



OPEN Photogrammetric assessment of quagga mussel growth shows no winter cessation in lake Geneva

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The quagga mussel (*Dreissena rostriformis bugensis*) is an invasive alien species present in many aquatic ecosystems. Although this species is known for its ecological and economic impacts, there are still significant gaps in our knowledge of its ecophysiology. This is particularly true when its growth rate under natural conditions is considered. Using a photogrammetry-based approach, we assessed bivalve growth in Lake Geneva during different seasons and for a variety of habitats. Based on the recorded changes in maximum shell length analysed during the period of this study (winter and spring 2023–2024), we measured average growth rates ranging from 0.142 ± 0.099 mm day⁻¹ for individuals smaller than 10 mm to 0.089 ± 0.071 mm day⁻¹ for larger individuals. The size class-dependent growth rate was analysed on the basis of the time of year, the type of environment (depth, substrate) or, again, the temperature. Our results reveal that the growth rate, obtained in situ and without manipulation, primarily depends on size and is independent of temperature or habitat within the studied range. This growth capacity in Lake Geneva is the highest found to date and is likely to explain the invasion success of this species.

Keywords Lake Geneva, Invasive alien species, (quagga) mussel, Growth rate, Photogrammetry

The introduction of invasive exotic species has numerous impacts on aquatic ecosystems^{1,2}. The environmental issues associated with these nonnative species are crucial for states and territories because of the potential ecological, economic, and health consequences of their introduction and spread^{1,3}.

Originating from the Black Sea and the Ponto-Caspian area, the quagga mussel (*Dreissena rostriformis bugensis*), similar to their close relative, e.g., the zebra mussel (*Dreissena polymorpha*), is an invasive species. They have significantly expanded their range of habitats, colonizing numerous lakes worldwide, and today, these two mussel species have large populations in the United States, Europe and Russia^{4–6}. They rapidly colonize new lotic and lentic environments, with zebra mussels generally being the first to establish⁴. However, quagga mussels often outcompete zebra mussels, taking advantage of their role as pioneer species to establish themselves more permanently^{4,7}. This shift is reportedly due to the quagga mussel's faster and more extended reproduction period⁷, which gives it a very rapid and aggressive colonization capacity.

The proliferation of quagga mussels can have a variety of impacts on ecosystem biodiversity and functioning^{3,8,9}. Some environmental parameters are altered as the invasive biomass increases in relation to the habitat modification and filtration capacity of the animal^{10–12}. Quagga mussels may deplete plankton biomass, which is likely to affect the entire pelagic food web^{13–15}. Additionally, bivalves can impact pelagic biogeochemical cycles at the water-sediment interface^{16,17} as well as in the water column¹⁸. The shift in energy production from the open pelagic region to the benthic region caused by quagga mussels, associated with increased water clarity, is a process known and termed benthification¹⁵.

Although the ecological impact of this species has begun to be well documented, our knowledge of its ecology remains limited for many natural environments. While some studies address the effects of environmental parameters on the growth of dreissenids^{19–21}, few studies have been carried out on the growth rates of quagga mussels, and growth rates have often been extrapolated from those found for zebra mussels²². Its rapid development, although recognized, is under exploration⁴, and to the best of our knowledge, in situ measurements without manipulation of the animals and without the use of artificial substrates (i.e., ropes or cages) remain scarce, if not unprecedented.

Our study highlights a noninvasive and nondestructive technique for accurately measuring the size and growth of quagga mussel populations. This original approach, which is based on photogrammetry, has

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already proven effective when studying coral growth and development^{23,24} through the observation of various metrics^{25,26}. Although photogrammetry has already been used in freshwater environments^{27,28}, its application to the construction of structure-from-motion (SfM) models for freshwater mussel aggregates is the first. After validating this novel approach, we were able to measure the growth rates of numerous individuals who are representative of a variety of lake conditions, namely, depth, substrate/support, and time of year. Our results suggest that the quagga mussel can grow more rapidly than previously reported, reaching up to 0.142 ± 0.099 mm day⁻¹ for small individuals during the study period (winter and spring), and this growth capacity is proposed as a key factor explaining the success of animal colonization in European lakes.

Results

Growth pattern

On the basis of 404 growth measurements, we recorded a decrease in the mussel growth rate with increasing animal size. Clearly, larger and older mussels (> 10 mm) grew more slowly (e.g., 0.089 ± 0.071 mm day⁻¹ on average for the size class [10–20 mm]) than smaller mussels (< 10 mm), for which the average growth rate was 0.142 ± 0.099 mm day⁻¹. Although we observed important variability, such growth rate differences between each size class were significant (p value $< 2e-16$, Fig. 1).

When all the measurements were plotted, the decrease in growth with increasing shell size was also clear (Fig. 2).

In contrast, we did not observe a significant habitat/substrate effect (p value = 0.0845, not shown) nor a seasonal effect (p value = 0.0652, Fig. 3), suggesting that the animals grow at similar rates, whatever the place, in winter and spring. Despite an average temperature of 7.95 °C in winter and 10.9 °C in spring, mean growth rates for the two periods were similar (e.g. 0.055 mm day⁻¹). When considering the maximal individual growth rate we measured, it is noteworthy that only a weak difference was found between the two periods, e.g. 0.25 mm day⁻¹ in winter vs. 0.28 mm day⁻¹ in spring, while temperatures were 7.7 and 10.4 °C, respectively. Temperature, which was hypothesized to be an important factor influencing animal growth, was thus not significant here (see discussion).

We did not observe neither a “group” effect on growth. Indeed, the size of the aggregates and thus the number (and size) of individuals per aggregate had no significant effect on growth. This may suggest that other factors, such as resource availability and/or environmental conditions, play a more crucial role in animal growth (see Discussion).

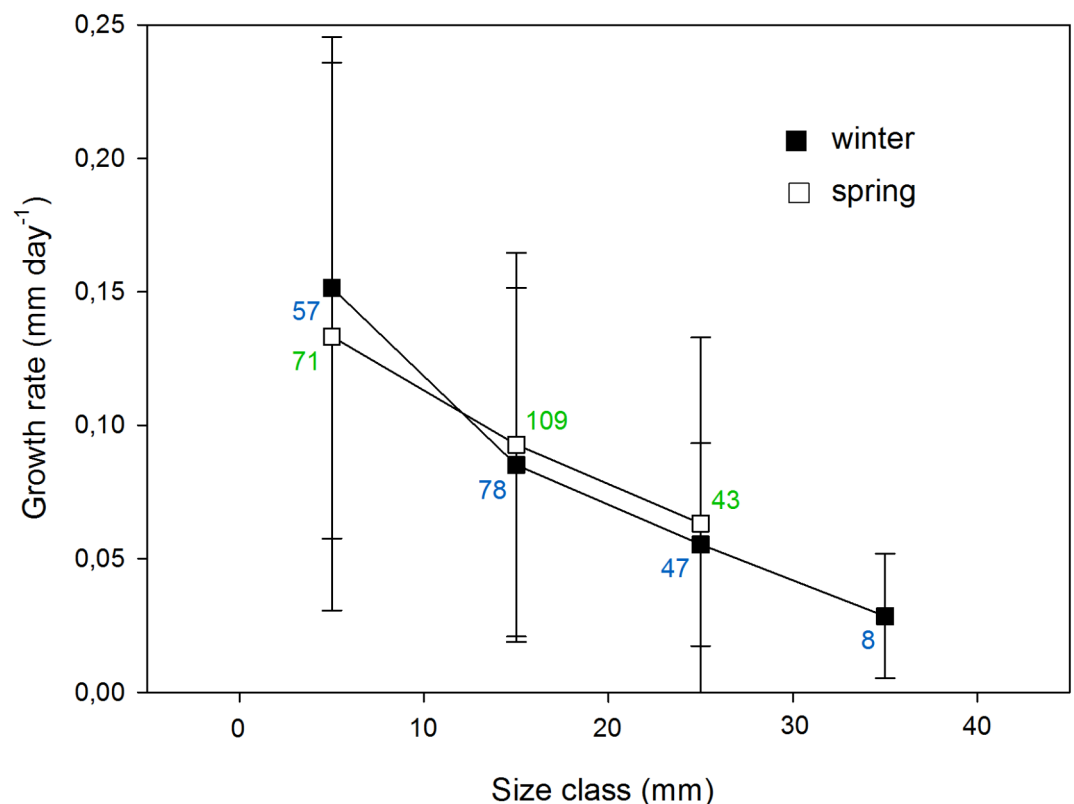


Fig. 1. Averaged growth rates as a function of size compared between winter and spring. The values correspond to the number of growth rate calculations performed for each size class.

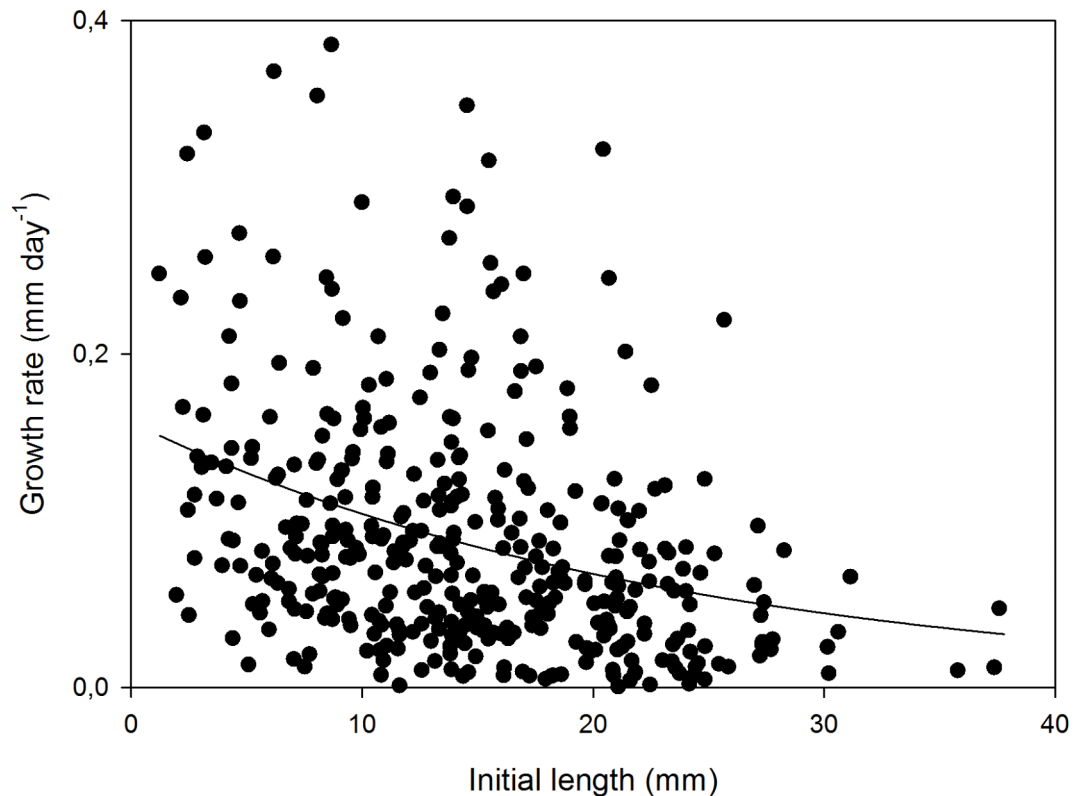


Fig. 2. Relationship between the growth rate and the initial size of measured individuals, regardless of the date ($r = 0.34$, $p < 0.001$, $n = 387$).

Technical validation

To validate underwater photogrammetry for our study model, we compared it with direct measurements via callipers. We monitored several aggregates, taking both photographs and direct shell measurements. A highly significant positive correlation ($r = 0.945$; $p < 0.01$; $n = 104$) was found between the direct and photogrammetric measurements. With an error of $< 6\%$, we considered our method very robust (Fig. 4), despite more pronounced differences for medium to large individuals than for smaller individuals.

Discussion

The first detection of quagga mussels in Lake Geneva dates back to 2016²⁹. Its invasion has thus been documented only recently, and different research programs have been proposed to better assess its animal distribution and impacts in Lake Geneva^{5,6}. However, the impact of dreissenid mussels is dependent on the biomass they represent, as this biomass is itself dependent on the number of individuals and the size structure of a population. The growth of the biomass represented by populations and the growth-at-length of individuals in Lake Geneva remain unexplored to date.

The method proposed here is original and appears strongly valid. However, we are aware that any comparison of growth is complicated by the fact that different measurement methods have been used to obtain them, in situ or not, with or without manipulation of the individuals likely to impact their physiology. In contrast to other studies, we observed that growth under natural conditions is likely to result in a reduction in animal stress, but conditions with multiple abiotic and biotic interactions are likely to positively or negatively impact animal growth. For example, Karatayev et al.³⁰ and Ozersky et al.³¹ reported that periphyton has a positive effect on mussel growth. However, when growth has been studied on artificial substrates such as ropes and cages, these interactions are likely erased, whereas the protective effect of cages can increase mussel survival rates³².

For the very few articles providing quantitative data on quagga mussel growth, we observed highly variable growth rates but higher values than those listed thus far in the current bibliography. While MacIsaac³³ reported that quagga growth reached 0.12 mm day^{-1} for 5 mm individuals, Elgin et al.³⁴ reported significantly lower values, i.e., approximately $0.002 \text{ mm day}^{-1}$ for 11–13 mm individuals. Such differences may be due, for example, to the size of the individuals examined, the water temperature, or the amount of food available but also to significantly different intervals between successive observations. In studies in which animal sizes ranged between 10 and 20 mm, the average growth-at-length was $0.035 \pm 0.01 \text{ mm day}^{-1}$ ^{122,32,35}. Comparatively, we observed an average growth rate of $0.089 \pm 0.071 \text{ mm day}^{-1}$ for the 10–20 mm individuals, which was 2.5 times greater than that of the other individuals, and $0.142 \pm 0.099 \text{ mm day}^{-1}$ for the $< 10 \text{ mm}$ individuals. Our measurements represent the first data of this type for European lakes. Only D'Hont et al.²² measured some growth rates for Europe, but they

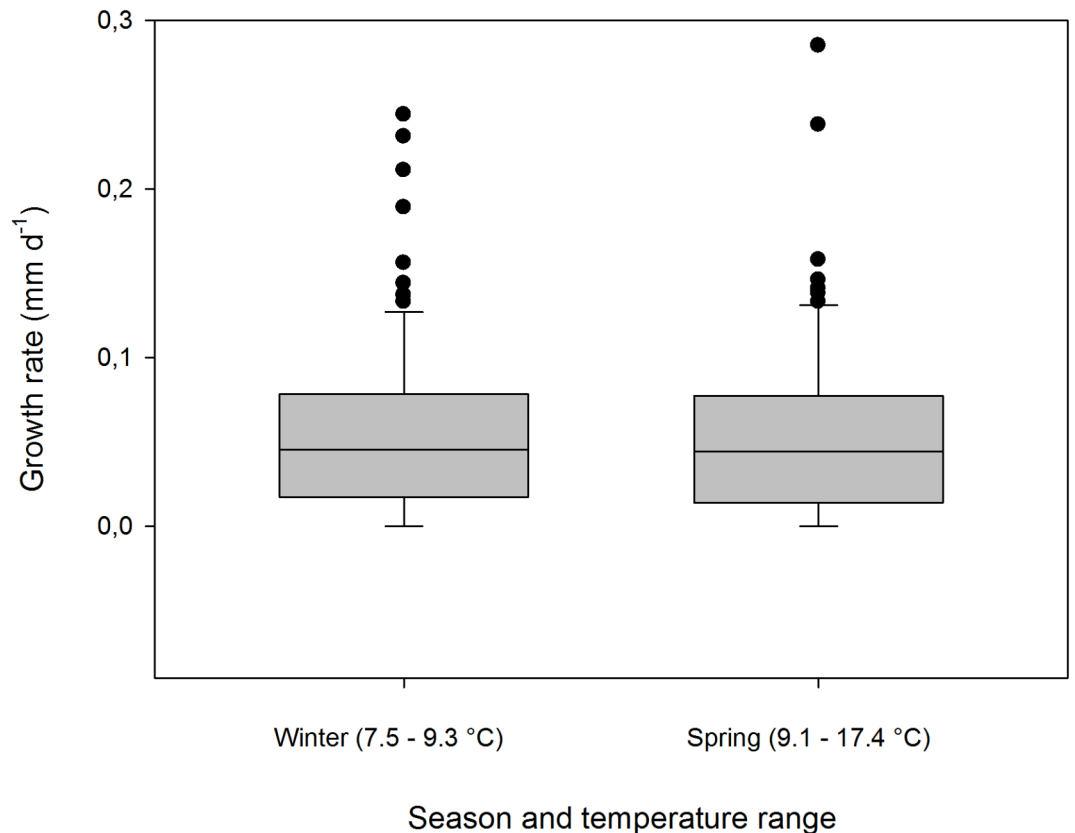


Fig. 3. Mean growth rates in winter and spring. Values for winter and spring correspond to the minimal and maximal temperature recorded during each period.

focused on the Rhine-Meuse River estuary in the Netherlands and individuals measured on plates deployed 1 m below the water surface, for which they reported average growth values of 0.09 mm day^{-1} or of $1.5\text{--}2.5 \text{ cm year}^{-1}$.

An important finding is that the growth of quagga mussels does not differ between winter and spring, regardless of the size of the individuals considered, indicating that temperature likely plays only a secondary role within the range of temperatures observed in Lake Geneva during the period of study (e.g. between 6 and 16°C , see Fig. S2 in the additional information section). This result contrasts with the widely accepted principle, never challenged by observations, of a slowdown in growth during winter in zebra mussels, although never resulting in a complete halt^{36,37}. Our results obtained for quagga mussels in Lake Geneva are likely due to the higher physiological activity of quagga mussels than zebra mussels at lower temperatures¹¹. For example, *D. bugensis* grows well in the cold profile zones of the Great Lakes, whereas the near-bottom temperatures are always less than 6°C ⁴. However, we did not find any articles reporting growth as strong in winter as in spring. In the same vein, and contrary to the literature, we found no effect of depth on growth. Existing studies have shown lower growth rates at much greater depths, such as 0.01 mm day^{-1} at approximately 50 m depth³⁰ or $0.002 \text{ mm day}^{-1}$ at 90 m depth versus $0.031 \text{ mm day}^{-1}$ at 15 m depth³⁴. Furthermore, a temperature-related effect, which is well documented in the literature^{4,20}, was not observed in our study. In contrast to Elgin et al.³⁴, we did not find any effects linked to the study site, which enabled us to examine growth at all sites combined and confirm previously reported growth rates. Our observations are only comparable with what MacIsaac et al.³³ reported during the first phase of colonization of the Great American lakes, likely at a moment when no limiting conditions occurred to prevent the quagga mussel from developing. We assume that the situation of Lake Geneva may be comparable and that, as a significant increase in biomass continues in the following years, quagga mussels will have to compete increasingly more for resources, resulting in probable decreasing growth rates in the future.

Conclusion

The growth rates of quagga mussels in Lake Geneva, which were calculated via a very original method, are the highest reported thus far. Such growth capacities could constitute an important ecophysiological process that enabled the animal to settle and colonize this lake and others in Europe so rapidly.

Highlights

Faster, higher, stronger ... together or not! Among the reasons for quagga mussel success in European lakes, the growth rates of the animals are likely important throughout the year, even during winter.

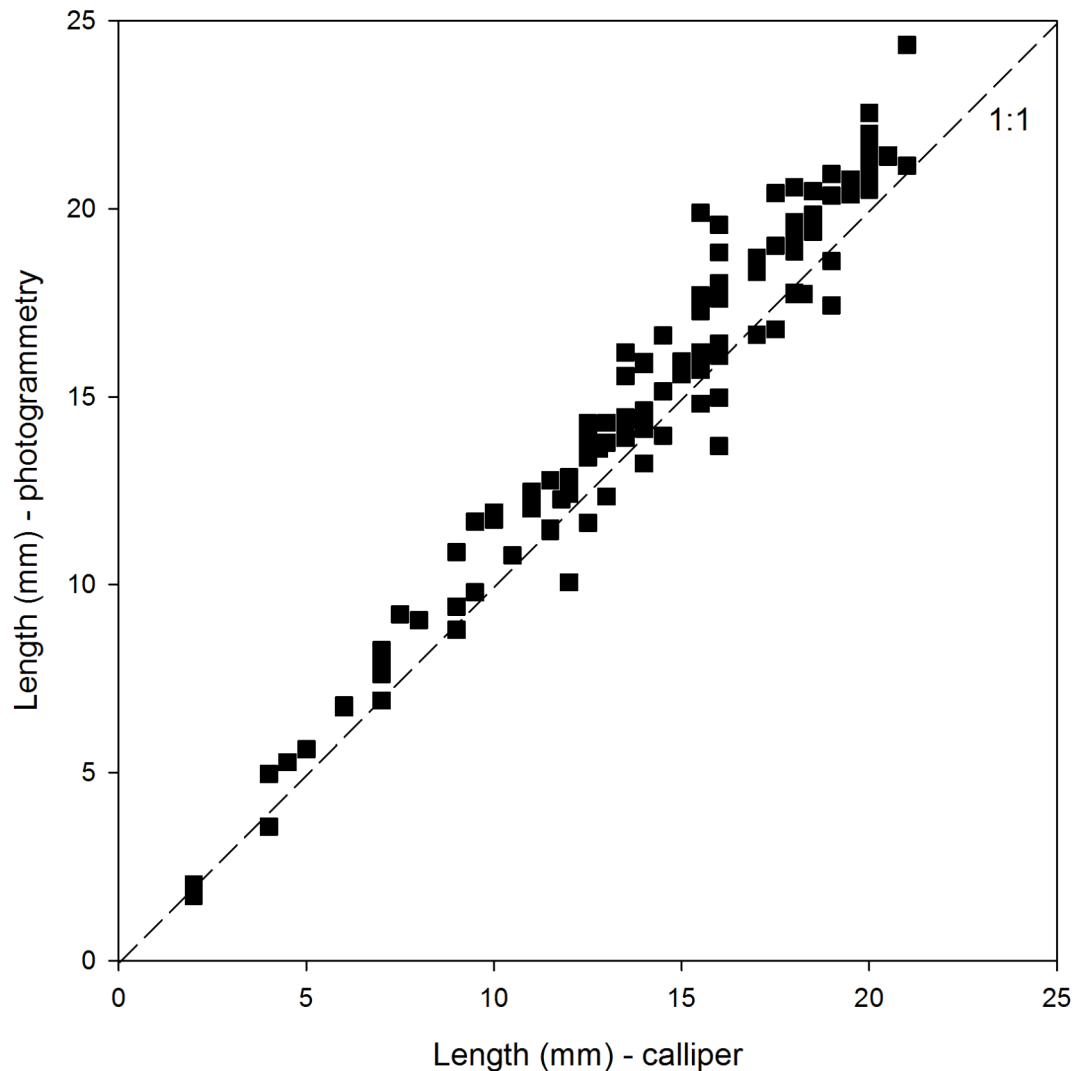


Fig. 4. Relationships between photogrammetric and calliper measurements.

Methods

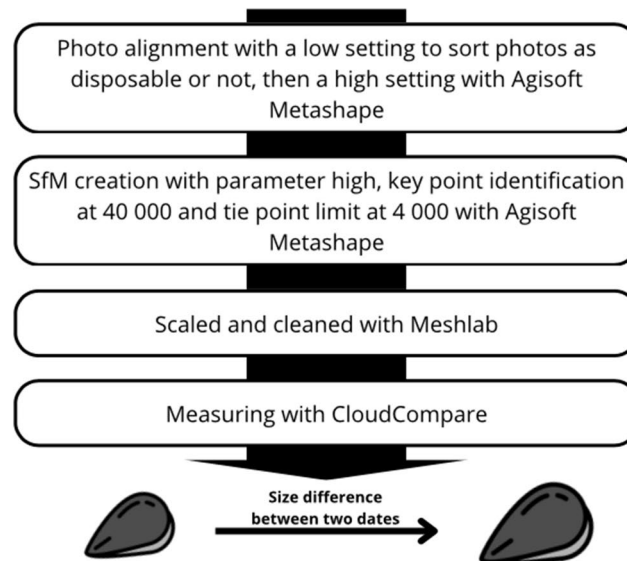
Study site and aggregate survey

We used to visit sites in Lake Geneva (named Saint-Disdille and Corzent), where we selected aggregates in different habitats, artificial or natural, reflecting the quagga mussel's ability to colonize various substrates. These habitats included an underwater upright dead tree between 22 and 30 m depth, the wreck of a small pleasant boat at 15–16 m depth, a brick and grate at 4–5 m depth, sediments or again an abandoned fish trap at 30 m depth. Each monitored colony/aggregate was easy to relocate because they were selected at known sites and associated with remarkable elements (i.e. a specific place of the tree, the brick, the grate or the wreck and precisely marked by small flags for the sediment). The study period ran from winter 2023 (e.g. November 15, 2023) to spring 2024 (e.g. July 2, 2024). Images were captured during several scuba dives (made approximately every 3 weeks) via two GoPro Hero cameras (versions 10 and 12). An average of 95 photos (ranging from 30 to 173) was taken for each aggregate at each dive following Tsuboi et al.³⁸. All photographed Dreissenids were assumed to be quagga mussels, as a previous study indicated that zebra mussels accounted for no more than 2% of the Dreissenids and were present in only one quarter of the samples (data not shown). Note also that our analysis was only performed on visually verified live individuals along the study and in aggregates easily identifiable (without ambiguity to relocate them from one sampling date to the next), each comprising a few dozens of individuals.

Environmental data

Submersible loggers measuring dissolved oxygen concentrations and temperature (miniDOT, PME, California) were deployed during this study and programmed to obtain one measurement every 15 min. The effect of temperature on animal growth was tested after considering the mean temperature between the two dates considered for each growth rate calculation.

(A)



(B)

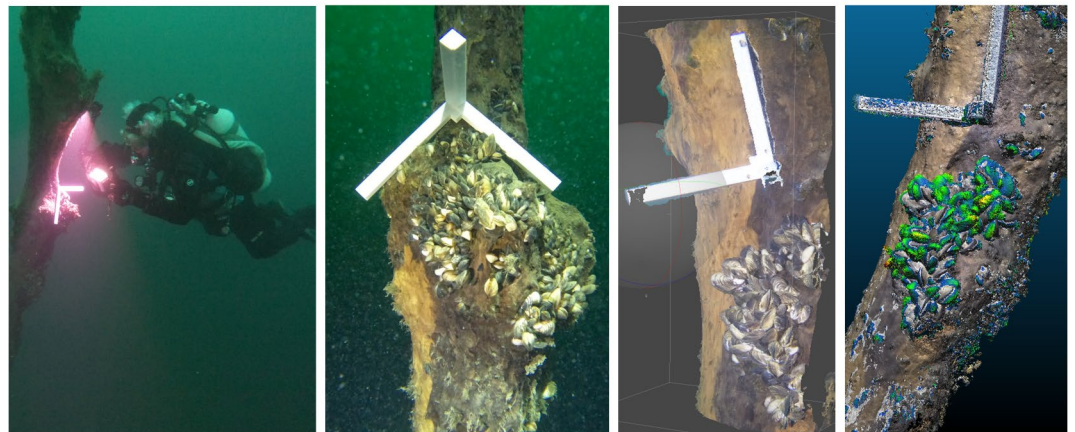


Fig. 5. Flowchart of the photogrammetric approach (A) and (B) series of images showing the passage from a typical initial photography of an aggerate to its model reconstruction to size individual evolution between dates, here illustrated by colors. Briefly you must (i) perform photo alignment using a low setting to preliminarily sort photos as disposable or not, followed by a high setting in Agisoft Metashape; (ii) generate a Structure-from-Motion (SfM) model with high-quality settings, using a key point limit of 40,000 and a tie point limit of 4,000 in Agisoft Metashape; (iii) scale and clean the model using Meshlab; (iv) perform measurements and analysis using CloudCompare. The demonstration that the applied method is adequate to measure the growth of mussel individuals between the recording dates is provided in the supplementary information (Fig. S3).

Photogrammetry processing and analysis

Photogrammetry consists of a technique for reconstructing 3-D objects from images. The method identifies similar points across different photos to enable software to reconstruct the scene. While commonly used for coral growth monitoring^{23,25,39}, this is the first application for monitoring bivalve growth, which is most often measured with callipers^{21,40–42} or caging experiments^{22,43,44}. Using Metashape software (Agisoft Metashape Standard version 2.0) on an HP Z2 Mini G9 workflow computer, we generated 3-D models of the aggregates. The computer, equipped with an Intel Core i7 processor, 16 GB of RAM, and 512 GB of storage, ensured optimal performance for running the software. Briefly, images were first aligned at low resolution to filter usable images. Following optimization on the basis of the camera type to reduce image distortion, the photos were then aligned at high resolution, generating a high-quality point cloud with key point identification limited at 40,000 and a tie point limit at 4,000 common feature points. Structure-from-motion (SfM) projection errors were monitored via Metashape-generated reports (Fig. 5). To increase efficiency, batch processing was employed from the high-

resolution alignment stage, optimizing the software performance by limiting the number of SfMs processed per batch⁴⁵.

Next, the generated SfMs were scaled and cleaned via Meshlab (2023.12). Meshlab's transform scale normalization function allows us to apply custom size scales, enabling accurate scaling of aggregates and individuals⁴⁶. Finally, growth measurements were performed using CloudCompare software (v2.13.0 Kharkiv - Feb 14 2024 [64-bit]) with the aid of a custom-designed 3-D graduated scale, marked at 1 cm intervals, specifically developed for this study and used during each underwater photo session (Fig. S3). Scatterplots were aligned to compare data across different dates to assess quagga mussel growth. We measured the maximum length of individuals and compared these measurements over time. Growth rates were estimated by calculating the difference between shell length measurements on different dates. To facilitate comprehension and comparison with the literature, the results are presented as daily mean values across four size classes: 0–10 mm, 10–20 mm, 20–30 mm, and greater than 30 cm. Width measurements were also taken on some individuals to assess growth as a function of size and to determine whether growth was proportional to size. Some variables were considered, such as the deep, the season or an assembly index. The assembly index was calculated as a function of the height of the colony and the potential interaction between 0 individuals and some individuals without interaction and 5 individuals forming an aggregate with individuals growing on other individuals.

Statistical analysis

Because of the movement of individuals, it was very difficult to track many individuals at any one time, and in total less than 5% (20/404) of our individuals were able to provide us with more than one growth measurement. We therefore considered our data to be independent. Using R (4.2.1), we normalized our data for monthly and seasonal growth. A growth model was created via linear regression, and mean comparison tests were conducted to evaluate the effects of different individual sizes. We used the packages *ade4* and *AICcmodavg* to determine our linear model. Linear models were generated with the base function present in R (4.2.1). The mean comparison test used was the Krustal test. First, to determine the difference between the classical method and our method, we perform a linear regression between these two measures. Second, we calculate the mean monthly growth for each class size, and we compare this with some Krustal tests. Finally, we studied the length and width growth with a Krustal test and linear regression.

Data availability

All data can be obtained from the corresponding author (both the pictures and the analysis).

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Author contributions

E.R. made the photogrammetric tests and analysis, he also participated to writing; J.G. was a scuba diver making the photographs; J.N.B. helped in writing and result interpretation; S.J. was the person in charge of the project, made the photographs underwater, participated to result interpretation, writing and all revisions.

Declarations

Competing interests

The authors declare no competing interests.

Additional information

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