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Dreissenid colonization during the initial invasion of the quagga mussel in the largest Central European shallow lake, Lake Balaton, Hungary

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ABSTRACT

The colonization progress of the invasive bivalve dreissenids, the formerly dominant *Dreissena polymorpha* and the recently (2008) introduced *Dreissena rostriformis bugensis* was studied between 2009 and 2013 in the largest Central European shallow lake, Lake Balaton, Hungary. The density of dreissenid planktonic veligers, new settlers (post-veligers and early juveniles), and the population structure (density, length frequency, relative abundance) of the two species were monitored on experimentally introduced natural stone substrata, on different time scales. Dreissenids started dynamic settling following a sudden veliger bloom. As substratum saturation progressed, competition between species for places was suggested, which, after two years, led to an increased number of large individuals (> 20 mm) and also recruits of *D. r. bugensis*. By contrast, the population of *D. polymorpha* confined to middle size (11-18 mm) individuals of the first settler generation. On local substrata, where the benthic community was already established, the replacement of *D. polymorpha* by *D. r. bugensis* took longer, but it happened in a similar way. The invasion speed of *D. r. bugensis* in Lake Balaton resembled the speed obtained in other European water bodies where *D. r. bugensis*, similar to Lake Balaton, was introduced much later than *D. polymorpha*. However, a longer replacement process was found in North America, where both species invaded new habitats at the same time. This suggests that the speed, and probably the success, of *D. r. bugensis* invasion depends on new surface availability, and whether the two dreissenid species are introduced together or at different times.

Index words: biological invasion, colonization dynamics, dreissenid, quagga mussel, population structure

Introduction

Invasive aquatic alien species, among them the freshwater bivalve dreissenids (*Dreissena polymorpha*, Pallas, 1771 [*D. polymorpha*, zebra mussel]) and *Dreissena rostriformis bugensis*, Andrusov 1897 [*D. r. bugensis*, quagga mussel]) are serious threats to and provoke dramatic changes in community abundance, species diversity, resource availability, nutrient cycling and functioning of the ecosystem (Crooks, 1998; Gutiérrez et al., 2003; Ward and Ricciardi, 2007; Ricciardi and MacIsaac, 2011). Due to their invasive nature and intensive filter-feeding behavior, dreissenids are counted among the most invasive and destructive invaders in North American and European freshwater ecosystems (OTA, 1993; DAISE, 2003; Pimentel et al., 2005).

Due to the fast spread of invasive species nowadays, a new invader is more likely to come into contact with a former dominant invader (van den Brink et al., 1993; van der Velde et al., 1994; Dick and Platvoet, 2000; Platvoet et al., 2009; Ricciardi, 2001; Gallardo and Aldridge, 2015; de Gelder et al., 2016). Although the occurrence and progression of *D. polymorpha* in Europe has long been described in many different habitats (Bij de Vaate, 1991; Pollux et al., 2003; Aldridge et al., 2004; Cianfanelli et al., 2010; Karatayev et al., 2010a; Palau Ibars et al., 2010; Stańczykowska et al., 2010), in contrast to North America (Mills et al., 1993; Watkins et al., 2007; Dermott and Dow, 2008; Nalepa et al., 2010; Karatayev et al., 2013a), and to the Ponto-Caspian region where dreissenids originated (Orlova et al., 2004; Zhulidov, et al., 2010), the characteristics of its population dynamics during the invasion of the new dreissenid, *D. r. bugensis*, has only rarely been observed and investigated (Bij de Vaate, 2010; Aldridge et al., 2014; Heiler et al., 2013; Matthews et al., 2014).

The dispersal speed of *D. polymorpha* was found to be much faster than that of *D. r. bugensis* throughout their invasion history (Karatayev et al., 2011). Therefore, in Europe, apart from the connected river systems (Orlova et al., 2004; Zhulidov et al. 2010; Heiler et al., 2012; Heiler et al., 2013; Matthews et al., 2014) which are known as invasion pathways, in lakes and reservoirs, *D. r. bugensis* has only appeared in the Kuybyshev, Saratov and Rybinsk Reservoirs (part of the Ponto-Caspian Volga River invasion corridor, Orlova, 2004), some Dutch lakes (Lake Ijsselmeer and Markermeer, Bij de Vaate et al., 2013), and recently in Great Britain (Aldridge et al., 2014). In contrast to the spread over long distances, in European water bodies where *D. r. bugensis* was introduced, its population increase rate was 26% per year within the dreissenid community, until the displacement of *D. polymorpha* (Heiler et al., 2013), which suggests the significant spread of this species in local habitats. Similar trends were reported from the Laurentian Great Lakes, where five years after the initial introduction, *D. r. bugensis* represented 44% of the dreissenid population (Dermott and Dow, 2008), and later increased up to 97% (Patterson et al., 2005), leading to total replacement of *D. polymorpha* in the deep parts of the lakes, and the balanced co-existence of the two dreissenids in shallow parts (Patterson et al., 2005; Watkins et al., 2007; Nalepa et al. 2010). It was also found that in some shallow lakes and reservoirs, or in shallow areas of deep lakes, dreissenids could live together for longer periods of time in the same habitat (Tzeyeb et al.1966; Zhulidov et al., 2010; Karatayev et al., 2011, 2013b), or exhibit a reversal, where *D. r. bugensis* was displaced by *D. polymorpha* (Zhulidov et al., 2006). Thus, the interaction between the two dreissenids can be characterized as competitive niche partitioning; however, the dynamics and progression of the co-existence remain unknown, and they seem to be influenced by environmental conditions.

The site of the present study, Lake Balaton, is the largest shallow lake in Central Europe connected to the Danube River via the Sió channel (Fig. 1). In 1932, *D. polymorpha* was the first Ponto-Caspian invader introduced from the Danube River to the lake, possibly via ship transport (Sebestyén, 1938). Around 75 years later (2008), *D. r. bugensis* was discovered as a new dreissenid invader in Lake Balaton (Majoros, 2009; Balogh and G.-Tóth, 2009; Benkő Kiss, Á. personal communication). *D. r. bugensis* may have been imported in the same way as *D. polymorpha* since the mussel was detected in the Hungarian region of the Danube River much earlier than it was estimated to appear in Lake Balaton (Szekeres et al., 2008). The recent introduction of *D. r. bugensis* to Lake Balaton makes this lake ideal to follow the invasion dynamics in real time, and study the early consequences of the invasion on the benthic community, including the dominant *D. polymorpha* population.

Studying the settlement and growth dynamics of the dreissenids would provide unique data to help understand the population trends and invasion success of *D. r. bugensis*, thus supporting the assessment and prediction of its environmental impact, ecological changes, and management (Wong and Gerstenberg, 2011). Shallow lakes invaded by *D. r. bugensis* have been reported by Karatayev et al. (2013b), who expected invasion dynamics to be different in shallow versus deep lakes. For these reasons, we investigated the colonization progress of dreissenids in Lake Balaton during the early invasion of *D. r. bugensis*. Colonization was evaluated on early, short-term (daily), medium-term (monthly), and long-term (yearly) time scales on experimentally introduced natural stone substrata by following the progression of the number (relative abundance, density) and growth (size and covered substratum area) of the two dreissenids. Data were compared with those sampled from the local stone substrata. Such a complex research approach, providing high resolution data in a medium-term study, has not yet been used for studying the invasion of *D. r. bugensis*. The objective was to analyze the colonization dynamics of dreissenids, in the knowledge that *D. r. bugensis* has been introduced to the lake recently, and the environmental conditions favor its settlement.

Materials and Methods

Study site with local conditions

The support structure for experimental substrata submerged in Lake Balaton was placed near to the riprap zone at 1.9 m depth, in front of the shoreline of the Balaton Limnological Institute, Tihany (Fig. 1). To compare the data obtained from the experimental substrata with natural trends, three sampling locations (T1, T2, T3) in the riprap along the shoreline of the Tihany peninsula were selected. The water characteristics of these local bottom substrata (type, size, shape, depth of their location [T1: 1.5 m; T2: 1.9 m; T3: 1.1 m]) were similar to those used for the experimental substrata. The only difference was that the local substrata had already been coated by natural biofilm, including dreissenids.

During each substratum sampling, at the same depth where the support structure for experimental substrata was placed, and the local sampling sites were situated, beside the substrata, water characteristic variables were recorded in the conventional manner, using a Horiba U-10 water multiparameter measuring instrument. In the first few months of the study, between the summer and winter period, the measured values were as follows: temperature: 7–29 °C; conductivity: 751–910 µS cm^{-1}; pH: 8.0–8.9; chlorophyll-*a* concentration: 5.4±3.15 µg L^{-1}, the highest content of suspended material: 25 mg (dw) L^{-1}.

Support structure for experimental substrata

To study the progression of surface colonization by dreissenids, stone holders were created from a massive metal frame measuring 1×1 m in size, and joined with protruding pipes, distributed at equal distances, and serving as holders (Fig. 2). Sixty palm-sized (surface was 0.0191±0.0038 m^2/ each) red sand stones of similarly irregular shape (hereafter referred to as ‘stones’) were collected from the shoreline, scrubbed and dried. They were drilled, inserted, and fixed onto metal pipes of uniform size with commercial glue. Stones with pipes could be slipped into and easily taken out of the holder pipes, ensuring a secure fit on the frame and sampling.

Sample collection

In each sampling session, three stones were randomly selected for retrieval by diving from both natural and experimental substrata. Each stone was placed in a plastic bag for protection, and transported to the laboratory, where the encrustation of the substrata was removed by knife and soft brush, and sieved through a 60 μm nylon net. The collected animal specimens were preserved in 70% ethanol.

Veligers were sampled with a 50 cm high (volume: 34 L) Schindler–Patalas sampler equipped with a 60 μm mesh-sized collector funnel near to the site, where experimental substrata were placed, on each occasion the substrata was sampled. Sampling was carried out at 50 cm increments along the entire vertical depth. The samples were pooled together and concentrated to 20 mL, then preserved with ethanol.

Sampling plan (dates and terms) and weather characteristics

The study began by submerging the instrument holding the experimental substrata on 3 August 2009. Sampling started from the second day of submersion and continued at a three-day frequency in August (short-term scale), monthly from September to December of 2009 (medium-term), and annually, beginning in the summer of 2010 for the following three years (long-term). In parallel, the local substrata were examined each August during the study period, until 2013.

The average summer temperature was 0.6 and 1 °C higher in 2012 than in 2010 and 2011, respectively. The hottest water temperature (29.1 °C) was also recorded in 2012, when a long dry period caused a significant decrease in water levels, which was low, as parts of the shoreline had dried up. In summer 2012, a number of days with stormy winds and waves were registered, which created harsh turbulences in the shallow water. Extreme weather phenomena, such as heavy storms (wind speed was 80–90 km/h) on the 5th and the 14th of August, and rapid cooling thereafter in September, occurred.

Density and size measurements

To calculate the surface area of sampled stones, the entire surface of the stones were traced onto wrapping paper. An algorithm for cut paper weight vs. surface area was derived. The density of dreissenids was represented as ind m^{-2} stone surface. The relative abundance of *D. r. bugensis* within the whole dreissenid population was calculated and given as percentage contribution in both introduced and local substrata.

The two dreissenids were distinguished from each other according to their unique morphological features (Spidle, et al., 1995; van der Velde et al., 2010). The two species were only differentiated if the dreissenid individual was >2 mm. New settlers were separated based on their sizes: <0.5 mm (post-veligers – plantigrade) and 0.5< and <2 mm (early juveniles – siphon-forming stage), according to Claudi and Mackie (1994), Kirpichenko (1964), and Ackerman, et al. (1994).

The number of dreissenids >2 mm was counted with the naked eye, and their length was measured with a digital caliper. Post-veligers and early juveniles were counted and measured under a stereomicroscope using a mm scale underneath the counter dish. Length frequency histograms were generated using 1 mm size classes to assess population size structure (Mills et al., 1993; Orlova et al., 2004, 2013; Dermott and Dow, 2008; Karatayev et al., 2013a). To count veligers, 2–5 mL multiple subsamples were taken from the concentrated 20 mL sample, and examined with a Zeiss–Opton inverted microscope.

Calculation of substratum surface saturation by dreissenids

Cover of experimental substrata by dreissenids was calculated using the following formula:

$$\sum_{(5-27)} \frac{\text{length} \times [\text{a} \times \text{length} + \text{b}] \times \pi \times \text{n}}{4}$$

Where,

length is the length of the individual in mm accuracy on a 5–27 mm scale;

a is the slope of the length–width regression line;

b is the intercept of the length–width regression line;

a × length + b is the calculated width;

length × [a × length + b] × $\pi/4$ is the surface of the ventral side of the animal;

n is the number of animals of a specific length;

$\Sigma_{(5-27)}$ is the total ventral surface of animals covering the surface.

The length– width correlation was obtained from the measurement of 30–40 *D. polymorpha* and *D. r. bugensis* individuals, respectively, in each length group (between 5 and 27 mm with 1 mm difference). The longest distance of the rostro-caudal axis was measured as the length, and the width was measured as the longest dimension in the direction perpendicular to the length. Dreissenids face the attaching surface with their ventral side, which looks like an ellipsoid in planar projection. The ventral side area of all mussels forming the dreissenid population was therefore calculated using the formula for elliptical area (a × b × π, where a and b are half of the length and width values, respectively), and finally, extrapolated to the number of animals on the substrata. The sum of the surface area of differently sized dreissenids colonizing the substrata simultaneously gave a total surface area, which would ideally cover the substrata if the animals settled side by side. This score overestimates the real surface area occupied by dreissenids, since animals attach to the substrata by their byssus and thus do not occupy the surface with their total base (ventral surface). In addition, as colonization progresses, many of the animals also use each other's shells as settling sites (multilayer aggregation). Nevertheless, with knowledge of these shortcomings, this calculation allows to assess the dynamics of substratum occupation and estimate the time when dreissenids reach total occupation.

Statistics

Before analysis, datasets were transformed to achieve homogeneity of variance and improve normality. The normality of the data was checked with a normal Q-Q plot of the model residuals (Sokal and Rohlf, 1995). A mixed model ANOVA was used to analyze differences in density (log-transformed) and average length (log-transformed) between the two species, on different time scales. The studied variables were species (within-subject, repeated measures factor) and time (between-subject factor). Separate analyses were carried out for different time scales (months, years). Sequential Bonferroni-corrected t-tests were used to show the significant interactions.

Yearly differences in the relative abundance of *D. r. bugensis* (percentage of *D. r. bugensis* in the dreissenid population) were compared between sampling sites using GLM ANOVA. The relative abundance of *D. r. bugensis* as a dependent (log-transformed) variable was analyzed with the independent categorical variables (fixed factors), time and sites (including experimental and local substrata) in the model. A Tukey test was used as a posthoc procedure for evaluating the main effects and interactions (for differences between the sites at a certain date, and differences between years at a given site).

Results

Densities of planktonic veligers and new settlers (size: 0.5–2 mm) on experimental substrata

Within a week of the onset of the settlement study, even though the veliger concentration in the water was low (1-1.3 ind L^{-1}), early colonization of post-veligers was already observed (Fig. 3). Shortly thereafter, an extraordinary boom of veliger expansion was detected (on the 14th August, 2009; 376±74 ind L^{-1}), which was limited only to single day, and could not be seen for the remainder of the month. A week after the veliger boom, on the 23rd of August, a peak appeared in the density of post-veligers (11500±6100 ind m^{-2}) which, within a month, showed a downward trend to a similar level as observed before the boom. The curve of density dynamics of early juveniles was similarly shaped, peaking in September with 27000±12000 ind m^{-2}. As the temperature dropped, and autumn transitioned to winter, veligers disappeared from the water sample, and post-veligers and early juveniles remained at low density levels on the substratum surface (2009 December, post-veligers: 300±130 ind m^{-2}; early juveniles: 2600±300 ind m^{-2}). In subsequent summers, veligers were consistently found at moderate levels (14-25 ind L^{-1}), whereas post-veligers and early juveniles showed a decreasing tendency to colonize with a density between 400–1400 ind m^{-2}, and 3400–11100 ind m^{-2}, respectively.

Dreissenid (size: >2 mm) density on experimental substrata

In the following months after substratum deployment (August 2009), no significant differences in density data were found either between the two dreissenids, or between the months (Fig. 4, Table 1a). The density of each species changed during this period, between 2652 and 2699 ind m^{-2}. From 2010 to the end of the study (2012), the density of *D. r. bugensis* significantly increased year by year (Fig. 4, Table 1b.), in contrast to *D. polymorpha* for which density slightly fluctuated, but did not change overall. By 2012, *D. r. bugensis* density reached up to 42453±10321 ind m^{-2}, which was six times higher than that of *D. polymorpha*.

Relative abundance of dreissenids (size: >2 mm) on experimental and local substrata

No difference in relative abundance was found on experimental substrata between the two dreissenids after one year of substratum implantation (Fig. 5). From 2010 onward, with increasing differences year by year, the abundance of *D. r. bugensis* (percentage of *D. r. bugensis* in the dreissenid community) significantly exceeded that of *D. polymorpha*, which was accompanied by the decline of the latter population (Fig. 5, Table 3).

Along with sampling from the experimental substrata during the study period (2009-2012), in each August, and also in the upcoming year (2013), the dreissenid population was also examined on natural (local) substrata at three points of the Tihany peninsula (see the sampling site map in Fig. 1). In the year of substratum implantation, the relative abundance of *D. r. bugensis* was significantly different at all three points (Fig. 5, Table 3). Percentage of *D. r. bugensis* was 29.6±8% in T1, 48.6±7.1% in T2, and 16.4±4.4% in T3. By 2010, the percentage of *D. r. bugensis* had significantly increased in all sampling sites, and a difference was only found between the T2 and T3 sites. At the same time, except in the T2 site, relative abundance was similar in the introduced as well as the local substrata. In 2011, the percentage of *D. r. bugensis* was further increased in experimental substrata, and T1. Trends of relative abundance equalization continued between the sampling sites. This resulted in around 80% relative abundance of *D. r. bugensis* in all sites and no annual differences between the sites by 2012. The decrease in water level resulted in high mortality for the dreissenid populations on the riprap, along which piles of shells could be traced in 2012; however, this had no significant impact on the growing relative abundance of *D. r. bugensis*, which reached 98% by 2013.

Size related composition of dreissenids (size: >2 mm) on experimental substrata

Fine resolution analysis of length distribution showed that both species were equally represented on the surface after two months of substratum deployment (Fig. 6). The most common sizes were within the 2–9 mm range, forming a bell shaped distribution. Interestingly, some adult animals also appeared on the substrata at this very early stage of colonization. In the subsequent months, the distribution of individuals within the 3–13 mm range equalized further, which resulted in a smoother distribution pattern (Fig. 6). By the end of 2009, five months after colonization started, the largest animals (> 12 mm) were mainly *D. r. bugensis*. A year later (2010), and in 2011, it was again evident that *D. r. bugensis* was more frequent among the largest animals (>12 mm), whereas the frequency of adult animals belonging to the size range of 10–13 mm was higher in *D. polymorpha*. Following the annual changes in length during the examination period, the whole size distribution pattern of *D. r. bugensis* (ranging from 2 to 28 mm) was found to be much wider than that of *D. polymorpha* (ranging from 2 to 17 mm). In 2010, the most abundant sizes found in the *D. polymorpha* population were within a narrow range of 7–11 mm in length, which slowly shifted to 10–16 mm by 2012. In contrast, the size frequencies of *D. r. bugensis* showed a rather heterogeneous distribution, resulting in a less coherent size distribution in the plot. In 2010 and 2011, dreissenids 4–7 mm in size, were missing or underrepresented in the samples.

The average length of settled *D. r. bugensis* reached its maximum as early as in 2010, whereas that of *D. polymorpha* in 2011-2012 (Fig. 7). As a straightforward consequence of the difference in the size distribution observed between the two dreissenids (see Fig. 6), the average length showed significant differences from December 2009 until 2011 (Fig. 7, Table 2a, 2b). By contrast, a difference in the average length was not seen in 2012.

Saturation of dreissenids (size: >2 mm) on experimental substrata

Both dreissenid species showed similar, linear correlations between length and width (Fig. 8a, b). The total surface occupied by the dreissenid population was estimated according to the ventral (attaching) surface of individuals and the quantity of settled animals of different sizes (see Fig. 6). Two months after deployment of the support structure for the experimental substrata, the total surface of colonizing dressenids occupied 10% of the available surface of the implanted stones (Fig. 8c). In the following cold season, this area did not increase significantly until the end of 2009. A year after deployment, the number of dreissenids attached to the substrata represented 122±28 cm^2 surface, which, supposing idealistic and homogeneous distribution, covered the whole available surface (Fig. 8c). In the forthcoming years (2011, 2012), the total surface of settled animals slightly increased, exceeding that of the substrata. Considering that surface occupation was overestimated, dreissenids could have saturated the whole surface around the summer of 2011. However, empty spots on experimental substrata could be seen until 2012 (Fig. 8d). From that time, the stratified appearance of dreissenid populations and phenomenon of multilayer aggregation could be more frequently observed on the experimental substrata (Fig 8d).

Discussion

Dreissenid population structure and dynamics on experimental and local substrata

Shortly after the experimental substrata were submerged into the lake, a huge boom of dreissenid larvae was observed, which could also be seen in the increasing number of post-veliger and early juvenile individuals attached to the new surface in the subsequent week and month. The spawning season of dreissenids lasts from late March to November depending on the lake temperature. The frequency of dreissenid larvae release has not been studied so far in Lake Balaton, but it is assumed to be influenced primarily by weather extremities, which occur more often nowadays rapidly changing the physical conditions of the shallow lake. Simultaneous release of a large number of larvae within days in the middle of the spawning period assumes the presence of some triggering substances, which affect gonadal activity and promote sudden rather than smooth production of new larvae. The veliger release coincided with a storm, which evoked big waves and mixed up the whole water column, increasing the amount of the suspended material. Nevertheless, correlation between the storm and the veliger release cannot be established, which was supported by the low number of veligers observed also at a stormy day just after the settlement. Taking into account that *D. polymorpha* larvae stay in the plankton for at least 7–15 days (Marsden, 1992; Ackerman et al., 1994), and because of the irregular larvae release, this implies that to address dreissenid larvae propagation, at least weekly sampling frequency is required.

It can be deduced from the density and length frequency data of dreissenids, which have been taxonomically identified (> 2 mm), that *D. r. bugensis* and *D. polymorpha* colonized the experimental substrata with equal success in the first few months. This theoretically suggests that at the beginning of the colonization study, veligers were distributed equally between the two species. However, due to its stronger attachment, *D. polymorpha* is a better colonizer and more often remain on the substratum (Peyer et al., 2009, Collas et al., 2016), also suggesting that *D. polymorpha* might have represented more on the substratum, albeit its veliger is less abundant in the water.

Some large individuals, found unexpectedly in the samples of early colonization, might come from the neighboring riprap by detaching and transporting via water currents or by active locomotion to the experimental substrata.

After an equalized abundance, from the first year of colonization, the *D. r. bugensis* population significantly increased on experimental and local substrata, implying the success of this dreissenid over the other species in the colonization process. However, the progression of *D. r. bugensis* colonization on local substrata took longer than on experimental substrata at the beginning of the study. This might be because of the established benthic community on local substrata including *D. polymorpha* and *C. curvispinum*, which saturated the surface and occupied the niche that is suitable for *D. r. bugensis*. In Lake Balaton, *D. polymorpha* was also found to rapidly colonize new substrata before the appearance of *D. r. bugensis* (Balogh et al., 2008), meaning that primarily the colonization speed is due to substratum saturation and not dependent on the type of dreissenid species. Nevertheless, the presence of competitors can significantly influence the process.

During the colonization process, the *D. polymorpha* population was mainly confined to a mid-size range (8-14 mm) that grew slowly. On the spat side, the *D. polymorpha* population could not be renewed, since after one year of colonization, *D. polymorpha* settlers were rarely found. On the adult side, the higher density of large (> 20 mm) *D. r. bugensis* individuals suggested more sexually mature *D. r. bugensis* in the sample. Pressure from both sides might lead to a decline, if not collapse, of the population of *D. polymorpha* during the simultaneous colonization of the two dreissenid species. Before *D. r. bugensis* was introduced to the lake, *D. polymorpha* grew larger (up to 2.4 cm, Balogh et al., 2008), which, considering that the general conditions of the lake have not changed in the past several decades, suggests that *D. r. bugensis* negatively affects *D. polymorpha* population development. The possible influence of the *D. r. bugensis* population on *D. polymorpha* growth may also be strengthened by the fact that neither in our sampling points nor at other sites of the lake (Balogh C., unpublished observation) can *D. polymorpha* individuals >2 cm be found.

From 2011, large *D. r. bugensis* individuals (between 20 and 28 mm), showing heterogeneous frequency, were counted on experimental substrata. These animals must have arisen from a compact group in which sizes were between 12 and 19 mm in 2010. The reduction of the number of these large animals in 2012 could be due to the decline of the first generation after the third year of settling, since, as found earlier in Lake Balaton (Balogh et al., 2008) and other water bodies (Whitney et al., 1996), the lifetime of dreissenids often does not exceed 3–4 years. However, different access to resources (food, oxygen), due to different site positions of the individuals in the substratum (i.e. at the bottom of the multilayer aggregation, or on that substratum side, which is relatively hidden from the water current), may contribute to the heterogeneous size distribution observed in large animals.

By the end of the study (August, 2012), the average length of the two species had equalized, which may be explained, on the one hand, by the decreasing number of large size (> 20 mm) individuals and the increasing number of young settling (3-10 mm) *D. r. bugensis* individuals, and on the other hand, by the smoothly growing population of the mid-size (10-17 mm) first colonizer generation of *D. polymorpha*.

While the veliger density was not significantly different in the summers of 2010–2012, the density of new settlers declined, suggesting that the progression of surface occupation, and hence, increasing saturation by growing dreissenids did not favor new settling generations. Parallel to the decrease in free settling places, the growing shell surfaces of earlier colonized individuals provided novel surfaces for larvae to attach, as observed from 2011. According to the experimental study of Tošenovský and Kobak (2016), the lower initial distances between settled mussels offered a higher possibility for aggregation, suggesting that as habitats are narrowed during the *D. r. bugensis* invasion, multilayer aggregation is facilitated. Substratum saturation by dreissenids was calculated to be completed around two years after substrata implanted to the lake, after which the competition for surfaces becomes more intense between the two dreissenids. This was confirmed recently in an experiment (Dzierzynska-Bialonczyk et al., 2017), where the formation of *D. polymorpha* aggregations was found as a consequence of the lack of available alternative attachment sites. On the other hand, saturation progression and in contrast, uncovered sites on experimental substratum found until the last year of the study (four years after substratum implantation), suggested that the shell of dreissenids appeared as an alternative attachment surface that promotes multilayer aggregation.

Abiotic and biotic factors that would explain the success of D. r. bugensis *colonization over* D. polymorpha

As the temperature dropped in the late autumn of 2009, the density of veligers decreased, and subsequently, the colonization of post-veligers was reduced. From 2010 onward, the new settlers were almost exclusively *D. r. bugensis,* which might be because *D. r. bugensis* starts spawning earlier at lower temperatures (4–9°C, Claxton and Mackie, 1998; Roe and MacIsaac 1997; Stoeckmann, 2003; Nalepa et al., 2010) than *D. polymorpha* (above 9°C, Sprung, 1987). In Lake Balaton, veligers could be found in the water column at 7.3 °C (late November), but they were missing in December when the temperature dropped below 7

°C. Interestingly, before the *D. r. bugensis* invasion, veligers were usually missing in the cold season, even in October, when the water temperature was higher than 8 °C (Balogh et al., 2008). The water temperature may explain the inability of *D. polymorpha* to produce larvae between October and April in Lake Balaton, and could be an environmental factor providing *D. r. bugensis* with an advantage for earlier spawning, and thus a settling opportunity.

From 2011 to 2012, the abundance of the two dreissenids on experimental substrata remained unchanged. This can be explained by the weather extremities (high water temperature, water level fluctuation, waves), which are less endurable for *D. r. bugensis* (Karatayev et al., 2013b), partly due to the mild attachment strength and fragility of the shell (Peyer et al., 2009; Casper and Johnson, 2010), and their low tolerance to temperatures above 30.5 °C (Spidle et al., 1995; Thorp et al., 1998; Karatayev et al., 1998). Conversely, in 2013, the lake was spared from weather extremities. In spring, the water level became so high that the local substrata suitable for colonization were submerged again. This allowed for the ongoing domination of *D. r. bugensis* on the rocks of the riprap in our sampling sites, resulting in almost total displacement of *D. polymorpha*.

Since there is no evidence of selective erasure from the substrata, or early death of *D. polymorpha* the different size distribution found between the two dreissenids after one year of substratum deployment could be due to the faster growth of *D. r. bugensis*. A similar difference in the growth rate between the two dreissenids was reported from the Laurentian Great Lakes (Jarvis et al., 2000; Diggins, 2001; Stoeckmann, 2003), which was attributed to the lower respiration and higher filtration rate of *D. r. bugensis*. A lower respiration rate enables *D. r. bugensis* to reduce the energetic expenditure on maintenance, and therefore promotes faster growth and ensures better chances for survival (Baldwin et al., 2002; Stoeckmann, 2003). *D. r. bugensis* grows faster and is heavier at the same shell length, so generally has a larger shell length and body mass than *D. polymorpha* (Mills et al. 1996, Jarvis et al. 2000, Diggins, 2001; Stoeckmann 2003; Karatayev et al., 2010b). It is known from field (Karatayev et al., 1998; Stoeckmann, 2003; Orlova et al., 2005), and from experimental studies (Stoeckmann and Garton, 2001; Baldwin et al. 2002) that the growth and body mass of *D. polymorpha* declines more on a poor-quality diet and in the presence of high suspended material concentration, than that of *D. r. bugensis*. Our experimental and local sampling points are situated in the oligotrophic part of the lake, and are characterized by low food (chlorophyll-*a* concentration was 5.4±3.15 μg L^{-1}), and high suspended material concentrations (25-600 mg dry weight L^{-1}, G.-Tóth et al., 2011), which may explain the faster growth of *D. r. bugensis*.

There is no evidence that *D. polymorpha* reaches sexual maturation at lower sizes than *D. r. bugensis*, but if this is the case, this could also explain why it develops slowly thereafter. In the years after substratum deployment, however, among the second and subsequent generations of post-veligers attached on the experimental substrata, *D. polymorpha* individuals were rarely found, suggesting that the aforementioned assumption might be false. Instead, the recruitment of *D. r. bugensis* implies that more larvae, and a larger number of individuals producing larvae belonging to this species, were present in the surroundings from 2010. Since local circumstances that would have influenced the selective depletion of *D. polymorpha* larvae are not known, the declined colonization of this species may due be to the decreasing number of sexually mature *D. polymorpha* individuals.

Fish and bird predation, which concerns mainly medium sized (8–17 mm) dreissenids (Czarnołęski, et al., 2006), regulates the dreissenid population in Lake Balaton (Ponyi, 1985; Specziár et al., 1997, Balogh et al., 2008). This, besides natural death, might cause the heterogeneous size distribution of the larger/older (> 20 mm) *D. r. bugensis* individuals found on experimental substrata. However, we do not know whether predation evokes any species selectivity. Other factors such as ice scours (MacIsaac, 1996; Chase and Bailey, 1999; Balogh et. al, 2008), and parasites (Molloy et al., 1997), considered as potential regulators of dreissenid population dynamics (Strayer and Malcom, 2006), are less feasibly involved in our study.

Comparison of dreissenid invasion dynamics in the eastern basin of Lake Balaton with other lakes

The colonization dynamics of dreissenids and the replacement of *D. polymorpha* with *D. r. bugensis* happened similarly in our experimental and local study sites to that found in the entire eastern basin of Lake Balaton (Balogh C., unpublished), where oligo-mesotrophic conditions are uniform (chlorophyll-a concentration: 2-3 µg L^{-1}, Sebestyén et al., 2017), and also in other European shallow reservoirs (Orlova et al., 2004; Heiler et al., 2013), and lakes (Matthews et al., 2014; Bij de Vaate et al., 2013). In these water bodies, *D. r. bugensis* almost entirely replaced *D. polymorpha* 3–4 years after its appearance. In the Laurentian Great Lakes, the progression of *D. r. bugensis*, mainly in deep areas, was much slower: it took more than 10 years, but finally led to a significant reduction of *D. polymorpha* population (Patterson et al., 2005; Watkins et al., 2007; Dermott and Dow, 2008; Nalepa et al. 2010). By contrast, in shallow areas of the Lakes, like the western basin of Lake Erie, the two dreissenids have lived together for a long time (Karatayev et al., 2014). Recently, we also found the co-existence of the two species in the western basin of Lake Balaton (Balogh C., unpublished), where the water trophity (chlorophyll-a concentration: 5-7 µg L^{-1}, Sebestyén et al., 2017) similar to that of the western basin of Lake Erie (Barbiero and Tuchman, 2004), is more eutrophic than the Eastern basin. Hence, in shallow lakes, it seems that rapid replacement of *D. polymorpha* with *D. r. bugensis* more likely happens if food availability is limited.

The difference between the colonization history of dreissenids in North America and in Europe is that North America was invaded by the two species simultaneously (Carlton, 2008, Mills et al., 1993), whereas in Europe, *D. polymorpha* colonized and became the dominant macroinvertebrate in the benthic community well before the appearance of *D. r. bugensis* (Van der Velde et al., 2010). Therefore, another possible explanation for the different duration of the replacement found between the continents is that parallel invasion could evoke a longer struggle for place and resources between dreissenids having similar ecological requirements. Where *D. polymorpha* was the first and prevailing dreissenid for years, the algal biomass and hence the trophic state of the habitat reduced, a condition that is much more tolerable for *D. r. bugensis* than *D. polymorpha.* Therefore, if *D. r. bugensis* is introduced to a habitat where *D. polymorpha* has already been colonized for a long time, the new invader has a competitive advantage as it better tolerates poor food conditions (Karatayev et al., 1998; Baldwin et al., 2002; Stoeckmann, 2003; Orlova et al., 2005). Similarly, the invasion of *D. polymorpha* and its competitor, the amphipod *Chelicorophium curvispinum* (Sars, 1895) gave different results in Lake Balaton and the river Rhine. In Lake Balaton, where the two species were introduced together (Sebestyén, 1938), they have lived side by side for a long time (Balogh et al., 2008). By contrast, in the river Rhine, the much later introduced amphipod gradually suppressed the mussel population over several years (van den Brink et al., 1993; van der Velde et al., 1994). Hence, it is possible that the progression and fate of the *D. r. bugensis* invasion highly depends on whether the invader comes simultaneously with or later than its competitors. In summary, it can be predicted that if *D. r. bugensis* appears later than *D. polymorpha*,in a shallow lake where food availability is low, then the replacement becomes rapid.

Conclusion

The colonization process of dreissenids (*D. polymorpha* and *D. r. bugensis*) on experimental and local substrata, simultaneously, at the time of the *D. r. bugensis* invasion, revealed that the new invasive species was very successful against its congener, the formerly dominating *D. polymorpha* in a large European shallow lake, where environmental conditions favor the settlement of the new invader. The differences found in the speed of replacement process between habitats in Europe and the Laurentian Great Lakes raise the necessity of running a cross-system analysis involving many lakes that have dreissenid population data. This would support the relevance of our hypothesis that the habitat previously occupied and modified by *D. polymorpha* facilitates the conduction of rapid invasion by *D. r. bugensis*. Detailed population analysis revealed that the success of *D. r. bugensis* is due to the increasing number of large (> 20 mm) reproducing individuals and the consequently recruited generations. The introduction of new substrata (e.g. setting piers, ship and boat stations) more likely favors the progression of *D. r. bugensis* invasion, which in turn implies that the proper selection of substratum type, or coating them with material inhibiting dreissenid attachment, might contribute to reducing or delaying the propagation of *D. r. bugensis* in newly invaded habitats. Nevertheless, it is necessary to study the reason for competition (ability to predominate, evidence of the impact of environmental factors, such as food availability and combined abiotic status) in the future, so as to make predictions about the invasion of dreissenids into shallow lakes.

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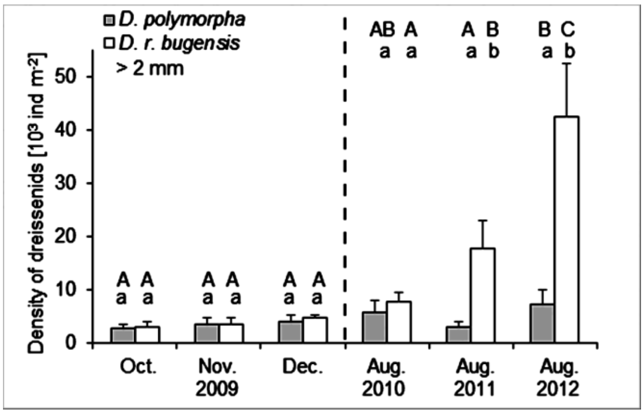
Figures and Legends

Fig. 1. Site map of the study site at Lake Balaton and the Tihany peninsula. Location where the experimental substrata were placed (rectangle), and natural sampling points (T, T2, T3) are indicated.

Fig. 2. Real and schematic views of the instrument used for studying the colonization process of dreissenids. The stone holder created from metal rods was capable of holding 60 red sand stones, which can be moved in and out the holder by the aid of a tube mounted on the stones with glue. In each sampling, three separate stones were randomly removed and analyzed.



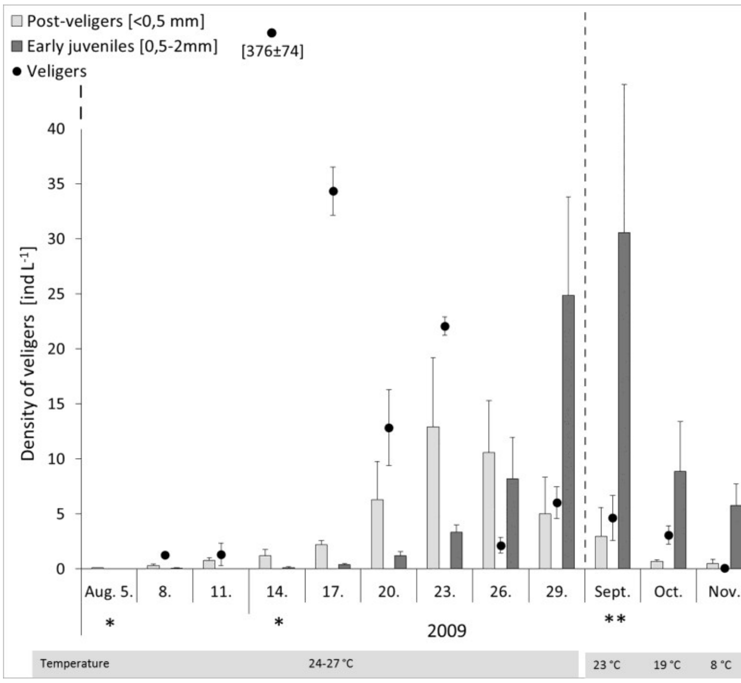


Fig. 3. Density of dreissenid veliger larvae in water, and recruitment dynamics of post-veligers (size <0.5 mm) and early juveniles (0.5 mm< <2 mm), named new settlers, on experimental substrata. Number of veligers was related to volume (ind L^{-1}), whereas the numbers of post-veligers and early juveniles were related to surface (ind m^{-2}). In each data point, post-veligers and early juveniles were obtained from three stones. Water samples were obtained near the substrata. Subsamples (n=3) were taken from a concentrated sample. For details of veliger sampling and counting, see Material and Methods. Sampling time scales were short (on every third day), medium (monthly) and long (yearly). Data are means ± SD. *: heavy storm, extreme waves; **: heavy storm, cooling.

Fig. 4. Density of dreissenids (size >2 mm) on experimental substrata. Substratum deployment was carried out in August 2009. Data are means ± SD. Letter symbols: upper case letters show the relationships between time (months and years, respectively), whereas lower case letters show the relationships between the species at given times. Bars labeled with different letters mean that they are significantly different, while the same letters indicate no significant difference.

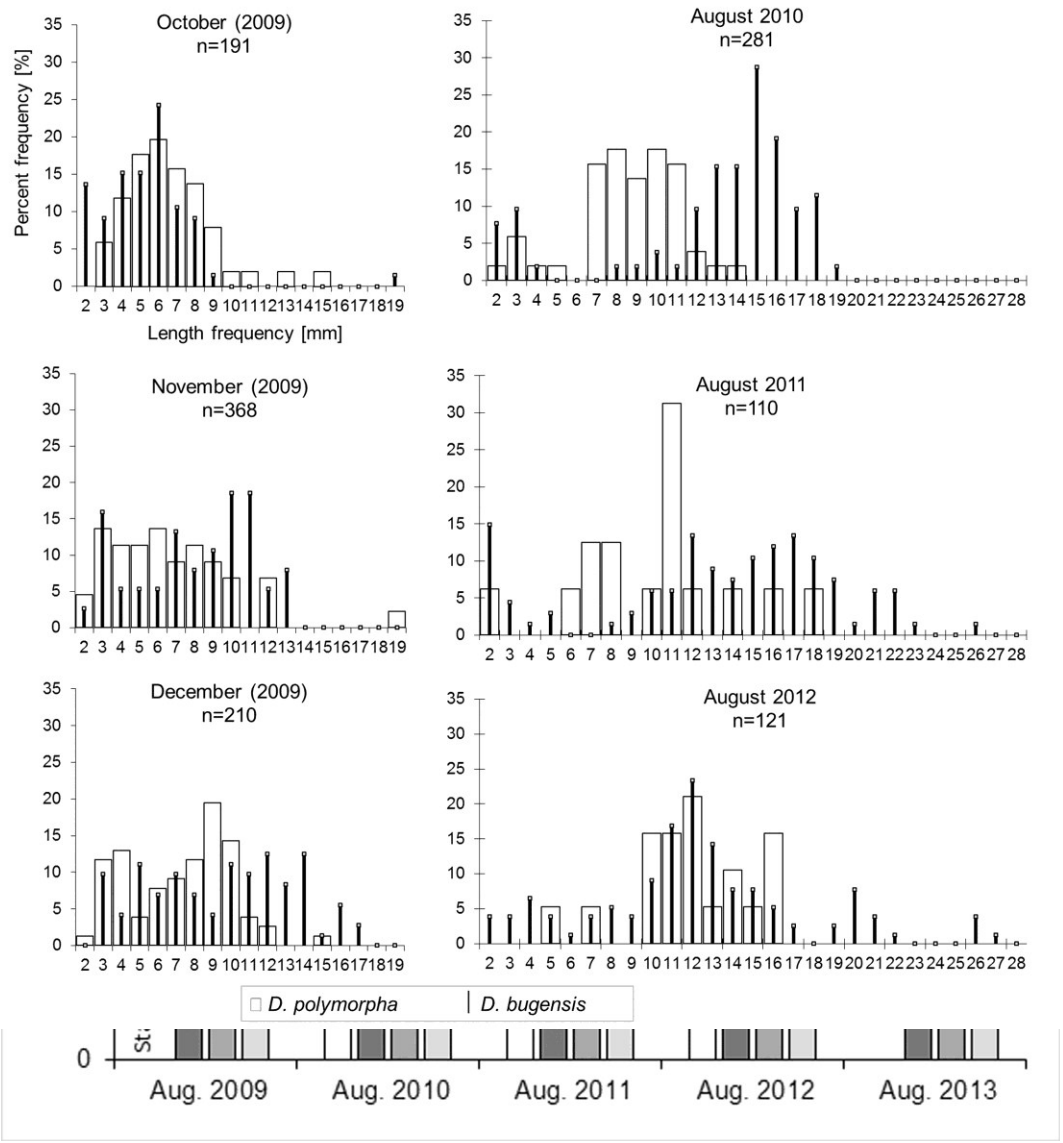
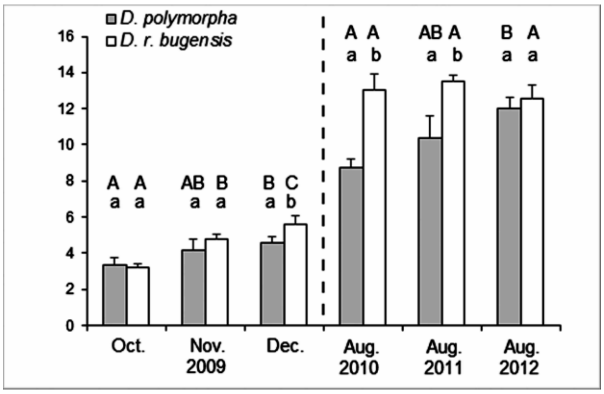


Fig. 5. Relative abundance of *D. r. bugensis* in the dreissenid population on experimental (open bar) and local (solid bars) substrata. Experimental substrata were deployed in early August 2009. Sampling was carried out in each August from 2009 to 2012. Local substrata were also sampled in 2013. Data are mean percentages of *D. r. bugensis* ± SD. In each data point, dreissenids were obtained from three stones. Letter symbols: upper case letters show the relationships between years, whereas lower case letters show the relationships between sites. Bars labeled with different letters mean that they are significantly different, while the same letters indicate no significant difference.

Fig. 6. Size frequency distribution of dreissenids (size >2 mm). Data are given as a percentage of the total number of animals measured (n, 100%), collected and counted at each time point. Data points obtained from three introduced stones deployed on Lake Balaton in early August 2009. Sampling was carried out over medium- (monthly) and long- (yearly) term scales.

Fig. 7. Shell length of dreissenids (size >2 mm) on experimental substrata. Each data point represents the average length of animals in medium- (month) and long- (year) term scales, which were obtained from three stones deployed on Lake Balaton in early August 2009. The number of animals (n) corresponds to the number given in Fig. 5. Data are means ± SD. Letter symbols: upper case letters show the relationships between sampling time (months and years, respectively), whereas lower case letters show the relationships between the species at given times (months and years, respectively). Bars labeled with different letters mean that they are significantly different, while the same letters indicate no significant difference.



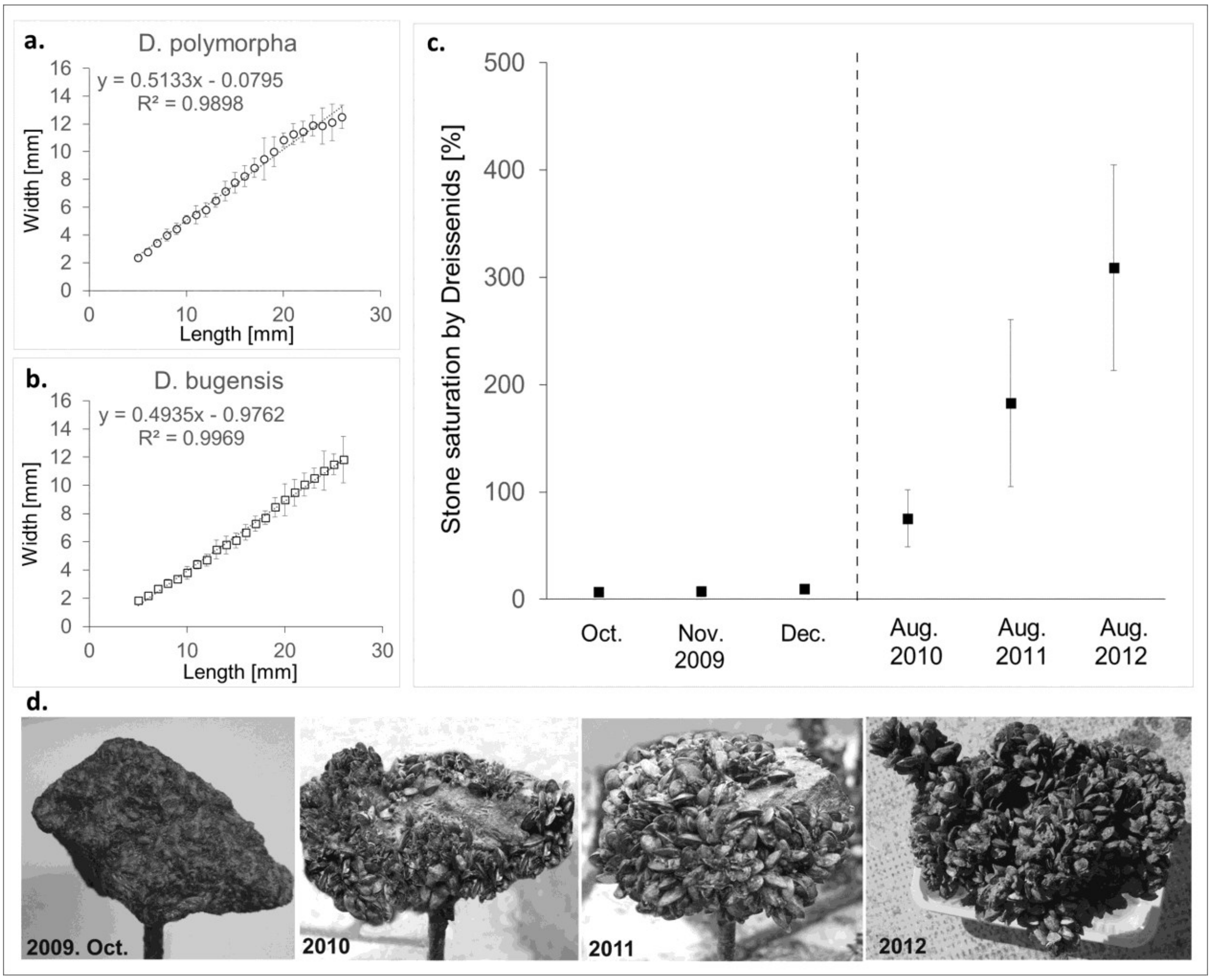


Fig. 8. Progression of surface saturation by dreissenids on experimental substrata. **a-b**. Length-width correlation of *D. polymorpha* (a) and *D. r. bugensis* (b). Each data point was obtained from the measurement of 30–40 individuals. **c**. Estimated surface cover at times when the population analysis was carried out. Each data point was obtained from the sum of surfaces corresponding to animal lengths 5–27 mm (see a and b) with 1 mm difference. Shape of the attaching surface of dreissenids was considered as ellipse, and therefore, the shell surface was calculated from the formula of ellipsis area: length × width × π /4 (detailed explanation in Material and Methods). Data obtained from three substrata are expressed as mean ± SD. **d**. Representative photos of experimental substrata covered by dreissenids two months after deployment (October 2009) and in the subsequent years.

934