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Competition between two congener invaders: Food conditions drive the success of the quagga over zebra mussel in a large shallow lake

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Abstract

1. *Dreissena rostriformis bugensis* (quagga mussel, QM) has spread into areas occupied by an earlier invader, *Dreissena polymorpha* (zebra mussel, ZM) in Europe and North America. Usually QM displaces ZM within a few years or both species coexist, although the mechanisms driving these outcomes have not been uncovered clearly.

2. In Lake Balaton (central-eastern Europe), QM displaced ZM in the oligotrophic (food-limited) basin, whereas they coexist in the eutrophic (food-rich) basin. Searching for the drivers of interactions in dreissenid assemblages, we compared survival, growth, allometry, shell hardness, biomacromolecule content and superoxide dismutase (SOD) expression (indicating nutrition stress) of dreissenids collected in both basins in a field survey, and in individuals collected from the food-rich basin and experimentally transplanted (10 weeks) to the food-limited or food-rich (i.e. the same) basin.

3. In the field survey, QM from the food-rich basin showed the greater height increment per unit length than coexisting ZM and food-limited conspecifics. ZM had the hardest shells of all the mussel populations. In the food-rich basin, ZM did not differ from QM in weight, protein, and carbohydrate contents, but had higher lipid content and SOD expression. Food-limited QM, compared to conspecifics from the food-rich basin, had weaker shells, but their protein, carbohydrate, and lipid contents showed faster increments per unit size, thus adults made up for the initial advantage of the food-rich population.

4. QM survived better than ZM after transplantation irrespective of the basin. Shells were harder in ZM versus QM and in the food-rich versus food-limited conditions. QM grew at both locations, whereas ZM only in the food-rich basin. The protein and carbohydrate contents were greater in the food-rich versus food-limited basin, with no interspecific differences. Lipid content in QM was higher in the food-limited versus food-rich basin, whereas the opposite held for ZM.

5. We demonstrated that the dreissenid species could coexist in food-rich conditions, despite the higher level of stress in ZM (as shown by weaker survival, higher SOD expression), whereas QM displaced ZM under food-limiting conditions, probably due to the ability to replace missing storage carbohydrates with

accumulated lipids. Nevertheless, QM from the food-limited basin also showed symptoms of nutritional stress (changes in biomacromolecule content, lower shell hardness). Results suggest that the ability to show a rapid change in metabolism could be an important advantage of QM over ZM in their competition.

1 | INTRODUCTION

The conquering of new habitats by invasive species has been enormously accelerated parallel to the expansion of global trade and climate change. In a given ecosystem, competition of the newcomer can take place not only against indigenous organisms, but also with other invasive species, introduced earlier. For the latter situation, one prominent example is the interaction between the invasive freshwater dreissenids (Bivalvia), which frequently spread over North American and European rivers and lakes by ship transport (Karatayev et al., 2011). In Europe, the quagga mussel (*Dreissena rostriformis bugensis*, Andrusov, 1897) is a relatively new invader that in recent decades started to populate habitats colonised earlier by its congener, the zebra mussel (*Dreissena polymorpha*, Pallas, 1771) (bij De Vaate et al., 2013). As their niches considerably overlap, especially in the shallow parts of water bodies (Baldwin et al., 2002; Quinn et al., 2014), a co-occurrence of the two dreissenids evokes competition, which in most cases leads to a replacement of the zebra mussel by the quagga mussel (Aldridge et al., 2014; Balogh et al., 2018; Bij de Vaate et al., 2013; Heiler et al., 2013; Matthews et al., 2014; Nalepa et al., 2010; Patterson et al., 2005; Ricciardi & Whoriskey, 2004; Strayer et al., 2019), or to a balanced co-existence (Balogh et al., 2018; Karatayev et al., 2011; Karatayev & Burlakova, 2022; Patterson et al., 2005; Tzeyeb et al., 1966; Zhulidov et al., 2010). The opposite outcome was observed in the Don River system within the native range for the zebra mussel, where the two species lived together for a long time before the zebra mussel displaced the quagga mussel (Zhulidov et al., 2006). Such a reversal of the general trend can take place in specific cases, e.g. when a molluscivorous predator depresses the quagga mussel population selectively (Rudstam & Gandino, 2020). Differences in the distribution pattern of the two dreissenids and their dynamics depend on multiple factors, but their exact explanation remains uncertain (Zhulidov et al., 2010). Dreissenids were found to share their habitat with each other under specific conditions supporting the zebra mussel or limiting the occurrence of the quagga mussel to a greater extent than that of the zebra mussel. These include shallow beds with higher temperatures, riverine flow, low calcium concentration, rich food resources, high macrophyte cover, and extensive fish predation (summarised in Zhulidov et al., 2010). Because dreissenids have significant impacts on the invaded ecosystem and cause economic damage (Mackie & Claudi, 2010), their biology, including the interaction between the two dreissenids and the nature of the competitive

advantage and success of quagga mussel, is a main research focus in this field.

Studies comparing physiological and ecological optima of the two dreissenids (Ram et al., 2012) reveal that the quagga mussel spends less energy on defence against predators (Balogh et al., 2019; Rudstam & Gandino, 2020), and detoxification of environmental contaminants (Kerambrun et al., 2018; Louis et al., 2019, 2021; Potet et al., 2016, 2018; Schäfer et al., 2012). Hence, the quagga mussel can allocate more energy into growth and reproduction, which has been suggested as the major difference in life strategy between the two dreissenids (Ram et al., 2012). While different allocation of energy budget in both species seems to contribute substantially to the shift of dominance, only Makhutova et al. (2012) compared the nutrient range (by analytical detection of lipids) between the two dreissenids to determine their energy budget. By contrast, a number of earlier studies on zebra mussel revealed that the body composition of this species contains 5%–10% carbohydrates, 5%–20% lipids, and 60%–70% proteins (Walz, 1979; Sprung & Borcherding, 1991; Nalepa et al., 1993, Bruner et al., 1994, Sprung, 1995; Smolders et al., 2004; Voets et al., 2006). Both carbohydrates and lipids are stored and used by dreissenids in a ratio depending on food availability and seasonal reproduction cycle (Nalepa et al., 1993; Sprung & Borcherding, 1991; Walz, 1979). Growth rate is strongly related to chlorophyll concentration, and less dependent on dissolved organic matter (Jantz & Neumann, 1998), which implies that dreissenids mainly consume phytoplankton. The size limit of filtered particles is between 5 and 35 μm with similar net clearance rate of algal assemblages by the two dreissenids (Tang et al., 2014). However, their food preference and selection among phytoplankton species was found to be different, which affects the diversity of the ecosystem (Tang et al., 2014), and may also influence the body composition. Not only the food quality, but also its quantity evokes different responses from dreissenids, as the quagga mussel better tolerates starvation (Baldwin et al., 2002; Karatayev et al., 2011; Sprung & Borcherding, 1991).

The two life strategies of dreissenids, differing from each other in allocation of energy into defence or growth and reproduction suggest the presence of differences in physical traits (size dimensions, weight, shell hardness), and metabolism between the congeners living in the same, as well between conspecifics living in different conditions. That is why, in the present study, we compared the changes in such metrics as linear shell dimensions (height, width), soft tissue wet weight, and biomacromolecule

content (protein, carbohydrate, and lipid) along a range of shell lengths among dreissenids living in the same lake, but at a location where both species co-exist and at a location where the quagga mussel has already displaced the zebra mussel. The existence of differences in these traits (or the lack of them) can help explain the phenomenon of the ongoing displacement of the zebra mussel by its congener in Europe and North America, as well as the occasional exceptions from this rule. The site of investigations was Lake Balaton, the largest shallow lake in Eastern Europe, where the quagga mussel (introduced in 2008) displaced the zebra mussel (introduced in 1932) from the eastern basin in 5 years (Balogh et al., 2018), but both species co-exist in the western basin (Balogh et al., 2019). The main difference between the two basins is the level of primary production, which is driven by the nutrient load from inlets in the western basin, resulting in eutrophic conditions in this area (chlorophyll *a* concentration ≥ 20 µg/L in summer, Istvánovics et al., 2022). By contrast, the eastern basin has lower nutrient inputs (chlorophyll *a* concentration < 5 µg/L in summer, Sebestyén et al., 2017). Hence, the sharp distribution pattern of nutrients and dreissenid populations make this lake an ideal site for studying the success of the quagga mussel over zebra mussel in relation to food conditions. Investigation of natural populations in a field survey was supported by a field transplant experiment, wherein the growth and condition of animals transplanted from the eutrophic western basin to the oligotrophic eastern basin was compared with that of mussels collected from and reinstated in the eutrophic location. Presumptive nutrient stress was assessed by the measurement of the anti-oxidant superoxide dismutase (SOD) expression, which is considered as an appropriate marker for starvation-induced cellular metabolic changes (Chen et al., 2009). SOD eliminates the superoxide anion accumulated because of insufficient reduction in oxygen at the end of the mitochondrial electron transport, which takes place during the nutrient stress. Starvation-induced autophagy is mediated by superoxide anion, and hence controlled by SOD (Redza-Dutordoir & Averill-Bates, 2021).

We hypothesised that dreissenid condition in the lake was affected by trophic conditions, to be reflected in intraspecific differences in their morphology, chemical body composition, and enzyme expression between the two lake basins in the field survey and transplant experiment. Furthermore, we expected that zebra mussels would be affected by poor food conditions to a greater extent than quagga mussels, which will be manifested in the transplant experiment by the higher intraspecific differences exhibited by zebra mussels between the basins and higher interspecific differences in the food-limited basin. We assume the examined traits will allow to infer the indicators and mechanisms of the adaptation strategy to low food abundance, as well as causatives of differences in acclimation to low food abundance between the two mussel congeners. Finally, the datasets allowed us to find possible correlations among traits, revealing how growth parameters (morphology, weight) and internal traits (biomacromolecule content) depend on each other in dreissenids.

2 | MATERIALS AND METHODS

2.1 | Study sites, field survey, and measurements of physical traits

Lake Balaton with its 600 km² surface is the largest shallow lake in Central Europe. Three sites in the lake were designated for the field survey and the field transplant experiment (Figure 1). Two sites were in the western basin (hereafter: food-rich basin) where both dreissenids co-occur, and one was in the eastern basin (hereafter: food-limited basin) where currently only the quagga mussel lives and zebra mussel has already been extirpated locally (Balogh et al., 2019). Nevertheless, as the distance between the sampling sites located in the two basins was considerable (50 km), the quagga mussels from both basins can be considered as separate groups. Water variables in both basins (depth of the water column, temperature, conductivity, transparency, and pH) were recorded routinely with standard equipment (water quality meter Horiba U-10, Secchi disc) at sampling and experimental sites (Table S1). Chlorophyll *a* (Chl-*a*) was measured according to Wetzel and Likens (2000).

For comparison of different traits between the two dreissenids living in these basins, animals of different sizes ($\Sigma_N \approx 200$
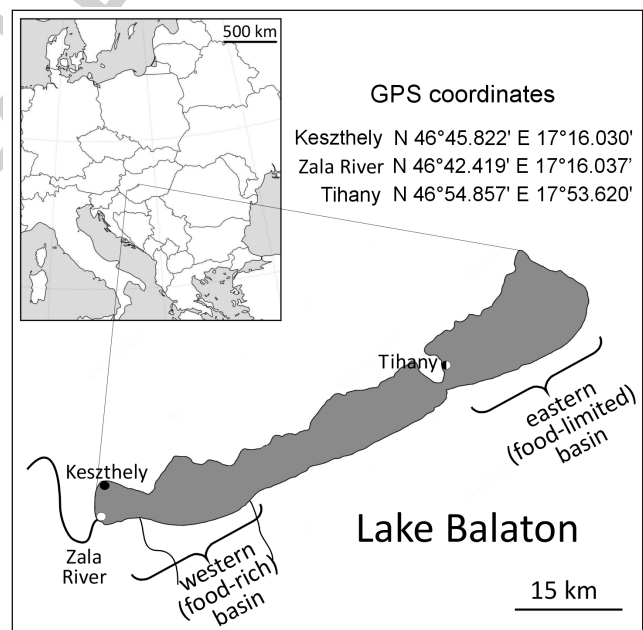

FIGURE 1 Location map of Lake Balaton with sampling and experimental sites. Schematic view of Lake Balaton enlarged from a blind map of Central Europe with indications of sampling (black circle) and transplantation sites (white circle) in the western basin, and for both (semi black and white circle) in the eastern basin. GPS coordinates give exact site locations, which are close to two residential areas (western: Keszthely, and eastern: Tihany). Note the difference in trophic status between the two basins (western: meso-eutrophic, food-rich, chlorophyll *a* concentration = 10–40 µg/L; eastern: oligotrophic, food-limited, chlorophyll *a* concentration = 0–5 µg/L).

ind./spec. and basin) were collected from the rocky shoreline in summer (July 2018) by gently removing them with a blade. Their valves were cleaned from fouling with a soft brush under water, and mussels were transported to the laboratory. Thereafter, the valve dimensions (the longest distance of the anterior–posterior axis [length], the longest distance of the dorso-ventral axis [height], and the longest distance between the left and right valve [width], Kerambrun et al., 2018) were measured with a digital caliper. Mussels from each population (denoting both species and basin) were divided into size classes every 1 mm within the length range of 5–25 mm, similar to our earlier work (Balogh et al., 2018). Within the 6–18 mm range, 10 individuals per each size class were used, whereas smaller and larger size classes contained fewer than three individuals because of the shortage of such small and large animals in the sample. Soft tissue wet weight and shell hardness were also measured in these individuals. Soft tissue wet weight of dreissenids was determined after excision of the soft tissue from the valves and removal of water from the pallial cavity by placing the tissue on a filter paper for 10 s. Shells were dried at room temperature for 1 hr and then both valves were cracked with a digital force gauge FH 50 (Sauter GmbH) to measure shell hardness (Balogh et al., 2019). We used an average value for both valves as a measure of shell hardness of each individual. As sample sizes allowed, a total of 10 dreissenids were sampled from each species, size class, and basin.

2.2 | Measurements of biomacromolecule content

6 In each size class of animals collected in the field survey, concentrations of biomacromolecule groups (proteins, carbohydrates, and lipids) were measured in three individuals randomly selected out of 10 animals per species, size class, and basin examined for physical traits. Total soft tissues were manually homogenised in small plastic tubes with a fitting pestle (Kimble-Kontes, PP 749521-1590) together with 100 μL of 0.1 M Tris–HCl buffer (pH 7.8). The homogenate was centrifuged at 12,500 g for 5 min at 4°C, and the supernatant was used for biomacromolecule analysis.

2.2.1 | Protein

Protein content was estimated by the BCA method using a protein assay kit (Pierce) according to the manufacturer's protocol. From the homogenate, 0.5–2.0 μL was added to 300 μL of working reagent containing 2% sodium-dodecylsulfate to avoid interference with lipids, and incubated at 37°C for 30 min. Colour intensity of the reaction was measured at 595 nm in a Hitachi U-2900 spectrophotometer, which was used for all biomacromolecule measurements. Concentration was calculated with a bovine serum albumin calibration standard in the linear range of 25–1,000 μg/mL. The result was expressed as the mg protein/mL homogenate ratio.

2.2.2 | Carbohydrate

The detailed description of the carbohydrate content measurement has been given elsewhere (Balogh et al., 2019). Briefly, 4 μL homogenate was heated in a mixture containing 1 mL of 96% ethanol, 200 μL of distilled water and 20 μL of saturated Na_2SO_4 at 95°C for 4 min in a block thermostat. Samples were chilled and centrifuged at 2,500 g for 20 min. The pellet was dried, dissolved in 50 μL of distilled water, and boiled in 1 mL of the 0.15% anthrone reagent (anthrone [Alfa Caesar] dissolved in 76% sulfuric acid) at 90°C for 20 min. The colour of the reaction was measured at 620 nm. Carbohydrate content was obtained in glucose equivalent (standard, linear range: 20–1,000 μg/mL) and expressed in mg glucose/mL homogenate ratio.

2.2.3 | Lipid

Lipid content measurement was carried out by the sulfo-phospho-vanillin assay adapted to dreissenids (Nalepa et al., 2010), with adjustment to small sample volumes. Two μL of the homogenate was added to 2×200 μL chloroform/methanol 2:1 solvent, shaken, and the lipid containing chloroform part was separated from methanol by adding 200 μL of 0.9% NaCl and using a pulse centrifugation (15 s) at 6,000 g. One hundred μL of the bottom (chloroform) fraction was removed quickly by a micropipette, and dried at 100°C. The dried sample was dissolved in 250 μL of sulfuric acid (96%) and heated at 100°C for 10 min. Then, 100 μL of this sample was added to 200 μL of sulpho-phospho-vanillin reagent prepared by mixing 15 mg of vanillin (Sigma-Aldrich, Hungary) with 2.5 mL of distilled water, and 10 mL of concentrated phosphoric acid. Vanillin was dissolved first in 250 μL of absolute ethanol. The sample was thoroughly mixed and left for 30 min before measuring the absorbance at 525 nm. Lipid content was estimated in relation to the calibration standard (olive oil, linear range: 25–500 μg/mL) and expressed as mg lipid/mL homogenate ratio.

2.3 | Measurements of the superoxide dismutase gene expression with reverse transcription–polymerase chain reaction

The expression of the enzyme eliminating superoxide (superoxide dismutase, SOD) was studied by reverse transcription–polymerase chain reaction (PCR) in field survey samples, using 5–14 mussels (shell length of 15 mm) per species and basin (for exact numbers, see Figure 5). RNA isolation and quantification was carried out as described by Balogh, Serfőző, and Kobak (2022). PCR primers for SOD gene expression (both forward and reverse) were designed according to the sequences published in the National Center of Biotechnology Information (NCBI USA, forward sequence: AGCAC TTACACACCCATTGCT; reverse sequence: ACAGGCTTAGCAGA GGGACA, Acc. No.: AY377970, efficiency: 1.96). These primers were also successfully used for both dreissenids elsewhere

(Kerambrun et al., 2018). High levels of homology between the SOD genes of the two species (91%–92%, Péden et al., 2019) made it possible to use the same primer for both dreissenids. Real-time PCR assays were run in a LightCycler® 96 System (Roche), using the gene-specific primers with SYBR Green protocol. For cycling, each 10-μL PCR reaction contained 1 μL cDNA (20 ng), 250 nM primers, and 5 μL qPCRBIO SyGreen Mix Lo-ROX (2X, PCR Biosystems). The PCR protocol was as follows: Enzyme activation at 95°C for 2 min, 45 cycles of denaturation at 95°C for 10 s, annealing at 60°C, and extension at 60°C for 10 s. All the quantitative PCRs were performed in three replicates. After amplification, the melting curve was checked to verify the specificity of the PCR reactions. The Ct values were normalised to β-actin gene for each time point.

2.4 | Transplant experiment

The experiment comprised collecting individuals of both species from the food-rich basin (where they were still present) and transplanting them into the food-limited basin or back to the food-rich basin (procedural control). Transplanted individuals were collected simultaneously with the collection of animals from the food-rich basin for trait measurements in the survey, and individuals from both species within the length range of 7–11 mm were selected and settled on the inner surfaces of PVC tubes (ø 5 cm, length 15 cm, Figure 2) in the laboratory (each species separately, 10
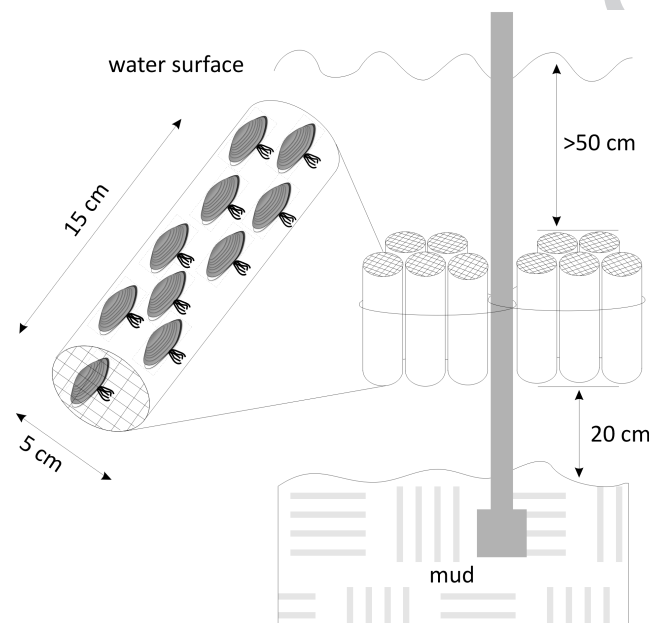

FIGURE 2 Schematic drawing of the configuration and situation of transplanted animals. Ten medium size dreissenids (7–11 mm) from one species were allowed to attach inside a PVC tube. The tube ends were sealed with mesh (size: 3 mm). Five replicate tubes for each species (10 tubes total) were bound together and fixed on a metal bar immersed in the mud, 20 cm above the mud surface and more than 50 cm below the water level.

individuals per tube). The exact length of each settled individual was measured with a calliper and recorded (Table S2). The outlets of the tubes were closed with a mesh (hole ø 3 mm) preventing animal loss and protecting the animals against predation after placement into the lake, whereas enabling water exchange. The tubes were kept in the research institute (Tihany, lakeside of the eastern basin), in aquaria supplied with a continuous flow of Balaton (the eastern, food-limited basin) water for a week. Then, half of the tubes with settled animals were deployed in the food-limited and the other half in the food-rich basin in the end of August (five tubes with zebra mussel and five tubes with quagga mussel at each location, Figure 1). The tube packs were fixed to metal bars pressed down the muddy substratum. The tubes were located 20 cm above the bottom and at least 50 cm below the surface (Figure 2), mimicking the natural depth position of dreissenid populations in Lake Balaton. After 10 weeks of exposure, the tubes were retrieved in early November. The mesh closing the tubes was checked for clogging debris, which, by blocking the water flow, could obscure the comparisons among the experimental groups. Such an extended covering or periphyton was not found on the mesh, thus conditions for mussel development were good and equal in the tubes (except for the differences between the basins).

Having determined the survival rate of mussels, the physical and chemical traits similar to those determined in the field survey were measured in a subset of survivors. The final shell length was measured in all the survivors (a maximum of 10 individuals from each tube). Moreover, seven dreissenids from each tube (as sample sizes allowed) were used to determine their final soft tissue wet weight and shell hardness, as well as protein, carbohydrate, and lipid content (the same individuals for all biomacromolecule measurements).

2.5 | Data analysis

General linear models (LMs) were run on the field survey dataset to reveal allometric relationships between mussel shell length (continuous independent variable) and dependent morphological variables: shell height, shell width, soft tissue wet weight, shell hardness, and biomacromolecule content (protein, carbohydrate, and lipid) for three mussel populations depending on basin and species (categorical independent variable; quagga mussel in the food-rich basin, zebra mussel in the food-rich basin, and quagga mussel in the food-limited basin). The models also included a population × length interaction. The continuous variables were log-transformed to linearise potentially allometric relationships among the measured traits. In these analyses, we first checked whether the slopes were significantly different from 0 (i.e. whether a relationship with length existed). If so, we tested whether the slopes differed among various mussel populations (when a population × length interaction was significant). For parallel or non-significant slopes, we tested whether the mean trait values (controlled for mussel shell length) differed among the mussel populations (difference in

a vertical position between the slopes). Furthermore, for biometric traits, we checked whether their relationship with length was isometric (i.e. whether the trait increased proportionately with an increase in mussel shell length), or whether its increase was relatively faster (positive allometry) or slower (negative allometry) than the increase in length.

Moreover, relationships between different biomacromolecule levels and their effect on shell hardness in individual mussels from the field survey were tested with LM: (1) protein content as a dependent variable, lipid and carbohydrate contents as independent variables, to test the relationship between storage materials and protein level; (2) carbohydrate content as a dependent variable, lipid content as an independent variable, to test the relationship between the storage materials; and (3) shell hardness as a dependent variable, protein, lipid, and carbohydrate contents as independent variables, to test the relationship between shell hardness and biomacromolecule content. In all these analyses, mussel population and length were included to control for their effects on tested traits. Additionally, SOD expression in the field survey samples was compared among mussel populations by a one-way LM.

Mussel survival in the transplant experiment was tested with a generalised linear model (GLM) with binomial distribution and log link function, suitable for frequency data (i.e. numbers of successes [surviving mussels] per a given number of trials [initially exposed mussels]). The model included basin (food-limited or food-rich), species, and their interaction. To check a difference in mussel growth in the transplant experiment, relative growth was estimated as a percent increase in mussel shell length, relative to the initial length. As particular mussels were not labelled at the experiment start, calculations were based on averages per each replicate: (mean final shell length—mean initial shell length)/ mean initial shell length. LMs were run on the following traits (log-transformed): relative mussel growth, soft tissue wet weight, shell hardness, and concentrations of biomacromolecules. The LMs included categorical variables: basin, species, and their interaction, as well as final mussel shell length as a continuous variable (except of the growth analysis, where mussel shell length was the part of the growth formula). Additionally, experimental tube was included in the models as a random factor in those analyses, in which measurements were made on individuals, to control for the tube effect (thus making them general linear mixed models). Furthermore, to check whether the mussels grew at all in particular treatments, (i.e. the increase in their size differed significantly from 0), one-sample t-tests comparing the mean percent increases in length with a theoretical value of 0 were used. In addition, a principal component analysis (PCA) (based on a correlation matrix, with varimax rotation of axes) was conducted to find sets of correlated mussel traits: final shell length, final soft tissue wet weight, shell hardness, protein, carbohydrate, and lipid contents.

Pairwise comparisons for significant effects in LMs and GLM were carried out using sequential Bonferroni corrected Fisher LSD tests.

3 | RESULTS

3.1 | Environmental variables in the food-rich and food-limited basins

Environmental variables (water depth, temperature, conductivity, and pH) did not differ decisively between the two basins at the time of the field study, or during the period of the transplant experiment (Table S1). Their values were typical for Lake Balaton in summer and autumn (Sebestyén et al., 2017). In contrast, the basins differed from each other in their Chl-*a* concentrations and water transparency. The seasonal means of Chl-*a* in the food-limited and food-rich basins were $2.42 \pm 1.3\,\mu g/L$ and $11.9 \pm 5.0\,\mu g/L$, respectively (Table S1).

3.2 | Differences in the relationships of physical traits and biomacromolecule content to shell length among dreissenids in the field survey

A significant interaction between mussel population and shell height in the LM resulted from the strong positive allometry of the shell height increase per unit length shown by quagga mussels from the food-rich basin compared to the other mussel populations (Figure 3a; Table S3). The relationship of the shell height of quagga mussels from the food-limited basin and zebra mussels (the food-rich basin) with shell length showed a negative allometry; hence, growing mussels in these populations became more elongated than quagga mussels in the food-rich basin.

Increases in shell width and soft tissue wet weight per unit length did not differ among the mussel populations and were positively allometric (except an isometric relationship between zebra mussel weight and length), meaning that these traits increased faster than length (Figure 3b,c; Tables S3 and S4).

Shell hardness developed differently among dreissenid populations, as indicated by a significant interaction between mussel population and length (Figure 3d; Tables S3 and S4). Zebra mussels, living only in the food-rich basin, had the hardest shells of all the populations, but the increase in their shell hardness per unit length was lower than that of the quagga mussels either from the food-rich or the food-limited basins. In result, the difference in shell hardness between zebra and quagga mussels was lower for larger individuals. The shell hardness versus length slopes did not differ between the quagga mussel populations from both lake basins. However, quagga mussels from the food-rich basin had stronger shells than those from the food-limited basin over the entire size range.

Analyses of biomacromolecule concentrations showed that body composition and its relationship with mussel shell length differed among mussel populations, as indicated by significant interactions between shell length and mussel population (Tables S3 and S4). Protein and carbohydrate contents increased with mussel shell length in all populations (Figure 4a,b). The increments of protein and carbohydrate contents with shell length were higher in quagga mussels in the
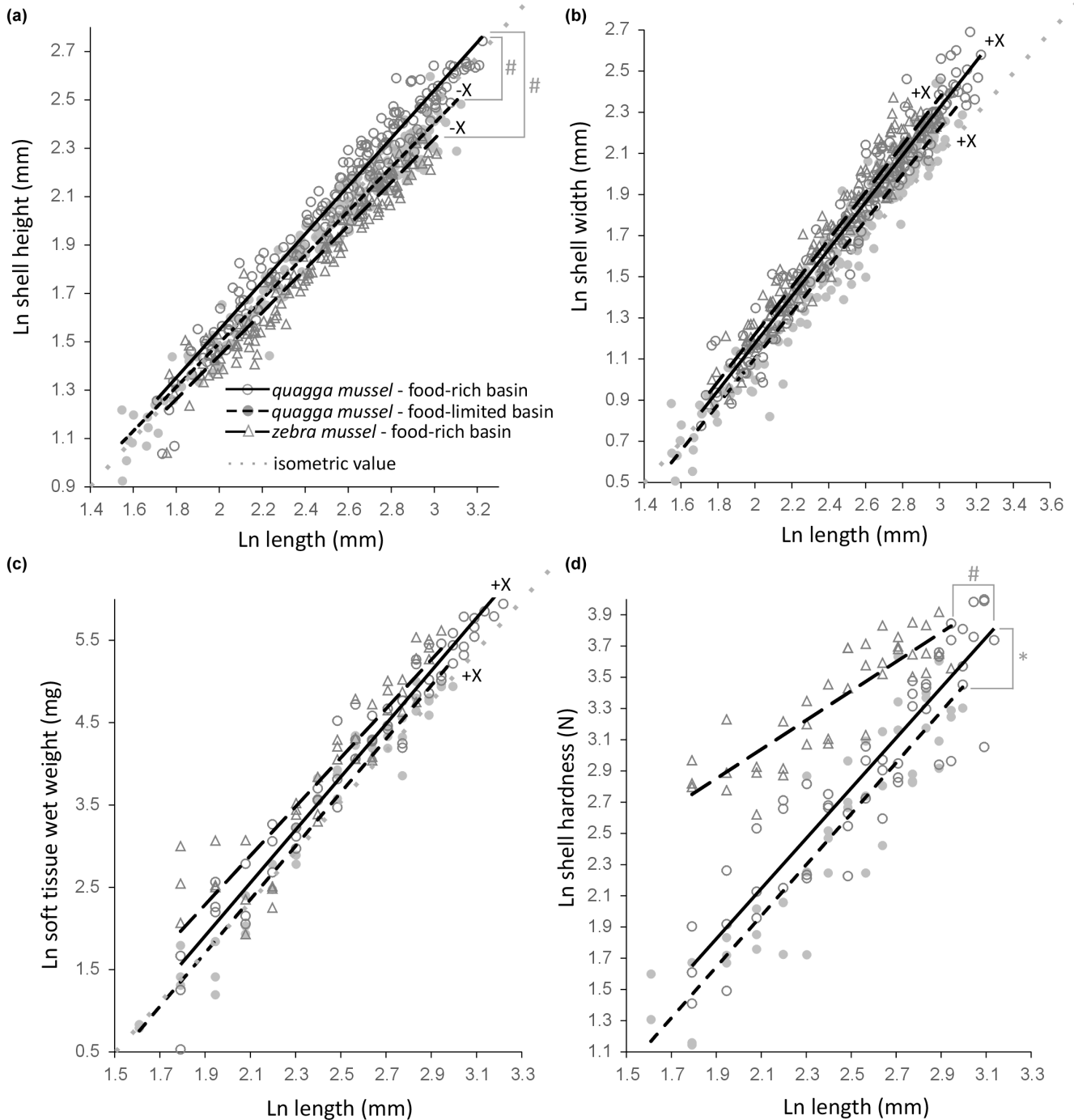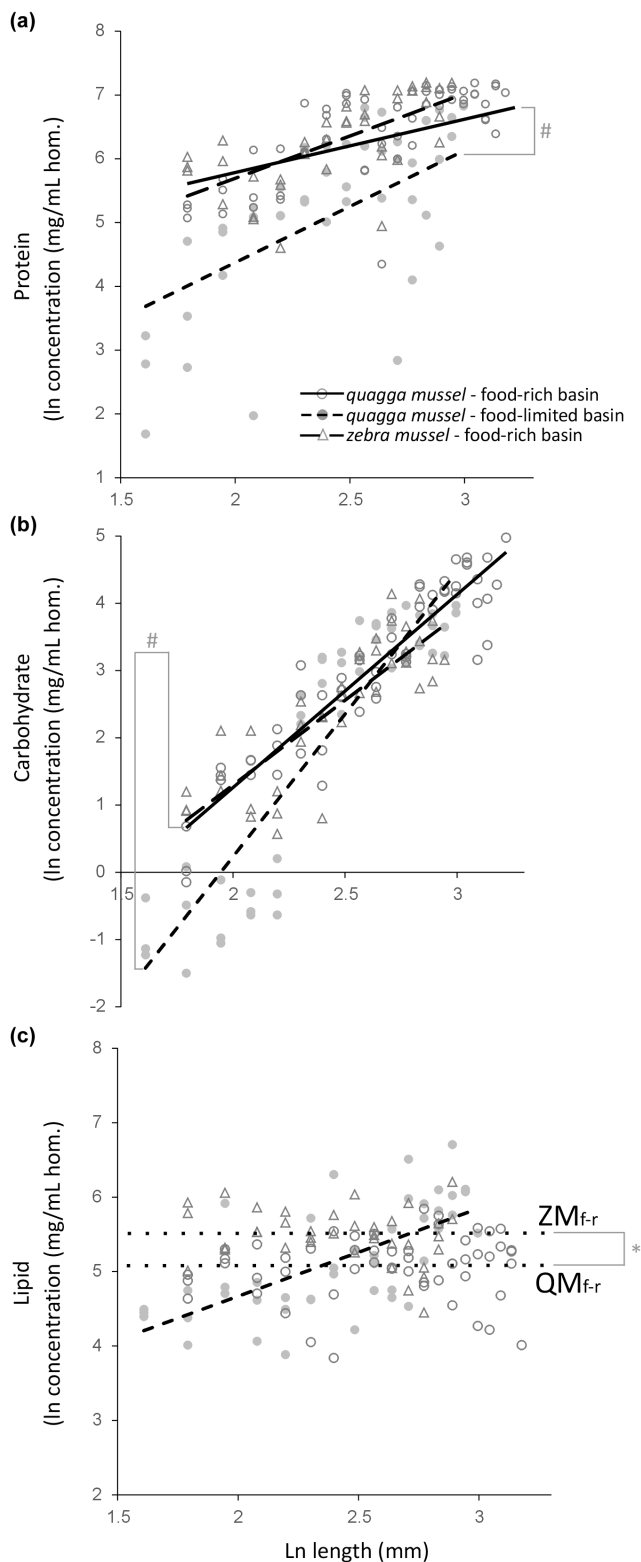
FIGURE 3 Development of size (length) related physical traits of dreissenids living in the western (food-rich) and eastern (food-limited) basins of Lake Balaton (the field survey). Changes in morphological traits (a: height, b: width), soft tissue wet weight (c), and shell hardness (d) measured as crack force per unit length are shown for different dreissenid populations. Data are log transformed. The regression lines are predicted by the general linear models. Hashtag (#) indicates regression lines with slopes significantly differing between mussel populations. Asterisks (*) indicate significant differences in mean trait values between mussel populations when the slopes are parallel. X marks indicate if the allometry of the regression slope differs positively (+X) or negatively (−X) from the isometric value (shown by the grey dotted line). Number of animals: a, b: quagga food-rich = 168, quagga food-limited = 176, zebra = 178; c, d: quagga food-rich = 55, quagga food-limited = 43, zebra food-limited = 39.

food-limited than food-rich basin, whereas no differences in these biomacromolecule contents were observed between both dreissenid species living in the food-rich basin. The lipid content increased with shell length only in quagga mussels from the food-limited basin, whereas it was independent of shell length in dreissenids living in the food-rich basin (Figure 4c; Tables S3 and S4). Moreover, zebra mussels had a higher mean lipid content than quagga mussels in the food-rich basin (Figure 4c; Table S4). As the protein content in the

FIGURE 4 Development of size (length) related body component biomacromolecules of dreissenids living in the western (food-rich) and eastern (food-limited) basins of Lake Balaton. (a) protein, (b) carbohydrate, (c) lipid. Data are log transformed. The regression lines are predicted by the general linear models. Hashtags (#) indicate regression lines with slopes significantly differing between mussel populations. The relationship of lipid content with body length was significant only for quagga mussels from the food-limited basin. However, the difference in mean lipid content between zebra (ZM_{f-r}) and quagga mussels (QM_{f-r}) from the food-rich basin (labelled by dotted lines, respectively) was significant across the entire length range. Number of animals: quagga food-rich $= 55$, quagga food-limited $= 45$, zebra $= 39$.

exceeded the values observed in the food-rich basin in larger con-specifics, at the size of 15 and 11 mm, respectively (Figure 4b,c).

3.3 | Relationships among biomacromolecules and shell hardness in dreissenids from the field survey

When data were corrected for mussel species, basin and shell length, the LM showed that protein level was positively related to carbohydrate content, but not to lipid content (Table S5). No cor-relation was found between carbohydrate and lipid contents. Shell hardness was positively related to carbohydrate and lipid contents, but not to protein content.

3.4 | Superoxide dismutase gene expression in dreissenids from the field survey

Reverse transcription–PCR on total homogenates of dreissenid indi-viduals taken from the field samples showed significant differences among mussel populations ($F_{2,24} = 75.1$, $p < 0.001$, Figure 5). Pairwise comparisons revealed interspecies ($p < 0.001$), but not inter-basin ($p = 0.348$) differences between the samples. The relative gene ex-pression level of SOD was significantly higher in zebra mussels than in quagga mussels, irrespective of the basin.

3.5 | Survival and changes in physical traits and biomacromolecule content in dreissenids from the transplant experiment

Ten weeks after transplantation, irrespective of the basin, almost 80% of quagga mussels and less than 40% of zebra mussels sur-vived, which resulted in a significant difference between the species survival in the GLM (Figure 6a; Table S6). According to a significant basin * species interaction in the LM, quagga mussels grew more in the food-limited than in the food-rich basin (procedural control), whereas the opposite was found for zebra mussels (Figure 6b; Ta-bles S2 and S6). There was no significant difference in growth rate between the two species in the food-rich basin. By contrast, in the food-limited basin, zebra mussels hardly grew at all, whereas quagga
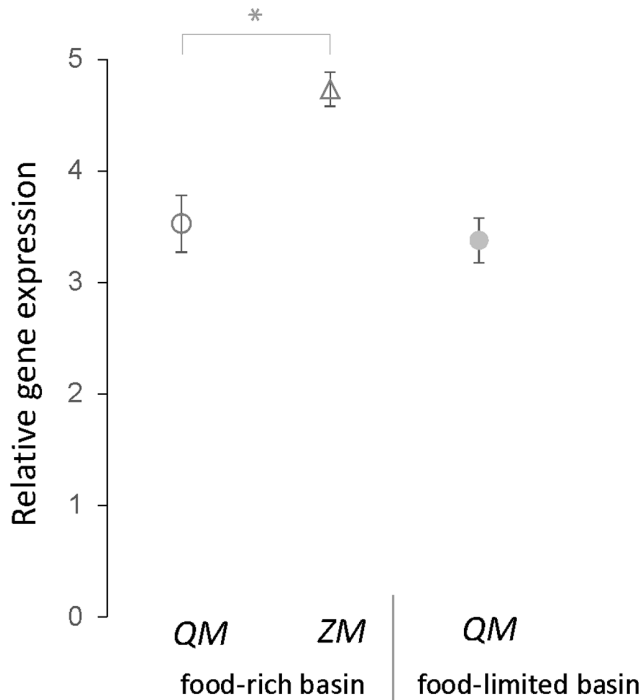
smallest (length <9 mm) quagga mussel individuals from the food-limited basin was very low, despite the fact that in this population the increment in protein content with shell length was larger than in the other populations, their absolute protein level never reached the level measured in animals from the food-rich basin (Figure 4a). By contrast, initially low carbohydrate and lipid values in small quagga mussel individuals from the food-limited basin reached and

FIGURE 5 Superoxide dismutase (SOD) mRNA copy numbers in total soft tissue of dreissenids collected during the field surveys in the western (food-rich) and eastern (food-limited) basins of Lake Balaton, revealed by reverse transcription–polymerase chain reaction. SOD is related to β-actin expression. Data are expressed as back transformed means predicted by the general linear model ± 95% confidence intervals. Asterisk (*) indicates a significant difference between species. QM: quagga mussel, ZM: zebra mussel. Number of animals: quagga food-rich = 5, quagga food-limited = 8, zebra = 14.

mussels became longer by 35% under the same conditions (Figure 6b; Table S7). Similar changes were detected when the increment in width was measured (not shown). Zebra mussel shells were more resistant to crushing than those of quagga mussels in both basins, and in the food-rich basin, mussel shells of both species were stronger than in the food-limited basin 10 weeks after transplantation, as shown by significant main effects of species and basin in the LM, with no interaction between them (Figure 6c; Table S6). The final soft tissue wet weight was greater in mussels in the food-rich than in the food-limited basin, but no weight difference was found between the two dreissenid species in the same basins (Figure 6d; Table S6). Protein and carbohydrate contents in transplanted mussels differed between the basins, but not between species (Figure 7a,b; Table S6). In the food-rich basin, both dreissenids had higher protein and carbohydrate contents than in the food-limited basin. Examining the effect of a basin × species interaction on the lipid content in dreissenids, no interspecies difference was observed in the food-rich basin (Figure 7c; Table S6). However, the lipid content was considerably higher in quagga mussels transplanted to the food-limited basin than in conspecifics transplanted to the food-rich basin (procedural control), and in zebra mussels deployed in the food-limited basin

(Figure 7c; Table S6). Zebra mussels had a higher lipid content in the food-rich than in the food-limited basin.

3.6 | Relationships among traits in transplanted dreissenids

The PCA on the dataset of transplanted mussels established two principal components: PC1 and PC2 explaining 51% and 28% of the total variance, respectively (Figure 8; Table S8). PC1 was strongly related to protein content, carbohydrate content, and final soft tissue wet weight (and final shell length to a lower extent). PC2 was negatively related to lipid content and length, as well as positively correlated with shell hardness. However, the relations of final shell length with lipid content and shell hardness were not significant in the LMs, suggesting that they were only tendencies (Table S6).

4 | DISCUSSION

4.1 | Food conditions for dreissenids in Lake Balaton

The Chl-*a* concentrations measured in the year of the study confirmed the difference in trophic conditions between the two basins; according to the commonly accepted classification (see: Pavluk & Bij de Vaate, 2008), the eastern basin is oligo-mesotrophic and the western basin is meso-eutrophic. The other variables did not differ profoundly between the basins nor showed extremes that could influence the distribution of the two dreissenids in Lake Balaton, according to the comparative biological limitations of dreissenids reviewed by Karatayev and Burlakova (2022).

Summarising the results of earlier studies, the limits of food tolerance of dreissenids were determined as Chl-*a* concentrations of 2.5–25 μg/L (Cross et al., 2011). Walz (1978) found that the algal food concentration required for the maintenance of a 1-year-old zebra mussel, corresponding to the mussels involved in our experiment (shell length of 7–11 mm), is equivalent to 0.1–0.3 mg C/L. It is known that carbon makes *c*. 48% of the algal biomass (Huntley et al., 2015), and the cellular amount of chlorophyll in algae ranges from 0.1% to 9.7% (Boyer et al., 2009). Assuming a middle chlorophyll content from this range (1%), the minimal algal concentration needed to sustain a zebra mussel corresponds to *c*. 2 μg/L Chl-*a*. The seasonal average Chl-*a* concentration in the food-limited basin of Lake Balaton was 2.4 μg/L, which is very close to the lower limit estimated by Cross et al. (2011) calculated from the Walz (1978) data. Noteworthy, during the experimental period, three measures of Chl-*a* concentrations (out of a total of five) were much below the threshold of 2.0 μg/L (1.67, 0.85, 1.55). Thus, the food availability for the zebra mussel living in the eastern basin was definitely low. Baldwin et al.'s (2002) experiments proved that low Chl-*a* concentrations (1–2 μg/L) inhibit the growth of zebra mussels in particular, while that of quagga mussels is either reduced or not affected. In
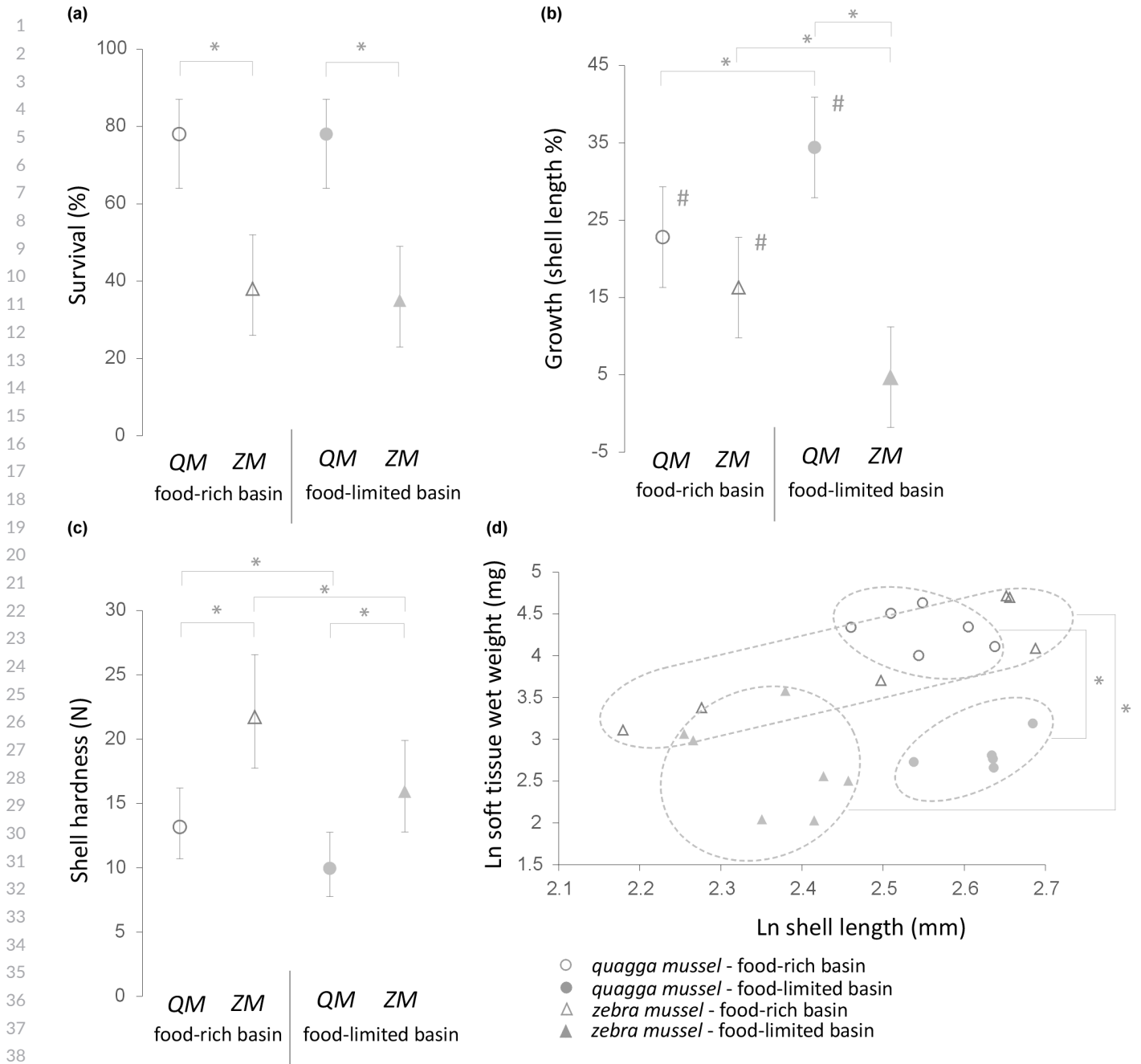
FIGURE 6 Survival and morphological traits of the two dreissenid species from the transplant experiment in the western (food-rich) and eastern (food-limited) basins of Lake Balaton. Animals obtained from the food-rich basin were allowed to attach to the inner surfaces of plastic tubes (each species separately), caged and placed in the food-limited or back to the food-rich basins for 10 weeks. Survival (a) and growth (relative length increment, (b) are expressed as percentage of the initial mussel number and length, respectively. (c) Shell hardness. (d) The relationship between the final length and soft tissue wet weight measured at the end of the experiment in different mussel categories. In (d), data points represent individual mussels and points belonging to the same mussel category are encircled with dashed lines. Data are expressed as back transformed means predicted by the generalised linear (a) or general linear (b–d) models ± 95% confidence intervals. In (b), hashtags (#) indicate mussel categories showing a significant growth (>0%). Asterisks (*) indicate significant differences between the species or basins revealed by the models. QM: quagga mussel, ZM: zebra mussel. Initial number of animals: 10 individuals per tube, five tubes per each species in each basin; number of animals for growth analysis (b): quagga food-rich, food-limited=39, zebra food-rich=19, zebra food-limited=17; number of animals for shell hardness (c) and weight analysis (d): quagga food-rich=6, quagga food-limited=5, zebra food-rich=7, zebra food-limited=6.

addition, food availability for mussels in Lake Balaton, which is rich in calcareous sediments (Tompa et al., 2014) and highly polymictic (Istvánovics et al., 2022), is adversely affected by frequent mixing

and the resulting redistribution of fine-grained inorganic sediments covering mussel beds. Hence, at similar Chl-*a* concentrations, food (algae) becomes diluted and its availability for filter-feeders, such
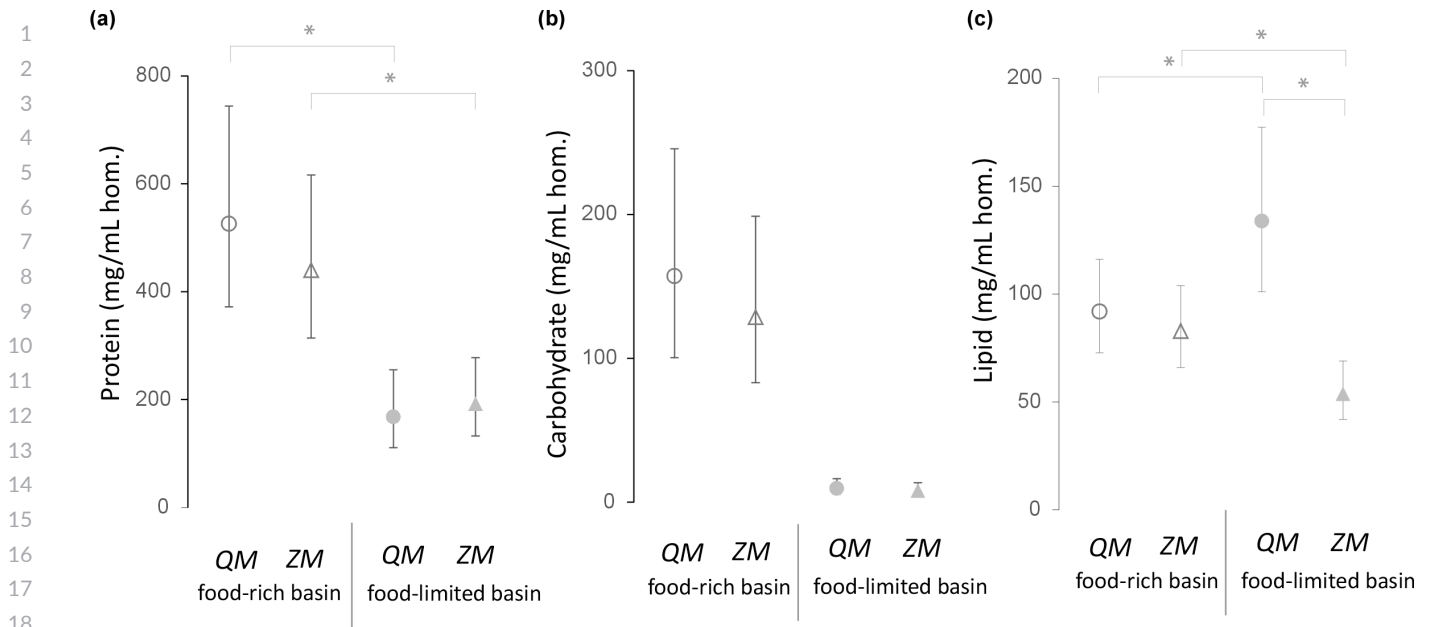
FIGURE 7 Body component biomacromolecules in dreissenids from the transplant experiment in the western (food-rich) and eastern (food-limited) basins of Lake Balaton. Ten weeks after transplantation of dreissenids of food-rich origin to both experimental sites, protein (a), carbohydrate (b) and lipid (c) concentrations were recorded. Data are expressed as back transformed means predicted by the general linear models $\pm$ 95% confidence intervals. Asterisks (*) indicate significant differences between species, or basins revealed by the general linear model. QM: quagga mussel, ZM: zebra mussel. Number of animals: quagga food-rich = 6, quagga food-limited = 5, zebra food-rich = 7, zebra food-limited = 6 (collected randomly from 5 tubes per species and basin).

as dreissenids, is lower compared to the situation in deep lakes (for review, see Karatayev et al., 2011). The zebra mussel is particulary sensitive for the combination of low food concentration and high water turbidity (Madon et al., 1998; Stoeckmann & Garton, 2001).

Besides the quantity, the quality of food, i.e. the composition of algal assemblage, is different between the two basins. According to the Report for the Lake Balaton Development Council for the year 2017 (2017), which can also be considered as relevant for the year 2018 and the following years until today (personal communication from B. Somogyi), the dinophyte, *Ceratium hirundinella* was a dominant species in the food-limited eastern basin between June and October. This species is known to be highly rejected by zebra mussels and was observed to reduce mussel population growth in Polish lakes (Stanczykowska et al., 1975). From May to November, the biomass of the large benthic filamentous diatom, *Aulacoseira granulate*, which, by contrast, can be filtered out effectively by the quagga mussel (Tang et al., 2014), became the highest in the water column of that basin (Report for the Lake Balaton Development Council, 2017). Some studies confirmed that the zebra mussel can also consume this algal species (Horgan & Mills, 1997; Vanderploeg et al., 2013), but only with a low clearance rate (Naddafi et al., 2007). Therefore, it seems that the eastern (food-limited) basin provides less palatable food for zebra mussels than for quagga mussels. Nevertheless, the issue of dreissenid preference for filamentous diatoms is quite complex, as it is dependent on the species of algae (Tang et al., 2014) and influenced by mussel size (Horgan & Mills, 1997) and food availability (Naddafi et al., 2007). The filamentous nitrogen-fixing

cyanobacteria (among them the dominant *Aphanizomenon flos-aquae*), which, besides Cryptophyta, are favoured by both dreissenids (Tang et al., 2014), as well as *Aulocoseria* (found also in high numbers in the food-limited eastern basin) are the main representatives of the phytoplankton and phytobenthos in the food-rich western basin from July to October (Report for the Lake Balaton Development Council, 2017). Therefore, in addition to the evidence of food amount for dreissenids being substantially different in the two basins, the food composition (algal species distribution) may also contribute to this effect.

4.2 | Physical traits and stress in the two dreissenids in the basins with different food availability

4.2.1 | Linear dimensions

The analysis of linear dimensions of dreissenids reveals that mussels become more elongated, wider and heavier as they grow. The height to length relationship seems to be related to nutrient availability, as the shell height–length allometry was positive in quagga mussels living under better food conditions, whereas negative in the food-limited basin. In addition, we found that height increase was also species dependent in growing mussels, similar to other works (Beggel et al., 2015; Kerambrun et al., 2018) wherein, at the same length, quagga mussels were taller than zebra mussels. Interestingly,
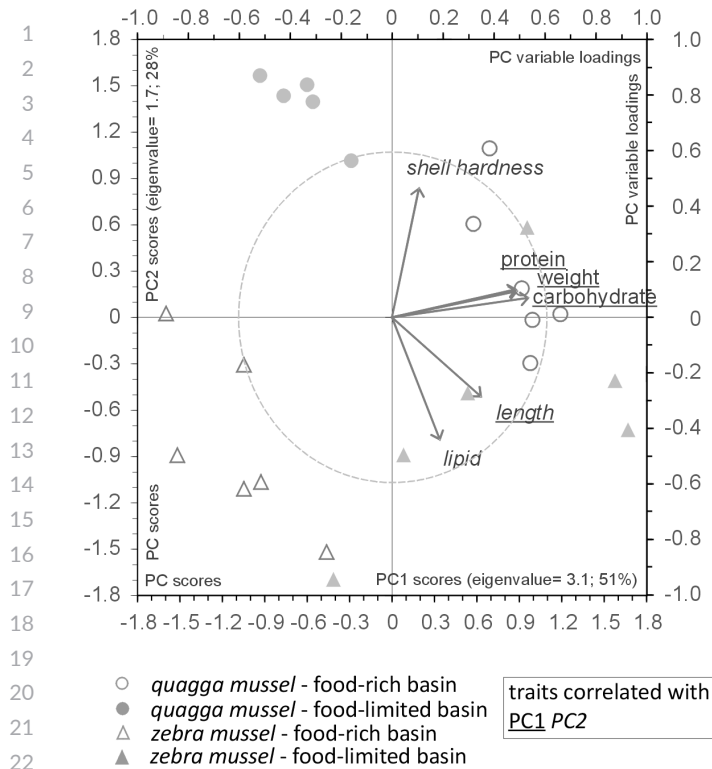
FIGURE 8 Principal component analysis based on the six examined traits of the two dreissenid species from the transplant experiment in the western (food-rich) and eastern (food-limited) basins of Lake Balaton. Two principal components (PC1 and 2) were established. The points show individual principal component scores for each individual. Arrows show correlations of measured mussel traits with particular PCs. Note a strong correlation among weight, protein, and carbohydrate level (the correlation between weight and protein is as strong that their arrow symbols highly overlap).

trends of the length–height relationship are very similar between quagga mussels living in food-limited conditions and zebra mussels in the food-rich basin. This means that quagga mussels can produce the same increment in height per unit length in worse conditions as zebra mussels do in better conditions. Although such a comparison of datasets obtained for different species in different basins should be interpreted with care, it might call attention to those environmental factors that could lead to this situation, including food, but also other traits, such as interspecific competition. Taking all these facts, we suggest that the shell height-length index can be introduced as a condition index of dreissenids, indicating also the environmental food capacity.

Dreissenid growth rates depend on a wide array of environmental variables, including temperature, food, season, depth, water velocity, and turbidity (Karatayev & Burlakova, 2022), of which food is the only factor differentiating the two studied basins of Lake Balaton. This provided us with a good opportunity to examine the pure effect of food conditions on mussel growth in the transplant experiment.

When dreissenids were kept for 10 weeks in transplant tubes in the food-rich basin, there were no significant interspecies

differences in their linear growth (shell length increase: 0.23 ± 0.05 and 0.16 ± 0.06 mm/week in the quagga and zebra mussels, respectively). During the initial stage of the quagga mussel invasion to Lake Balaton (10 years before the present study), a shell length growth of 0.25 mm/week was exhibited by new settlers in the eastern (food-limited) basin (Balogh et al., 2018), which is similar to our current results, despite some differences in environmental conditions (lower Chl-*a* concentration and older mussels tested in the present study). In Lake Erie, the quagga mussel growth was calculated as 0.23 mm/week (at a depth of 13–19 m, at 15–18°C) based on the data from Karatayev et al. (2018). In Dutch lakes, the zebra mussel growth was estimated as 0.32 mm/week (0.59 mm/week when juveniles were taken into account) by Dorgelo and Smeenk (1988) and Dorgelo (1993). A similar growth rate of 0.25 mm/week was also shown by zebra mussels in the laboratory experiment by Nichols (1992) in optimal food conditions. From this review, we can conclude that dreissenids in the food-rich part of Lake Balaton grow at similar rates as in other well-nourished shallow lakes. Dreissenid growth is directly proportional to the mussel feeding activity, and inversely related to their age (size) and spawning activity (Dorgelo, 1993; Stoeckmann, 2003).

Our results showed that low food conditions in the food-limited, eastern basin of Lake Balaton were still suitable for quagga mussels. The quagga mussels transplanted to the food-limited basin still increased their shell length, whereas the zebra mussels stopped growing under such conditions. Also in Lake Erie, where the situation is similar to that observed in Lake Balaton (both dreissenids co-occur in the food-rich shallow western basin, while only the quagga mussel occurs in the deep, food-limited eastern basin), the quagga mussels transplanted from the food-rich basin to the food-limited basin still increased in length, whereas the zebra mussels were unable to sustain their growth (MacIsaac, 1994). Moreover, the quagga mussel grew faster than the zebra mussel in food-limited southwestern Lake Ontario (Mills et al., 1999), as well as under low food conditions in the laboratory experiment by Baldwin et al. (2002). These results support our findings on interspecies differences in growth dynamics, suggesting that the poorer the food conditions, the greater competitive advantage of the quagga over zebra mussel.

Surprisingly, the quagga mussels transplanted to low food conditions grew even faster (0.34 ± 0.07 mm/week) than conspecifics left in the food-rich basin (procedural control). We assume that, at least shortly after transplantation, the nutrient stress can promote liberation of the stored energy to fuel a brief period of accelerated growth of quagga mussels. As a mechanism, we propose the mobilisation of some growth factors induced by food deprivation after transplantation to the food-limited basin, which might activate longitudinal shell growth. This could be the part of a strategy to reach the sexual maturation quickly, which can be adaptive for the quagga mussel under competition for limited food resources and settling sites. A similar mechanism can account for the faster growth of the quagga mussel than zebra mussel under competition pressure (Metz et al., 2018).

4.2.2 | Soft tissue wet weight

In contrast to the above-described shell length–height relationship, we did not find corresponding differences in soft tissue wet weight between the basins and species, similar to what was found by Kerambrun et al. (2018) for shell volume increment. By contrast, a positive allometry of the quagga mussel weight increment per unit length and isometry observed for this relationship in the zebra mussel implies a more progressive development of the quagga mussel weight. Noteworthy, after the quagga mussel invasion, the weight increment per unit length was reduced in co-existing zebra mussels in most of the lakes studied by Balogh et al. (2019), which suggests the impact of the interspecies competition on the deterioration of the zebra mussel condition, at least in certain situations.

In the transplant experiment, food availability strongly influenced the soft tissue wet weight of both dreissenids; however, an interspecies difference in this trait occurred in neither of the basins. The final soft tissue wet weight of the transplanted mussels showed a similar trend as those obtained for proteins and carbohydrates, which suggests that differences in food conditions between the two basins profoundly influence the condition of both dreissenids. It is also possible that in lower food conditions, the quagga mussel could grow effectively (as indicated by lipid accumulation in the food-limited basin), but allocated energy to shell length increase rather than to soft tissue weight gain. The result of a reciprocal transplant experiment, implying that shell growth not always reflects changes in soft tissue weight due to flexible energy allocation (Casper et al., 2014), supports this hypothesis. This phenomenon could be the part of the quagga mussel adaptation strategy to low food conditions (reviewed by Karatayev & Burlakova, 2022).

4.2.3 | Shell hardness

In accordance with earlier studies (Balogh et al., 2019; Grutters et al., 2012; Naddafi & Rudstam, 2013; Nalepa et al., 2010), shell hardness showed the most unequivocal difference between the two species in both field and experimental studies suggesting that this trait is an intrinsic, genetically conserved property of dreissenids. However, within each species, shell hardness was dependent on food availability across all dreissenid sizes, as shown by the lower values of this trait in both species transplanted from the food-rich to food-limited conditions. Supporting our observations on the relationship between food availability (basin trophic status) and shell growth rate, Jantz and Neumann (1998) found that the availability of phytoplankton, which is the primary source of food for dreissenids, strongly determines shell growth. Shell thickening is a dynamic process; hence, the difference in shell hardness observed between mussels transplanted to the same (procedural control) and worse food conditions in our experiment implies that calcium remobilisation from the shell matrix to the soft tissue can happen within quite a short time and depends on food-driven metabolic changes. Supporting this hypothesis, the reabsorption of the shell was found after

transplantation of zebra mussels to poor diet conditions (Stoeckmann & Garton, 2001).

4.2.4 | Stress marker (SOD level)

The expressional level of SOD indicates cellular oxidative stress induced by different stressors, including nutrient deprivation (Redza-Dutordoir & Averill-Bates, 2021). Since the most important morphometric and condition indices did not show differences between the two dreissenids within the length range investigated in the food-rich basin where they naturally coexist, we consider that the elevated SOD level indicates stress caused by competition rather than food availability, which otherwise is not an issue in the food-rich basin. Although we do not know any direct evidence for the connection of competition, stress, and stress-mediated physiological changes in invertebrates, the discovered mechanism shows remarkable similarities with that of vertebrates (Creel et al., 2013; Stefano et al., 2002). Hence, we suppose that competition might evoke the higher stress level in the weaker competitor, which would explain why in our study SOD level was higher in zebra than in quagga mussels. This suggestion is consistent with the former finding showing that the zebra mussel is less tolerant to the presence of congeners in a mixed-species assemblage, being more often fouled and avoiding attachment to congener shells (Jermacz et al., 2021). The increased level of stress in zebra mussels coexisting with quagga mussels in the food-rich basin is also suggested by their weaker survival in the experiment, irrespective of the basin of deployment. In the present study, other environmental factors, such as temperature, oxygen saturation, or contaminants probably evoke less stress response in dreissenids than described in other studies (Potet et al., 2016; Novicki & Kashian, 2018), as the basins of Lake Balaton are free from extreme physico-chemical conditions (Balogh, Kobak, et al., 2022).

4.3 | Biomacromolecule content of the two dreissenids in the basins with different food availability

Results of the field survey show that the consequence of malnutrition on biomacromolecule content mostly affects young animals. In other words, the larger the quagga mussel, the lower difference between conspecifics living in worse and better food conditions. Carbohydrate level became equal in the food-limited and food-rich basin for quagga mussels of shell longer than 15 mm. Moreover, lipid content in the food-limited basin exceeded that in the food-rich basin for quagga mussels longer than 11 mm. This suggests that quagga mussels that reached adulthood under food-limited conditions had sufficient energy to maintain growth, even though their protein level did not reach that of mussels living in better food environment. This is supported by the similarity between large quagga mussels from both basins in weight and storage material content. It was found earlier that dreissenids increased their reproductive effort with

age (Bayne et al., 1983; Sprung, 1995), hence we speculate that to increase reproductive capacity adult quagga mussels accumulate storage materials even in limited food conditions probably by intensifying filtering activity (Sprung & Rose, 1998; Baldwin et al., 2002). The fact that large individuals show lower differences between the basins can be supported, on the one hand, by earlier observations showing that large animals can consume long filamentous algae (summarised in: Tang et al., 2014), which dominate in both basins in summer, with high efficiency. On the other hand, it is also conceivable that dense, intensively filtering mussel beds, as well as the large amount of re-suspended sediments typical for shallow lakes, influence the nutrient access to small mussels to a greater extent than to large mussels. This could lead to the poor condition of young animals and their retarded growth when food is limited, as summarised in a recent review (Karatayev & Burlakova, 2022).

Transplantation of quagga mussels to low food conditions resulted in lower carbohydrate storage, protein content, and soft tissue wet weight compared to conspecifics kept in the food-rich basin (procedural control). However, quagga mussels in low food conditions were still able to sustain their linear growth, making up the storage materials with accumulation of lipids. In contrast, this was not possible in the case of zebra mussels, in which the lipid storage in the food-limited basin was also depleted. These findings are similar to what was found in nutritional research on mammals, showing that a low protein diet provokes lipid accumulation associated with weight loss (Aparecida De França et al., 2009; Du et al., 2000; Pezeshki et al., 2016; White et al., 2000). Hence, it seems that metabolic consequences of malnutrition are general in the animal kingdom. Storage materials have an annual cycle in dreissenids, transforming glycogen to lipid during gametogenesis and depleting lipid stores at spawning (Gabbott, 1983; Kwan et al., 2003; Louis et al., 2019). Both the field survey and transplant experiment were conducted in summer, when mature animals produce and discharge large amount of gametes. Probably, besides the dismantling of other body parts, including the shell, which was found weaker under low food abundance in the field survey and transplant experiment, the lipid rich gonads of quagga mussels might be preserved and hence larval production could be more effective during the spawning period, opposite to zebra mussels. Environmental stress increases reproductive effort in mussels (Bayne et al., 1983), according to the optimisation theory (Sebens, 1982), by diverting energy from growth to reproduction to the extent that the net energy (difference of feeding and basal metabolism) allows (Stoeckmann & Garton, 2001). This could also be the case in the present experiment, where, although the length of quagga mussels increased, the other traits, which strongly determined growth, such as weight, protein, and carbohydrate amount, were significantly reduced. Lipid content is the only body constituent showing a difference between the two dreissenids under low food conditions. Consequently, we assume that the quagga mussel can tolerate the nutrient stress in the food-limited basin by the ability to accumulate lipids, which can support gamete production, and thus the long-term population maintenance in the food-limited basin, as it was found in a recent long term

monitoring study (Balogh et al., 2018). The assumption that the success of the quagga mussel over zebra mussel is due to enhanced energy allocation into reproduction even in extreme conditions fits in the idea that the earlier invader, the zebra mussel, changed from the *r* strategy to the *k* strategy while establishing their existence in the ecosystem (Louis et al., 2019). Regardless of this idea, the quagga mussel proved definitely much more flexible than the zebra mussel to adapt to worse food conditions, as is confirmed by other authors (Baldwin et al., 2002; Karatayev et al., 2011; Sprung & Borcherding, 1991). Interestingly, in the field survey, the zebra mussel had a constantly higher lipid level than the quagga mussel in the food-rich basin. By analogy to quagga mussel responses to limited food conditions in the eastern basin, such a raised lipid content suggests that zebra mussels in the food-rich western basin may also suffer from hunger (or some level of stress, as survival rate and SOD level also indicate) and that is why they accumulate lipids. In this case, the environmental conditions for the zebra mussel in the food-rich basin can be similar to that established for the quagga mussel in the food-limited basin.

Taking the protein concentrations measured in dreissenids from the field survey and transplant experiment together, it can be stated that food availability significantly influences the protein content in dreissenids regardless of the species and size. Ten weeks after transplantation, the protein and carbohydrate contents in dreissenids became comparable to those measured in conspecifics of similar size taken from the relevant basin in the field study (i.e. outside the experimental tubes), showing that the animals had adapted to the local food conditions within this short time. In the food-limited basin, the lipid content of the quagga mussel increased with shell length along the field survey, while parallel to the growth in length, lipid content also increased in the transplanted mussels. Hence, biomacromolecule measurements show clearly that the transplant experiment was able to reproduce the situation experienced by mussels living naturally in both basins. The greater adaptation ability of the quagga mussel to limited food conditions (Baldwin et al., 2002; Karatayev et al., 2011; Sprung & Borcherding, 1991) was also proved by the transplant experiment, suggesting a mechanism underlying the rapid disappearance of the zebra mussel from the food-limited environment of Lake Balaton following the appearance of the quagga mussel (Balogh et al., 2018).

4.4 | Relationships among dreissenid traits

Both the LM performed on the field survey data and the PCA run for the field transplant experimental data showed that the soft tissue protein and carbohydrate levels in dreissenids strongly correlated with one another, implying that carbohydrates can be the primary energy source for protein synthesis by dreissenids, and hence determine soft tissue weight. If we add this to the fact that carbohydrate pool was found to depend on food availability, then carbohydrate body concentration can be a good proxy for estimating the fitness of dreissenids. By contrast, the concentration of lipids, the other

storage material, relates neither to protein nor to carbohydrate levels, suggesting that its accumulation is rather connected to some functions unrelated to growth, such as gamete production. Besides, the quagga mussel turned out to be able to substitute lipids for the missing carbohydrates in relatively short-term (10 weeks of the experimental study) low food conditions. Increased lipid storage can provide the energy source to maintain longitudinal growth under food-limited conditions to reach the maturation size.

5 | CONCLUSION

Invasion progress of the quagga mussel and interspecies competition between the two dreissenid species happen differently in lake basins with different food availabilities. The ability to increase lipid storage under limiting food conditions seems to be a key metabolic property of the quagga mussel, which helps this species thrive and provides it with a definitive advantage in the competition against the zebra mussel in poorly nourished areas. The zebra mussel puts relatively more effort to energetically costly self-defence than the quagga mussel, which is manifested in enhanced shell hardness and SOD activity. However, such a strategy might not be optimal in such waterbodies like the eastern basin of Lake Balaton, where food resources are limited, whereas predator pressure (Balogh, Serfőző, & Kobak, 2022) and contaminant stress (Balogh, Kobak, et al., 2022) are low. The progression of the primary energy source (carbohydrates) content seen in quagga mussels developing in food-limited conditions suggests that although young individuals show a significant drawback against those living in suitable conditions, they make up for the disadvantages in adulthood. As an ecological consequence, it is proposed that better tolerance to food limitation could have led to the rapid replacement of the former invader, the zebra mussel, by the quagga mussel, taking place within a few generations (Balogh et al., 2018). By contrast, when food availability is not an issue, the traits are very similar between dreissenids, enabling their co-existence. In this case, the outcome of the competition is far less predictable. In addition, measurements revealed that height increment per unit length (as an external trait) and carbohydrate content per unit length (as an internal trait) indices can be introduced as potential proxies for the assessment of food driven condition in dreissenids.

For the future perspective, it would be beneficial to know what happens if quagga mussels are transplanted in an opposite direction: from the food-limited to the food-rich basin. To explain the contribution and role of lipid accumulation under food-limited conditions, a time resolved analysis of changing macromolecule content, particularly focusing on lipids, will be mandatory both in field transplant and laboratory experiments with frequent sampling and extended examination period. It is also important to uncover the metabolic background of accelerated lipid accumulation, and to follow the gonad status in food-limited conditions.

The zebra mussel profoundly restructures inhabited freshwater littoral ecosystems by, among others, intensive filtering the suspended material out of the water column, which in turn makes them vulnerable because of their low tolerance to food limitation (Strayer et al., 2019). By contrast, this enables the quagga mussel, which seems evolutionary capable of better using decreasing food sources, to be a successful competitor against the zebra mussel. Therefore, revealing structural and physiological mechanisms of the quagga mussels allowing it to endure harsh food conditions will contribute to our understanding why it is more successful in the competition with its congener in serial invasions of dreissenids.

CONFLICT OF INTEREST STATEMENT
The authors have no financial or proprietary interests in any material discussed in this article.

DATA AVAILABILITY STATEMENT
Data are available from the authors upon reasonable request.

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