

RESEARCH ARTICLE

Sediment contributing invasive dreissenid species in a calcareous shallow lake – Possible implications for shortening life span of lakes by filling

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Although the ecosystem transforming impact of the invasive dreissenid mussels has been widely reported in short-to-mid time scale studies, little is known about the contribution of the spent shells to sediments accumulating on the lake bottom. The question whether the shell production significantly reduces the lifespan of the lake by increasing sedimentation rate is particularly interesting in those shallow lakes where the calcium supply is sufficient to maintain the high mussel biomass production permanently, and where the alkaline water does not favor shell dissolution. Lake Balaton, a large calcareous, shallow lake in Central Europe invaded by dreissenids (*Dreissena polymorpha*, *Dreissena rostriformis bugensis*), provides an ideal testing ground for this scenario. Therefore, we made calculations based on recent population abundance datasets (2000–2018), estimated the whole habitable, hard surface coastline and the muddy bottom of the pelagic area which is also gradually becoming inhabited by *D. r. bugensis*, using high resolution aerial photographs and analyzing seismic sections. We created four scenarios: (1) if no dreissenids are present (applying basic sedimentation rate); (2) if *D. r. bugensis* had not been introduced to the lake (only *D. polymorpha*); (3) if *D. r. bugensis* occupies the hard surfaces of the coastline (the current dominant situation); (4) if *D. r. bugensis* colonizes the entire lake bottom (a probable future model). Different sedimentation rates obtained from the literature were used to model the filling of Lake Balaton. The shell production of the new invader, *D. r. bugensis* can shorten the lake's lifespan by one to two-thirds, depending on the model, and whether the mussel density currently observed at the shoreline is extended to the whole lake bottom. Attention is called to shallow calcareous lakes with low pre-invasion sedimentation rates in which the shell contribution of invasive mollusks has the potential to shorten lifespan.

Keywords: Dreissenids; Shell production; Biogenic sedimentation; Basin filling; Limnogeology; Biohorizon

1. Introduction

Recently, increasing attention is being paid to shallow lakes due to their vulnerability. The focus is on environmental changes over annual and decadal time spans. Typically, the natural filling process of a lake basin over a longer time scale, resulting in the termination of the lake is overlooked. Quantifying this process by attempting to model it, is however of great interest in learning the fate of shallow lakes.

The expanding global trade on waterways brings invasive species to lakes, where some of these species become

very successful, by colonizing and creating a large biomass. Among these, invasive mollusks produce inorganic external skeletons, which then add to the sediment and contribute to biogenic sedimentation. Dreissenid species, *Dreissena polymorpha* (Pallas 1771, common name: zebra mussel) and *Dreissena rostriformis bugensis* (Andrusov, 1897, quagga mussel) originated from the Ponto-Caspian region, but have now become widely distributed. These invasive bivalves are now in North America and Europe, where they are rapidly colonizing freshwater bodies (Karatayev et al., 2013; Matthews

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et al., 2014). Dreissenids live 1.5 to 9 years (Mackie and Schloesser, 1996), thereafter, their shells drift and finally become part of the sediment.

The invasive dreissenids can reach a biomass ten times larger than the native benthic invertebrates (Karatayev et al., 1997), more than 300,000 ind m⁻² density in the Laurentian Great Lakes (Nalepa and Fahnenstiel, 1995). Consequently, their current impact on the local environment has been extensively studied (Strayer et al., 1999; Karatayev et al., 2002, 2014; Sousa et al., 2009; Higgins and Vander Zanden, 2010; Ozersky et al., 2015). It was found that dreissenids are functioning as an “ecosystem engineer”, because they significantly modify the structure and the material flux of the ecosystem. However, the effect of dreissenids over longer timescales has been neither investigated, nor has it been assessed, in spite of evidence of large mussel shell druses that accumulate at the shoreline in many places.

Historical studies documenting the spread of dreissenids, e.g. in North America (Hebert et al., 1989; Mills et al., 1996; Ricciardi and MacIsaac, 2000; Carlton, 2008; Karatayev et al., 2014), cover decades. European studies, started in the mid-1800s, span well over a century. They review the moving of dreissenids since the mid-1800s in Europe (Karatayev et al., 1997; Orlova et al., 2005). The few deep-time evolutionary studies that consider the phylogeny of the taxa (Geary et al., 2000; Harzhauser and Mandic, 2004; Harzhauser and Mandic, 2010) are on the million-year scale, but these works have not considered the ecosystem engineering impact of these species.

In the present study, we aimed to estimate the possible contribution of dreissenid shell production to sedimentation and the resulting acceleration of filling the lake basin. We tested our hypothesis in a large, shallow, calcareous lake, because shallow lakes are more vulnerable to environmental changes, their filling up process is more pronounced. The high Ca²⁺ concentration provides an ideal geochemical environment for both dreissenid shell production, and for the inhibiting of spent-shell dissolution, due to the maintaining of alkaline pH.

Lake Balaton, the largest lake of Central Europe, fulfills all these criteria. There were two dreissenid species introduced to Lake Balaton. First around 1932 and then around 2008, when these species spread in Europe (Bidwell, 2010). Until the later arrival of *D. r. bugensis*, the first arriving *D. polymorpha* was the dominant member of the shoreline benthic macroinvertebrate community, reaching a density level of 220,000 ind/m², and the biomass of 1,100 g/m² (Balogh et al., 2008). Three to four years after the arrival of *D. r. bugensis*, this newcomer almost entirely replaced the *D. polymorpha* population in the oligotrophic Siófok (eastern) basin, and significantly reduced it in the meso-eutrophic Keszthely (western) basin, rapidly reaching an equilibrium in population dynamics (Balogh et al., 2018). The Lake Balaton dataset on annual dreissenid biomass from 2000 provided useful information on population dynamics (Balogh et al., 2008, 2018), and on the evaluation of the interspecific competition between the two species (Strayer et al., 2019). This dataset is used in the present study, appended with the calculation of biomass

conversion to shell volume, and with the estimation of the entire colonization surface. We calculated the thickness of deposited spent shell layers as sediment created in four possible scenarios and three sedimentation rates: (1) if no dreissenids are present (2) if *D. r. bugensis* had not been introduced to the lake (counting only with *D. polymorpha*); (3) if *D. r. bugensis* occupies only the coastline hard surfaces (current situation); (4) if *D. r. bugensis* colonizes the entire bottom of the lake. The first two do not represent realistic situations at present, but they can serve as comparisons to scenarios 3 and 4. The probability of either scenario 3 or 4, is as yet unknown, however, according to our sampling results, *D. r. bugensis* continues to form aggregates in high abundance on the mud surface. Conditions in all four possible situations were assumed to be constant over time and represent the currently existing state, that is, fish predation, and other difficult to estimate causes, like water level fluctuation, food source limitation, population collapse due to parasites, or competition were not considered. Hence, these four possible scenarios are simplified, they only involve biomass data.

1.1. Regional settings

Lake Balaton is one of the best-studied large (with 600 km² surface) calcareous shallow lakes in the world. It is in the Pannonian Basin in Hungary (**Figure 1**). There are numerous publications available, ranging from early works in the last century to more recent ones (Lőrentsey, 1911; Herodek et al., 1988a). Among these, studies of lake limnogeology (Cserny and Nagy-Bodor, 2000; Cserny, 2002; Jordan et al., 2005; Van Dessel et al., 2008) and seismics (Novák et al., 2010; Tóth et al., 2010; Zlinszky et al., 2010; Visnovitz et al., 2015) are also numerous.

Lake Balaton is relatively young, just 13–15,000 years old. It is originally endorheic. Water is supplied to the lake by one large (River Zala) and several small rivers from the limestone and dolomite mountains surrounding it to the north, and from Late Miocene sediments and Quaternary loess from the south side. The water level is increasing as described in the water budget of van Straten et al. (1979), thus since the Sió flood-gate was built, the water level has been kept around a constant 104 m level above the Adriatic Sea. The average water depth is only 3.25 m, based on a bathymetric data set (Zlinszky et al., 2010). Due to its shallow nature and artificially controlled water level, the accommodation space for sediments is limited, making it sensitive to increased sedimentation, thus justifying all concerns about the vanishing of this lake.

Assesing pre-invasion sedimentation rates without the additional dreissenid shells is of utmost importance for evaluating the impact of dreissenid shells in the present work. However, reliable sedimentation rates based on recent measurements are scarce, and are limited to few locations. At the same time, making multiple measurements representative of the entire lake is beyond the scope of this present work. Because, in general, the measurement of sedimentation rates is problematic in Lake Balaton, we had to rely on published literature. As a direct measurement, sediment traps are not an adequate method (Malmaeus, 2004), because resuspension is a

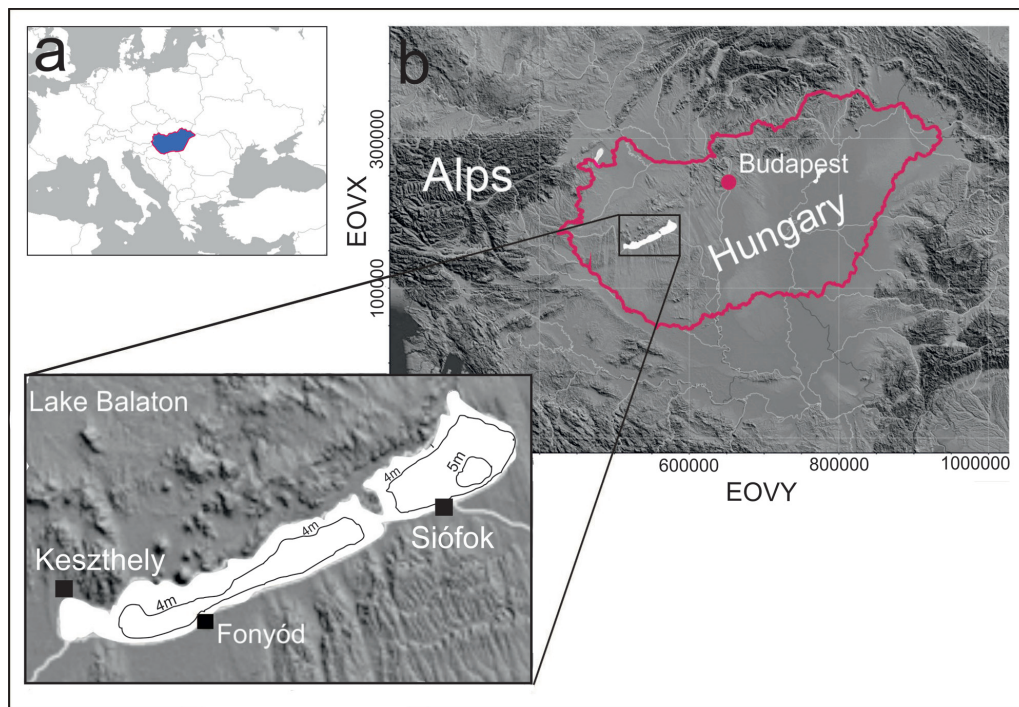


Figure 1: The location of Lake Balaton in the Pannonian Basin, with the case study area at Fonyód on the southern coast of the lake. **a)** A modified thumbnail map of Europe with Hungary taken from https://commons.wikimedia.org/wiki/File:Europe_map_hungary.png. **b)** Slightly modified maps of the study area taken from the geodynamic atlas of Hungary (Horváth et al., 2006) with bathymetry of the lake. Available at: <https://www.scopus.com/record/display.uri?origin=inward&eid=2-s2.0-34248398045>. DOI: <https://doi.org/10.1525/elementa.380.f1>

major process in Lake Balaton (Istvánovics et al., 2004). Radiocarbon dating is complicated by the high carbonate and low organic matter content of sediments which make it less reliable, but, in spite of this, perhaps it is still the best available method (Buczko et al., 2018; Cserny, 2002; Cserny and Nagy-Bodor, 2000; Tullner and Cserny, 2003). Detection of the anthropogenic Cs^{134} and Cs^{137} isotopes is an appealing method, as these isotopes are originating from two sources; the 1950's experimental nuclear explosions and the Chernobyl nuclear plant catastrophe (1986), but only a few measurements are available. Such measurements were made only in the southwest part of the lake (Keszthely and Szigliget basins). Biohorizons, e.g. the appearance of *Dreissena polymorpha*, was used in Korponai et al. (2011). With additional taxa, biohorizons might become a feasible method.

A linear sedimentation rate of longer, geological timespan, can be calculated based on the thickness of a several meters thick Holocene lacustrine sediment layer, that covers the underlying peat-layer under Lake Balaton. The thickness of this Holocene lacustrine sediment is decreasing from the southwest Keszthely basin to the northeast Siófok basin. At the Keszthely basin where the Zala river, the main water supply of the lake enters, Holocene deposits are 8 m thick, compared to barely 4 m in the Siófok basin. Generally, a sedimentation rate (SR) of 0.38–0.48 mm/yr is accepted; averaged as **0.43 mm/yr** was used in the present work (Cserny, 2002; Tullner and Cserny, 2003). Near the mouth of the Zala river (in Keszthely and Szigliget basins) the SR varied between 1 and 14 mm/yr (Cserny and Nagy-Bodor, 2000; Tullner and Cserny, 2003;

Korponai et al., 2011). Also in this area, Korponai et al. (2011) found dreissenid shells 40 cm deep and thus used 0.55 mm/yr for this upper 40 cm layer, but **1 mm/yr** below, which we adopted in the present study. In the Siófok basin Buczko et al. (2018) calculated **0.15 mm/yr**, based on two recent radiocarbon measurements carried out as part of their project.

In the present work, based on the available published literature the following values were used:

1. Southwest part of the lake, 1 mm/yr; 2. average sedimentation rate, 0.43 mm/yr; 3. Northeast part of the lake, 0.15 mm/yr.

The most common sediment of Lake Balaton is calcareous mud, but clastic sediments (silts, sands) brought from the drainage area are also common. The average free Ca concentration of the water is high (36.5–47.3 g/m³). Water Ca content is at steady state, because water supply from the inflows and condensation equals the outflow and evaporation (van Straten et al., 1979). As the inflows are supersaturated with CO₂, around 70% of the Ca transported by the inflows are retained in Lake Balaton as CaCO₃ deposition (~20.000 t [Ca,Mg]CO₃) (Müller, 1970; Cserny, 2002; Tompa et al., 2014; Nyiró et al., 2018). The calcareous sediment is mainly calcite, built with inorganic C from HCO₃⁻ in the water, but also partly biogenic, obtained from the side product of the excess CO₂ fixation by algae in the summer (Tompa et al., 2014). The aragonite form of CaCO₃, which has animal origin, can also be found in the lake sediment, although it has not been studied quantitatively as yet.

In addition to the high free Ca concentration, other factors, such as the long shoreline (240 km) with large expanses of reeds, the 105 km length of the shoreline which is reinforced with rip-rap, the numerous piers and harbors, all provide substrata and create ideal conditions for dreissenids to colonize, develop, and reproduce (Balogh et al., 2008). The bottom sediments of the lake are mostly soft (Lőrenthey, 1911). While *D. polymorpha* preferred hard substrata, for the species *D. r. bugensis* both hard and soft surfaces are suitable for colonization (Dermott and Munawar, 1993).

Human impact on the lake grew substantially in the last century. The emerging agricultural activity, with intensive vineyard development, animal farming, including fish farming along the south side of the lake, urbanization, growing human population, and the increasing popularity of lakes for recreation and tourism, led to eutrophication by the end of the last century (Herodek et al., 1988a). The organic matter produced contributes to the accumulating sediments, but the generally oxidative condition of the lake might hinder this process and make it in the long term less significant than it is in other lakes. This eutrophication trend was successfully halted (Herodek et al., 1988b), thanks to extensive scientific activity and fruitful cooperation between limnologists and property-holders. Phosphorus, the main element driving eutrophication was removed from the upper layer of the sediment at the mouth of the main inlet River Zala. More importantly, reservoirs were built (Kis-Balaton I-II) to prevent phosphorus and other contaminants from entering Lake Balaton and a sewage system was completed around the lake (Herodek et al., 1988b; Somlyódi et al., 1997). Hence, all these events

in the past 30 years have resulted in a significant improvement of water quality, which most likely also lowers the SR. Although clastic sediments arriving from the drainage area are influenced by land use, the political changes of the 90's have not created drastic changes here, unlike in other Eastern-European countries (Jordan et al., 2005; Van Dessel et al., 2008). The Fonyód area of Lake Balaton is of particular interest in the present study due to an Upper Miocene “hard rock” underwater outcrop which constitutes a special study site for dreissenid colonization in the pelagic water. Thanks to the descriptions of some early naturalists (Lőrenthey, 1911), it is known that the beach sediment near the outcropping was silty sand a century ago. This situation must have lasted until the arrival of *D. polymorpha* (~1932). The only dreissenid-related bivalve that might have been encountered in Lőrenthey's time, was the fossil “*Congeria ungula caprae*” (valid name *Mytilus ungula caprae*), (Harzhauser and Mandic, 2010), washed in by erosion from the Late Miocene (Pannonian) rocks. Finding fossil “*Congeria*” in the lake mud may have been quite common in past centuries (see local Balaton folk legend of rounded, worn fossil *Congeria umbos* as “goat hooves”), unlike nowadays, when Late Miocene fossils (“*Congeria*”, *Viviparus*, *Lymnocardium*) in the Holocene mud have vanished or became extremely rare. A case study was carried out in the Fonyód area, based on seismic profiles. In this unique area of Lake Balaton, the hard rock bottom protrudes from under a continuous layer of soft, calcareous mud in a wide zone, running parallel to the coastline. Dreissenids particularly favor this place on the south shore. The knee-high dunes of lumashell evidence that dreissenids are a major present-day sediment contributor (**Figure 2**).



Figure 2: Photographs taken at the Fonyód shoreline demonstrate the contribution of dreissenid shell remains to sedimentation. **a.** Accumulated shell fragments from the size of sand-grains to less fragmented lumashell cover the shoreline, mixed with broken reed stalks. **b.** Half-meter high dunes of lumashell formed along the waterfront of the beach. **c.** Enlarged view of dreissenid shells with a pair of sunglasses as a scale reference. Photos by Renáta Rigó. Scale bars: 1 m in a, 0.5 m in b, and 5 cm in c. DOI: <https://doi.org/10.1525/elementa.380.f2>

2. Data and methods

2.1. Estimation of the habitable area

In order to calculate the amount of shells produced in Lake Balaton, the habitable area both at the shoreline and at the mud in the pelagic zone were estimated. As the settling substrate preference and temporal dominance of the two dreissenids do not totally overlap, the habitable areas of the two species were counted separately.

2.1.1. *D. polymorpha* limited to hard surfaces – data acquisition between 2000–2005

D. polymorpha biomass was calculated first for the coastline providing solid surface for dreissenid colonization in individual basins, then for the shoreline of the whole lake, using datasets obtained between 2000 and 2005 from previous publications (Muskó and Bakó, 2005; Balogh et al., 2008). The calculation was based on point samples of mussel densities measured on reeds, on stones in the rip-rap, and on different underwater substrates (concrete

revetments, pier pilings). The length of the habitable coastline for *D. polymorpha* was measured by using the high resolution (40 × 40 cm) aerial photographs (ortho-photos) taken from 2002 June (Eurosense Ltd., Székely & Co, Pécs), and from the collection of an approx. 10,000 digital photos taken during the year of low water level (2003, Table S1). The COLIM Image Analysis software (Pictron Computer and Videotechnics Ltd., Budapest) with necessary corrections (G.-Tóth, 2005) was used for photo analysis. The calculated yearly average shell production was extrapolated to the underwater surfaces related to the water level of the lake. Samples from the mussel beds were collected by scuba divers.

2.1.2. Special off shore habitat of *D. polymorpha* – Fonyód sampling campaign 2006

At times of extremely low water level, off the coast of Fonyód rocks became visible as they jutted out of the water (Novák et al., 2010; **Figure 3**). These rocks are

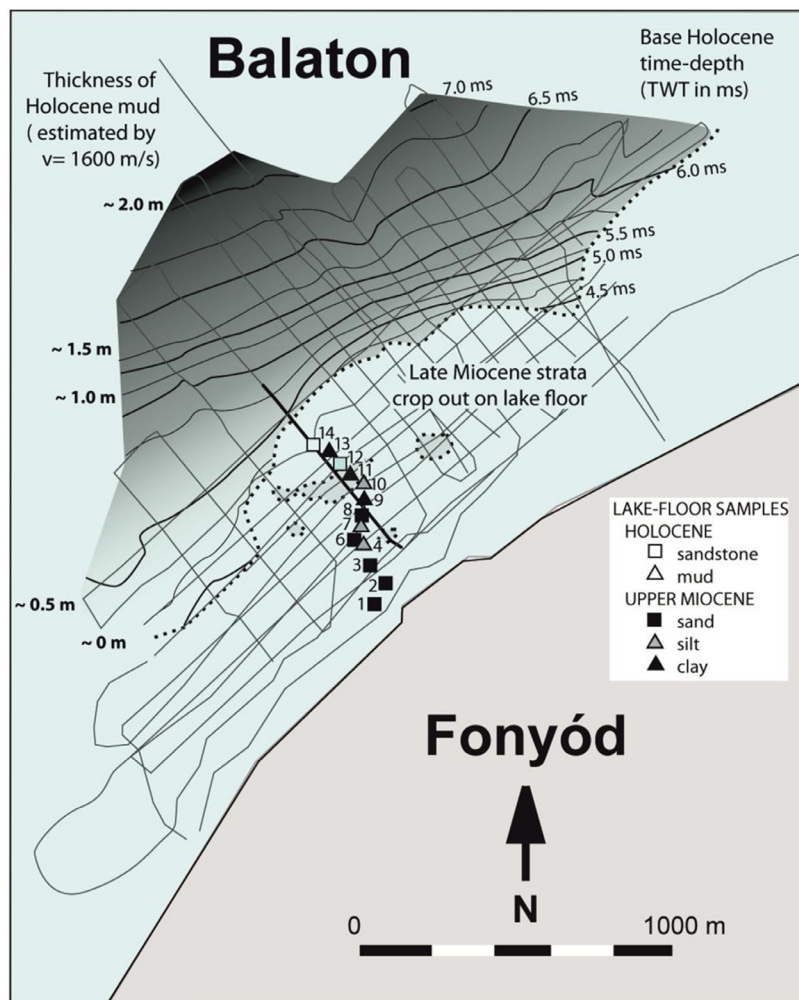


Figure 3: The thickness of Holocene mud is mapped from data of the 2005 ultra-high-resolution seismic acquisition offshore of Fonyód (Novák et al., 2010). Thickness and depth in meters were calculated from two-way-travel-time (TWT) data by applying 1600 m/s as seismic velocity. The seismic line M is found in Figure 4. Brief description of sediment samples: The first six near-shore samples (sample 1–6) consist of silty fine sands with occasional microlamination. Samples 6–8 both contain hard rock and soft sediment with very fine sand, and the hard rock surface is covered by thick carpet of lumashell. Samples 9–10 clay to sandstone, sample 11 is Holocene mud and lumashell. Sample 12 has many Late Miocene fossil mollusks besides dreissenid lumashell. Sample 14 is sandstone. Details are found in Table S2. DOI: <https://doi.org/10.1525/elementa.380.f3>

serving as a unique, off-shore, hard colonization surface for dreissenids in a pelagic environment, exceptional in Lake Balaton, as generally, soft calcareous mud, or fine sand covers the lake floor (**Figure 4**). The GPS coordinates of the outcropping layers were chosen based on the ultra-resolution seismics. Sampling was carried out here on June 22, 2005. Fourteen samples were taken along a transect perpendicular to the shoreline from open water towards the coast (**Figures 3, 4**). Based on these samples and the seismics, it was established that the underwater outcrop is indeed identical to the Late Miocene Tihany Formation on the shore (Novák et al., 2010).

2.1.3. Soft dwelling surfaces for *D. r. bugensis* settling since 2008

As *D. r. bugensis* is capable of colonizing on soft surfaces, this habitat was also considered in the calculation of the colonizing surface (see also in the Introduction). However, calculation of shell production is challenging here, as *D. r. bugensis* do not colonize the mud uniformly. Occasionally, the living specimens might form only a single knot/drusse in the mud, but usually it can be found penetrating deep into the mud in many layers, forming 3 to 6 layers of mat, occasionally up to 10 layers as a thick mussel bed. Therefore, an easy to calculate scenario with a single unified layer on the sediment surface is unrealistic. Moreover, the strongly scattered distribution pattern of these dreissenid beds makes it impossible to estimate the colonized area precisely, in spite of widespread and repeated samplings. For simplification, an upper limit situation was considered and applied, proposing that all the soft calcareous mud covering the bottom can serve as habitable area for *D. r. bugensis*.

2.2. Calculation of dreissenid spent shell sedimentation rate (SR_{biDre})

We used earlier (2000–2005) and recent (2008–2018) annual datasets (Table S3) of dreissenid biomass in Lake Balaton for estimating the contribution of dreissenid shell production (SR_{biDre}) to total sedimentation post-invasion

(SR_{tpi}). These biomass data were obtained in biovolume (the volume of the living dreissenid population [between the 5–25 mm shell length interval], which is equivalent to the water volume displaced by the animals). This form of biomass has been found more useful for estimating dreissenid biomass, because of its simplicity and reliability (Balogh et al., 2019).

From the biovolume of dreissenids given in volume/surface/year, we calculated the volume of shells of the dead mussels produced annually. First, we had to define the mean body density (ρ) of living mussels and the shell dry mass to body wet mass ratio. These values were obtained from the measurement of biovolume (v), wet mass (m_{wet}), and shell dry mass (m_{shell}) of about 450 *D. polymorpha* and *D. r. bugensis* individuals of different sizes (length range 5–25 mm), collected from two sites of Lake Balaton in 2018 (Table S4). Body density (ρ_{body}) was calculated as

$$\rho_{body} = m_{wet} / v$$

With knowledge of body density and m_{shell}/m_{wet} ratio, the biovolume of living dreissenids ($V_{bodyDre}$, datasets 2000–2005, 2008–2015) could be converted to mass ($M_{bodywet}$), then to shell mass (M_{biDre}) with the following equations:

$$M_{bodywet} = \rho_{body} \times V_{bodyDre}$$

$$M_{biDre} = M_{bodywet} \times m_{shell}/m_{wet}$$

The shell mass must be related to shell volume when its contribution to sediment thickness is assessed. The carbonate shells, as part of the sediment, are expected to break into smaller parts and the carbonate in them could dissolve in the pore water depending on the pH. The first (physical) process does not change the volume, and the second (chemical) process was regarded as negligible in Lake Balaton, in the present work (see reasoning in discussion). For the conversion of shell mass to shell volume, the shell density (ρ_{shell}) was determined for both dreis-

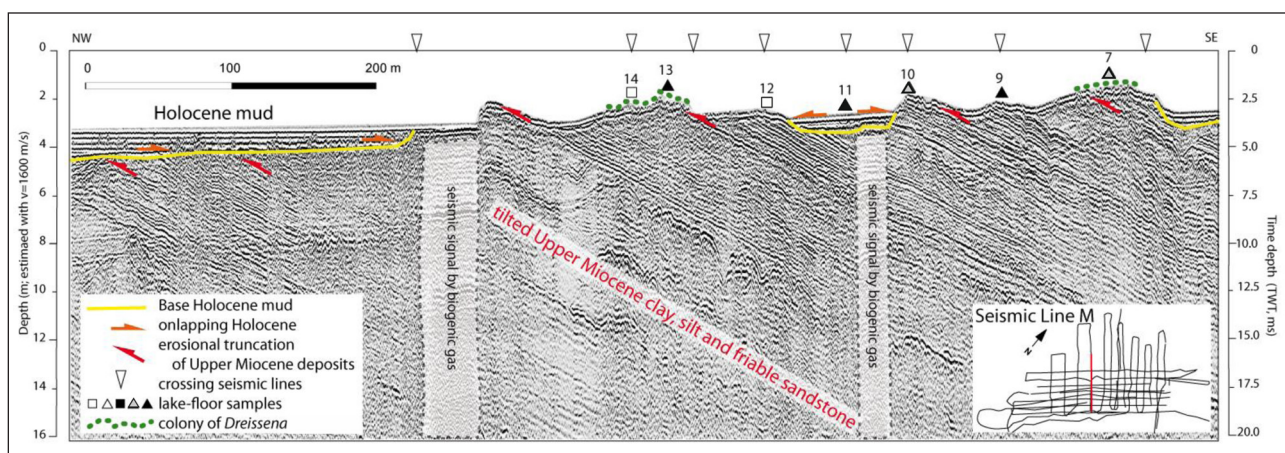


Figure 4: Lake-floor lithology at the sampling site of Fonyód with indication of dreissenid colonies. An ultra high-resolution seismic line near the sample locations reveals the deep structure of the lake floor. Nearshore tilted Late Miocene strata comprise the floor of Lake Balaton without significant Holocene cover here (Novák et al., 2010), giving rise to dreissenid colonies. Description of the sediments are found in Figure 3, and in Table S2. DOI: <https://doi.org/10.1525/elementa.380.f4>

senid species with a simple experiment. Different sizes of dreissenid shells, representing the whole population in the near-shore region of Tihany (northern shore of Lake Balaton) were collected and cleaned from the mussel spit. The following procedure was carried out five times: 10 g of shells were immersed in 30% (v/v) hydrogen peroxide in 150 cm³ glass beakers for a month. Then the shells were air dried and put into a graduated cylinder to determine the volume displaced by the shells. Thus, shell density is calculated for both dreissenid species using the equation:

$$\rho_{\text{shell}} = M_{\text{shell (10 g)}} / (V_{\text{displaced}})$$

Next, the volume of shells contributed to the sediment by dreissenids (V_{biDre}) is:

$$V_{\text{biDre}} = M_{\text{biDre}} / \rho_{\text{shell}}$$

Finally, to get the sediment thickness (sedimentation rate, SR_{biDre}) produced by dreissenid spent shells annually, the V_{biDre} was related to a given surface (hard surface along the shoreline [scenario 2, 3, 4], or soft mud in the pelagic zone [scenario 4]):

$$SR_t = SR_{\text{me}} + SR_{\text{che}} + SR_{\text{bi}}$$

2.3. Calculation of total sedimentation rate after dreissenid invasion (SR_{tPi})

Sedimentation rate (SR) was calculated from the thickness of the sediment layer deposited annually at the bottom of a lake. Total SR (SR_t) is derived from the total sediment volume (V_t) per m² area in a year, the thickness of the sediment layer in the usual units (m³/m² year = m/year). We expressed our results for SR in mm/year for convenience. The SR_t can be subdivided into three categories depending on the origin of the sediment; the clastic (solid) particles come from mechanical erosion (SR_{me}), the dissolved material from chemical erosion (SR_{che}), while the biogenic sediment (SR_{bi}) is autochthonous in the lake. Thus, we can write (after Einsele and Hinderer, 1998):

$$SR_{\text{biDre}} = V_{\text{biDre}} / \text{surface area}$$

Based on the massive amount of shells accumulating on the shores, especially emphasized in the case study area at Fonyód, we suppose that dreissenid shell production (SR_{biDre}) is added to the already existing biogenic sedimentation (SR_{bi}) in Lake Balaton. This new biogenic SR formed “postinvasion” (Pi) is called SR_{biPi} . This makes the equation after the arrival of dreissenids:

$$SR_{\text{biPi}} = SR_{\text{bi}} + SR_{\text{biDre}}$$

The SR_t after the invasion (SR_{tPi}) is given as:

$$SR_{\text{tPi}} = SR_{\text{me}} + SR_{\text{che}} + SR_{\text{biPi}} = SR_{\text{me}} + SR_{\text{che}} + (SR_{\text{bi}} + SR_{\text{biDre}}) = SR_t + SR_{\text{biDre}}$$

Therefore, to know how sedimentation SR_{tPi} has changed since the invasion of dreissenids, and how it will change in the future, the SR_{biDre} has to be estimated. We based our calculations on SR_{biDre} values taken from the literature.

According to the available data in the literature (see difficulties of SR determination in Lake Balaton in the Introduction), the average SR_t before the invasion of dreissenids was considered in three different locations in order to describe its variation:

- The southwest part of the lake (Keszthely Basin) after Korponai et al., (2011), dreissenid shells were found at 40 cm, thus this upper part was formed almost instantly on our time scale in 80 years since the arrival of dreissenids in the lake. Thus, below 40 cm the 1 mm/yr was used in the present study, more matching our millennial timescale. Hence, the expected lifetime of Lake Balaton without the dreissenid invasion, using SW part of lake data is **2.93 kyr**.
- The usually accepted 0.43 mm/yr value (Cserny, 2002; Cserny and Nagy-Bodor, 2000; Tullner and Cserny, 2003) of the SR was used for the average 3.25 m lake depth resulting in a **7.5 kyr** expected life time.
- The northeast part of lake (Siófok Basin) rather low sedimentation rates of about 0.15 mm/yr were used in Buczkó et al. (2018) to fill the average 3.25 m depth of the lake in **21.6 kyr**.

3. Results

3.1. Habitable areas on the shoreline and in the pelagic zone

The orthophoto analysis suggests that the hard substrates along the shoreline could be separated into stone, reed, concrete, angling area, and piers. In this order, the total surfaces of these substrates in Lake Balaton were estimated to 1.75 km², 15.79 km², 0.07 km², 0.02 km², 0.01 km², respectively. Altogether, these areas amounted to 17.64 km² (**Table 1**, line 6; Table S3).

Samples and observations both underwater and on the beach, as well as seismic sections in the Fonyód area make clear that there are two underwater ridges of Upper Miocene outcrops along the coastline (Novák et al., 2010) which are thickly covered by *D. polymorpha*. No hard rocks were found at sampling sites 8 and 11, and the depression visible on the seismic section was filled with “spent shells” consisting of the broken shells of *D. polymorpha*. Shells were also found at other sampling sites, but after some digging the hidden hard rocks became visible, except near the shore, where the rocks were covered with mud. This shell bulk consisted only of the shells of *D. polymorpha*. It was established that the area of the outcrop hard surface could cover a 6 m wide and 2 km long area, providing 0.012 km² habitable hard surface (**Figure 3**, **Table 1**, line 6; Table S3).

In determining the habitable area of soft dwelling for *D. r. bugensis*, the entire lake-floor, except for the anthropogenic and reed covered areas, was taken into account. This amounted to 506.21 km² (**Table 1**, line 6; Table S3).

Table 1: Summary of filling Lake Balaton basin under different scenarios, considering dreissenid shell production and different preinvasion sedimentation rates. * Shell weight was directly obtained from sampling of spent shells from the Miocene outcrop at Fonyód. Find calculations of this table with the mathematical formulas applied in Excel in the supplement (Table S5). DOI: <https://doi.org/10.1525/elementa.380.t1>

Scenarios	Scenario 1	Scenario 2	Scenario 3		Scenario 4	Supplementary information
	In the absence of invasive dreissenids	<i>D. polymorpha</i> (datasets 2000–2005)	<i>D. polymorpha</i> (Fonyód Miocene outcrop)*	<i>D. r. bugensis</i> (datasets 2008–2015) hard substrate	<i>D. r. bugensis</i> (datasets 2008–2018) hard substrate extended to the whole lake	
Mean biovolume of living dreissenids (cm ³ /m ² ·yr) Suppl. 1		1,017,36	1,618,75	171,73	1,618,75	
Total whole body wet weight of living dreissenids (body density × biovolume/m ² ·g/yr) Suppl. 2		1,281,87	1,991,06	211,23	1,991,06	average body density of <i>D. polymorpha</i> (1.26 g/cm ³); <i>D. r. bugensis</i> (1.23 g/cm ³)
Total shell weight (dry shell/body wet weight × whole body wet weight)/m ² ·g/yr) Suppl. 2		502,49	748,64	79,42	748,64	dry shell/ body wet weight (g/g) of <i>D. polymorpha</i> (0.392); <i>D. r. bugensis</i> (0.376)
Total shell volume (total shell weight/shell density; cm ³ /m ² ·yr)		206,36	307,45	32,62	307,45	shell density (2.435 g/cm ³)
Biogenic accumulation rate (total shell volume/surface; mm/yr)		0,21	0,31	0,03	0,31	
Total surface (km ²)		17,64	17,64	506,4	524,04	
Total spent shell production (SR×total surface; m ³ /yr)		3639,99	5423,03	16517,57	21940,60	
Total spent shell sediment thickness (sedimentation rate, SR; related to the whole lake surface (total "lumashell"/lake surface; m ³ /m ² ·yr in mm/yr)		0,01	0,01	0,03	0,04	0,31 whole lake surface (524.04 km ²)
South West part of lake filling time (mean water depth/sedimentation rate, SR; kyr) + 80 yrs top 40 cm	2,93	2,91	2,90	2,84	2,82	Estimated total sedimentation rate (SRt): 1mm/yr (Korponai et al. 2011); water depth (2.85 m)
Percentage of lake lifespan with dreissenids compared to the lifespan without dreissenid	–	99,33	99,00	97,03	96,09	77,13
Lake filling time (mean water depth/average sedimentation rate, SR; kyr)	7,56	7,44	7,38	7,04	6,89	4,41
Percentage of lake lifespan with dreissenids compared to the lifespan without dreissenid		98,41	97,65	93,17	91,13	58,31
North East part of lake filling time (mean water depth/sedimentation rate, SR; kyr)	21,67	20,71	20,27	17,90	16,94	7,10
Percentage of lake lifespan with dreissenids compared to the lifespan without dreissenid		95,57	93,55	82,64	78,18	32,79
						Estimated total sedimentation rate (SRt) based on Buczko et al. (2019) (0.15 mm/yr) mean water depth (3.25 m)

3.2. Dreissenid shell production in Lake Balaton (Table 1)

Mean body density of living *D. polymorpha* individuals was found to be 1.26 g/cm³, and *D. r. bugensis* for 1.23 g/cm³ (Table S4). Hence, the wet mass of living dreissenids was 1,281.87 g/m²yr before 2008 (only *D. polymorpha* presented, scenario 2), 1,991.06 g/m²yr in the rocky shoreline (scenarios 3, 4) and 211.23 g/m²yr in the pelagic zone after 2008 (Table S3). For simplicity, we calculated only with *D. r. bugensis* data from 2008, in scenario 3. Using the dry shell weight to wet body weight ratio (0.392 for *D. polymorpha* and 0.376 for *D. r. bugensis*, Table S3, S4) the shell mass of living dreissenids could be calculated. The results are 502.49 g/m²yr before 2008, and 748.64 g/m²yr and 79.42 g/m²yr for the shoreline and the pelagic zone, respectively, after 2008 (Table S3). The dry, organics-free shell density was 2.435 g/cm³, obtained from laboratory measurements (Table S4). Then, using the shell density, the volume of the shells produced for each m² surface annually, can be calculated. These results were 206.36 cm³ for *D. polymorpha*, and 307.45 cm³ on the hard surface, and 32.62 cm³ on the soft dwelling for *D. r. bugensis* (Table S3). This means that the SR_{biDre} increased annually by 0.21 mm, and 0.31 mm on the shoreline if *D. polymorpha* or *D. r. bugensis* occupies the habitat, respectively. If *D. r. bugensis* were to uniformly colonize the pelagic zone of the entire lake, then the SR would increase by 0.03 mm, annually.

Considering the whole Miocene outcrop surface at Fonyód (0.012 km²) and the spent shell mass collected from this area (75.29 g/m²), approximately 1 ton of shells is produced yearly at this site, which is enough to make a difference in the landscape locally, but, as we will see later, it has not much effect on the lake, overall.

3.3. Estimated times of filling the lake basin (Table 1, lines 9, 11, 13)

According to our results, the estimated times of filling a lake basin much depends on pre-invasion sedimentation rates, in addition to the various post-dreissenid-invasion scenarios. In order to make our data comparable with other shallow lakes that may have different sedimentation rates, substrates, and different invasive dreissenid species, we paid special attention to the existing variations in Lake Balaton, resulting in three distinct scenarios (scenarios 2–4) concerning dreissenids. Also, we used three preinvasion sedimentation rate values, one for the southwest, another for the northeast part of the lake, and an overall average value calculated for the entire Holocene period.

Scenario 1

Disregarding the influence of the invasive dreissenids, the sedimentation rate is strongly decreasing from southwest to northeast in Lake Balaton. Using the highest values from Keszthely Basin (1 mm/yr) the lake would fill in just 2.9 kyr. The Holocene average (0.43 mm/yr) results in a 7.5 kyr life expectancy, while the lowest northeast sedimentation rate (0.15 mm/yr) would fill the lake in 21.6 kyr.

Scenario 2

D. polymorpha colonizes only hard surfaces on the shoreline (17.64 km²), therefore the SR_{biDre} of the shells produced (0.2064 mm/yr, see also in 3.2 subsection) when dispersed over the whole area of the lake (506.4 km²), would create a 0.0069 mm of shell/year sedimentation. This SR would only slightly increase the SR_{fill}, i.e. there would be only a very small change in the filling time whether the southwest, average, or northeast SR_i values are used.

Compared to the area of the entire lake, the submerged Upper Miocene layer at Fonyód is a relatively small area (0.012 km²). However, it produced a large amount of shells, and, though it has not much overall impact on the filling of the entire lake, it has changed the local landscape and ecosystem services.

Scenario 3

By now, *D. r. bugensis* has almost displaced *D. polymorpha* in Lake Balaton, hence the scenarios considering only *D. r. bugensis* seem more realistic. Shell depositions on the shoreline and the pelagic zone were considered separately, due to the different colonization rates of *D. r. bugensis* on the two surface types. Taking these differences in the two habitats into account, we calculated an average value for shell layer thickness deposited in the whole lake to be 0.041 mm/yr. This means that Lake Balaton would fill in 2.8, 6.9, or 16.9 kyr, using the southwest, the average, or the northeast SR_i values, respectively.

Scenario 4

If we assume that *D. r. bugensis* colonize on the mud at the same rate as on the shoreline, perhaps because spent shells scattered over the mud make a suitable surface for further generations, then shell deposition rate of the shoreline can be applied to the whole lake bottom. In this case, the lake would fill in 2.2, 4.4 or 7.1 kyr, again depending on which of the three, southwest, average, or northeast SR_i value is used.

The results presented in **Table 1** suggest, that, concerning the life expectancy of Lake Balaton, the local variation of pre-invasion sedimentation rates is more significant, than the different dreissenid shell production scenarios. According to pre-invasion scenario 1, values range from the southwest 2.9 kyr to seven times higher 21.6 kyr for northeast values. Keeping the same SR_i, dreissenids may reduce the life expectancy of the lake by one third (**Table 1**, line 10). It seems, that in the northeast parts of the lake where sedimentation rates are low, the different dreissenid scenarios can reduce life expectancy of the lake by two thirds (**Table 1**, line 14). If we choose to calculate with the highest (southwest) Lake Balaton SR_i values, the life expectancy is almost 3 kyr. This can be reduced by about one third in scenario 4 to just 2.2 kyr (**Table 1**, line 9). So, in our particular Lake Balaton data set, although dreissenids do impact life expectancy of the lake, this impact is less significant than the one caused by the natural variation in the original, pre-invasion sedimentation rates from high SR in front of inlet Zala in the northwest to low SR in the southeast.

4. Discussion

4.1. Filling of the lake basin caused by dreissenid invasion at Lake Balaton

In the present study, the idea of invasive dreissenid shell production contributing to sedimentation was examined. The question was whether such shell production significantly accelerates the natural filling of a shallow calcareous lake on a relatively short time scale. Shell production by invading bivalves as a source of sediment has not been considered in the literature, perhaps due to the fact that most of the well-studied lakes are deep lakes, or are not saturated with carbonates. This made the dreissenid production data of Lake Balaton ideal, as well as unique, allowing us to consider the dreissenid shell contribution to the original sediment flux. The different SR_t s (northwest, average, and southeast) and the case study at Fonyód demonstrated that, if the initial parameters, like supersaturation of the lake water with carbonates remain unchanged, and the current water level is maintained, shell production by the new invader, *D. r. bugensis* can considerably shorten the lifespan of a shallow lake, providing that it colonizes the mud surface with the same density as it does the shoreline (scenario 4). Shoreline data indicated that the biovolume of *D. r. bugensis* is larger nowadays than that of *D. polymorpha* was earlier (before 2008), when the latter had dominant position in the benthic community. Moreover, unlike *D. polymorpha*, *D. r. bugensis* can colonize the mud surface. This makes *D. r. bugensis* a far more significant sediment contributor than *D. polymorpha*. Preferences and limitations of colonization on the mud are not well understood, therefore, it is not easy to predict how this process will develop in the future. Will the present situation (scenario 3) remain, or will the whole mud surface be occupied (scenario 4), resulting in high values of shell production in the whole lake area? In two large shallow, non-calcareous European lakes (Lake IJsselmeer, Lake Markermeer, The Netherlands) where *D. r. bugensis* appeared around 13 years ago, biovolume values in the whole bottom (soft sediment) was $140.43 \text{ cm}^3/\text{m}^2\text{yr}$ (Matthews et al., 2014) which correlates well with what is measured in the pelagic zone of Lake Balaton ($171.3 \text{ cm}^3/\text{m}^2\text{yr}$). This suggests that, at least for decades, the present partitioned biovolumes of the shoreline (hard substrate) and the pelagic mud (soft dwelling) in Lake Balaton will remain unchanged, implying that scenario 3 is the most probable one.

Obviously, lake filling time is much dependent on the SR_t , the sedimentation rate without dreissenid contribution (the part of SR_{tPI} which is independent of SR_{biDre}). The value of this SR_t used in the present study is known from literature (Cserny and Nagy-Bodor, 2000; Tullner and Cserny, 2003; Korponai et al., 2011; Buczkó et al. 2018). The results presented in **Table 1** show that if dreissenid shell sedimentation rates are on the scale of lake sedimentation rates, then dreissenid shells can indeed change life expectancy, reducing it by one, or two thirds (**Table 1** line 9, 13). Concerning other lakes, based on our Lake Balaton dataset we note that lakes with low pre-invasion sedimentation rates and with extremely shallow average depth are

the most sensitive to dreissenid invasion, while lakes with high pre-invasion sedimentation rates are not affected significantly. For example, if we take the extremely high $14 \text{ mm/yr } SR_t$ observed at the mouth of the Zala River, and extend this (fortunately) impossibly high value for the entire Lake Balaton, then the lake would fill in 2–300 years without dreissenid invasion, and the invasion would reduce this time by only a few decades. Everything considered, it seems that the greatest impact of dreissenids would have on a lake is when SR_{biDre} of the dreissenid shell production has similar values to the pre-invasion SR_t of the lake, and the lake is shallow. Naturally, there are some other conditions that must be met if a lake is to be affected by dreissenids in the long term. The lake must be a calcareous lake, where Ca supply for the dreissenids is available for shell building, and also the water and sediment pore water are oversaturated with carbonates for shell preservation.

4.2. Landscape change and dreissenids-hampered ecosystem services at Fonyód

An issue not much addressed in published papers is the landscape-altering effect of accumulating dreissenid shells. The spent shells accumulating on the shore degrade any fine, sandy beach ideal for bathing, to a less favorable to walk on sharp shell debris covered beach, and thereby changing the ecosystem services of the lake. The Fonyód case study perfectly demonstrates this effect. At Fonyód, in 2006, before the arrival of *D. r. bugensis*, it was observed that the Late Miocene hard rock layers off shore were heavily occupied by *D. polymorpha*, already producing shells in pelagic setting for eighty years since the arrival of the species in the 1930's (Sebestyén, 1935, 1937). A massive amount of approximately 80 tons of shell was produced at that location, that changed the lake bottom and drastically altered the landscape. Before the arrival of this invasive mussel to the lake, the sediments there were described as “grey muddy sand” containing fossils identical to layers on land, like “*Congerina*, *Viviparus*, *Lymnocardium*”, etc. (Lőrenthey, 1911). The rarity of such Late Miocene fossil molluscs in the beach sediments is related, we must suppose, to the living dreissenid colony covering the underwater outcrops, protecting them from erosion and preventing the dilution of fossils among the dreissenid shells locally. In addition, the lake-wide spreading of pavements and water drainage systems along the coasts reduced the transport of fossil shells from the shore to the lake thereby making them scarce.

4.3. Calculation accuracy – model reliability

To assess the feasibility of dreissenid shell production contribution accelerating the natural filling of Lake Balaton basins by sedimentation, a simplified calculation scheme was followed which did not take into account numerous difficult to predict abiotic and biotic impacts that are part of the complexity of real sedimentation processes in nature. Primarily, shell production is depended on biomass, which is influenced by many changes in the ecosystem balance, such as, for example, food and set-

ting surface availabilities, interspecies competition, parasites, and human intervention. The lake eutrophication recorded in the 1960–1980s (Herodek et al., 1988a, b) has been successfully arrested by attenuating nutrient load from inlets (Somlyódy et al., 1997), leading to low food availability for dreissenids at present (Présing et al., 2008; Pálffy et al., 2013). This, together with the large suspended material content characterizing the lake, provides competitive superiority for *D. r. bugensis* over *D. polymorpha*, resulting in the ongoing domination by the former species in Lake Balaton (Balogh et al., 2018). The wide-spread propagation of *D. r. bugensis* (Stoeckmann, 2003) results in greater shell production, and the accumulating of shells on the soft mud can significantly increase the colonization surface, which has been so far the limiting factor for the dreissenid expansion in the pelagic zone. Dreissenids can also enlarge the settling surface indirectly by enhancing water transparency through filter-feeding, that is beneficial to the light-limited growing of submerged macrophytes (Dermott and Munawar, 1993), that provide new colonization surface by increasing the area of reed stalks and leaves (Muskó and Bakó, 2005; Balogh et al., 2008). However, with the changing climate, accelerated ecological processes, such as the arrival of new invaders to Lake Balaton, can tilt the biological equilibrium of benthic life, usually negatively influencing the dreissenid population dynamics in the community. Such event happened in the river Rhine, where an introduced amphipod gradually suppressed the dreissenid population, over several years (Van den Brink et al., 1993; Van der Velde et al., 1994).

Other uncertainties in the result might be due to not taking into account shell diminishing factors, as neither shell dissolution, nor compression was incorporated into our calculations. Dissolution might be negligible in Lake Balaton, because Mg-calcite and protodolomites are undoubtedly formed as autogenous sediment (Müller, 1970; Cserny, 2002; Tompa et al., 2014; Nyirő-Kósa et al., 2018), indicating that the water is saturated with these elements. Carbonate balance maintains the stable alkali pH of Balaton water (pH 8.5–8.6), which is not favorable for Ca dissolution. In the sediment, where shells ultimately settle, the pH of the pore water was measured to be between 8.5 and 7.5, depending on the sampling method used (Gelencsér et al., 1982). The surface water has always been highly oxidative, and partly due to turbulence that mixes surface and bottom layers, organic materials decompose quickly through oxidation in Lake Balaton. This, unlike anaerobic decomposition, does not increase acidity (Elbaz-Poulichet et al., 1997). Moreover, in light of the general trend of diminishing nutrient load in the past decades and improved water quality in Lake Balaton (Istvánovics et al., 2007; Jeppesen et al., 2007; Hatvani et al., 2014), high organic content with greater acidic scenario which favors shell dissolution occurs only occasionally. The resulting equilibrium in the concentration of Ca in the form of carbonates in Lake Balaton water makes significant chemical dissolution of spent shells in the sediment less likely. An experimental study (Strayer and Malcolm, 2007) showed that in natural waters with

over 30 mg/L Ca concentration, as in the case of Lake Balaton, the decay rate of dreissenid shells is negligible. Moreover, they concluded that in waters where high dreissenid productivity combines with high water hardness, dead shell accumulation could be substantial, creating important consequences for habitat structure and biogeochemical cycling. Therefore, for reasons explained above, we believe that neglecting the calcium carbonate loss from spent shells in the sediment would be the best approach in assessing shell mass productivity in our scenarios.

Compression of dreissenid shells is also considered insignificant for the present scenarios, for two reasons. First, the calculation scheme which makes the conversion of biovolume of living animals to shell volume feasible (see subsection 2.2) served strictly volumetric data, which is not affected by flattening, or fragmenting the shells, or by any change in the shape or size due to transport and compression as part of the sediment. Second, dreissenid shells consist of non-porous, hard carbonates of incompressible nature (Immel et al., 2016). Studying the preservation potential of shells in the sediment in several works (Gutierrez et al., 2003; Strayer and Malcom, 2007; Ilarri et al., 2015) revealed, that invasive species had a slower decay rate, hence higher contribution in sediment production, than indigenous species (Schmidlin et al., 2012). The thin, organic coat of the shell (Belcher et al., 1996) which is lost through decomposing upon burial and would change the density can be ignored, because of the use of the oxidizer hydrogen peroxide in our calculation method.

5. Conclusions

If we suppose that the water in Lake Balaton is supersaturated with carbonates and that the prevalence of dreissenids along the shoreline is the same in the pelagic zone, then the invasive dreissenids have the potential to considerably shorten the lifespan of Lake Balaton and other similar, shallow, calcareous lakes, based on our calculations (**Table 1**). In the case of Lake Balaton, the fill-time is on the order of thousands of years due to generally low SRs. However, although dreissenid shell production is not an immediate threat, the calculated life span of the lake is reduced by one or two thirds, depending on whether we use the pre-invasion SR of the higher southwestern, or lower northeastern part of the lake.

Based on the Lake Balaton results the dreissenid shell sedimentation rates (0.03–0.3 mm/yr) are on a scale comparable to normal pre-invasion sedimentation rates of any other lake, and thus have the potential to significantly affect the filling time of lake basins. Most susceptible lakes are those where the pre-invasion SRs are low compared to SR_{bDre} , thus the invasion makes a significant difference. If such a lake is shallow, it becomes vulnerable on a short, human time scale.

The case study at a particular area of the lake (Fonyód) exemplifies that the last 80 years were long enough for just the first-arriving dreissenid, *D. polymorpha* to change the local landscape from a silty beach to the present-day spent shell covered beach (**Figure 2**). Our observations and calculations show that the population of the new invader,

D. r. bugensis has significantly higher capacity for shell production than *D. polymorpha*, and could potentially have an even more devastating impact if they were to colonize even the soft sediments in the pelagic environment, that would result in changing the ecosystem of the lake more severely. Our work might help assess the long-term consequences of an invasion to an aquatic biota of other lakes, and might help with proper decision making in environmental management concerning the dredging of beach sediments.

In the case of Lake Balaton, dating sediments and establishing SRs are challenging and must become the focus of future research. The idea of using biohorizons, as, for example, the appearance of dreissenids, is appealing. And, with regard to stratigraphy, the thought of this present sedimentation as FAD (First Appearance Date) of the “Dreissenid Zone” guiding future geologists, is compelling.

Data Accessibility Statement

The presented results are based on several original datasets provided full or as a summary in different sheets of a supplementary attached Excel file. This file is called “Supplement data” and uploaded with the manuscript. The source of Figures 1, 2, 3, 4 was noted in the legends.

Supplemental files

The supplemental files for this article can be found as follows:

- **Sheet 1: Table S1.** Detailed substrata. DOI: <https://doi.org/10.1525/elementa.380.s1>
- **Sheet 2: Table S2.** Fonyód case study – Sampling details. DOI: <https://doi.org/10.1525/elementa.380.s1>
- **Sheet 3: Table S3.** Biovolume, substrate surface assessment, SR_{biDre} calculation, Lake Balaton filling time scenarios. DOI: <https://doi.org/10.1525/elementa.380.s1>
- **Sheet 4: Table S4.** *D. polymorpha* (Keszthely) and *D. r. bugensis* (Keszthely, Tihany) samples were collected in 2018 for calculating body density (wet weight/biovolume) and shell/wet weight ratio. DOI: <https://doi.org/10.1525/elementa.380.s1>

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Competing interests

The authors have no competing interests to declare.

Author contributions

- Báldi, K** Substantial contributions to conception and design, basic idea of the manuscript, writing the article. Seismics, sedimentology and analysis Table 1, interpretation of data. Figures 1–4; Table S2
- Balogh, C** Acquisition of substrate surface and biovolume data, analysing and interpreting the data. Helping to draft the article and revising it critically for important intellectual content. Table S1, S3, S4
- O. Sztanó** Acquisition of data in seismics. Figures 3, 4
- K. Buczkó** Drafting the article and revising it critically for important intellectual content.
- I. B. Muskó** Acquisition of older biovolume datasets (2000–2005).
- L. G.-Tóth** Acquisition of data orthophotography.
- Z. Serfőző** Writing the article, preparing the revised version. Table 1, S3

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