Biometry, shell resistance and attachment of zebra and quagga mussels at the beginning of their co-existence in large European lakes

Csilla Balogh[a,b], Zoltán Serfőző[a,b], Abraham bij de Vaate[c], Ruurd Noordhuis[d], Jarosław Kobak[e]*

[a]Centre for Ecological Research, Balaton Limnological Institute, Hungarian Academy of Sciences, Tihany, Klebelsberg Kuno u. 3., Hungary

[b]MTA Centre for Ecological Research, GINOP Sustainable Ecosystems Group, 8237 Tihany, Klebelsberg Kuno u. 3., Hungary

[c]Waterfauna Hydrobiological Consultancy, Oostrandpark 30, NL- 8212 AP Lelystad, The Netherlands

[d]Deltares, P.O. Box 177, 2600 MH Delft, The Netherlands

[e]Nicolaus Copernicus University, Faculty of Biology and Environmental Protection, Department of Invertebrate Zoology, 87-100 Toruń, Lwowska 1, Poland, e-mail: jkob73@umk.pl, phone: +48 56 611 2647, fax: +48 56 611 4772

*Corresponding author

C.B and Z.S. equally contributed to this work

Abstract

In invasive dreissenid communities, the zebra mussel usually appears earlier and then is displaced by the quagga mussel. We analysed length-weight allometric relationships, attachment strength (2 days, 1 week and 1 month of exposure), shell crushing resistance and glycogen content across the entire size range of both species in large shallow European lakes where this displacement has recently occurred. In Lake Balaton (Hungary) and Ijsselmeer (The Netherlands), the soft tissue dry weight increment of zebra mussels per unit length decreased after the quagga mussel invasion and became lower than that of quagga mussels. In Lake Markermeer (The Netherlands), having relatively worse environmental conditions, dry weight increment per unit length was always higher in quagga mussels than in zebra mussels, but no negative change in dry weight increment occurred in zebra mussels during the quagga mussel invasion. Small zebra mussels had more resistant shells and stronger attachment than quagga mussels. These differences were reduced (shell hardness) or reversed (long-term attachment) in larger individuals. Zebra mussels had lower glycogen content than quagga mussels across the entire size range. Thus, the quagga mussel advantage over zebra mussel likely consists in the faster dry weight increment per unit length and higher storage product contents of the former, due to its lower investments in attachment strength and shell crushing resistance.

Keywords: Dreissena polymorpha, Dreissena rostriformis bugensis, allometric relationships, attachment strength, shell resistance, glycogen

Introduction

Sessile Ponto-Caspian dreissenids, the zebra (*Dreissena polymorpha* (Pallas, 1771)) and quagga (*Dreissena rostriformis bugensis* Andrusov, 1897) mussels share similar habitats and food requirements (Quinn et al. 2013). They are invasive in Europe and North America, causing habitat changes and economic losses (Pimentel et al., 2005; Oreska and Aldridge, 2010; Ricciardi and MacIsaac, 2011). While in North America both species appeared within a few years, in Europe (apart from their native area) only the zebra mussel has occurred since the 19th century (Bidwell, 2010) until the recent spread of the quagga mussel in the second half of the 20th century (Van der Velde et al., 2010). Despite the faster spread of the zebra mussel, its populations are usually reduced or displaced within a few years after the appearance of the quagga mussel (Ricciardi and Whoriskey, 2004; Karatayev et al., 2011). This phenomenon also occurs in great lakes of Europe (Orlova et al., 2004; Heiler et al., 2012; Matthews et al., 2014; Balogh et al., 2018) and North America (Patterson et al., 2005), that are commonly being invaded and affected by both species. Nevertheless, a few notable exceptions of the co-existence of the two dreissenids exist (Zhulidov et al., 2010; Strayer and Malcom, 2013).

The competitive superiority of the quagga over zebra mussel is an intriguing issue. Morphological (shell thickness), behavioural (attachment, anti-predator responses) and physiological (growth, depending on filtration, respiration and/or thermal tolerance) differences between them have been postulated as feasible explanations (Orlova et al., 2005; Peyer et al., 2009; Naddafi and Rudstam, 2013a, b, D’Hont et al., 2018).

Shell and byssus strengths are influenced by the energy budget of mussels (Babarro et al., 2008). They affect resistance to hydrodynamic forces and anti-predator defense (Bell and Gosline, 1997; Czarnołęski et al., 2006). The zebra mussel was found to allocate relatively more energy to shell development compared to the quagga mussel (Roe and MacIsaac, 1997;

Casper and Johnson, 2010). However, these studies compared shallow water zebra mussel populations with deep water quagga mussels, thus including a confounding factor (Roe and MacIsaac, 1997), or focused mainly on large individuals (mean length: 22 mm) (Casper and Johnson, 2010), while the impact of species on length vs. shell strength relationship was not investigated. Zebra mussels also had higher short time (<48 h) attachment strength than quagga mussels (Peyer et al., 2009), whereas no differences between them were found in 2-3-month attachment (Peyer et al., 2009). Furthermore, Grutters et al. (2012) found limited differences in the number of byssal threads produced by the two species. However, these studies only included small individuals (<12 mm) and no changes in attachment with individual size/age have been compared between both species so far. Nevertheless, it seems that zebra mussels allocate more energy to increase shell strength and attachment under predation stress, which, by contrast, may allow the quagga mussel to exhibit relatively faster soft tissue growth, resulting in its competitive advantage in areas of low predation pressure (Naddafi and Rudstam, 2013a, b).

The faster growth rate of the quagga mussel (Jarvis et al., 2000; Diggins, 2001; Stoeckmann, 2003; D’Hont et al., 2018; Metz et al., 2018) was attributed to lower energetic expenditure on maintenance (respiration) and higher filtration rate (Baldwin et al., 2002; Stoeckmann, 2003), which however was not confirmed by Kemp and Aldridge (2018).

Carbohydrates, particularly glycogen, are prominent energy sources of dreissenids used to maintain physiological state under low food conditions (Palais et al., 2011), hence it is proposed as a condition marker (Bódis et al., 2014), reflecting another potential cause of the quagga mussel dominance in mixed communities. Glycogen level varies seasonally, diminishing from late autumn to spring and reaching its maximum in late summer-early autumn following the temperature and nutrient increase (Sprung, 1995; Palais et al., 2011). To our knowledge, glycogen storage has not yet been compared between the two dreissenids.

Although many studies concern the topic, the advantage of the quagga over zebra mussel is not clearly known or understood. It is still not known whether any differences between the two dreissenids, which would explain the success of the quagga mussel, are intrinsic species properties, or appear in the response to the competitive pressure from the other species. Therefore, we raise the issue to compare the length-weight allometric relationships, shell crush resistance, attachment strength and energy storage of the two dreissenids along the body length increase over a fine resolution scale. This novel approach led us to deeper insight into the dynamics of development of both species, which can contribute to explaining the ongoing displacement of the zebra by quagga mussel.

We studied all three large lakes in central and western Europe, which have been invaded by the quagga mussel and still had viable zebra mussel populations during the study course: Lakes Markermeer and IJsselmeer in The Netherlands, as well as Lake Balaton in Hungary (Bij de Vaate et al., 2013; Balogh et al., 2018). Traits of co-existing mussel populations were compared with corresponding historical data obtained before the quagga mussel invasion. We applied a unified sampling strategy and biomass calculation in all the lakes because the lack of this is still the obstacle to making a comprehensive picture of the properties of dreissenid invasion (Strayer et al., 2019).

Our hypothesis was that the zebra mussel would exhibit lower increment of soft tissue weight per unit length compared to the quagga mussel, irrespective of the competitor presence (suggesting the general superiority of the latter species), or, alternatively, this parameter would decrease in the presence of the new competitor (suggesting a negative impact of the newcomer). Moreover, we hypothesized that the zebra mussel would attach more strongly to the substratum, develop a shell more resistant to crushing and contain lower amount of glycogen, which could explain its slower increment of the soft tissue weight. Finally, we expected that these differences between species could be size (i.e. age) and time dependent.

Material and Methods

Sampling sites and the history of dreissenid introductions

Lake IJsselmeer and Lake Markermeer (The Netherlands) are parts of a former estuarine bay, called Zuiderzee, dammed in 1932 and turned into a freshwater lake called Lake IJsselmeer (Fig. 1). Wide parts of this lake were turned into land and the remaining part was separated into two large water bodies, northern Lake IJsselmeer and southern Lake Markermeer, by another dam in 1975 (De Jong and Bij de Vaate, 1989).

During the study period (2008-12), water quality surveys in both lakes took place with a four week interval as part of a national monitoring program conduted by the Dutch Ministry of Infrastructure and the Environment (Table S1). Transparency was measured as Secchi disk depth and water samples were taken with a pump at 1 m below the surface to analyse concentrations of total suspended matter, chlorophyll-a (by spectrophotometry) and total phosphorus (by Continuous Flow Analysis) according to Noordhuis (2007).

Lake IJsselmeer has mainly sandy sediments, and the concentration of suspended solids varies considerably between the southern and central part (Table S1). The lake was eutrophicated until the 1980s, but phosphorus concentration dropped substantially in the second half of the 1980s (Noordhuis, 2007). Lake Markermeer has clay sediments that erode into silt-sized particles, resulting in higher concentrations of suspended matter when compared to Lake IJsselmeer (Table S1). Suspended silt interacts with phytoplankton, resulting in relatively poor food conditions for dreissenids (Penning et al., 2013; De Lucas Pardo et al., 2015). Nevertheless, average concentration of seston in the lake also depends on the location (Table S1) and season (Fig. S1) and has been relatively low during our study. The biggest difference in the concentration of suspended solids between both lakes was observed in spring, while it disappeared in late summer and early autumn (Fig. S1). Since 1990, trophic level in both lakes has been similar and slowly decreased. In 2011-12, they approached mesotrophic conditions (R. Noordhuis, unpublished data).

Zebra mussel colonisation of Lake IJsselmeer started soon after it was separated from the sea (Van Benthem Jutting, 1954). In 2006, the quagga mussel was first observed in the Netherlands (Molloy et al. 2007), and soon thereafter it appeared in Lakes IJsselmeer (2007) and Markermeer (2008) (Bij de Vaate and Jansen, 2009; Matthews et al., 2014).

Lake Balaton (Fig. 1) has soft bottom sediments (Lóczy, 1894; Miller and Wagner, 1978). Its shoreline has large expanses of reeds, is reinforced with rip-rap and includes numerous piers and harbours, providing suitable substrata for dreissenid colonization. Environmental data (Table S1) for Lake Balaton (Hungary) were monitored according to Somogyi et al. (2017). Seston in Lake Balaton consists mainly from resuspended fine mineral particles (0.2–10 μm) and biogenic lime. The organic content in the suspended matter is very low (<4%) (Entz and Sebestyén, 1942; Entz, 1981; Máté, 1987). A trophic gradient exists from the eutrophic western part to the oligo-mesotrophic eastern basin (Istvánovics et al., 2007; Tátrai et al., 2008). Temperature in Lake Balaton, particularly in summer, was clearly higher than in the Dutch lakes (Table S1).

In 1932, the zebra mussel was introduced into Lake Balaton from the Danube River, possibly via ship transport (Sebestyén, 1938). Ca. 75 years later, the quagga mussel was detected in the lake (Majoros, 2009; Balogh and G.-Tóth, 2009). It was most probably imported through the same route as the zebra mussel, as it was earlier observed in the Hungarian part of the Danube River (Szekeres et al., 2008).

Sampling and preliminary processing of mussels

We colected mussels from the sandy or clay lake bottom with a trawl net (depth ≈3 m) or cut from the rip-rap (depth ≈0.5 m) at 6 sites in Lake IJsselmeer and 4 sites in Lake Markermeer

(Fig. 1). There were no differences in species distribution or biometric traits (volume x length relationship) between these substratum types (A. bij de Vaate, personal information), so all mussels were pooled for further analyses. Sampling took place between 2008-12, from January/March until October/December each year, except in 2012 when sampling took place from January until June. In Lake Balaton, we collected mussels from the western part of the lake, where both species still co-exist. We sampled mussels from the rip-rap (depth: 1.2-1.5 m) in July 2005 (before the quagga mussel appearance) and, together with quagga mussels, in August 2015 (Fig. 1). After sampling, we transported mussels to the laboratory, cleaned them of epibionts, contaminants and mud, and identified to the species level.

In selected years, we have determined the biovolume of mussels (the volume of fouling bivalves per unit area) to indicate the load of the fouling community (Smit and Dudok van Heel, 1992). Briefly, biovolume was calculated from the measured density (ind. per unit area) and population size structure using an empirical body volume vs. length relationship equation. To determine this relationship, body volume was measured as an equivalent of the water volume displaced by an animal. The mussel biovolume combines mussel size and density, showing the level of their crowding on the substratum per unit bottom area. We also calculated the percentage shares of both dreissenid species in the community.

Soft tissue dry weight measurement

We measured mussel lengths and soft tissue weights to determine the rate of their soft tissue growth per unit length depending on species, location and time. We assumed that in within-species comparisons (zebra mussels before and after the competitor invasion or each species between the years), higher soft tissue weight increments would indicate a better condition (the ability to develop higher biomass), whereas in between-species comparisons (between two co-existing dreissenids) may also point to a different allocation of available resources.

We measured mussel length to the nearest 1 mm with a calliper (Lake Balaton) or ruler (Dutch lakes). Soft tissue was removed from 10-40 animals per size class (size classes every 1 mm for a range of 7-26 mm) after boiling them for 1-2 min in a microwave at 800 W (A. bij de Vaate, personal information). Then the soft tissue was dried for 24 h at 80 ºC and weighed yielding the average soft tissue dry weight (DW). The average soft tissue ash free dry weight (AFDW) was obtained after incineration during 4 h at 450 ºC. These average values per each size class were used as data points in further analyses following the protocol by Bij de Vaate (1991).

Attachment and shell strength measurement

Mussel attachment and shell strength allow for the assessment of resistance to environmental dangers (predators, hydrodynamics) (Czarnołęski et al., 2006; Naddafi and Rudstam, 2013a).

We collected mussels from the rip-rap of Lake Balaton in August 2015. After a 2-week acclimation period under laboratory conditions, we placed animals onto circular polypropylene (pp) plates (diameter 85 mm, thickness 5 mm) with a raised edge (6 mm), 15 mixed sized individuals per plate. The plates were covered with plastic 1-mm mesh to prevent animal loss and placed (each species separately) in aerated 200-L tanks (4 plates per tank, 6 tanks per each species and each of the 3 exposure times – see below). Each tank was independently connected to Lake Balaton with a flow-through system (flow rate: 62 L/h), so the water quality experienced by the exposed mussels were the same as outdoors. We randomized the positions of the experimental tanks with both species within the laboratory room to reduce the effect of unknown external stimuli. The conditions during the acclimation and experiment (equal in all experimental tanks) were as follows: temperature: 20-24°C; suspended material: 1.5-3 mg/L; chlorophyll-a: 1.5-3 μg/L. The tanks were uniformly illuminated with natural light coming through the window of the laboratory room, at natural photoperiod (14L:10D). After two days, when the animals had attached to the plastic surface, the mesh was removed. We measured the attachment strength of mussels after two days (i.e. immediately after removing the mesh), one week and one month of exposure (different 6 tanks on each term). Only individuals found attached to the substratum were analysed.

We measured byssal attachment and shell strength of mussels with a digital force gauge FH 50 (Sauter GmbH, Balingen, Germany). The device was connected with forceps to the mussel and pulled gently perpendicularly to the plate until it was detached from the substratum. This approach simulates an attack of a predator attempting to detach its prey from the substratum. Then, we measured the length of the detached mussel, opened its shell and broke both valves with the force gauge to record the force needed to crush them. The shell strength of each individual was expressed as the mean of both valves.

Glycogen content measurement

Mussels were collected from the rip-rap of Lake Balaton in August 2018. We selected 3 individuals of each species per each 1-mm size class (across the range of 6-23 mm). They were fast dried on filter paper, frozen and kept in plastic boxes at -80 °C until use. Their soft tissues were pulled out from the melted samples and hand-homogenized them in microtest tubes with plastic pestles.

We measured glycogen (total carbohydrate) content according to Van Handel (1965), adapted to mussels by De Zwaan and Zande (1972). We added a mixture containing 1 mL 96% ethanol, 200 µL distilled water and 20 µL saturated Na_2SO_4 to 40 µL of each sample and heated it at 95 °C for 4 min in a block thermostat. Then the sample was cooled down in a fridge at 4 °C and centrifuged at 2000 g for 20 min. The pellet was dried at 95 °C and filled up to 50 µL with distilled water. To prepare the calibration line, we diluted 20 mg/mL glucose (used as a standard) stock in a 5-14-fold range having 10 different concentrations of the solution. Within this range, the reaction was linear with the glucose concentration. We incubated the standards and samples with 1 mL of anthrone reagent (0.15% anthrone [Alfa Caesar, Kalsruhe, Germany] solution in 76% sulfuric acid) at 90°C for 20 min. The samples were kept on ice for 15 min to stabilize the colour of the reaction and measured within 10 min at 620 nm in a Hitachi U-2900 spectrophotometer (Hitachi Ltd, Tokyo, Japan). Glycogen content was expressed as a glucose equivalent in mg glucose/g soft tissue wet weight ratio.

Data analysis

The relationship between mussel size and weight is described by the allometric equation: $W = a L^b$ where W – mussel weight (dry weight (DW) or ash free dry weight (AFDW), L – mussel length, a, b – constants). We linearized this equation by log-transforming all length and weight measurements for further analyses. The higher value of the allometric coefficient b indicates the higher increment of soft tissue weight per unit length. Thus, we assumed the higher allometric coefficient to be associated with the greater relative investment of energetic resources into soft tissues during the animal growth.

To analyse length-weight relationships of mussels in Lakes IJsselmeer and Markermeer, we pooled samples from each year to avoid random month to month fluctuations and focus on interannual differences depending on changing shares of dreissenids in the community. We tested mussel DW and AFDW with a General Linear Model (GLM) with (1) Lake, (2) Species and (3) Sampling Year as fixed categorical factors and (4) Mussel Length as a continuous independent variable. All main effects and interactions between Species and other variables were included in the model.

To analyse length-weight relationships of mussels in Lake Balaton (DW and AFDW) we used a GLM with (1) Species/Year as a fixed categorical factor with three levels: (i) quagga mussels sampled in 2015, (ii) zebra mussels co-occurring with quagga mussels in 2015 and

(iii) zebra mussels sampled in 2005, before the quagga mussel appearance and (2) Mussel Length as a continuous independent variable.

Attachment strength and shell strength were log-transformed before the analyses, as they are also likely to depend on dimensions (attachment on the number and diameter of byssal threads and shell strength on its thickness). To check factors affecting mussel attachment, we applied a GLM with (1) Species and (2) Exposure Time (2 days, 1 week, 1 month) as fixed categorical factors, (3) Tank as a random factor nested within Species (included to avoid pseudoreplications, as each tank contained a group of mussels) as well as (4) Mussel Length (log-transformed) and (5) Shell Strength as continuous independent variables. Mussel length was included in the model to control for its influence on attachment strength (Kobak 2006) and check its potential effect on interspecific differences in attachment. We assumed that attachment strength can vary within a short timeframe, depending on current conditions (Kobak, 2006), whereas shell strength is a lifetime parameter, reflecting the entire life of an animal. Therefore, it was possible that shell strength would shape attachment, e.g. by reflecting animal condition or its past experiences with predation pressure (Czarnołęski et al. 2006). All main effects, the interaction between the fixed factors as well as interactions involving Species and the continuous variables were included in the model.

To check factors affecting mussel shell strength, we applied a GLM with (1) Species as a fixed categorical factor, (2) Tank as a random factor nested within Species and (3) Mussel Length (log-transformed) as a continuous independent variable. All exposure times were pooled for this analysis as it was unlikely that such a short timeframe would affect the strength of a shell developed throughout a mussel life. All main effects and an interaction between the fixed factor and continuous variable were included in the model.

To analyse differences in glycogen content (log-transformed), we used a GLM with (1) Species as a fixed factor and (2) Mussel Size as a continuous independent variable.

For significant interactions of continuous variables with categorical factors, we compared the regression slopes for particular levels of grouping variables with one another according to Sokal and Rohlf (1995). If two slopes did not differ from each other (indicating parallel regression lines), we checked whether the lines differed in their vertical position using ANCOVAs. The results of these post-hoc comparisons were sequential-Bonferroni corrected to control for Type I error inflation. Calculations were carried out with SPSS 22.0 (IBM inc.).

Results

Length-weight relationship

During the study period, a shift from the zebra to quagga mussel dominance occurred in all the lakes (Table 1). The biovolumes observed in Lake Balaton were much higher than in Lakes IJsselmeer and Markermeer. Moreover, a considerable increase in mussel biovolume was observed in Lake IJsselmeer, following the collapse that had occurred between 1999 and 2007 (Table 1).

The GLMs have shown significant Lake x Year x Species x Length interactions for both DW ($F_{2, 200} = 3.73$, $P = 0.026$) and AFDW ($F_{2, 200} = 7.21$, $P = 0.001$, see Table S2 for detailed results) of the Dutch lake populations. Thus, both species grew differently in both lakes and their length-weight relationships changed with time.

In Lake IJsselmeer, the weight increment per unit length of zebra mussels were greater than that of quagga mussels in 2008 and 2009, whereas this tendency was reversed in 2010 and 2011 (Fig. 2, Fig. S2). The highest weight increments per unit length were observed in 2008-9 for zebra mussels and 2010 for quagga mussels (Table S3). The body weight of both species gradually decreased in consecutive years, as shown by significant differences in vertical position among lines with the same slopes (Table S3).

In Lake Markermeer, the weight increment per unit length was higher in quagga than in zebra mussels in 2009 (only AFDW), 2010 and 2012. In the other cases (year 2011 and DW in 2009), body weight of quagga mussels was uniformly greater than that of zebra mussels across the entire size range (Fig. 2, Fig. S2). Body weight of both species increased from 2009 till 2011, with no differences in allometric coefficients (i.e. slopes) between the consecutive years (Table S3).

Significant Species x Length interactions in the GLMs (DW: $F_{2, 47} = 7.59$, $P = 0.001$, AFDW: $F_{2, 47} = 3.81$, $P = 0.029$, see Table S4 for detailed results) indicated that length-weight relationships differed between both species in Lake Balaton. DW and AFDW of quagga mussels increased faster per unit length compared to zebra mussels (Fig. 3, Fig. S3). The DW increment of zebra mussels co-occurring with quagga mussels (in 2015) was lower than that exhibited by this species before the appearance of quagga mussels (in 2005). AFDW of zebra mussels co-occurring with quagga mussels was constantly lower than in 2005 across the entire size range. It should be noted that large (length >15 mm) zebra mussels were very rare in the 2015 samples, despite collecting thousands of animals.

Attachment strength

Mussel attachment was affected by species, exposure time and mussel length, as shown by a significant interaction between these factors in the GLM ($F_{2, 1206} = 8.26$, $P < 0.001$, see Table S5 for detailed results). After 2 days, zebra mussels were more strongly attached than quagga mussels irrespective of their length (Fig. 4A), which resulted in a significant difference in vertical position between the parallel regression lines for both species ($t_{606} = 3.28$, $P = 0.001$). After 1 week, the attachment of both species did not differ from each other (Fig. 4B). After 1 month, a significant difference appeared between the regression slopes for both species ($t_{212} = 4.08$, $P < 0.001$). The increment of attachment strength per unit length was greater in quagga than in zebra mussels. In consequence, small zebra mussels were more strongly attached than small quagga mussels, whereas the opposite was true for the largest individuals (Fig. 4C).

The shell strength appeared to correlate positively (as shown by the positive value of the estimated parameter B = 0.074 ±0.058 SE for the shell strength effect) with attachment strength, though this relationship was rather weak (shell strength main effect: $F_{1, 1206} = 4.48$, $P = 0.034$).

Shell strength

Zebra mussels had harder shells than quagga mussels (Fig. 5), though this difference decreased with size, as shown by a significant Species x Length interaction in the GLM ($F_{1, 1216} = 8.40$, $P = 0.004$, see Table S6 for detailed results). Thus, the increment of shell strength per unit length was greater in quagga mussels than in zebra mussels.

Glycogen content

A significant Species effect in the GLM ($F_{1, 89} = 12.32$, $P = 0.001$, see Table S7 for detailed results) reflected the higher glycogen content in quagga mussels (Fig. 6) across the entire size range studied (as the length effect was non-significant: $F_{1, 89} = 2.94$, $P = 0.090$).

Discussion

Soft tissue increment per unit length is faster in quagga than zebra mussels

We observed a gradual replacement of zebra by quagga mussels in all three lakes studied. A similar process took place within 4-13 years in most of the European and North American freshwater bodies in which they co-occur (Mills et al., 1996; Orlova et al., 2004; Ricciardi and Whoriskey, 2004; Patterson et al., 2005; Dermott and Dow, 2008; Nalepa et al., 2010; Zhulidov et al., 2010; Bij de Vaate et al., 2013; Heiler et al., 2012; Matthews et al., 2014). Comparison of our data obtained at various stages of the quagga mussel invasion allowed us to get insight into the process of the species displacement. Notable intra- and interspecies differences in soft tissue weight increment per unit length were observed during the process of invasion.

Higher soft tissue weight increment per unit length may have two causes: (1) higher energetic allocation into soft tissue growth or (2) different proportions in linear growth in the two species (i.e. the heavier species might increase more in width and/or height than the other, having the same length increment). Beggel et al. (2015) and Kerembrun et al. (2018) provided data on zebra and quagga mussel shell proportions, showing that quagga mussels have narrower and taller shells than zebra mussels of the same length. Nevertheless, detailed calculations based on the numerical data by Kerembrun et al. (2018) indicate that the overall shell volume of a quagga mussel is smaller (though only slightly) than that of a zebra mussel of the same length. Thus, we can argue that the heavier soft tissue mass of the quagga mussel must be attributed to its higher content in the shell volume rather than to the larger shell volume per unit length. The higher amount of soft tissue may allow faster maturation, more efficient reproduction (gonad mass and gamete production), feeding (gill size), movement (muscle mass) and/or accumulation of storage materials. Thus, the high soft tissue amount and its fast increment per unit length is likely to be beneficial for a mussel (Metz et al., 2018).

At the beginning of the quagga mussel invasion in Lake IJsselmeer (years 2008-9), zebra mussels had higher weight increments than after the establishment of the newcomer (2010-11). In Lake Balaton, we also observed a reduction in zebra mussel soft tissue increment per unit length after the appearance of the quagga mussel and the higher value of this parameter exhibited by the latter species. This suggests that either (1) quagga mussels negatively affected zebra mussels (so individuals of the same length had less soft tissue), or (2) some external factors negatively affected zebra mussels, whereas quagga mussels remained less influenced. The body weight of all size classes of both species in Lake IJsselmeer tended to decrease with time. Perhaps, it could follow from the increasing overall dreissenid biovolume during the study period in this lake (Table 1) and/or from the resulting considerable decrease in chlorophyll-a concentration observed in the southern part of the lake (Table S1).

In Lake Markermeer, quagga mussels had higher body weight and/or its increment rate per unit length than zebra mussels from the beginning of their appearance. In this lake, intrinsic differences between both species, rather than a relationship between them, seemed to be responsible for the advantage of the former. The hypothesis of the intrinsic difference between the species being related to the displacement in this lake is supported by (1) the fact that the displacement took place despite the absence of a negative change in the zebra mussel length-weight relationship after the appearance of its competitor, (2) the relatively constant advantage of quagga over zebra mussels from the beginning of the invasion of the former, and (3) the improvement of the relative soft tissue weight of zebra mussels in 2010-11, despite the increasing quagga mussel population. In addition, the relatively low densities and small size of the mussels of both species in this lake suggest other limitation parameters than intraspecific competition. These are probably related to high silt content of suspended matter and flocculation of algae with silt particles (De Lucas Pardo et al., 2015). The absence of a reduction in the zebra mussel body weight increment after the appearance of its congener in Lake Markermeer might also result from the generally lower increments observed in this lake, which could prevent detection of any further decrease in this parameter. The quagga mussel has been found to have generally larger body weight/shell ratio than zebra mussel (Mills et al., 1996; Jarvis et al., 2000; Diggins, 2001; Stoeckmann, 2003; Karatayev et al., 2010), which, similarly to the results of our study, indicates its higher investment into soft tissue growth.

The different pattern of dreissenid length-weight relationships in Lake Markermeer may result from the high concentration of suspended particles (Vijverberg et al., 2011) particularly in spring (Fig. S1, Table S1), which negatively affects the living conditions and growth of dreissenids (Mandemakers, 2013; Penning et al., 2013). The superiority of the quagga mussel in such a turbid lake may result from their higher resistance to such conditions. The faster growth rate of the quagga mussel compared to its congener was reported under stressful conditions (low food quantity and quality) in the field (Karatayev et al., 1998; Baldwin et al. 2002; Stoeckmann, 2003; Orlova et al., 2005) and experimental studies (Stoeckmann and Garton, 2001; Baldwin et al., 2002). It was attributed to lower metabolic rate and faster filtration (Baldwin et al., 2002; Stoeckmann, 2003), advantageous mainly in suboptimal conditions (Karatayev et al., 1998; Madon et al., 1998; Stoeckmann and Garton 2001; Baldwin et al., 2002; Stoeckmann, 2003; Orlova et al., 2005). On the other hand, in the southern part of Lake IJsselmeer, the amount of suspended particles was moderate (Table S1) and the largest dreissenid community existed (Table 1). The more sandy sediments in this lake in comparison to Lake Markermeer may result in the higher food quality of the suspended matter. Also, this part of the lake is closest to the mouth of the River IJssel, which supplies most of the nutrients to Lake IJsselmeer. Nevertheless, a study involving a greater number of lakes differing in turbidity is needed to confirm the importance of this factor.

To summarize, in the view of all the lakes studied here, the displacement of the zebra mussel takes place irrespective of whether they respond to the appearance of the quagga mussel with changes in soft tissue growth parameters or not. Therefore, other parameters are likely to lead to the superiority of quagga mussels. These can include generally faster soft tissue weight increment per unit length under poor environmental conditions, shown in our study. Quagga mussels were showed to grow faster and therefore exhibit higher fitness than zebra mussels under a range of densities of both coexisting species (Metz et al., 2018). Moreover, the quagga mussel better tolerates low temperature and food concentration (Karatayev et al., 1998; Baldwin et al., 2002; Stoeckmann, 2003; Orlova et al., 2005). Thus, it can reproduce at lower temperatures (4-9 °C, Roe and MacIsaac, 1997; Thorp et al., 1998;

Claxton and Mackie, 1998; Stoeckmann, 2003; Nalepa et al., 2010) and therefore colonize substrata earlier in spring (Balogh et al., 2018). On the other hand, according to D'Hont et al. (2018), quagga mussels may be able to dominate the dreissenid community even when they settle later in spring than zebra mussels. Furthermore, the quagga mussel survives at a lower oxygen concentration (Karatayev et al., 1998).

Attachment strength and shell resistance are greater in zebra than in quagga mussels

The 2-day attachment of zebra mussels was significantly stronger than that of quagga mussels. This supports the short-term results of Peyer et al. (2009) and shows that the zebra mussel invests more energy into initial adhesion. This strategy allows it to gain faster protection against environmental dangers, such as predators or hydrodynamics. Moreover, the youngest zebra mussels invested more energy into their shell hardness and long-term attachment than quagga mussels. Roe and MacIsaac (1997) and Casper and Johnson (2010) also reported zebra mussels to allocate relatively more energy to shell than to soft tissue growth compared to the quagga mussel. However, in our study, larger quagga mussels made up for this difference and approached (shell strength) or exceeded (attachment) the values measured for large zebra mussels. The long-term attachment strength of quagga mussels surpassed that of zebra mussels at the size of ca. 12-13 mm (Fig. 4C). In contrast, Peyer et al. (2009) showed no difference in long-term (2-3 months) attachment strength between the species. Also, Grutters et al. (2012), comparing byssal production at different temperatures, found the advantage of zebra mussels only at 25 °C. The difference between these results and our study could be due to the fact that we tested the whole size range of mussels, up to 24 mm in length. We showed that neither species can be actually considered as having stronger long-term attachment. Instead, quagga mussels exhibit faster increment of attachment per unit length (though starting from a lower initial value for the smallest individuals), resulting in the stronger adhesion of the largest specimens. It should be noted that byssogenesis is influenced by multiple environmental cues: temperature, salinity, dissolved oxygen, light, hydrodynamics, adhesion surface and season (Rajagopal et al. 1996, 2005, 2006; Clarke and McMahon, 1996; Kobak, 2001; 2006; Peyer et al., 2009), which can also modify the results.

Stronger attachment and more resistant shell can protect mussels from predation (Naddafi and Rudstam, 2013a). Anti-predator defences involving stronger attachment (Côté 1995; Reimer and Tedengren, 1996; Dolmer, 1998; Nagarajan et al., 2006) and thicker shells have also been described for marine mussels (Leonard et al., 1999; Smith and Jennings, 2000; Freeman and Byers, 2006). However, only specifically adapted fish (e.g. cyprinids), birds and large invertebrates (crayfish, crabs) are capable of consuming dreissenids (Molloy et al., 1997). Fish and bird predation affects the dreissenid population in Lake Balaton (Ponyi, 1994; Specziár et al., 1997; Balogh et al., 2008). In Lake IJsselmeer, predation pressure by ducks on zebra mussels as well as impact on densities used to be relatively high during the 1980s and early 1990s (van Eerden et al., 1997), when availability of alternative prey was low. Their stomach contents contained as much as 95% zebra mussels in winter (de Leeuw and van Eerden, 1995). In more recent years, abundance of aquatic macrophytes has increased, and stomachs of ducks contained less mussels and more gastropods and amphipods (Van Rijn et al., 2012). Proportions of both dreissenid species in the stomachs were roughly similar to their proportions in the mussel community on the lake bottom at that time.

Fish and bird predation concerns mainly small and medium sized (8–17 mm) dreissenids (Czarnołęski et al. 2006). De Leeuw and van Eerden (1992) showed that tufted ducks *Aythya fuligula* fed on smaller zebra mussels in Lake IJsselmeer using a suction technique, which was more profitable than picking up larger mussels individually. Thus, large mussels are relatively less susceptible to predation compared to small individuals. Our results indicate that small zebra mussels seem better protected against predation than quagga mussels of the same size.

Moreover, Naddafi and Rudstam (2013a, b) found stronger responses (increase in shell thickness and attachment strength) of zebra mussels to the presence of predators compared to quagga mussels. Nevertheless, despite of their apparently better anti-predation protection, zebra mussels are still being displaced by their congeners. Naddafi and Rudstam (2013a, b) suggested that different energy partitioning by the two dreissenid species into growth and anti-predation defences might explain the competitive advantage of the quagga mussel. By decreasing the allocation of energy into attachment and shell building, quagga mussels are able to invest more resources into growth and/or reproduction, resulting in faster growth and greater soft tissue weight increments per unit length, also shown in our results. This may be advantageous for an animal which, due to its hard shell and gregarious occurrence, is likely to be exposed to generally lower predation risk compared to soft zoobenthos.

The stronger attachment of zebra mussels can be advantageous in areas exposed to variable physical conditions, e.g. water currents and waves (e.g. upper littoral). Zebra mussels are commonly observed in such locations, e.g. at a shallow depth (Karatayev et al., 2013) or on shells of actively moving unionid mussels (Bódis et al., 2014). Conversely, quagga mussels are more often found at higher depths and/or on muddy bottoms with more stable conditions (Mills et al., 1996; Coakley et al., 1997; Berkman et al., 1998, 2000; Peyer et al., 2011). On the other hand, no differences in the distribution of both species were observed in Lakes IJsselmeer and Markermeer (A. bij de Vaate, personal observation).

The strong attachment and resistant shell also makes the zebra mussel more durable than the quagga mussel during transport with vessels and sailing equipment that might have resulted in its higher spread rate at the initial invasion stage, particularly over long distances and between water bodies (Karatayev et al., 2011; Collas et al., 2016). Further, this durability likely delays displacement of the zebra by quagga mussel and allows for the co-existence of the two species at some places (Patterson et al. 2005; Watkins et al. 2007; Nalepa et al. 2010).

Habitat partitioning was also found in some co-existing intertidal marine mussels (Harger, 1970; Witman and Suchanek, 1984; Gardner and Skibinski, 1991; Willis and Skibinski, 1992). Among them, marine counterparts of dreissenids, *Mytillus trossulus* and *M. californianus,* have different attachment strength, which is associated with their location on wave-exposed shores (Witman and Suchanek, 1984; Bell and Gosline, 1997).

Quagga mussels accumulate more energy storage products than zebra mussels

We showed that zebra mussels had significantly lower level of glycogen than quagga mussels. Lower glycogen content may reflect unfavorable conditions inhibiting production of storage materials by zebra mussels and/or exhausting these resources. Quagga mussels under the same conditions seem capable of keeping higher levels of storage materials and thus sustaining better physiological condition. This corresponds to the reduction in the abundance of zebra mussels during the initial stage of the quagga mussel invasion in Lake Balaton (Balogh et al., 2018). Lower glycogen content could reduce reproduction, and hence provide an advantage for the quagga mussel to displace the zebra mussel from the common habitat. Moreover, the difference in glycogen content between the species accounts for our earlier finding of the higher soft tissue weight increment per unit length observed in quagga mussels, supporting the hypothesis that this species accumulates its soft tissue weight faster than its congener.

Summary and conclusions

Zebra mussels in our study had generally lower weight increment per unit length, lower glycogen content, more resistant shells and higher initial attachment strength than quagga mussels. Moreover, small zebra mussels exhibited stronger long-term adhesion than quagga mussels. The displacement of zebra by quagga mussels occurred in all the lakes, irrespective of whether a negative change in the weight increment per unit length of the zebra mussel appeared in the presence of its congener or not. Thus, the displacement between the dreissenids is likely to depend on some intrinsic differences between the species, including lower energetic investment of the quagga mussel into processes other than growth and reproduction (i.e. attachment and shell strength), its higher content of storage products and/or higher resistance to negative environmental factors. Nevertheless, its negative impact on the zebra mussel also cannot be excluded, at least occasionally. The differences between the species act mainly at early stages of mussel life, when intra- and interspecific competition for space and food is most important due to common detachment events and searching for suitable sites (Kobak et al., 2009). The faster growth at this stage, enabled due to weaker development of anti-predation structures, may promote the competitive success of the quagga mussel over its congener. Older quagga mussels offset their initial lower attachment strength and shell resistance with faster growth, suggesting that after establishing permanent attachment sites they start to allocate more energy into these processes as well.

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Figure captions

Fig. 1. Map of the study sites in Lake IJsselmeer, Lake Markermeer and Lake Balaton. Mussel sampling sites are indicated as solid circles and those used for environmental parameter measurements are shown as white asterisks.

Fig. 2. Soft tissue dry weight (DW) increments per unit length of zebra (solid lines) and quagga mussels (dashed lines) in Lakes IJsselmeer (IJM) and Markermeer (MM) in 2008-2012. The lines (±SE) are predicted by the General Linear Model. Asterisks (*) indicate regression lines with slopes significantly differing between species. “X” marks indicate regression lines significantly differing in their vertical position (valid for parallel slopes only) between species. Note the log scale. See Table S3 for regression equations and differences among years.

Fig. 3. Soft tissue dry weight (DW) increments per unit length of zebra mussels in 2000 (dotted line) as well as zebra (solid line) and quagga mussels (dashed line) in 2015 in Lake Balaton. The lines (±SE) are predicted by the General Linear Model. Asterisks (*) indicate regression lines with significantly different slopes. Note the log scale. See Table S3 for regression equations.

Fig. 4. Attachment strength increments per unit length of zebra (solid line) and quagga mussels (dashed line) from Lake Balaton after different exposure times. N values show the numbers of mussels measured in each treatment. The lines (±SE) are predicted by the General Linear Model. Asterisks (*) indicate regression lines with slopes significantly differing between species. “X” marks indicate regression lines significantly differing in their vertical position (valid for parallel slopes only) between species. Note the log scale.

Fig. 5. Shell strength increments per unit length of zebra (solid line) and quagga mussels (dashed line) from Lake Balaton. The lines (±SE) are predicted by the General Linear Model. Asterisks (*) indicate regression lines with slopes significantly differing between

species. Note the log scale.

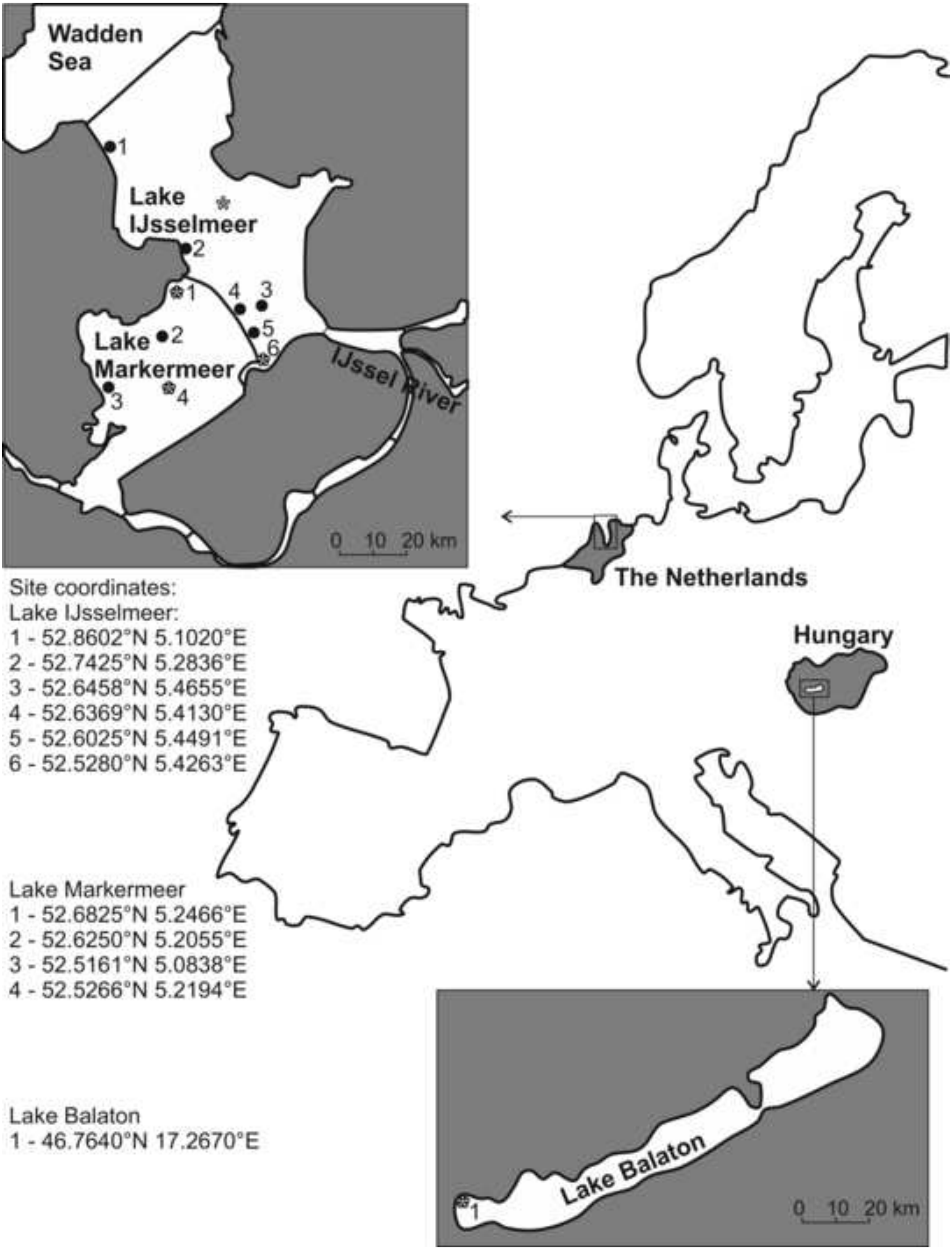
Fig. 6. Glycogen content in zebra and quagga mussels of various sizes collected from Lake Balaton. Open symbols show single data points, solid symbols (with standard errors of the mean) represent least squares (LS) means predicted by the General Linear Model. Asterisks (*) indicate a significant difference between mussel species ($p<0.001$).

Table 1. Percentage contribution of the quagga mussel to the dreissenid community (PQ) and dreissenid (both species pooled) biovolume (DB) (as an indicator of crowding, combining density and size) in the studied lakes.

Lake	Year	PQ (%) mean ±SD	DB (mL/m^2) mean ±SD		
			North	Center	South
Lake IJsselmeer	1999	0	97.7±235.4	196.2±425.1	582.7±504.5
	2007	0	10.6±28.3	40.1±101.8	56.6±71.4
	2008	27±19			199.8±273.7
	2009	57±10			
	2010	48±24			
	2011	86±8			
	2012	95±6	39.2±170.5	290.2±619.0	963.0±921.7
			North		
Lake Markermeer	2000	0	22.8±37.5		
	2006	0	16.0±18.9		
	2007	0			
	2008	8±3			
	2009	32±10			
	2010	54±5			
	2011	72±4	58.0±89.5		
	2012	74±8			
Lake Balaton	2005	0	68406±20487		
	2015	96±2	3531.8±2501.4		

Sources: for Lake IJsselmeer and Markermeer: Matthews et al. (2014); A. bij de Vaate (unpublished), for Lake Balaton: original data

Figure1



Site coordinates:

Lake IJsselmeer:

1 - 52.8602°N 5.1020°E
2 - 52.7425°N 5.2836°E
3 - 52.6458°N 5.4655°E
4 - 52.6369°N 5.4130°E
5 - 52.6025°N 5.4491°E
6 - 52.5280°N 5.4263°E

Lake Markermeer

1 - 52.6825°N 5.2466°E
2 - 52.6250°N 5.2055°E
3 - 52.5161°N 5.0838°E
4 - 52.5266°N 5.2194°E

Lake Balaton

1 - 46.7640°N 17.2670°E

Figure2

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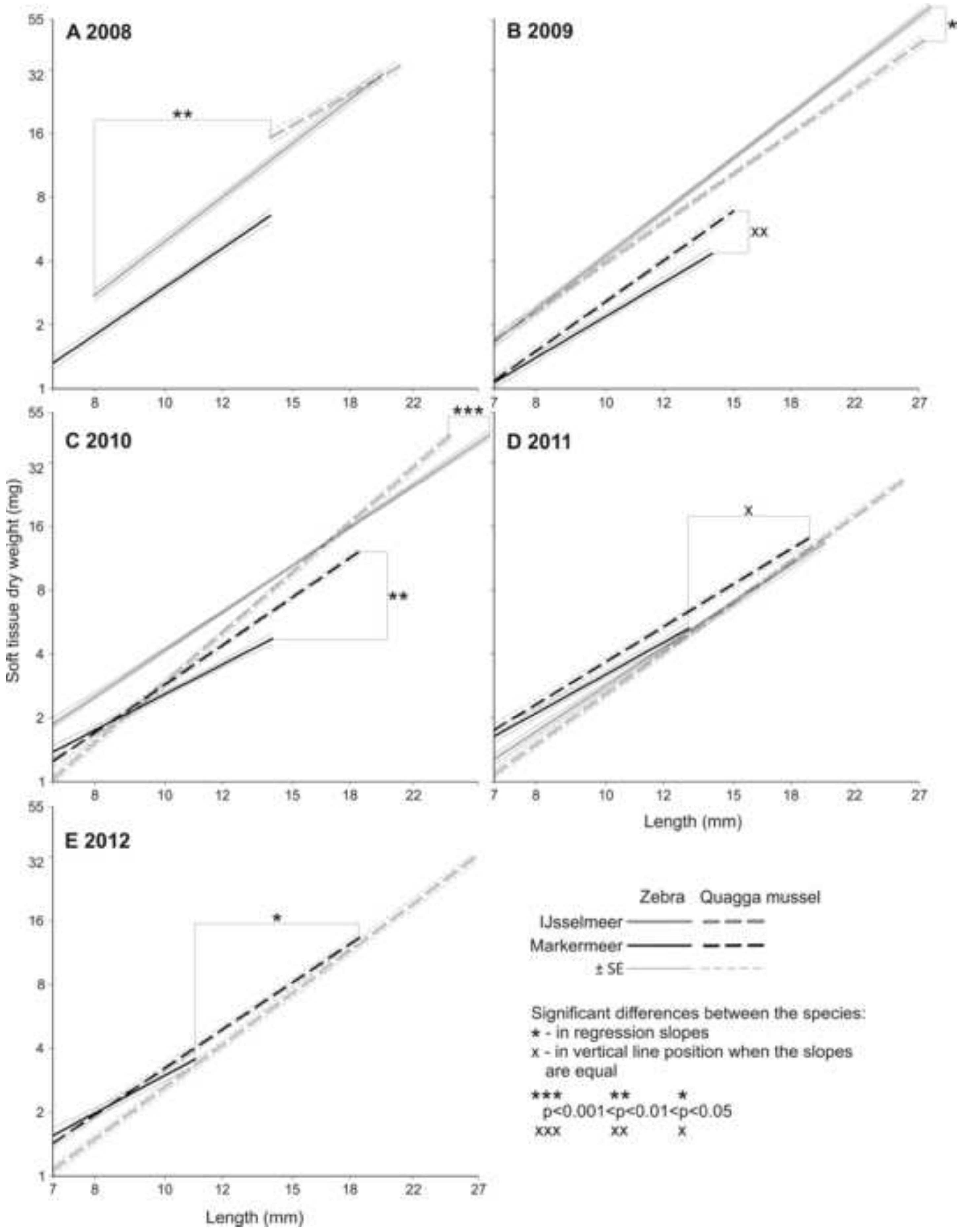

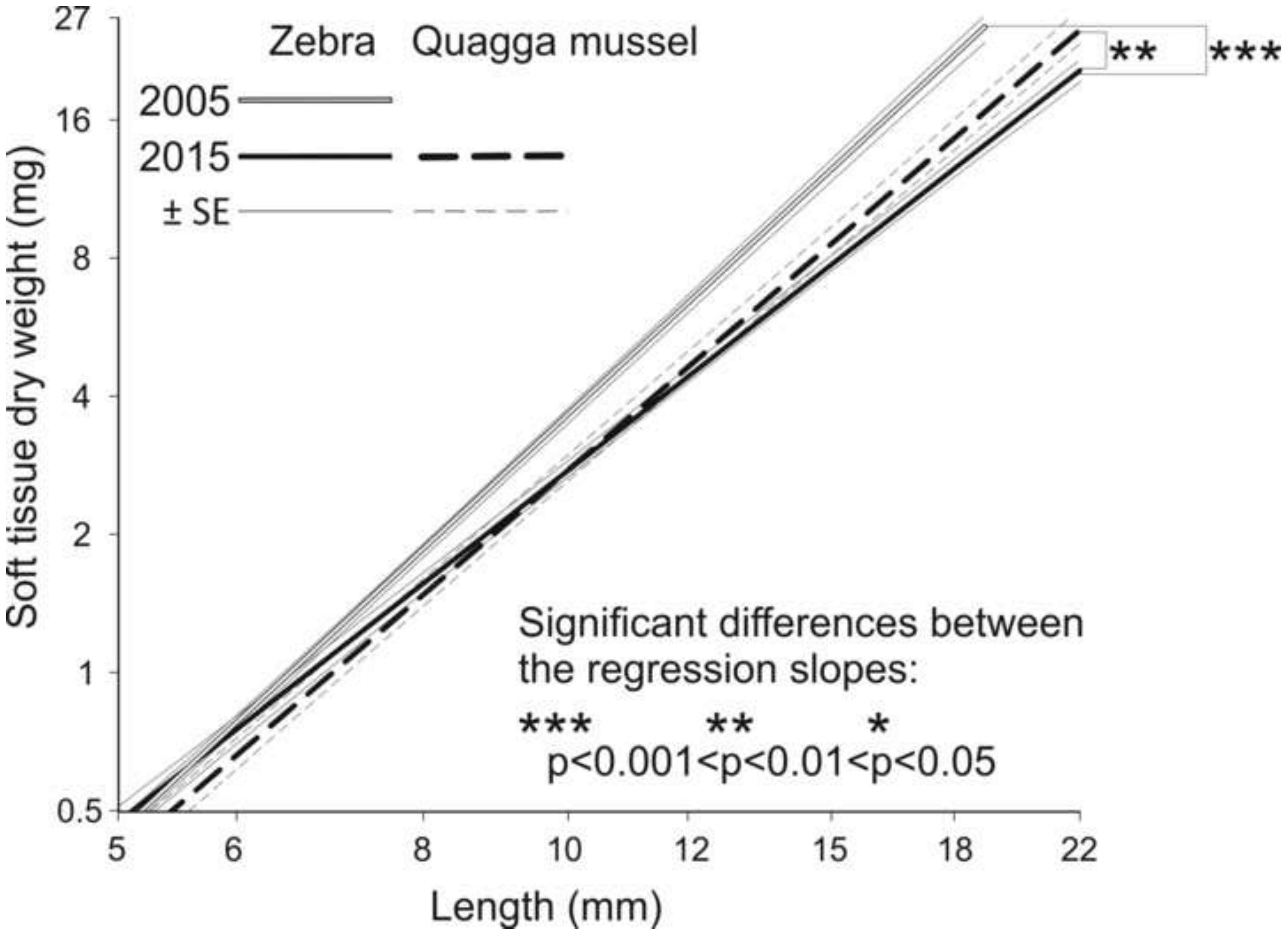
Zebra
Quagga mussel
2005
2015
± SE
**
***
Significant differences between the regression slopes:
*** p<0.001<** p<0.01<* p<0.05
Soft tissue dry weight (mg)
27
16
8
4
2
1
0.5
5
6
8
10
12
15
18
22
Length (mm)

Figure4

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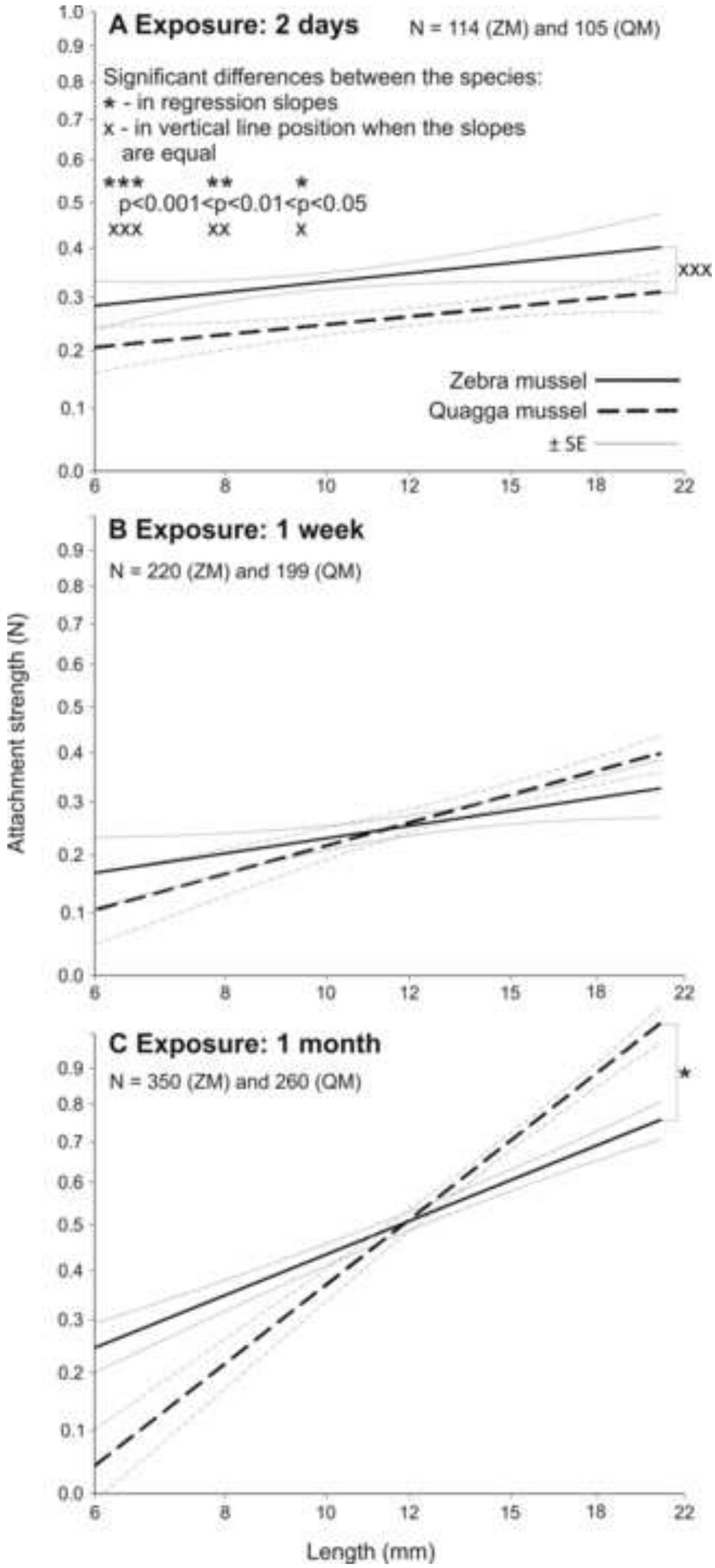

Figure5

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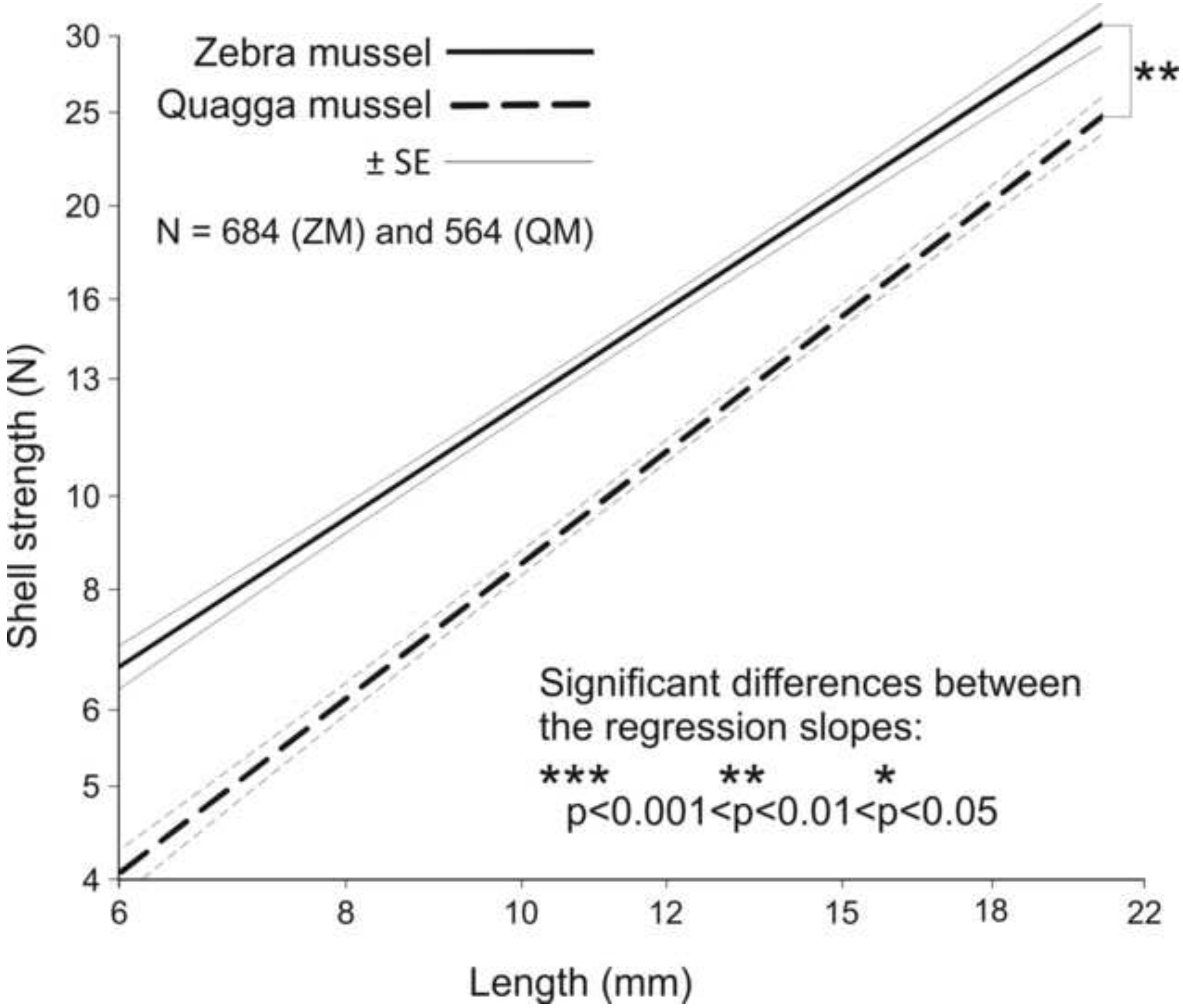

Figure6

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