

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

3

4 Csilla Balogh^{a,b}, Zoltán Serfőző^{a,b}, Abraham bij de Vaate^c, Ruurd Noordhuis^d, Jarosław
5 Kobak^{e*}

6 ^aCentre for Ecological Research, Balaton Limnological Institute, Hungarian Academy of
7 Sciences, Tihany, Klebelsberg Kuno u. 3., Hungary

8 ^bMTA Centre for Ecological Research, GINOP Sustainable Ecosystems Group, 8237 Tihany,
9 Klebelsberg Kuno u. 3., Hungary

10 ^cWaterfauna Hydrobiological Consultancy, Oostrandpark 30, NL- 8212 AP Lelystad, The
11 Netherlands

12 ^dDeltares, P.O. Box 177, 2600 MH Delft, The Netherlands

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

16 *Corresponding author

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

18

19

20 **Abstract**

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

38

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

41

42 **Introduction**

43 Sessile Ponto-Caspian dreissenids, the zebra (*Dreissena polymorpha* (Pallas, 1771)) and
44 quagga (*Dreissena rostriformis bugensis* Andrusov, 1897) mussels share similar habitats and
45 food requirements (Quinn et al. 2013). They are invasive in Europe and North America,
46 causing habitat changes and economic losses (Pimentel et al., 2005; Oreska and Aldridge,
47 2010; Ricciardi and MacIsaac, 2011). While in North America both species appeared within a
48 few years, in Europe (apart from their native area) only the zebra mussel has occurred since
49 the 19th century (Bidwell, 2010) until the recent spread of the quagga mussel in the second
50 half of the 20th century (Van der Velde et al., 2010). Despite the faster spread of the zebra
51 mussel, its populations are usually reduced or displaced within a few years after the
52 appearance of the quagga mussel (Ricciardi and Whoriskey, 2004; Karatayev et al., 2011).
53 This phenomenon also occurs in great lakes of Europe (Orlova et al., 2004; Heiler et al., 2012;
54 Matthews et al., 2014; Balogh et al., 2018) and North America (Patterson et al., 2005), that
55 are commonly being invaded and affected by both species. Nevertheless, a few notable
56 exceptions of the co-existence of the two dreissenids exist (Zhulidov et al., 2010; Strayer and
57 Malcom, 2013).

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

63 Shell and byssus strengths are influenced by the energy budget of mussels (Babarro et al.,
64 2008). They affect resistance to hydrodynamic forces and anti-predator defense (Bell and
65 Gosline, 1997; Czarnołęski et al., 2006). The zebra mussel was found to allocate relatively
66 more energy to shell development compared to the quagga mussel (Roe and MacIsaac, 1997;

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

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

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

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

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

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

117

118 **Material and Methods**

119 *Sampling sites and the history of dreissenid introductions*

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

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

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

142 level in both lakes has been similar and slowly decreased. In 2011-12, they approached
143 mesotrophic conditions (R. Noordhuis, unpublished data).

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

148 Lake Balaton (Fig. 1) has soft bottom sediments (Lóczy, 1894; Miller and Wagner,
149 1978). Its shoreline has large expanses of reeds, is reinforced with rip-rap and includes
150 numerous piers and harbours, providing suitable substrata for dreissenid colonization.
151 Environmental data (Table S1) for Lake Balaton (Hungary) were monitored according to
152 Somogyi et al. (2017). Seston in Lake Balaton consists mainly from resuspended fine mineral
153 particles (0.2–10 μm) and biogenic lime. The organic content in the suspended matter is very
154 low (<4%) (Entz and Sebestyén, 1942; Entz, 1981; Máté, 1987). A trophic gradient exists
155 from the eutrophic western part to the oligo-mesotrophic eastern basin (Istvánovics et al.,
156 2007; Tátrai et al., 2008). Temperature in Lake Balaton, particularly in summer, was clearly
157 higher than in the Dutch lakes (Table S1).

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

163

164 *Sampling and preliminary processing of mussels*

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

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

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

184

185 *Soft tissue dry weight measurement*

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

192 We measured mussel length to the nearest 1 mm with a calliper (Lake Balaton) or ruler
193 (Dutch lakes). Soft tissue was removed from 10-40 animals per size class (size classes every 1
194 mm for a range of 7-26 mm) after boiling them for 1-2 min in a microwave at 800 W (A. bij
195 de Vaate, personal information). Then the soft tissue was dried for 24 h at 80 °C and weighed
196 yielding the average soft tissue dry weight (DW). The average soft tissue ash free dry weight
197 (AFDW) was obtained after incineration during 4 h at 450 °C. These average values per each
198 size class were used as data points in further analyses following the protocol by Bij de Vaate
199 (1991).

200

201 *Attachment and shell strength measurement*

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

204 We collected mussels from the rip-rap of Lake Balaton in August 2015. After a 2-week
205 acclimation period under laboratory conditions, we placed animals onto circular
206 polypropylene (pp) plates (diameter 85 mm, thickness 5 mm) with a raised edge (6 mm), 15
207 mixed sized individuals per plate. The plates were covered with plastic 1-mm mesh to prevent
208 animal loss and placed (each species separately) in aerated 200-L tanks (4 plates per tank, 6
209 tanks per each species and each of the 3 exposure times – see below). Each tank was
210 independently connected to Lake Balaton with a flow-through system (flow rate: 62 L/h), so
211 the water quality experienced by the exposed mussels were the same as outdoors. We
212 randomized the positions of the experimental tanks with both species within the laboratory
213 room to reduce the effect of unknown external stimuli. The conditions during the acclimation
214 and experiment (equal in all experimental tanks) were as follows: temperature: 20-24°C;
215 suspended material: 1.5-3 mg/L; chlorophyll-a: 1.5-3 µg/L. The tanks were uniformly
216 illuminated with natural light coming through the window of the laboratory room, at natural

217 photoperiod (14L:10D). After two days, when the animals had attached to the plastic surface,
218 the mesh was removed. We measured the attachment strength of mussels after two days (i.e.
219 immediately after removing the mesh), one week and one month of exposure (different 6
220 tanks on each term). Only individuals found attached to the substratum were analysed.

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

228

229 *Glycogen content measurement*

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

235 We measured glycogen (total carbohydrate) content according to Van Handel (1965),
236 adapted to mussels by De Zwaan and Zande (1972). We added a mixture containing 1 mL
237 96% ethanol, 200 µL distilled water and 20 µL saturated Na₂SO₄ to 40 µL of each sample and
238 heated it at 95 °C for 4 min in a block thermostat. Then the sample was cooled down in a
239 fridge at 4 °C and centrifuged at 2000 g for 20 min. The pellet was dried at 95 °C and filled
240 up to 50 µL with distilled water. To prepare the calibration line, we diluted 20 mg/mL glucose
241 (used as a standard) stock in a 5-14-fold range having 10 different concentrations of the

242 solution. Within this range, the reaction was linear with the glucose concentration. We
243 incubated the standards and samples with 1 mL of anthrone reagent (0.15% anthrone [Alfa
244 Caesar, Kalsruhe, Germany] solution in 76% sulfuric acid) at 90°C for 20 min. The samples
245 were kept on ice for 15 min to stabilize the colour of the reaction and measured within 10 min
246 at 620 nm in a Hitachi U-2900 spectrophotometer (Hitachi Ltd, Tokyo, Japan). Glycogen
247 content was expressed as a glucose equivalent in mg glucose/g soft tissue wet weight ratio.

248

249 *Data analysis*

250 The relationship between mussel size and weight is described by the allometric equation:
251 $W = a L^b$ where W – mussel weight (dry weight (DW) or ash free dry weight (AFDW), L –
252 mussel length, a, b – constants). We linearized this equation by log-transforming all length
253 and weight measurements for further analyses. The higher value of the allometric coefficient
254 b indicates the higher increment of soft tissue weight per unit length. Thus, we assumed the
255 higher allometric coefficient to be associated with the greater relative investment of energetic
256 resources into soft tissues during the animal growth.

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

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

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

269 Attachment strength and shell strength were log-transformed before the analyses, as they
270 are also likely to depend on dimensions (attachment on the number and diameter of byssal
271 threads and shell strength on its thickness). To check factors affecting mussel attachment, we
272 applied a GLM with (1) Species and (2) Exposure Time (2 days, 1 week, 1 month) as fixed
273 categorical factors, (3) Tank as a random factor nested within Species (included to avoid
274 pseudoreplications, as each tank contained a group of mussels) as well as (4) Mussel Length
275 (log-transformed) and (5) Shell Strength as continuous independent variables. Mussel length
276 was included in the model to control for its influence on attachment strength (Kobak 2006)
277 and check its potential effect on interspecific differences in attachment. We assumed that
278 attachment strength can vary within a short timeframe, depending on current conditions
279 (Kobak, 2006), whereas shell strength is a lifetime parameter, reflecting the entire life of an
280 animal. Therefore, it was possible that shell strength would shape attachment, e.g. by
281 reflecting animal condition or its past experiences with predation pressure (Czarnołowski et al.
282 2006). All main effects, the interaction between the fixed factors as well as interactions
283 involving Species and the continuous variables were included in the model.

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

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

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

298

299 **Results**

300 *Length-weight relationship*

301 During the study period, a shift from the zebra to quagga mussel dominance occurred in all
302 the lakes (Table 1). The biovolumes observed in Lake Balaton were much higher than in
303 Lakes IJsselmeer and Markermeer. Moreover, a considerable increase in mussel biovolume
304 was observed in Lake IJsselmeer, following the collapse that had occurred between 1999 and
305 2007 (Table 1).

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

310 In Lake IJsselmeer, the weight increment per unit length of zebra mussels were greater
311 than that of quagga mussels in 2008 and 2009, whereas this tendency was reversed in 2010
312 and 2011 (Fig. 2, Fig. S2). The highest weight increments per unit length were observed in
313 2008-9 for zebra mussels and 2010 for quagga mussels (Table S3). The body weight of both
314 species gradually decreased in consecutive years, as shown by significant differences in
315 vertical position among lines with the same slopes (Table S3).

316 In Lake Markermeer, the weight increment per unit length was higher in quagga than in

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

322 Significant Species x Length interactions in the GLMs (DW: $F_{2, 47} = 7.59$, $P = 0.001$,
323 AFDW: $F_{2, 47} = 3.81$, $P = 0.029$, see Table S4 for detailed results) indicated that length-weight
324 relationships differed between both species in Lake Balaton. DW and AFDW of quagga
325 mussels increased faster per unit length compared to zebra mussels (Fig. 3, Fig. S3). The DW
326 increment of zebra mussels co-occurring with quagga mussels (in 2015) was lower than that
327 exhibited by this species before the appearance of quagga mussels (in 2005). AFDW of zebra
328 mussels co-occurring with quagga mussels was constantly lower than in 2005 across the entire
329 size range. It should be noted that large (length >15 mm) zebra mussels were very rare in the
330 2015 samples, despite collecting thousands of animals.

331

332 *Attachment strength*

333 Mussel attachment was affected by species, exposure time and mussel length, as shown by a
334 significant interaction between these factors in the GLM ($F_{2, 1206} = 8.26$, $P < 0.001$, see Table
335 S5 for detailed results). After 2 days, zebra mussels were more strongly attached than quagga
336 mussels irrespective of their length (Fig. 4A), which resulted in a significant difference in
337 vertical position between the parallel regression lines for both species ($t_{606} = 3.28$, $P = 0.001$).
338 After 1 week, the attachment of both species did not differ from each other (Fig. 4B). After 1
339 month, a significant difference appeared between the regression slopes for both species ($t_{212} =$
340 4.08 , $P < 0.001$). The increment of attachment strength per unit length was greater in quagga
341 than in zebra mussels. In consequence, small zebra mussels were more strongly attached than

342 small quagga mussels, whereas the opposite was true for the largest individuals (Fig. 4C).

343 The shell strength appeared to correlate positively (as shown by the positive value of the
344 estimated parameter $B = 0.074 \pm 0.058$ SE for the shell strength effect) with attachment
345 strength, though this relationship was rather weak (shell strength main effect: $F_{1, 1206} = 4.48$, P
346 $= 0.034$).

347

348 *Shell strength*

349 Zebra mussels had harder shells than quagga mussels (Fig. 5), though this difference
350 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
351 per unit length was greater in quagga mussels than in zebra mussels.

353

354 *Glycogen content*

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

358

359 **Discussion**

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

361 We observed a gradual replacement of zebra by quagga mussels in all three lakes studied. A
362 similar process took place within 4-13 years in most of the European and North American
363 freshwater bodies in which they co-occur (Mills et al., 1996; Orlova et al., 2004; Ricciardi and
364 Whoriskey, 2004; Patterson et al., 2005; Dermott and Dow, 2008; Nalepa et al., 2010;
365 Zhulidov et al., 2010; Bij de Vaate et al., 2013; Heiler et al., 2012; Matthews et al., 2014).
366 Comparison of our data obtained at various stages of the quagga mussel invasion allowed us

367 to get insight into the process of the species displacement. Notable intra- and interspecies
368 differences in soft tissue weight increment per unit length were observed during the process of
369 invasion.

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

384 At the beginning of the quagga mussel invasion in Lake IJsselmeer (years 2008-9), zebra
385 mussels had higher weight increments than after the establishment of the newcomer (2010-
386 11). In Lake Balaton, we also observed a reduction in zebra mussel soft tissue increment per
387 unit length after the appearance of the quagga mussel and the higher value of this parameter
388 exhibited by the latter species. This suggests that either (1) quagga mussels negatively
389 affected zebra mussels (so individuals of the same length had less soft tissue), or (2) some
390 external factors negatively affected zebra mussels, whereas quagga mussels remained less
391 influenced. The body weight of all size classes of both species in Lake IJsselmeer tended to

392 decrease with time. Perhaps, it could follow from the increasing overall dreissenid biovolume
393 during the study period in this lake (Table 1) and/or from the resulting considerable decrease
394 in chlorophyll-a concentration observed in the southern part of the lake (Table S1).

395 In Lake Markermeer, quagga mussels had higher body weight and/or its increment rate
396 per unit length than zebra mussels from the beginning of their appearance. In this lake,
397 intrinsic differences between both species, rather than a relationship between them, seemed to
398 be responsible for the advantage of the former. The hypothesis of the intrinsic difference
399 between the species being related to the displacement in this lake is supported by (1) the fact
400 that the displacement took place despite the absence of a negative change in the zebra mussel
401 length-weight relationship after the appearance of its competitor, (2) the relatively constant
402 advantage of quagga over zebra mussels from the beginning of the invasion of the former, and
403 (3) the improvement of the relative soft tissue weight of zebra mussels in 2010-11, despite the
404 increasing quagga mussel population. In addition, the relatively low densities and small size
405 of the mussels of both species in this lake suggest other limitation parameters than
406 intraspecific competition. These are probably related to high silt content of suspended matter
407 and flocculation of algae with silt particles (De Lucas Pardo et al., 2015). The absence of a
408 reduction in the zebra mussel body weight increment after the appearance of its congener in
409 Lake Markermeer might also result from the generally lower increments observed in this lake,
410 which could prevent detection of any further decrease in this parameter. The quagga mussel
411 has been found to have generally larger body weight/shell ratio than zebra mussel (Mills et al.,
412 1996; Jarvis et al., 2000; Diggins, 2001; Stoeckmann, 2003; Karatayev et al., 2010), which,
413 similarly to the results of our study, indicates its higher investment into soft tissue growth.

414 The different pattern of dreissenid length-weight relationships in Lake Markermeer may
415 result from the high concentration of suspended particles (Vijverberg et al., 2011) particularly
416 in spring (Fig. S1, Table S1), which negatively affects the living conditions and growth of

417 dreissenids (Mandemakers, 2013; Penning et al., 2013). The superiority of the quagga mussel
418 in such a turbid lake may result from their higher resistance to such conditions. The faster
419 growth rate of the quagga mussel compared to its congener was reported under stressful
420 conditions (low food quantity and quality) in the field (Karatayev et al., 1998; Baldwin et al.
421 2002; Stoeckmann, 2003; Orlova et al., 2005) and experimental studies (Stoeckmann and
422 Garton, 2001; Baldwin et al., 2002). It was attributed to lower metabolic rate and faster
423 filtration (Baldwin et al., 2002; Stoeckmann, 2003), advantageous mainly in suboptimal
424 conditions (Karatayev et al., 1998; Madon et al., 1998; Stoeckmann and Garton 2001;
425 Baldwin et al., 2002; Stoeckmann, 2003; Orlova et al., 2005). On the other hand, in the
426 southern part of Lake IJsselmeer, the amount of suspended particles was moderate (Table S1)
427 and the largest dreissenid community existed (Table 1). The more sandy sediments in this lake
428 in comparison to Lake Markermeer may result in the higher food quality of the suspended
429 matter. Also, this part of the lake is closest to the mouth of the River IJssel, which supplies
430 most of the nutrients to Lake IJsselmeer. Nevertheless, a study involving a greater number of
431 lakes differing in turbidity is needed to confirm the importance of this factor.

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

442 Claxton and Mackie, 1998; Stoeckmann, 2003; Nalepa et al., 2010) and therefore colonize
443 substrata earlier in spring (Balogh et al., 2018). On the other hand, according to D'Hont et al.
444 (2018), quagga mussels may be able to dominate the dreissenid community even when they
445 settle later in spring than zebra mussels. Furthermore, the quagga mussel survives at a lower
446 oxygen concentration (Karatayev et al., 1998).

447

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

449 The 2-day attachment of zebra mussels was significantly stronger than that of quagga
450 mussels. This supports the short-term results of Peyer et al. (2009) and shows that the zebra
451 mussel invests more energy into initial adhesion. This strategy allows it to gain faster
452 protection against environmental dangers, such as predators or hydrodynamics. Moreover, the
453 youngest zebra mussels invested more energy into their shell hardness and long-term
454 attachment than quagga mussels. Roe and MacIsaac (1997) and Casper and Johnson (2010)
455 also reported zebra mussels to allocate relatively more energy to shell than to soft tissue
456 growth compared to the quagga mussel. However, in our study, larger quagga mussels made
457 up for this difference and approached (shell strength) or exceeded (attachment) the values
458 measured for large zebra mussels. The long-term attachment strength of quagga mussels
459 surpassed that of zebra mussels at the size of ca. 12-13 mm (Fig. 4C). In contrast, Peyer et al.
460 (2009) showed no difference in long-term (2-3 months) attachment strength between the
461 species. Also, Grutters et al. (2012), comparing byssal production at different temperatures,
462 found the advantage of zebra mussels only at 25 °C. The difference between these results and
463 our study could be due to the fact that we tested the whole size range of mussels, up to 24 mm
464 in length. We showed that neither species can be actually considered as having stronger long-
465 term attachment. Instead, quagga mussels exhibit faster increment of attachment per unit
466 length (though starting from a lower initial value for the smallest individuals), resulting in the

467 stronger adhesion of the largest specimens. It should be noted that byssogenesis is influenced
468 by multiple environmental cues: temperature, salinity, dissolved oxygen, light,
469 hydrodynamics, adhesion surface and season (Rajagopal et al. 1996, 2005, 2006; Clarke and
470 McMahon, 1996; Kobak, 2001; 2006; Peyer et al., 2009), which can also modify the results.

471 Stronger attachment and more resistant shell can protect mussels from predation (Naddafi
472 and Rudstam, 2013a). Anti-predator defences involving stronger attachment (Côté 1995;
473 Reimer and Tedengren, 1996; Dolmer, 1998; Nagarajan et al., 2006) and thicker shells have
474 also been described for marine mussels (Leonard et al., 1999; Smith and Jennings, 2000;
475 Freeman and Byers, 2006). However, only specifically adapted fish (e.g. cyprinids), birds and
476 large invertebrates (crayfish, crabs) are capable of consuming dreissenids (Molloy et al.,
477 1997). Fish and bird predation affects the dreissenid population in Lake Balaton (Ponyi, 1994;
478 Specziár et al., 1997; Balogh et al., 2008). In Lake IJsselmeer, predation pressure by ducks on
479 zebra mussels as well as impact on densities used to be relatively high during the 1980s and
480 early 1990s (van Eerden et al., 1997), when availability of alternative prey was low. Their
481 stomach contents contained as much as 95% zebra mussels in winter (de Leeuw and van
482 Eerden, 1995). In more recent years, abundance of aquatic macrophytes has increased, and
483 stomachs of ducks contained less mussels and more gastropods and amphipods (Van Rijn et
484 al., 2012). Proportions of both dreissenid species in the stomachs were roughly similar to their
485 proportions in the mussel community on the lake bottom at that time.

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

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

503 The stronger attachment of zebra mussels can be advantageous in areas exposed to
504 variable physical conditions, e.g. water currents and waves (e.g. upper littoral). Zebra mussels
505 are commonly observed in such locations, e.g. at a shallow depth (Karatayev et al., 2013) or
506 on shells of actively moving unionid mussels (Bódis et al., 2014). Conversely, quagga
507 mussels are more often found at higher depths and/or on muddy bottoms with more stable
508 conditions (Mills et al., 1996; Coakley et al., 1997; Berkman et al., 1998, 2000; Peyer et al.,
509 2011). On the other hand, no differences in the distribution of both species were observed in
510 Lakes IJsselmeer and Markermeer (A. bij de Vaate, personal observation).

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

517 Habitat partitioning was also found in some co-existing intertidal marine mussels (Harger,
518 1970; Witman and Suchanek, 1984; Gardner and Skibinski, 1991; Willis and Skibinski,
519 1992). Among them, marine counterparts of dreissenids, *Mytilus trossulus* and *M.*
520 *californianus*, have different attachment strength, which is associated with their location on
521 wave-exposed shores (Witman and Suchanek, 1984; Bell and Gosline, 1997).

522

523 *Quagga mussels accumulate more energy storage products than zebra mussels*

524 We showed that zebra mussels had significantly lower level of glycogen than quagga mussels.
525 Lower glycogen content may reflect unfavorable conditions inhibiting production of storage
526 materials by zebra mussels and/or exhausting these resources. Quagga mussels under the same
527 conditions seem capable of keeping higher levels of storage materials and thus sustaining
528 better physiological condition. This corresponds to the reduction in the abundance of zebra
529 mussels during the initial stage of the quagga mussel invasion in Lake Balaton (Balogh et al.,
530 2018). Lower glycogen content could reduce reproduction, and hence provide an advantage
531 for the quagga mussel to displace the zebra mussel from the common habitat. Moreover, the
532 difference in glycogen content between the species accounts for our earlier finding of the
533 higher soft tissue weight increment per unit length observed in quagga mussels, supporting
534 the hypothesis that this species accumulates its soft tissue weight faster than its congener.

535

536 *Summary and conclusions*

537 Zebra mussels in our study had generally lower weight increment per unit length, lower
538 glycogen content, more resistant shells and higher initial attachment strength than quagga
539 mussels. Moreover, small zebra mussels exhibited stronger long-term adhesion than quagga
540 mussels. The displacement of zebra by quagga mussels occurred in all the lakes, irrespective
541 of whether a negative change in the weight increment per unit length of the zebra mussel

542 appeared in the presence of its congener or not. Thus, the displacement between the
543 dreissenids is likely to depend on some intrinsic differences between the species, including
544 lower energetic investment of the quagga mussel into processes other than growth and
545 reproduction (i.e. attachment and shell strength), its higher content of storage products and/or
546 higher resistance to negative environmental factors. Nevertheless, its negative impact on the
547 zebra mussel also cannot be excluded, at least occasionally. The differences between the
548 species act mainly at early stages of mussel life, when intra- and interspecific competition for
549 space and food is most important due to common detachment events and searching for
550 suitable sites (Kobak et al., 2009). The faster growth at this stage, enabled due to weaker
551 development of anti-predation structures, may promote the competitive success of the quagga
552 mussel over its congener. Older quagga mussels offset their initial lower attachment strength
553 and shell resistance with faster growth, suggesting that after establishing permanent
554 attachment sites they start to allocate more energy into these processes as well.

555

556 **Acknowledgements**

557 Mrs. Ildikó Starkné Mecsnóbel, Ms Brigitta Baranyai, Ms. Judit Tóth, Éva Koltai and Balázs
558 Kutasi provided excellent technical assistance in experimental work. We are indebted to
559 Balázs Németh for generous share of the TSM data of Lake Balaton. The study was
560 financially supported by the GINOP-2.3.2-15-2016-00019, the MAHOP-2.1.1.-2016-2017-
561 00005.

562

563 **References**

564 Baldwin, B.S., Mayer, M.S., Dayton, J., 2002. Comparative growth and feeding in zebra and
565 quagga mussels (*Dreissena polymorpha* and *Dreissena bugensis*). Implications for North
566 American lakes. Can. J. Fish. Aquat. Sci. 59, 680–694.

567 Balogh, C., G-Tóth, L., 2009. A Balaton bevonatlakó gerinctelen állatvilágának vizsgálata a
568 2008. évben. In: Bíró, P., Banczerowsky, J.A. (Eds.), Balaton kutatásának 2008. évi
569 eredményei. MTA, Budapest, pp. 45-53.

570 Balogh, C., Muskó, I.B., G-Tóth, L., Nagy, L., 2008. Quantitative trends of zebra mussels in
571 Lake Balaton (Hungary) in 2003-2005 at different water levels. *Hydrobiol.* 613, 57-69.

572 Balogh, C., Vlácilová, A., G-Tóth, L., Serfőző, Z., 2018. Dreissenid colonization during the
573 initial invasion of the quagga mussel in the largest Central European shallow lake, Lake
574 Balaton, Hungary. *J. Great Lakes Res.* 44, 114–125.

575 Babarro, J.M.F., Reiriz, M.J.F., Labarta, U., 2008. Secretion of byssal threads and attachment
576 strength of *Mytilus galloprovincialis*: the influence of size and food availability. *J. Mar.*
577 *Biol. Assoc. UK* 88, 783-791

578 Beggel, S., Cerwenka, A.F., Brandner, J., Geist J., 2015. Shell morphological versus genetic
579 identification of quagga mussel (*Dreissena bugensis*) and zebra mussel (*Dreissena*
580 *polymorpha*). *Aquat. Inv.* 10, 93-99.

581 Bell, E.C., Gosline, J.M., 1997. Strategies for life in flow: tenacity, morphometry, and
582 probability of dislodgment of two *Mytilus* species. *Mar. Ecol. Prog. Ser.* 159, 197–208.

583 Berkman, P.A., Haltuch, M.A., Tichich, E., Garton, D.W., Kennedy, G.W., Gannon, J.E.,
584 Mackey, S.D., Fuller, J.A., Liebenthal, D.L., 1998. Zebra mussels invade Lake Erie muds.
585 *Nature* 393, 27–28.

586 Berkman, P.A., Garton, D.W., Haltuch, M.A., Kennedy, G.W., Febo, L.R., 2000. Habitat shift
587 in invading species: Zebra and quagga mussel population characteristics on shallow soft
588 substrates. *Biol. Inv.* 2, 1–6.

589 Bidwell, J.R., 2010. Range expansion of *Dreissena polymorpha*: a review of major dispersal
590 vectors in Europe and North America. In: Van der Velde, G., Rajagopal, S., Bij de Vaate,
591 A. (Eds.), *The zebra mussel in Europe*. Backhuys Publishers, Leiden, Margraf Publishers,

592 Weikersheim, Germany. pp. 69–78.

593 Bij de Vaate, A., 1991. Distribution and aspects of population dynamics of the zebra mussel,
594 *Dreissena polymorpha* (Pallas, 1771), in the Lake IJsselmeer area (The Netherlands).
595 *Oecologia* 86, 40-50.

596 Bij de Vaate, A., van der Velde, G., Leuven, S.E.W.R., Heiler, K.C.M., 2013. Spread of the
597 quagga mussel (*Dreissena rostriformis bugensis*) in western Europe. In: Nalepa, T.F.,
598 Schloesser, D.W. (Eds.), Quagga and zebra mussels: biology, impacts, and control. CRC
599 Press, Boca Raton, Florida, USA, pp. 83-92.

600 Bij de Vaate, A., Jansen, E.A., 2009. De verspreiding van de quaggamossel in de
601 Rijkswateren. *Spirula* 368, 72-75.

602 Bódis, E., Tóth, B., Sousa, R., 2014. Impact of *Dreissena* fouling on the physiological
603 condition of native and invasive bivalves: interspecific and temporal variations. *Biol. Inv.*
604 16, 1373-1386.

605 Casper, A.F., Johnson, L.E., 2010. Contrasting shell/tissue characteristics of *Dreissena*
606 *polymorpha* and *Dreissena bugensis* in relation to environmental heterogeneity in the St.
607 Lawrence River. *J. Great Lakes Res.* 36, 184–189.

608 Clarke, M., Mcahon, R.F., 1996. Effects of current velocity on byssal-thread production by
609 the freshwater mussel, *Dreissena polymorpha*. *Can. J. Zool.* 74, 63–69.

610 Claxton, W.T., Mackie, G.L., 1998. Seasonal and depth variation in gametogenesis and
611 spawning of *Dreissena polymorpha* and *Dreissena bugensis* in eastern Lake Erie. *Can. J.*
612 *Zool.* 76, 2010–2019.

613 Coakley, J.P., Brown, G.R., Ioannou, S.E., Charlton, M.N., 1997. Colonization patterns and
614 densities of zebra mussel *Dreissena* in muddy offshore sediments of western Lake Erie,
615 Canada. *Water Air Soil Pollut.* 99, 623–632.

616 Collas, F.P.L., Karatayev, A.Y., Burlakova, L.E., Leuven, R.S.E.W., 2018. Detachment rates

617 of dreissenid mussels after boat hull-mediated overland dispersal. *Hydrobiologia* 810(1),
618 77-84.

619 Côté, I.M., 1995. Effects of predatory crab effluent on byssus production in mussels. *J Exp.*
620 *Mar. Biol. Ecol.* 188, 233–241.

621 Czarnołęski, M., Kozłowski, J., Kubajak, P., Lewandowski, K., Müller, T., Stańczykowska,
622 A., Surówka, K., 2006. Crosshabitat differences in crush resistance and growth pattern of
623 zebra mussels (*Dreissena polymorpha*): effects of calcium availability and predator
624 pressure. *Arch. Hydrobiol.* 165, 191–208.

625 De Jong, J., Bij de Vaate, A., 1989. Dams and the environment: The Zuiderzee damming.
626 International Commission on Large Dams (IOCLD) Bulletin, pp. 66. Paris.

627 De Lucas Pardo, M.A., Sarpe, D., Winterwerp, J.C., 2015. Effect of algae on flocculation of
628 suspended bed sediments in a large shallow lake. Consequences for ecology and sediment
629 transport processes. *Ocean Dynam.* 65, 889-903.

630 Dermott, R., Dow, J., 2008. Changing benthic fauna of Lake Erie between 1993 and 1998. In:
631 Munawar, M., Heath, R. (Eds.), *Checking the Pulse of Lake Erie*. Goodwords Books, New
632 Delhi, India, pp. 409–438.

633 De Leeuw, J.J., Van Eerden, M.R., 1992. Size selection in diving tufted ducks *Aythya fuligula*
634 explained by differential handling of small and large mussels. *Ardea* 80, 353-362.

635 De Leeuw, J.J., Van Eerden, M.R., 1995. *Duikeenden in het IJsselmeergebied*. Herkomst,
636 populatie-structuur, biometrie, rui, conditie en voedselkeuze. *Flevobericht* 373, RWS
637 Directie IJsselmeergebied, Lelystad.

638 De Zwaan, A., Zande, D.I., 1972. Body distribution and seasonal changes in the glycogen
639 content of the common sea mussel *Mytilus edulis*. *Comp. Biochem. Physiol.* 43, 53-58.

640 D’Hont, A., Gittenberger, A., Hendricks, A.J., Leuven, R.S.E.W., 2018. Drivers of dominance
641 shifts between invasive Ponto-Caspian dreissenids *Dreissena polymorpha* (Pallas, 1771)

642 and *Dreissena rostriformis bugensis* (Andrusov, 1897). *Aquat. Inv.* 13, 449-462.

643 Diggins, T.P., 2001. A seasonal comparison of suspended sediment filtration by quagga
644 (*Dreissena bugensis*) and zebra (*D. polymorpha*) mussels. *J Great Lakes Res* 27, 457–466.

645 Dolmer, P., 1998. The interactions between bed structure of *Mytilus edulis L.* and the predator
646 *Asterias rubens L.* *J Exp. Mar. Biol. Ecol.* 228, 137–150.

647 Entz, G., Sebestyén, O., 1942. The life of Lake Balaton. Királyi Magyar Természettudományi
648 Társulat, Budapest, Hungary.

649 Entz, B. 1981. Windgeschwindigkeit, Schwebstoffmengen und Lichtverhältnisse im
650 Balatonsee. *BFBericht* 42, 69–78.

651 Freeman, A.S., Byers, J.E., 2006. Divergent induced responses to an invasive predator in
652 marine mussel populations. *Science* 313, 831–833.

653 Gardner, J.P.A., Skibinski, D.O.F., 1991. Biological and physical factors influencing
654 genotype-dependent mortality in hybrid mussel populations. *Mar. Ecol. Prog. Ser.* 71, 235–
655 243.

656 Grutters, B.M.C., Verhofstad, M.J.J.M., van der Velde, G., Rajagopal, S., Leuven, R.S.E.W.,
657 2012. A comparative study of byssogenesis on zebra and quagga mussels: the effects of
658 water temperature, salinity and light-dark cycle. *Biofouling* 28, 121–129.

659 Harger, J.R.E., 1970. The effect of wave impact on some aspects of the biology of sea
660 mussels. *Veliger* 12, 401–414.

661 Heiler, K.C.M., Brandt, S., Albrecht, C., Hauffe, T., Wilke, T., 2012. A new approach for
662 dating introduction events of the quagga mussel (*Dreissena rostriformis bugensis*). *Biol*
663 *Inv.* 14, 1311–1316.

664 Istvánovics, V., Clement, A., Somlyódy, L., Specziár, A., G-Tóth, L., Padisák, J., 2007.
665 Updating water quality targets for shallow Lake Balaton (Hungary), recovering from
666 eutrophication. *Hydrobiologia* 581, 305-318.

667 Jarvis, P., Dow, J., Dermott, R., Bonnell, R., 2000. Zebra (*Dreissena polymorpha*) and quagga
668 mussel (*Dreissena bugensis*) distribution and density in Lake Erie 1992–1998. Can Tech
669 Rep. Fish. Aquat. Sci. 2304, 1-46.

670 Karatayev, A.Y., Burlakova, L.E., Padilla, D.K., 1998. Physical factors that limit the
671 distribution and abundance of *Dreissena polymorpha* (Pall.). J Shellfish Res. 17, 1219–
672 1235.

673 Karatayev, A.Y., Burlakova, L.E., Mastitsky, S.E., Padilla, D.K., Mills, E.L., 2011.
674 Contrasting rates of spread of two congeners, *Dreissena polymorpha* and *Dreissena*
675 *rostriformis bugensis* at different spatial scales. J. Shellfish. Res. 30, 923–931.

676 Karatayev, A.Y., Mastitsky, S.E., Padilla, D.K., Burlakova, L.E., Hajduk, M.M., 2010.
677 Differences in growth and survivorship of zebra and quagga mussels: size matters.
678 Hydrobiologia 668, 183-194.

679 Karatayev, A.Y., Burlakova, L.E., Padilla, D.K., 2013. In Quagga and zebra mussels: biology,
680 impacts, and control. Nalepa, T.F., Schloesser, D.W. (Eds.), General overview of zebra and
681 quagga mussels: what we know and do not know. CRC Press, Boca Raton, Florida, USA,
682 pp. 695–703.

683 Kemp, J.S., Aldridge, D.C., 2018. Comparative functional responses to explain the impact of
684 sympatric invasive bivalves (*Dreissena spp.*) under different thermal regimes. J. Mollus.
685 Stud. 84, 175-181.

686 Kerambrun, E., Delahaut, L., Geffard, A., David, E., 2018. Differentiation of sympatric zebra
687 and quagga mussels in ecotoxicological studies: A comparison of morphometric data, gene
688 expression, and body metal concentrations. Ecol. Environ. Safety 154, 321-328.

689 Kobak, J., 2001. Light, gravity and conspecifics as cues to site selection and attachment
690 behaviour of juvenile and adult *Dreissena polymorpha* Pallas, 1771. J Moll. Stud. 67, 183–
691 189.

692 Kobak, J., 2006. Factors influencing the attachment strength of *Dreissena polymorpha*
693 (Bivalvia). *Biofouling* 22, 141–150.

694 Kobak, J., Poznańska, M., Kakareko, T., 2009. Effect of attachment status and aggregation on
695 behaviour of the zebra mussel, *Dreissena polymorpha*, Bivalvia. *J. Moll. Stud.* 75, 109-
696 117.

697 Leonard, G.H., Bertness, M.D., Yund, P.O., 1999. Crab predation, waterborne cues, and
698 inducible defences in the blue mussel *Mytilus edulis*. *Ecology* 80, 1–14.

699 Lóczy, L., 1894. A Balaton környékének geológiai történetéről és jelenlegi geológiai
700 jelentőségéről. *Földrajzi Közlöny* 22, 1-62.

701 Mandemakers, J., 2013. The impact of suspended sediments and phosphorous scarcity on
702 zebra mussel and quagga mussel growth. Wageningen. Master's thesis, Utrecht University
703 / NIOO-KNAW. pp. 1-50.

704 Madon, S.P., Schneider, D.W., Stoeckel, J.A., Sparks, R.E., 1998. Effects of inorganic
705 sediment and food concentrations on energetic processes of the zebra mussel, *Dreissena*
706 *polymorpha*: implication for growth in turbid rivers. *Can. J. Fish. Aquat. Sci.* 55, 401-413.

707 Majoros, G., 2009. Invazív kagylófajok terjeszkedése a Balatonban: esetismertetés és a
708 probléma felvetése. *Halászatfejlesztés. Fish. Aquacult. Dev.* 32, 57-64.

709 Matthews, J., Van der Velde, G., Bij de Vaate, A., Collas, F.P.L., Koopman, K.R., Leuven,
710 R.S.E.W., 2014. Rapid range expansion of the invasive quagga mussel in relation to zebra
711 mussel presence in The Netherlands and Western Europe. *Biol. Inv.* 16, 23-42.

712 Máté, F., 1987. Mapping of recent sediments in Lake Balaton. *A Magyar Állami Földtani*
713 *Intézet évi jelentése az 1985. évről.* 367–379.

714 Metz, O., Temmen, A., von Oheimb, C.M., Albrecht, C., Schubert, P., Wilke, T., 2018.
715 Invader vs. invader: intra- and interspecific competition mechanisms in zebra and quagga
716 mussels. *Aquat. Inv.* 13, 473-480.

717 Miller, G., Wagner, F., 1978. Holocene carbonate evolution in Lake Balaton (Hungary) a
718 response to climate and impact. Special Publ. Internat Assoc. Sedimentol. 2, 57-81.

719 Mills, E.L., Rosenberg, G., Spidle, A.P., Ludyanskiy, M., Pligin, Y., May, B., 1996. A review
720 of the biology and ecology of the quagga mussel (*Dreissena bugensis*), a second species of
721 freshwater *Dreissenid* introduced to North America. Am. Zool. 36, 271–286.

722 Molloy, D.P., Karatayev, A.Y., Burlakova, L.E., Kurandina, D.P., Laruelle, F., 1997. Natural
723 enemies of zebra mussels: predators, parasites, and ecological competitors. Rev. Fish. Sci.
724 5, 27–97.

725 Molloy, D.P., bij de Vaate, A., Wilke, T., Giamberini, L., 2007. Discovery of *Dreissena*
726 *rostriformis bugensis* (Andrusov 1897) in Western Europe. Biol. Inv. 9, 871–874.

727 Naddafi, R., Rudstam, L.G., 2013a. Predator-induced behavioural defences in two
728 competitive invasive species: the zebra mussel and the quagga mussel. Anim. Behav. 86,
729 1275–1284.

730 Naddafi, R., Rudstam, L.G., 2013b. Predator diversity effects in an exotic freshwater food
731 web. Plos One 8, e72599.

732 Nagarajan, R., Lea, S.E.G., Goss-Custard J.D., 2006. Seasonal variations in mussel, *Mytilus*
733 *edulis* L. shell thickness and strength and their ecological implications. J. Exp. Mar. Biol.
734 Ecol. 339, 241–250.

735 Nalepa, T.F., Fanslow, D.L., Pothoven, S.A., 2010. Recent changes in density, biomass,
736 recruitment, size structure, and nutritional state of *Dreissena* populations in southern Lake
737 Michigan. J. Great Lakes Res. 36, 5–19.

738 Noordhuis, R., 2007. Water quality and ecological changes in Lake Markermeer-IJmeer.
739 Landschap 2014, 13-21.

740 Oreska, M.P., Aldridge, D.C., 2010. Estimating the financial costs of freshwater invasive
741 species in Great Britain: a standardized approach to invasive species costing. Biol Inv. 13,

742 305–319.

743 Orlova, M.I., Muirhead, J.R., Antonov, P.I., 2004. Range expansion of quagga mussels
744 *Dreissena rostriformis bugensis* in the Volga River and Caspian Sea basin. *Aquat. Ecol.*
745 38, 561–573.

746 Orlova, M.I., Therriault, T.W., Antonov, P.I., Shcherbina, G.K., 2005. Invasion ecology of
747 quagga mussels (*Dreissena rostriformis bugensis*): A review of evolutionary and
748 phylogenetic impacts. *Aquat. Ecol.* 39, 401–418.

749 Patterson, M.W.R., Ciborowski, J.J.H., Barton, D.R., 2005. The distribution and abundance of
750 *Dreissena* species (Dreissenidae) in Lake Erie, 2002. *J. Great Lakes Res.* 31, 223-237.

751 Palais, F., Mouneyrac, C., Dedourge-Geffard, O. Giambérini. L., Biagianti-Risbourg, S.,
752 Geffard, A., 2011. One-year monitoring of reproductive and energy reserve cycles in
753 transplanted zebra mussels (*Dreissena polymorpha*). *Chemosphere* 83, 1062-1073.

754 Penning, W.E., Pozzato, L., Vijverberg, T., Noordhuis, R., Bij de Vaate, A., Van Donk, E.,
755 Dionisio Pires, M., 2013. Effects of suspended sediments on seston food quality for zebra
756 mussels in Lake Markermeer, The Netherlands. *Inland Waters* 3, 437-450.

757 Peyer, S.M., McCarthy, A.J., Lee, C.E., 2009. Zebra mussels anchor byssal threads faster and
758 tighter than quagga mussels in flow. *J Exp. Biol.* 212, 2027–2036.

759 Peyer, S.M., Hermanson, J.C., Lee, C.E., 2011. Effects of shell morphology on mechanics of
760 zebra and quagga mussel locomotion. *J. Exp. Biol.* 214, 2226-2236.

761 Pimentel, D., Zuniga, R., Morrison, D., 2005. Update on the environmental and economic
762 costs associated with alien-invasive species in the United States. *Ecol. Econom.* 52, 273-
763 288.

764 Ponyi, J., 1994. Abundance and feeding of wintering and migrating aquatic birds in two
765 sampling areas of Lake Balaton in 1983-85. *Hydrobiologia* 279/280, 63-69.

766 Quinn, A., Gallardo, B., Aldridge, D.C., 2013. Quantifying the ecological niche overlap

767 between two interacting invasive species: the zebra mussel (*Dreissena polymorpha*) and
768 the quagga mussel (*Dreissena rostriformis bugensis*). *Aquat. Conserv. Mar. Freshwat.*
769 *Ecosyst.* 24, 324–337.

770 Rajagopal, S., Van der Velde, G., Van der Gaag, M., Jenner, H.A., 2005. Factors influencing
771 the upper temperature tolerances of three mussel species in a brackish water canal: size,
772 season and laboratory protocols. *Biofouling* 21, 87–97.

773 Rajagopal, S., Venugopalan, V.P., van der Velde, G., Jenner, H.A., 2006. Mussel colonization
774 of a high flow artificial benthic habitat: Byssogenesis holds the key. *Mar. Environ. Res.* 62,
775 98-115.

776 Rajagopal, S., Van der Velde, G., Jenner, H.A., Van der Gaag, M., Kempers, A.J., 1996.
777 Effects of temperature, salinity and agitation on byssus thread formation of zebra mussel;
778 *Dreissena polymorpha*. *Neth J. Aquat. Ecol.* 30, 187–195.

779 Reimer, O., Tedengren, M., 1996. Phenotypical improvement of morphological defences in
780 the mussel *Mytilus edulis* induced by exposure to the predator *Asterias rubens*. *Oikos* 75,
781 383–390.

782 Ricciardi, A., Whoriskey, F., 2004. Exotic species replacement: Shifting dominance of
783 dreissenid mussels in the Soulanges Canal, upper St. Lawrence River, Canada. *J North*
784 *Am. Benthol. Soc.* 23, 507–514.

785 Ricciardi, A., MacIsaac, H.J., 2011. Impacts of biological invasions on freshwater
786 ecosystems. In: Richardson, D. M. (Eds.), *Fifty Years of Invasion Ecology: The Legacy of*
787 *Charles Elton*. Wiley-Blackwell, West Sussex, UK, pp. 211-224.

788 Roe, S.L., MacIsaac, H.J., 1997. Deepwater population structure and reproductive state of
789 quagga mussels (*Dreissena bugensis*) in Lake Erie. *Can. J. Fish. Aquat. Sci* 54, 2428–
790 2433.

791 Sebestyén, O., 1938. Colonization of two new fauna-elements of Pontus-origin (*Dreissena*

792 *polymorpha* Pall. and *Corophium curvispinum* G. O. Sars forma *devium* Wundsch) in Lake
793 Balaton. Verh. Int. Ver. Theor. Angew. Limnol. 8, 169–182.

794 Smit, H., Dudok van Heel, E., 1992. Methodical aspects of a simple allometric biomass
795 determination of *Dreissena polymorpha* aggregations. In: Neumann, D., Jenner, H.A.
796 (Eds.), The zebra mussel *Dreissena polymorpha*. Ecology, biological monitoring and first
797 applications in the water quality management. Limnol. Aktuell., Stuttgart, Germany:
798 Fischer Verlag 4, 79–86.

799 Smith, L.D., Jennings, J.A., 2000. Induced defensive responses by the bivalve *Mytilus edulis*
800 to predators with different attack modes. Mar. Biol. 136, 461–469.

801 Sokal, R.R., Rohlf, F.J., 1995. Biometry, 3rd edn. WH Freeman and Company, New York.

802 Somogyi, B., Pálffy, K., V-Balogh, K., Botta-Dukát, Z., Vörös, L., 2017. Unusual behaviour
803 of phototrophic picoplankton in turbid waters. Plos One 12 (3), e0174316.

804 Specziár, A., Tölg, L., Bíró, P., 1997. Feeding strategy and growth of cyprinids in the littoral
805 zone of Lake Balaton. J. Fish Biol. 51, 1109-1124.

806 Sprung, M., 1995. Physiological energetics of the zebra mussel *Dreissena polymorpha* in
807 lakes. I. Growth and reproductive effort. Hydrobiologia. 304,117-132.

808 Stoeckmann, A., 2003. Physiological energetics of Lake Erie dreissenid mussels: a basis for
809 the displacement of *Dreissena polymorpha* by *Dreissena bugensis*. Can. J. Fish Aquat. Sci.
810 60, 126–134.

811 Stoeckmann, A., Garton, W., 2001. Flexible energy allocation in zebra mussels (*Dreissena*
812 *polymorpha*) in response to different environmental conditions. J. North Am. Benthol Soc.
813 20, 486–500.

814 Strayer, D.L., Malcom, H.M., 2013. General overview of zebra and quagga mussels: what we
815 know and do not know. In: Nalepa T.F., Schloesser, D.W. (Eds.), Quagga and zebra
816 mussels: biology, impacts, and control. CRC Press, Boca Raton, Florida, USA. pp. 695–

817 703.

818 Strayer, D.L., Adamovich, B.V., Adrian, R., Aldridge, D.C., Balogh, C., Burlakova, L., G.-
819 Tóth, L., Hetherington, A.L., Jones, T., Karatayev, A., Madill, J.B., Makarevich, O.A.,
820 Marsden, J.E., Martel, A.L., Minchin, D., Nalepa, T.F., Noordhuis, R., Fried-Petersen, H.,
821 Robinson, T.J., Rudstam, L.G., Schwalb, A.N., Smith, D.R., Steinman, A.D., Jeschke, J.M.
822 2019. Long-term population dynamics of zebra and quagga mussels (*Dreissena*
823 *polymorpha* and *D. rostriformis bugensis*): a cross-system analysis. *Ecosphere*, 10, 1-22.

824 Szekeres, J., Szalóky, Z., Bodolai, K. 2008. Első adat a *Dreissena bugensis* (Andrusov, 1897)
825 (*Bivalvia: Dreissenidae*) magyarországi megjelenéséről. 26, 33-36.

826 Tátrai, I., Istvánovics, V., G-Tóth, L., Kóbor, I., 2008. Management measures and long-term
827 water quality changes in Lake Balaton (Hungary). *Fund. Appl. Limnol.* 172, 1–11.

828 Thorp, J.H., Delong, M.D., Casper, A.F., 1998. In situ experiments on predatory regulation of
829 a bivalve mollusc (*Dreissena polymorpha*) in the Mississippi and Ohio Rivers. *Freshwat.*
830 *Biol.* 39, 649–664.

831 Van Benthem Jutting, W.S.S., 1954. Mollusca. In: de Beaufort De Boer, L.F., Helder, D.
832 (Eds.), *Veranderingen in de flora en fauna van de Zuiderzee (thans IJsselmeer) na de*
833 *afsluiting in 1932. the Netherlands*., pp. 233-252.

834 Van der Velde, G., Rajagopal, S., Bij de Vaate, A., 2010. In: Van der Velde, G., Rajagopal,
835 S., Bij de Vaate, A. (Eds.), *The zebra mussel in Europe. From zebra mussels to quagga*
836 *mussels: an introduction to the Dreissenidae* Backhuys Publishers, Leiden, Margraf
837 Publishers, Weikersheim, Germany, pp. 1–10.

838 Van Eerden, M.R., De Leeuw, J.J., Munsterman, M.J., 1997. Factors determining the
839 availability of Zebra Mussels *Dreissena polymorpha* for diving ducks: evidence for a
840 possible feed-back mechanism between predation pressure and long-term prey availability.
841 In: Van Eerden, M. R. (Eds.), *Patchwork. Patch use, habitat exploitation and carrying*

842 capacity for water birds in Dutch freshwater wetlands. Ministry of Transport and Public
843 Works, The Netherlands, pp. 265-282.

844 Van Handel, E., 1965. Estimation of glycogen in small amounts of tissue. *Analyt Biochem* 11,
845 256-265.

846 Van Rijn, S., Bovenberg, M., Hasenaar, K., Roos, M., Van Eerden, M.R., 2012. Voedsel van
847 overwinterende duikeenden in het IJsselmeergebied. Rapport Delta Milieu, Culemborg.

848 Vijverberg T., Winterwerp J.C., Aarninkhof S.G.J., Drost H. 2011. Fine sediment dynamics in
849 a shallow lake and implication for design of hydraulic works. *Ocean Dynam.* 61, 187-202.

850 Watkins, J.M., Dermott, R., Lozano, S.J., Mills, E.L., Rudstam, L.G., Scharold, J.V., 2007.
851 Evidence for remote effects of dreissenids mussels on the amphipod *Diporeia*: Analysis of
852 Lake Ontario benthic surveys, 1997–2003. *J. Great Lakes Res.* 33, 642–657.

853 Willis, G.L., Skibinski, D.O., 1992. Variation in strength of attachment to the substrate
854 explains differential mortality in hybrid mussel (*Mytilus galloprovincialis* and *Mytilus*
855 *edulis*) populations. *Mar. Biol.* 112, 403–408.

856 Witman, J.D., Suchanek, T.H., 1984. Mussels in flow: drag and dislodgement by epizoans.
857 *Mar. Ecol. Prog. Ser.* 16, 59–268.

858 Zhulidov, A.V., Kozhara, A.V., Scherbina, G.H., Nalepa, T.F., Protasov, A., Afanasiev, S.A.,
859 Pryanichnikova, E.G., Zhulidov, A.A., Gurtovaya, T.Y., Pavlov, D.F., 2010. Invasion
860 history, distribution, and relative abundances of *Dreissena bugensis* in the old world: A
861 synthesis of data. *Biol. Inv.* 12, 1923–1940.

862

863

864 **Figure captions**

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

868 Fig. 2. Soft tissue dry weight (DW) increments per unit length of zebra (solid lines) and
869 quagga mussels (dashed lines) in Lakes IJsselmeer (IJM) and Markermeer (MM) in 2008-
870 2012. The lines (\pm SE) are predicted by the General Linear Model. Asterisks (*) indicate
871 regression lines with slopes significantly differing between species. “X” marks indicate
872 regression lines significantly differing in their vertical position (valid for parallel slopes
873 only) between species. Note the log scale. See Table S3 for regression equations and
874 differences among years.

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

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

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

889 species. Note the log scale.

890 Fig. 6. Glycogen content in zebra and quagga mussels of various sizes collected from Lake

891 Balaton. Open symbols show single data points, solid symbols (with standard errors of the

892 mean) represent least squares (LS) means predicted by the General Linear Model.

893 Asterisks (*) indicate a significant difference between mussel species ($p < 0.001$).

894

895

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

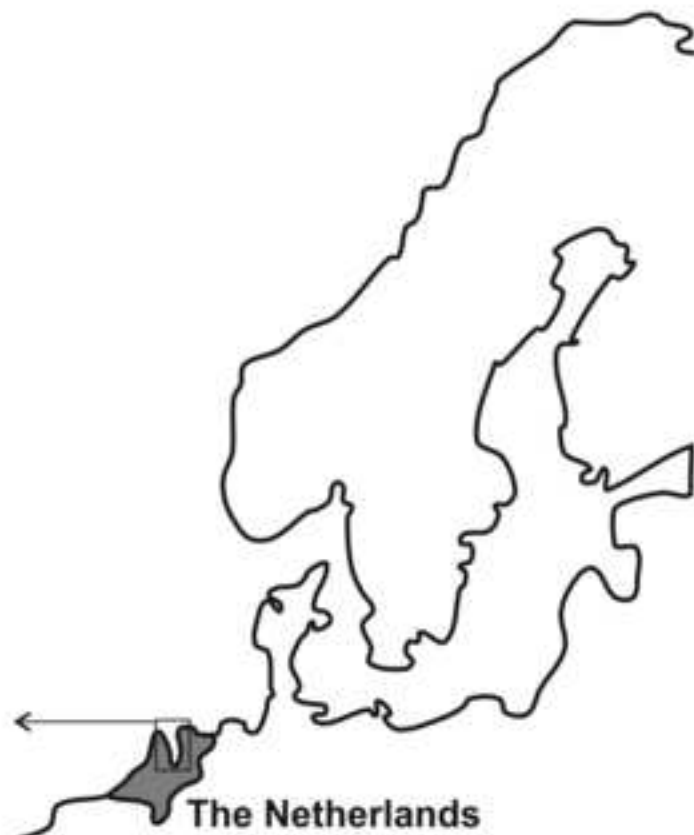
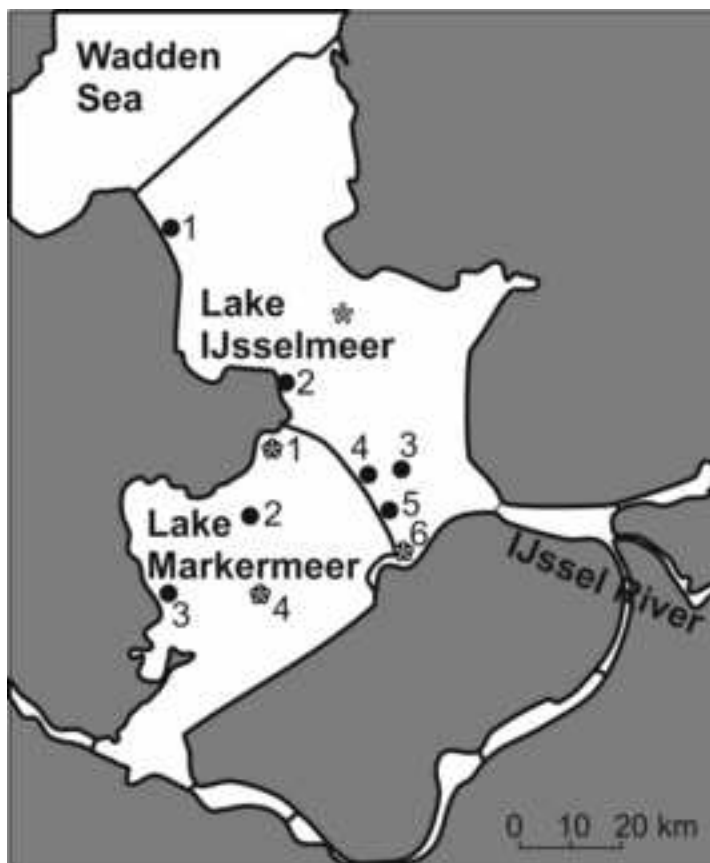
Lake	Year	PQ (%) mean \pm SD	DB (mL/m ²) mean \pm SD		
			North	Center	South
Lake	1999	0	97.7 \pm 235.4	196.2 \pm 425.1	582.7 \pm 504.5
IJsselmeer	2007	0	10.6 \pm 28.3	40.1 \pm 101.8	56.6 \pm 71.4
	2008	27 \pm 19			199.8 \pm 273.7
	2009	57 \pm 10			
	2010	48 \pm 24			
	2011	86 \pm 8			
	2012	95 \pm 6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

899 Sources: for Lake IJsselmeer and Markermeer: Matthews et al. (2014); A. bij de Vaate

900 (unpublished), for Lake Balaton: original data

Figure1

[Click here to download high resolution image](#)



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

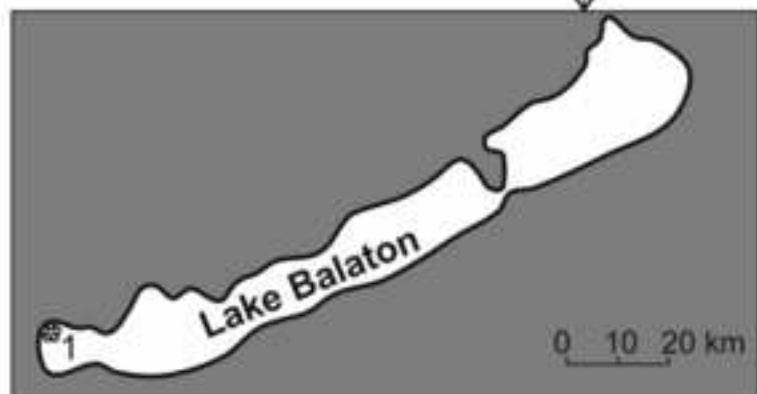


Figure2
[Click here to download high resolution image](#)

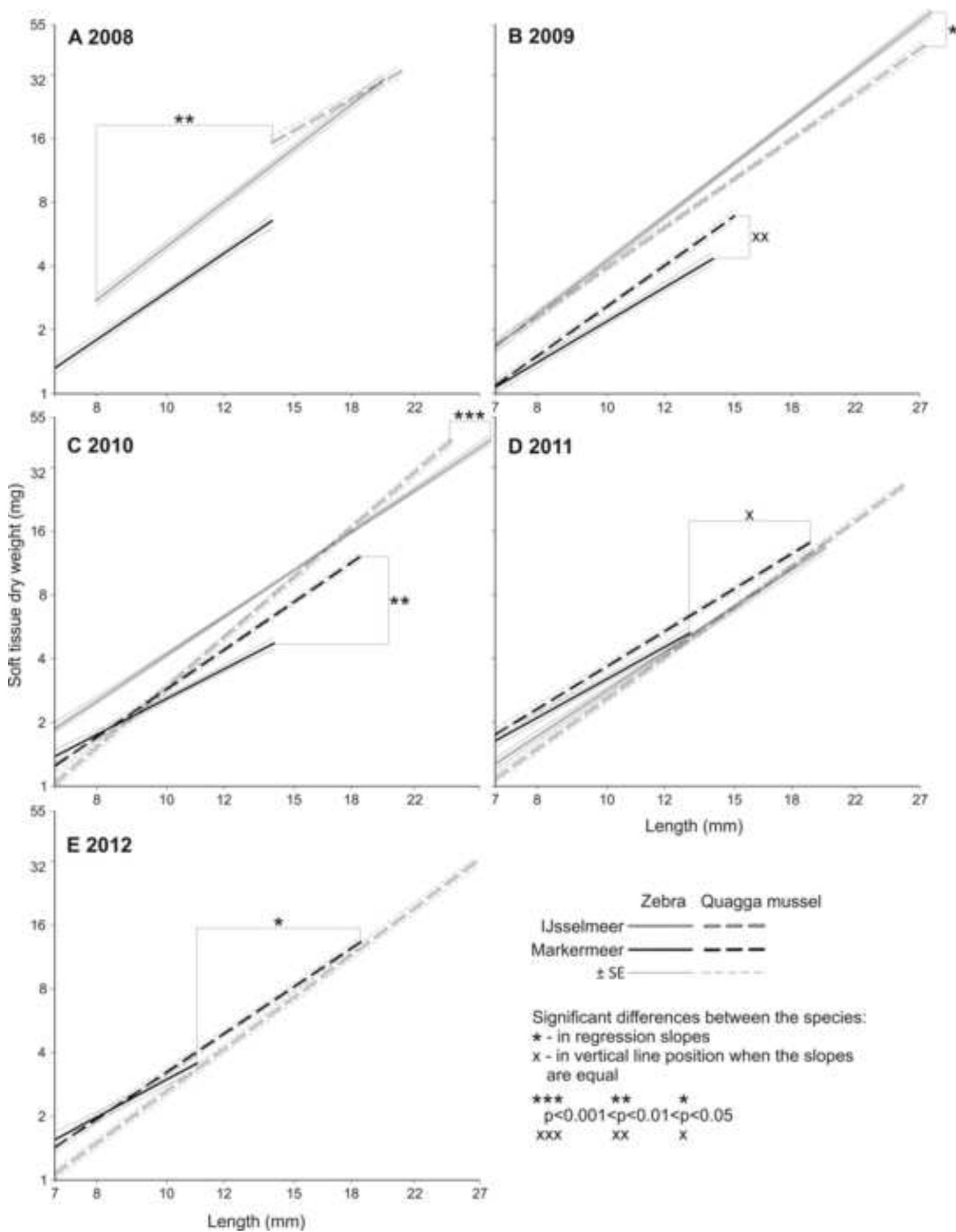


Figure3
[Click here to download high resolution image](#)

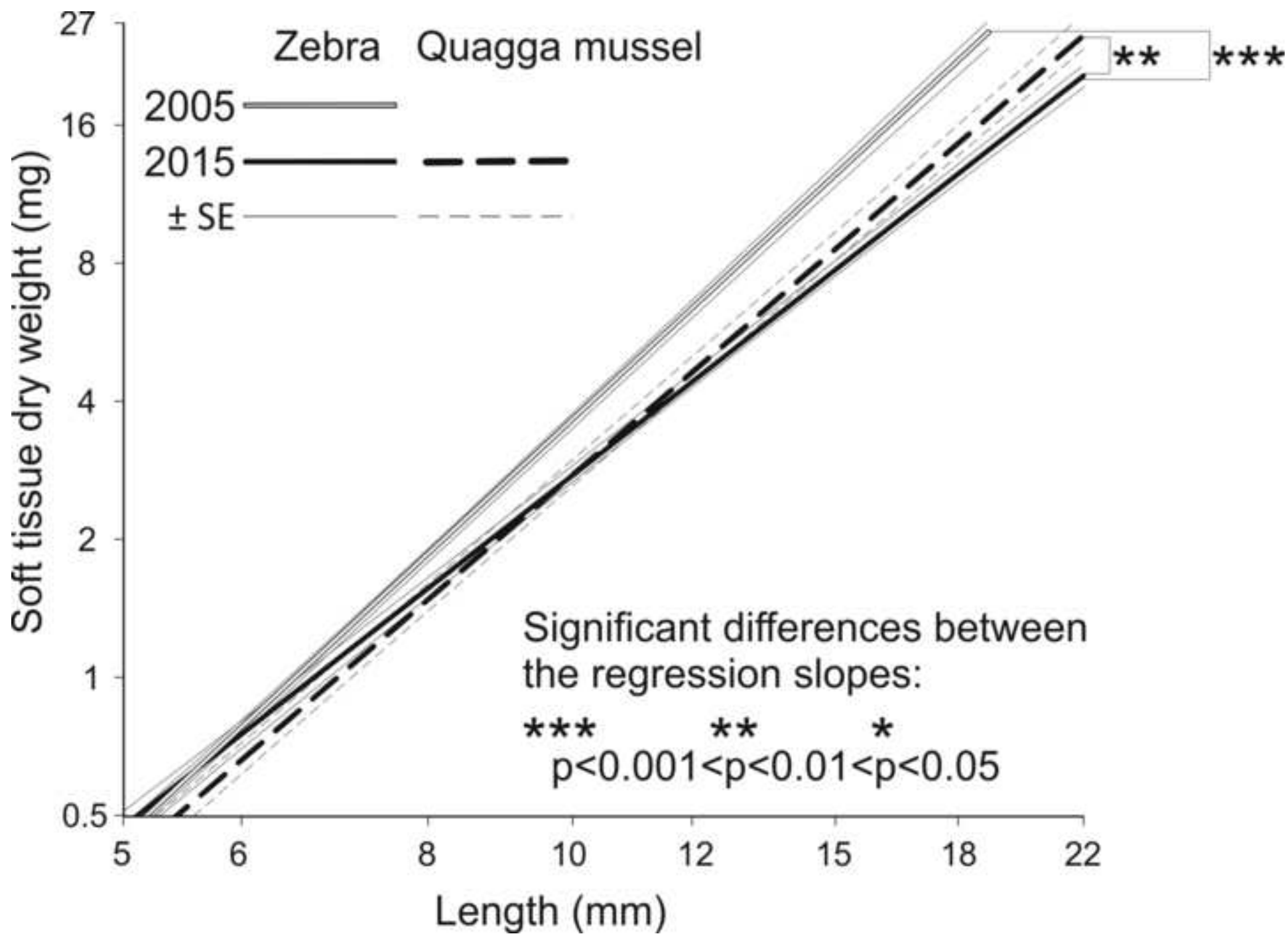


Figure4

[Click here to download high resolution image](#)

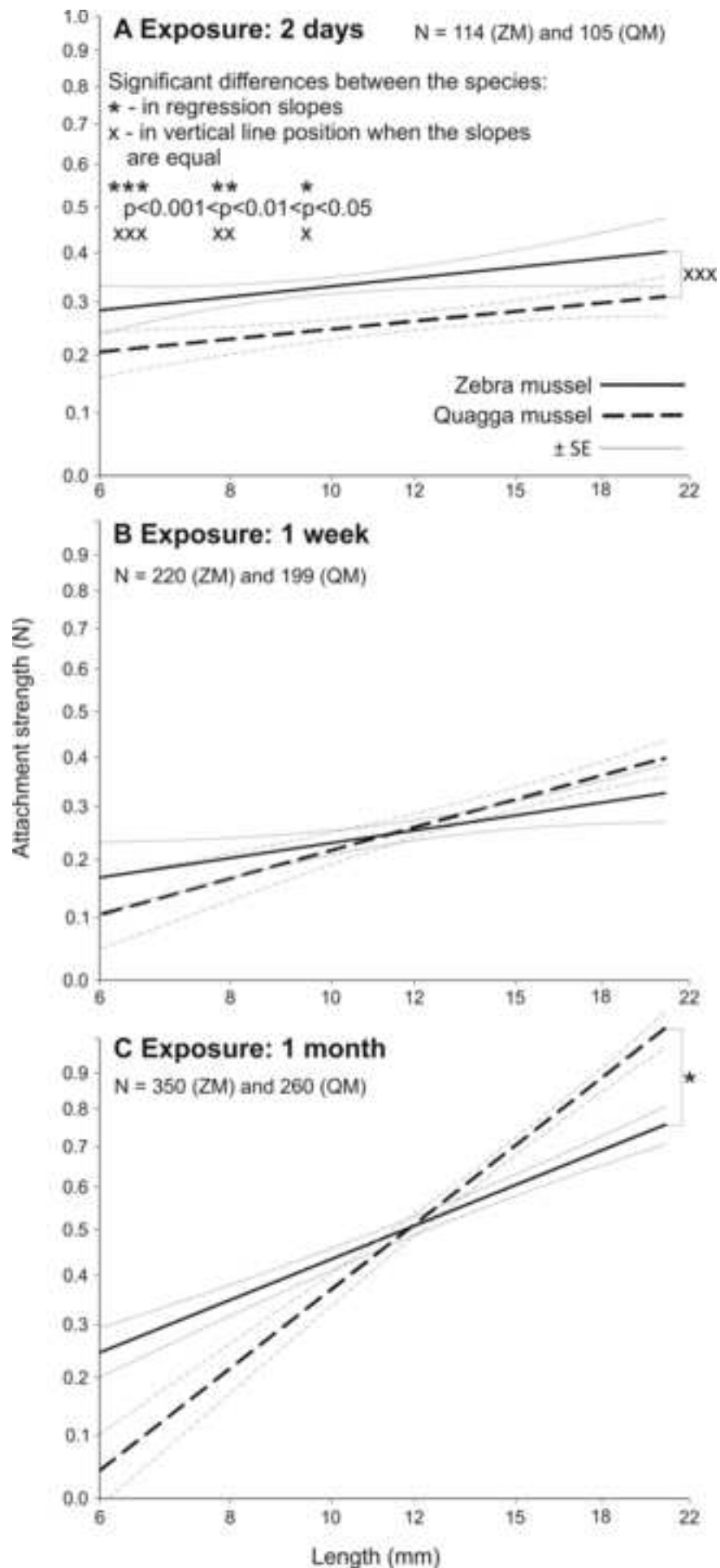


Figure5

[Click here to download high resolution image](#)

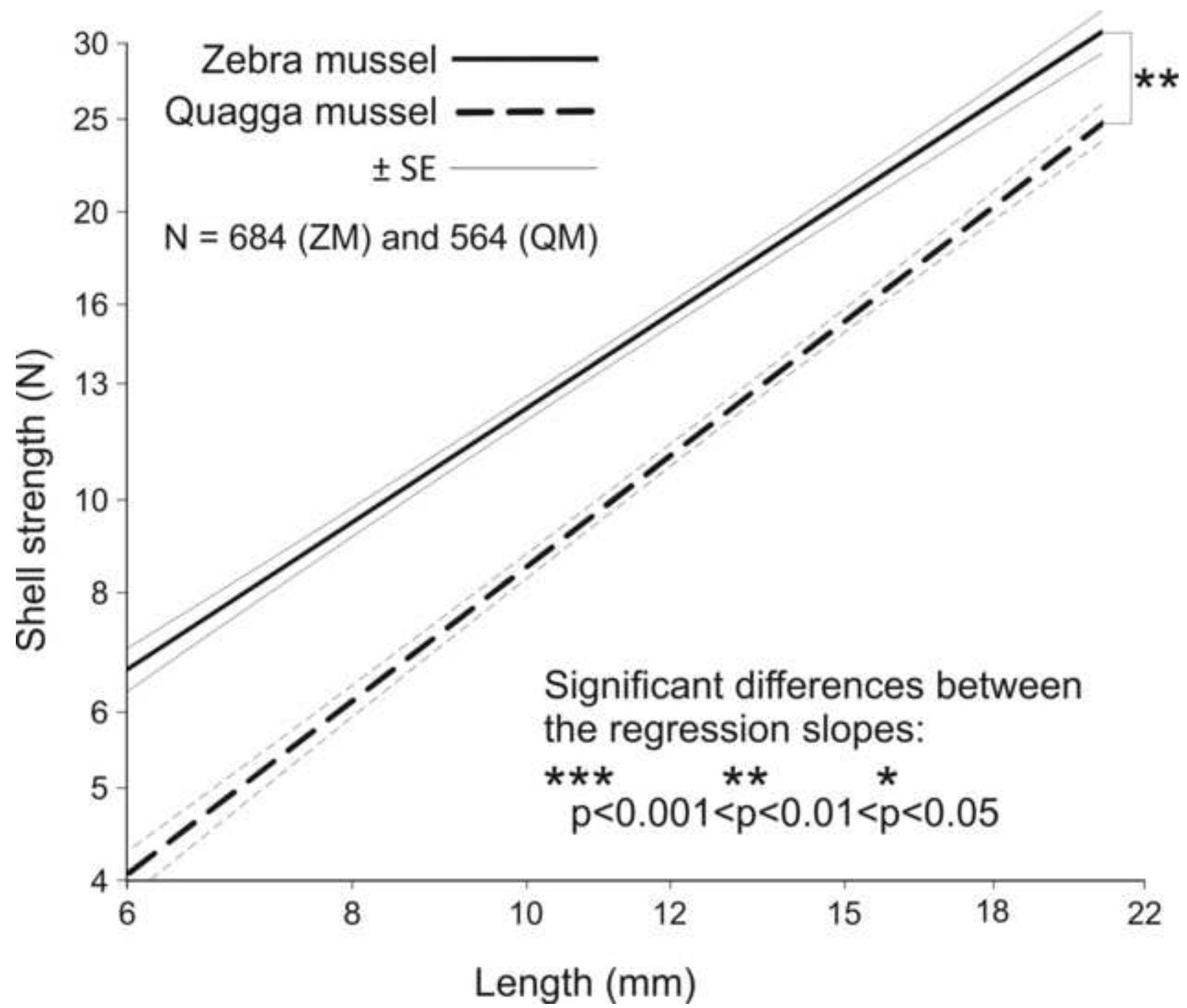


Figure6
[Click here to download high resolution image](#)

