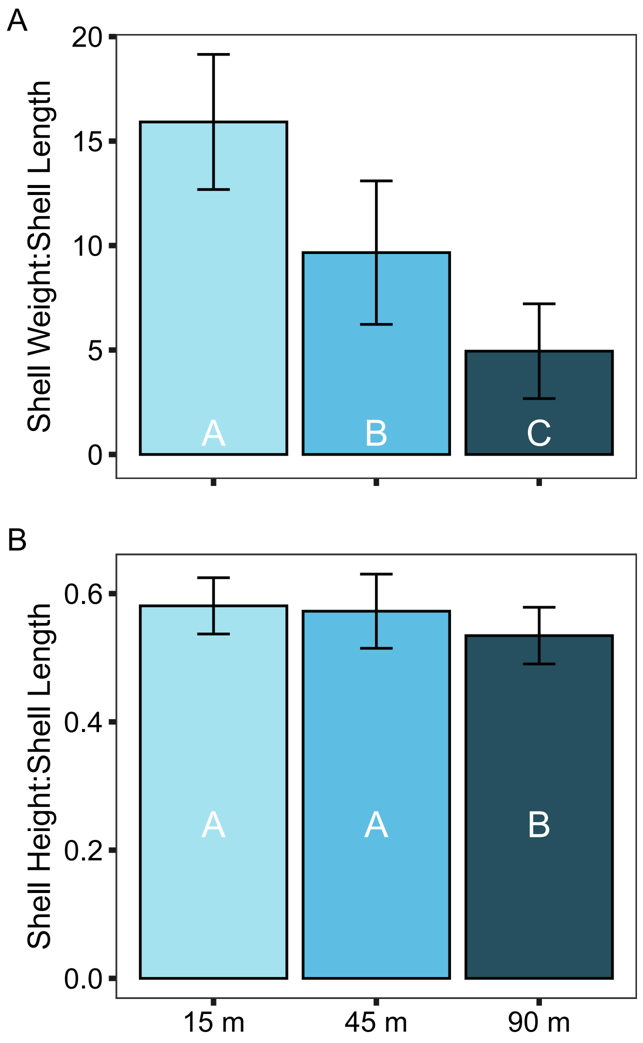

Fig. 7. Ratios of Lake Ontario quagga mussel (*Dreissena rostriformis bugensis*) shell ratios: (A) shell weight in mg to shell length in mm, which is a metric related to shell thickness and (B) shell height to shell length in mm compared across depths. Categories with different letters differ significantly ($\alpha = 0.05$), according to pairwise comparisons. Error bars represent SD and measurements are from mussels deployed from June 13, 2018 until May 7, 2019.

significantly affected growth, but food was not included as a factor (all mussels received Lake Erie water with potentially "low seston concentration or low food quality"; Karatayev et al., 2011). A multi-year study reported lower growth rates for quagga mussels exposed to lower temperatures and lower food quantities, which were tested separately so there was no opportunity to see the combined effect of low food and low temperature (Peyer et al., 2010). Our results from 90 m confirm that quagga mussel growth is minimal in low food, low temperature environments. It will be important for future field and laboratory studies to observe growth over a wider variety of food and temperature conditions in order to differentiate the relative roles of these factors on dreissenid growth.

Cages are commonly employed to estimate mussel growth, but they have the potential to interfere with the *in situ* measurements they are designed to capture. Such cage and experimental artifacts are not always well-tested (Karatayev et al., 2006). We compared mussel body condition between caged and non-caged mussels in order to quantify potential cage effects. The 10% higher relative tissue weight of the 90-m caged mussels compared to the uncaged mussels suggests that the mesh size used for the cages did not inhibit feeding. In addition, we did not observe periphyton growth fouling the cages, which has been suggested to contribute to mussel mortality in other cage studies (Karatayev et al., 2006). However, the lack of background mussels at the 15 m and 45 m locations did not allow us to evaluate cage effects at depths with higher food levels. Another potential experimental artifact can arise from mussels being elevated above the lakebed. Our mooring was designed to minimize the height of the cages from the lake bed (8 cm) because growth rate increases with increasing height in the water column. Karatayev et al. (2018) observed about 50% higher growth when cages were 0.7 m vs. 0 m from the lake bed for quagga mussels. However, a similar difference in cage height did not have a significant effect on zebra mussel growth in the littoral zone of Lake Wawasee, Indiana (Garton and Johnson, 2000). We recommend that future growth studies use the largest mesh size that still retains the study organisms; situate the mussel cages as close to the lakebed as possible without burying them in the sediments; and compare metrics between caged to non-caged mussels in order to detect experimental artifacts.

The levels of mortality that we observed in our cages did not track linearly with depth and exceeded values reported by studies conducted in other lakes. Wave disturbance and increased suspended sediments have been thought to limit success of dreissenid mussels in shallow, nearshore waters (Roe and MacIsaac, 1997; Vanderploeg et al., 2010) and in a laboratory study, mussels exposed to warmer temperatures (4-25 °C) had lower survival rates than mussels in colder water (5-8 °C; Karatayev et al., 2011). Further, quagga mussels acclimated at 5 °C experienced high levels of mortality at temperatures exceeding 30 °C (Mills et al., 1996), with references therein citing lethal temps beginning at 28 °C. Based on these mechanisms, we would have expected mortality to be highest at 15 m and decline with depth. However, we observed highest mussel mortality at the intermediate depth (45 m, 49%), which was more thermally similar to the 90-m site

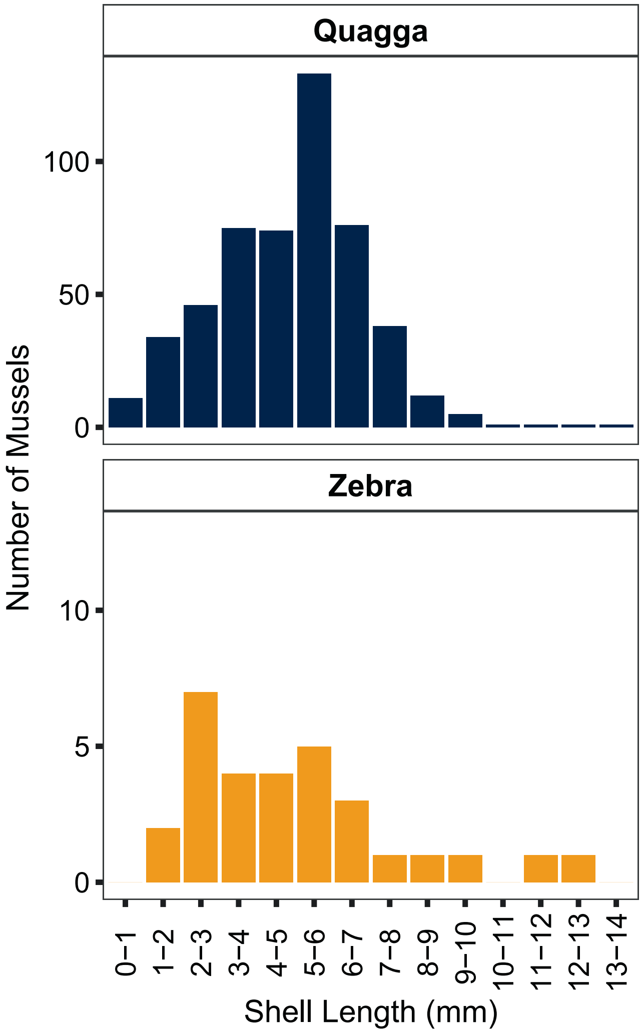

Fig. 8. Size distribution of quagga mussels (*Dreissena rostriformis bugensis*; upper panel) and zebra mussels (*D. polymorpha*; lower panel) that were found inside of the Group cages at 15 m. The colonization and growth would have occurred between June 13, 2018 and May 7, 2019. Note the order of magnitude difference in the y-axis scale between the two species.

(5% mortality). The 15-m site experienced the greatest temperature fluctuations (e.g., from 24 to 6 °C within one week in July) and had the highest temperature recorded during our study (24.6 °C), but mortality was more moderate at 30%. As a result, we do not expect that the higher mortality of caged mussels at 45 m was due to thermal stress. Overall, our caged mussel mortalities (0–100%) were higher than other field studies (0–4% in Karatayev et al., 2018; 0–15% in MacIsaac, 1994), which may partially be explained by our study having a longer observation period. For example, at 45 m, the mussels that died achieved an average shell length that was 73% of that measured for the mussels that survived the duration of the experiment, indicating that those mussels that died likely lived for a majority of the year before perishing.

The environmental conditions that impacted the caged mussels may partially explain the limited number of mussels in the adjacent lakebed at 15 m and 45 m. At <125 mussels/m^2, the background densities of mussels at these sites were much lower than the lake-wide mean abundances for these depth zones (<30 m and 31–50 m, respectively; Karatayev et al., this issue). Another indication of high mortality among the quagga mussel populations is that neither site had mussels greater than 5 mm in length in the sediments surrounding the moorings. While predation would seem a plausible explanation since round goby are frequently caught at these sites, the mortality we observed in the cages, which excluded predators, suggests other environmental and physical processes contribute to mussel mortality as well. Because quagga mussels appear to survive in low temperature and food environments, local sedimentation and resuspension events may be the most plausible explanation for our observations. In addition to mortality, the supply of settling veligers also likely influences mussel abundance and size distribution across depths.

The patterns we observed in colonizing mussels provide insight into the settlement and drivers of Lake Ontario dreissenid mussel distributions. The number of colonizing mussels and size of the mussels found in and on experimental gear at the 15-m site contrasts with the low densities in the surrounding natural substrates suggesting the lack of stable, hard substrates in this habitat with greater physical disturbance may limit mussel density. The similarity in sizes of mussels between the mooring platform grate and inside the cages suggests two things. First, that predation was likely not sufficient to eliminate mussels on the mooring outside of the protective cages. Second, the mussels on the grate grew from settlement as opposed to large mussels migrating up from the sediments. The dearth of colonizing mussels on the experimental gear at 45 m and 90 m suggests recruitment may be sporadic at these depths. That no mussels < 9 mm were found in the natural populations surrounding the 90 m mooring provides further support for sporadic recruitment at that site. In Lake Erie, colonization occurred at shallow depths but reduced food resources and interspecific competition in hypolimnetic habitats limited deeper dreissenid recruitment (Karatayev et al., 2018). The scarcity of mussels at depths > 130 m across the Great Lakes in the initial stages of invasion has been partially attributed to low propagule supply at these depths (Karatayev et al., 2021). The presence of zebra mussels on the moorings confirms that this species still has viable propagules in the water column. However, their absence in the background Ponar samples, as well as their conspicuous absence from the Lake Ontario whole-lake benthic surveys since 2008 (Karatayev et al., this issue), confirms that zebra mussels depend on hard substrates for settlement success. Veligers are present in the water column for much of the sampling season in Lake Ontario, with peak abundances observed in August and September (Bowen et al., 2018). Based on long-term veliger dynamics in Lake Michigan, veliger densities further offshore tend to be lower than nearshore and peak in the autumn (Pothoven and Elgin, 2019). Less is known about the settling patterns of veligers after they complete their planktonic life stage; recruitment may not synchronize with spawning activity or veliger abundances (Nalepa et al., 2010). Deploying settlement traps to quantify the incoming supply of settling veligers over time at multiple depths could help to address knowledge gaps about dreissenid recruitment patterns, particularly in mid-depth zones where reasons for limited recruitment are poorly understood.

The slow mussel growth we observed in deep water has important implications for understanding Lake Ontario quagga mussel invasion dynamics. May and Marsden (1992) genetically identified and named quagga mussels from 1991 samples in Lake Erie and Ontario, and quagga mussels comprised up to 50% of the dreissenids collected in Ponar samples in 1990 near our study site (Nine Mile Point, Oswego, NY; Mills et al., 1993). In 1992, zebra mussels up to 22 mm and quagga mussels up to 24 mm in shell length were collected at multiple sites in 85–130 m of water along Lake Ontario's south shore (Mills et al., 1993). Given our estimated growth of 0.7 mm/y at 90 m, either mussel growth has radically slowed in deep regions following initial invasions and/or mussels may have been present in Lake Ontario deep water much earlier than 1990. Mussel growth rates have likely declined since they first invaded due to reduced food resources since spring phytoplankton biomass has decreased from 5.8 to 0.14 g/m^3 from 1990 to 2013 (Munawar et al., 2015; Munawar et al., 2016). However, water temperature also regulates mussel growth (Karatayev et al., 2011; MacIsaac, 1994) and temperatures at those depths have likely changed little since dreissenid invasion. The large-shelled mussels observed in deep habitats in 1992 could have grown in shallower habitats and moved deeper, but an estimated migration rate of 0.5 km/y (calculated from Toomey et al. (2002) and assuming non-stop, linear progress), suggests movement is an unlikely explanation. Interestingly, the large mussels found at depths > 85 m in 1992 were collected using bottom trawls, which would have swept approximately 10,000–15,000 m^2 of lake bottom in single 10-minute tow (Weidel et al., 2017). The likelihood of detecting deep dreissenid mussels would have been much greater with this non-traditional sampling gear in contrast to benthic invertebrate surveys that employed Ponar grabs which collect ~ 0.05 m^2 lake area per sample (Dermott and Geminiuc, 2003). Recent evidence has shown species invasions can often go undetected for years before specific conditions trigger enough population growth such that the invasion can be detected (Spear et al., 2021). Here we illustrate how quantifying dreissenid growth rates and inferred longevity could improve estimation of dreissenid invasion timing.

Addressing the remaining unknowns about quagga mussel biology will require additional targeted investigations. To validate our hypothesis of slow growth and high longevity in deeper regions, we recommend conducting long-term growth studies (5 years or longer) to better capture quagga mussel growth and mortality over extended time periods. We estimated that a deepwater 25-mm quagga mussel could be more than 30 years old. An estimate of 17–19 years was given for zebra mussels in the Volga River in Russia (summarized by Karatayev et al., 2006). New analysis techniques could provide a promising avenue to determine dreissenid age with more certainty. For example, laser ablation–inductively coupled plasma–mass spectrometry has been used to retrospectively estimate age of oyster shells by analyzing seasonal peaks and troughs in their Mg/Ca ratio profiles (Durham et al., 2017). Frequent (annual or less) collections of mussels and analysis of their size distributions are another way to test if our measured rates accurately represent growth in the field. Ultimately, a better understanding of individual growth, longevity, and energy allocation is necessary to predict long-term population dynamics of dreissenid mussels and their impacts on aquatic ecosystems. Not only will these investigations elucidate the past and future population trajectories for dreissenid mussels, they will also provide updated parameter estimates for models developed to explain mussel impacts, such as recent work by Li et al. (2021) to demonstrate the critical role dreissenids play in the Great Lakes phosphorus cycle.

Regardless of how growth rate has changed over time, nearly half of Lake Ontario is 90 m or deeper, and mussels are now abundant at those depths. Quagga mussels that successfully settle in deep regions of the Great Lakes may establish populations that could persist for more than 20 years, during which time they will have long-term impacts on the local benthic environment as well as benthic and pelagic food webs.

CRediT authorship contribution statement

Ashley K. Elgin: Conceptualization, Funding acquisition, Methodology, Investigation, Resources, Data curation, Writing - original draft, Writing - review & editing. **Paul W. Glyshaw:** Methodology, Investigation, Data curation, Formal analysis, Visualization, Writing - original draft, Writing - review & editing. **Brian C. Weidel:** Investigation, Resources, Formal analysis, Writing - original draft, Writing - review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

This work was supported by the Great Lakes Restoration Initiative [award 2017-183]. We thank the vessel, administrative, and science support staff at the USGS Lake Ontario Biological Station, as well as M. Wensman and G. Carter from the Cooperative Institute for Great Lakes Research and K. Beadle, D. Burlingame, S. Constant, G. Lang, and L. Mason from NOAA GLERL. This manuscript was improved by comments from A. Karatayev, B. Baldigo, and three anonymous reviewers. Any use of trade, product, or firm names is for descriptive purposes only and does not imply endorsement by the U.S. Government. This is NOAA GLERL Contribution No. 1987.

References

Andraso, G.M., Ganger, M.T., Adamczyk, J., 2011. Size-selective predation by round gobies (*Neogobius melanostomus*) on dreissenid mussels in the field. J. Great Lakes Res. 37, 298–304.

Arnott, D.L., Vanni, M.J., 1996. Nitrogen and phosphorus recycling by the zebra mussel (*Dreissena polymorpha*) in the western basin of Lake Erie. Can. J. Fish. Aquat. Sci. 53, 646–659. https://doi.org/10.1139/f95-214.

Bates, D., Machler, M., Bolker, B.M., Walker, S.C., 2015. Fitting linear mixed-effects models using lme4. J. Stat. Softw. 67 (1). https://doi.org/10.18637/jss.v067.i01.

Birkett, K., Lozano, S.J., Rudstam, L.G., 2015. Long-term trends in Lake Ontario's benthic macroinvertebrate community from 1994–2008. Aquat. Ecosyst. Health Manag. 18 (1), 76–88.

Borrero, F.J., Hilbish, T.J., 1988. Temporal variation in shell and soft tissue growth of the mussel *Geukensia demissa*. Mar. Ecol. Prog. Ser. 4, 9–15.

Bowen, K.L., Conway, A.J., Currie, W.J.S., 2018. Could dreissenid veligers be the lost biomass of invaded lakes? Freshw. Sci. 37, 315–329.

Burlakova, L.E., Karatayev, A.Y., Hrycik, A.R., Daniel, S.E., Mehler, K., Rudstam, L.G., Watkins, J.M., Dermott, R., Scharold, J., Elgin, A.K., Nalepa, T.F., (this issue). Six decades of Lake Ontario ecological history according to benthos. J. Great Lakes Res. https://doi.org/10.1016/j.jglr.2021.03.006 (this issue).

Chapra, S.C., Dolan, D.M., Dove, A., 2016. Mass-balance modeling framework for simulating and managing long-term water quality for the lower Great Lakes. J. Great Lakes Res. 42, 1166–1173.

Dermott, R., Geminiuc, M., 2003. Changes in the benthic fauna of Lake Ontario 1990-1995, with local trends after 1981. In: Munawar, M. (Ed.), State of Lake Ontario: Past, present and future. In: Munawar, M. (Ed.), Ecovision World Monograph Series. Backhuys Publishers, Leiden, The Netherlands, pp. 323–345.

Durham, S.R., Gillikin, D.P., Goodwin, D.H., Dietl, G.P., 2017. Rapid determination of oyster lifespans and growth rates using LA-ICP-MS line scans of shell Mg/Ca ratios. Palaeogeogr. Palaeoclimatol. Palaeoecol. 485, 201–209.

Environment and Climate Change Canada and the U.S. Environmental Protection Agency, 2018. Lake Ontario Lakewide Action and Management Plan, 2018-2022. https://binational.net/wp-content/uploads/2021/03/FINAL-EN-2018-22-Lake-Ontario-LAMP-2021-01-13.pdf.

Estepp, L.R., Reavie, E.D., 2015. The ecological history of Lake Ontario according to phytoplankton. J. Great Lakes Res. 41, 669–687.

Foley, C.J., Andree, S.R., Pothoven, S.A., Nalepa, T.F., Höök, T.O., 2017. Quantifying the predatory effect of round goby on Saginaw Bay dreissenids. J. Great Lakes Res. 43, 121–131.

Garton, D.W., Johnson, L.E., 2000. Variation in growth rates of the zebra mussel, *Dreissena polymorpha*, within Lake Wawasee. Freshw. Biol. 45, 443–451.

Glyshaw, P.W., Riseng, C.M., Nalepa, T.F., Pothoven, S.A., 2015. Temporal trends in condition and reproduction of quagga mussels (*Dreissena rostriformis bugensis)* in southern Lake Michigan. J. Great Lakes Res. 41, 16–26.

Hilbish, T.J., 1986. Growth trajectories of shell and soft tissue in bivalves: seasonal variation in *Mytilus edulis* L. J. Exp. Mar. Biol. Ecol. 96, 103–113.

Horgan, M.J., Mills, E.L., 1997. Clearance rates and filtering activity of zebra mussel (*Dreissena polymorpha*): implications for freshwater lakes. Can. J. Fish. Aquat. Sci. 54 (2), 249–255. https://doi.org/10.1139/f96-276.

Karatayev, A.Y., Burlakova, L.E., Padilla, D.K., 2006. Growth rate and longevity of *Dreissena polymorpha* (Pallas): a review and recommendations for future study. J. Shellfish Res. 25, 23–32.

Karatayev, A.Y., Mastitsky, S.E., Padilla, D.K., Burlakova, L.E., Hajduk, M.M., 2011. Differences in growth and survivorship of zebra and quagga mussels: size matters. Hydrobiologia 668, 183–194.

Karatayev, A.Y., Karatayev, V.A., Burlakova, L.E., Rowe, M.D., Mehler, K., Clapsadl, M. D., 2018. Food depletion regulates the demography of invasive dreissenid mussels in a stratified lake. Limnol. Oceanogr. 63, 2065–2079.

Karatayev, A.Y., Burlakova, L.E., Mehler, K., Daniel, S.E., Elgin, A.K., Nalepa, T.F., 2020. Lake Huron benthos survey Cooperative Science and Monitoring Initiative 2017. Technical Report. USEPA-GLRI GL00E02254. Great Lakes Center, SUNY Buffalo State, Buffalo, NY.

Karatayev, A.Y., Burlakova, L.E., Mehler, K., Elgin, A.K., Rudstam, L.G., Watkins J.M., Wick, M., (this issue). Dreissena in Lake Ontario 30 years post-invasion. J. Great Lakes Res. https://doi.org/10.1016/j.jglr.2020.11.010 (this issue).

Karatayev, A.Y., Karatayev, V.A., Burlakova, L.E., Mehler, K., Rowe, M.D., Elgin, A.K., Nalepa, T.F., 2021. Lake morphometry determines Dreissena invasion dynamics. Biol. Invasions. https://doi.org/10.1007/s10530-021-02518-3.

Lenth, R.V., 2016. Least-squares means: the *R* package lsmeans. J. Stat. Softw. 69 (1). https://doi.org/10.18637/jss.v069.i01.

Li, J., Ianaiev, V., Huff, A., Zalusky, J., Ozersky, T., Katsev, S., 2021. Benthic invaders control the phosphorus cycle in the world's largest freshwater ecosystem. Proc. Natl. Acad. Sci. U.S.A. 118, e2008223118.

Link, C.L., 2010. Filtration and growth rate of Lake Mead quagga mussels (Dreissena bugensis) in laboratory studies and analyses of bioaccumulation (M.Sc. thesis). University of Nevada, Las Vegas, USA.

MacIsaac, H.J., 1994. Comparative growth and survival of *Dreissena polymorpha* and *Dreissena bugensis,* exotic molluscs introduced to the Great Lakes. J. Great Lakes Res. 20, 783–790.

Madon, S.P., Schneider, D.W., Stoeckel, J.A., Sparks, R.E., 1998. Effects of inorganic sediment and food concentrations on energetic processes of the zebra mussel, Dreissena polymorpha: implications for growth in turbid rivers. Can. J. Fish. Aquat. Sci. 55, 401–413.

May, B., Marsden, J.E., 1992. Genetic identification and implications of another invasive species of dreissenid mussel in the Great Lakes. Can. J. Fish. Aquat. Sci. 49, 1501–1506.

Mills, E.L., Dermott, R.M., Roseman, E.F., Dustin, D., Mellina, E., Conn, D.B., Spidle, A. P., 1993. Colonization, ecology, and population structure of the "quagga" mussel (bivalvia: dreissenidae) in the lower Great Lakes. Can. J. Fish. Aquat. Sci. 50, 2305–2314.

Mills, E.L., Rosenberg, G., Spidle, A.P., Ludyanskiy, M., Pligin, Y., May, B., 1996. A review of the biology and ecology of the quagga mussel (*Dreissena bugensis*), a second species of freshwater dreissenid introduced to North America. Am. Zool. 36, 271–286.

Munawar, M., Munawar, I.F., Fitzpatrick, M., Niblock, H., Lorimer, J., 2015. The phytoplankton community of Lake Ontario in 2008: structure, biodiversity and long term changes. Aquat. Ecosyst. Health Manag. 18 (1), 28–42. https://doi.org/10.1080/14634988.2014.936808.

Munawar, M., Niblock, H., Fitzpatrick, M., Rudstam, L. 2016. Phytoplankton and primary productivity. Lake Ontario Cooperative Science and Monitoring Initiative (CSMI) 2013. Summary Report.

Naddafi, R., Rudstam, L.G., 2014. Predator-induced morphological defences in two invasive dreissenid mussels: implications for species replacement. Freshw. Biol. 59, 703–713.

Nalepa, T.F., Fanslow, D.L., Lang, G.A., 2009. Transformation of the offshore benthic community in Lake Michigan: recent shift from the native amphipod *Diporeia* spp. to the invasive mussel *Dreissena rostriformis bugensis*. Freshw. Biol. 54, 466–479. https://doi.org/10.1111/j.1365-2427.2008.02123.x.

Nalepa, T.F., Fanslow, D.L., Pothoven, S.A., 2010. Recent changes in density, biomass, recruitment, size structure, and nutritional state of *Dreissena* populations in southern Lake Michigan. J. Great Lakes Res. 36 (Supplement 3), 5–19.

Nalepa, T.F., Pavlova, V., Wong, W.H., Janssen, J., Houghton, J.S., Mabrey, K., 2013. Variation in the quagga mussel *(D. r. bugensis)* with emphasis on the deepwater morphotype in Lake Michigan. In: Nalepa, T.F., Schloesser, D.W. (Eds.), Quagga and Zebra Mussels: Biology, Impacts, and Control. 2nd edition. CRC Press, Boca Raton, FL, pp. 315–329.

O'Gorman, R., Elrod, J.H., Owens, R.W., Schneider, C.P., Eckert, T.H., Lantry, B.F., 2000. Shifts in depth distributions of Alewives, Rainbow Smelt, and age-2 Lake Trout in southern Lake Ontario following establishment of dreissenids. Trans. Am. Fish. Soc. 129, 1096–1106.

Pennuto, C.M., Mehler, K., Weidel, B., Lantry, B.F., Bruestle, E., 2021. Dynamics of the seasonal migration of Round Goby (Neogobius melanostomus, Pallas 1814) and implications for the Lake Ontario food web. Ecol. Freshw. Fish. 30, 151–161.

Peyer, S.M., Hermanson, J.C., Lee, C.E., 2010. Developmental plasticity of shell morphology of quagga mussels from shallow and deep-water habitats of the Great Lakes. J. Exp. Biol. 213, 2602–2609.

Pothoven, S.A., Elgin, A.K., 2019. Dreissenid veliger dynamics along a nearshore to offshore transect in Lake Michigan. J. Great Lakes Res. 45, 300–306.

R Core Team, 2019. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org.

Roe S.L., MacIsaac H.J., 1997. Deepwater population structure and reproductive state of quagga mussels (Dreissena bugensis) in Lake Erie. Can. J. Fish. Aquat. Sci. 54, 2428–33.

Smith, S.D.P., McIntyre, P.B., Halpern, B.S., Cooke, R.M., Marino, A.L., Boyer, G.L., Buchsbaum, A., Burton, G.A., Campbell, L.M., Ciborowski, J.J.H., Doran, P.J., Infante, D.M., Johnson, L.B., Read, J.G., Rose, J.B., Rutherford, E.S., Steinman, A.D., Allan, J.D., 2015. Rating impacts in a multi-stressor world: a quantitative assessment of 50 stressors affecting the Great Lakes. Ecol. Appl. 25, 717–728.

Spear, M.J., Walsh, J.R., Ricciardi, A., Vander Zanden, M.J., 2021. The invasion ecology of sleeper populations: prevalence, persistence, and abrupt shifts. BioScience 71, 357–369.

Sprung, M., 1991. Costs of reproduction: a study on metabolic requirements of the gonads and fecundity of the bivalve *Dreissena polymorpha*. Malacologia 33, 63–70.

Stoeckmann, A.M., Garton, D.W., 2001. Flexible energy allocation in zebra mussels (Dreissena polymorpha) in response to different environmental conditions. J. N. Am. Benthol. Soc. 20, 486–500.

Strayer, D.L., Adamovich, B.V., Adrian, R., Aldridge, D.C., Balogh, C., Burlakova, L.E., Fried-Petersen, H.B., Tóth, L., Hetherington, A.L., Jones, T.S., Karatayev, A.Y., Madill, J.B., Makarevich, O.A., Marsden, J.E., Martel, A.L., Minchin, D., Nalepa, T.F., Noordhuis, R., Robinson, T.J., Rudstam, L.G., Schwalb, A.N., Smith, D.R., Steinman, A.D., Jeschke, J.M., 2019. Long-term population dynamics of dreissenid mussels (*Dreissena polymorpha* and *D. rostriformis*): a cross-system analysis. Ecosphere 10,. https://doi.org/10.1002/ecs2.2701 e02701.

Toomey, M.B., McCabe, D., Marsden, J.E., 2002. Factors affecting the movement of adult zebra mussels (*Dreissena polymorpha*). J. N. Am. Benthol. Soc. 21, 468–475.

Vanderploeg, H.A., Liebig, J.R., Nalepa, T.F., Fahnenstiel, G.L., Pothoven, S.A., 2010. Dreissena and the disappearance of the spring phytoplankton bloom in Lake Michigan. J. Great Lakes Res. 36 (Supplement 3), 50–59.

Wacker, A., Von Elert, E., 2008. Body size and food thresholds for zero growth in *Dreissena polymorpha*: a mechanism underlying intraspecific competition. Freshw. Biol. 53, 2356–2363.

Walsh, M.G., Dittman, D.E., O'Gorman, R., 2007. Occurrence and food habits of the round goby in the profundal zone of southwestern Lake Ontario. J. Great Lakes Res. 33, 83–92.

Walz, N., 1978. The energy balance of the freshwater mussel *Dreissena polymorpha* Pallas in laboratory experiments and in Lake Constance. IV. Growth in Lake Constance. Arch. Hydrobiol. Suppl. 55, 142–156.

Watkins, J.M., Dermott, R., Lozano, S.J., Mills, E.L., Rudstam, L.G., Scharold, J.V., 2007. Evidence for remote effects of dreissenid mussels on the amphipod *Diporeia*: analysis of Lake Ontario benthic surveys, 1972–2003. J. Great Lakes Res. 33, 642–657.

Weidel, B.C., Walsh, M.G., Connerton, M.J., Lantry, B.F., Lantry, J.R., Holden, J.P., Yuille, M.J., Hoyle, J.A., 2017. Deepwater sculpin status and recovery in Lake Ontario. J. Great Lakes Res. 43, 854–862.

Wong, W.H., Gerstenberger, S., Baldwin, W., Moore, B., 2012. Settlement and growth of quagga mussels (*Dreissena rostriformis bugensis* Andrusov, 1897) in Lake Mead, Nevada-Arizona, USA. Aquat. Invasions 7, 7–19.