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Research Article

Invader vs. invader: intra- and interspecific competition mechanisms in zebra and quagga mussels

Olivia Metz[1],*, Anja Temmen[1], Katharina C. M. von Oheimb[1,2], Christian Albrecht[1], Patrick Schubert[1] and Thomas Wilke[1]

[1]*Department of Animal Ecology & Systematics, Justus Liebig University Giessen, Heinrich-Buff-Ring 26 (IFZ), 35392 Giessen, Germany*
[2]*Life Sciences Department, The Natural History Museum, Cromwell Road, London, SW7 5BD, United Kingdom*

Author e-mails: olivia.metz@bio.uni-giessen.de (OM), anja1105@gmx.de (AT), katharina.von.oheimb@gmx.de (KO), christian.albrecht@allzool.bio.uni-giessen.de (CA), patrick.schubert@fg.bio.uni-giessen.de (PS), tom.wilke@allzool.bio.uni-giessen.de (TW)

**Corresponding author*

Abstract

The zebra mussel, *Dreissena polymorpha* (Pallas, 1771), is considered to be one of the world's worst invasive species with a large impact on local biodiversity and ecosystem services in Europe and North America. Recently, a large-scale displacement of the invasive zebra mussel by the similarly invasive quagga mussel, *Dreissena rostriformis* (Deshayes, 1838), is occurring in large parts of Western and Central Europe. While the exact reasons for the competitive advantage of the quagga mussel remain unknown, its potentially higher fitness might play a role. This replacement of one invasive species by a closely related invasive species offers a unique opportunity for unravelling patterns and processes of competition. To test whether the quagga mussel derives its competitive advantage from higher growth rates, a fully closed and controlled microcosm system was used to subject specimens of both species to different intensities of intraspecific and interspecific competition. The study revealed that both species reacted qualitatively similar to the different treatments. However, under all competition scenarios the quagga mussel showed substantially higher growth rates and larger growth ranges. Therefore, these characteristics might provide the quagga mussel with a higher flexibility in fluctuating environments and allow it to reach adult size earlier. This, in turn, can make the quagga mussel less prone to parasite pressure and other biological constraints during growth, and provides an advantage in the competition for space (hard substrates) and food.

Key words: *Dreissena polymorpha*, *Dreissena rostriformis*, Western Europe, growth rates, microcosm

Introduction

Invasive species are considered to be a major driver of biodiversity loss (e.g., Sala et al. 2009). They can have dire consequences for ecosystem services and may cause enormous economic damage (Pimentel et al. 2005; Charles and Dukes 2007; Connelly et al. 2007; Pejchar and Mooney 2009; Sousa et al. 2014). While today almost all ecosystems are affected by invasive species, brackish and freshwater systems are particularly vulnerable (e.g., Gherardi 2007; Gherardi et al. 2009).

The zebra mussel *Dreissena polymorpha* (Pallas, 1771) is one of the "100 of the World's Worst Invasive

Alien Species" (Global Invasive Species Database 2017). Native to the fresh and brackish waters of the Caspian and Black Sea drainage basins, it quickly spread throughout much of Europe after the construction of several inter-basin canals (e.g., Black Sea-Baltic Sea) at the end of the 18th and the beginning of the 19th century (Karatayev et al. 2007). The zebra mussel continues to spread throughout Europe and was, for example, first reported in the southern Balkans in 2010 (Wilke et al. 2010).

Only 30 years ago, the zebra mussel arrived in North America, most likely by release of its larvae with ship ballast water into Lake St. Clair near Detroit, Michigan (Hebert 1989). From there it quickly

spread throughout much of eastern North America and was recently discovered in Mexico (Naranjo-García and Castillo-Rodríguez 2017). However, despite hundreds of relevant studies, the invasion biology of the zebra mussel remains unclear. In fact, scientists only realized in 1991 that several years earlier a congener, the quagga mussel *Dreissena rostriformis* (Deshayes, 1838), had also been introduced into the Great Lakes (formerly known as *D. rostriformis bugensis*; for a revised nomenclature see Stepien et al. 2013). Confined to the northeastern part of the United States for decades, it was only recently reported from southwestern states (Stokstad 2007). At about the same time, the quagga mussel was also introduced into western Europe and quickly spread along major water pathways (Bij de Vaate et al. 2013; Heiler et al. 2013; Marescaux et al. 2016b). Moreover, it is outcompeting the zebra mussel in many sympatric populations (Heiler et al. 2012, 2013; Matthews et al. 2014; Marescaux et al. 2015, 2016b).

Strong competition between invasive species, in general, has been suggested before (e.g., Gérard et al. 2014), and the displacement of one invasive species by another is typically attributed to higher competitive strength in regard to resource exploitation (e.g., Braks et al. 2004). Specifically, Diggins et al. (2004) found that the quagga mussel is expelling the zebra mussel from hard substrate at sites in Lake Erie, while the latter is seeking refuge on macrophytes. In addition, the quagga mussel is able to colonize silty sediment and has a higher tolerance towards low oxygen concentrations, resulting in a better adaptation to the profundal zones of deep lakes (Karatayev et al. 1998, 2014).

Preliminary analyses indicate that growth rates of quagga and zebra mussels, as a proxy for competition strength, are differentially affected by, for example, food availability and water temperatures. Accordingly, the quagga mussel outcompetes the zebra mussel at low food concentrations (Baldwin et al. 2002) and at lower temperatures (Karatayev et al. 2010). However, despite ample research aimed at understanding the competitive advantage of the quagga mussel, the direct influence of intra- and interspecific competition on the growth rates of both species has not yet received adequate attention. The major goal of this study was therefore to experimentally assess the effects of different intra- and interspecific competition levels on growth rates of quagga and zebra mussels. To minimize the possibility of other factors influencing the outcome, we established a closed microcosm system using artificial waters with controlled biotic and abiotic conditions and a defined food supply.

Material and methods

Origin and acclimatization of mussels

All mussels were collected from the back waters of the River Main in Hanau-Steinheim in Germany (50.1103ºN; 8.9169ºE). The two species were kept separately in fish tanks and acclimated to laboratory conditions over four days.

Experimental setups

To examine the response of zebra and quagga mussels to changing densities of both intra- and interspecific competition, we studied their growth for 82 days. All experiments were conducted under fully controlled conditions in climate chambers (12h/12h light/dark cycle) at Justus Liebig University in Giessen, Germany (Figure 1). The basic experimental setup was inspired by Grudemo and Bohlin (2000).

Individual competition experiments were performed in 900 mL polyethylene terephthalate containers with 800 mL of artificial water, a base sand layer of 3 cm, and a small brick of aragonite-sand cement (3 × 2.5 × 1 cm) as hard substrate. Each container was also equipped with a wadding-wrapped foam filter with a pore size of 1 mm. Prior to the experiments, substrate and filter materials were inoculated with nitrifying bacteria (Sera Bio-Nitrivec, sera GmbH, Heinsberg, Germany). Artificial water supply was prepared from de-ionized water supplemented with biocalcium (Tropic Marin, Wartenberg, Germany) to a final concentration of 0.25 g L^{-1} to increase water hardness to approximately 8 °dH. Approximately 5 µL L^{-1} vitamin/highly unsaturated fatty acid (HUFA) solution was added to support the growth of nitrifying bacteria and to avoid potential dietary deficits. The latter solution consisted of 2 mL Lipovit (Tropic Marin), 5.25 g lecithin and 25 mL glycerin. Air supply was provided through glass pipettes. Both water flow and water exchange were achieved by using medical infusion bags and a tube through which fresh water ran into the container at a rate of approximately 200 mL per day. Excess water overflowed through a small hole near the top of each container. During the experiments, mussels were fed daily with one drop (approximately 50 µL) per container of Rotifer Diet® HD and two drops of Shellfish Diet® 1800 (both products of Reed Mariculture, Campbell, CA, USA), which is the food concentration we have been using for our mussel cultures since 2010. Water temperatures (mean of 19.1 °C, minimum 18 °C, maximum 22 °C) were recorded with Hobo Pendant® Temperature/Light Data Loggers (Onset, Bourne, MA, USA).
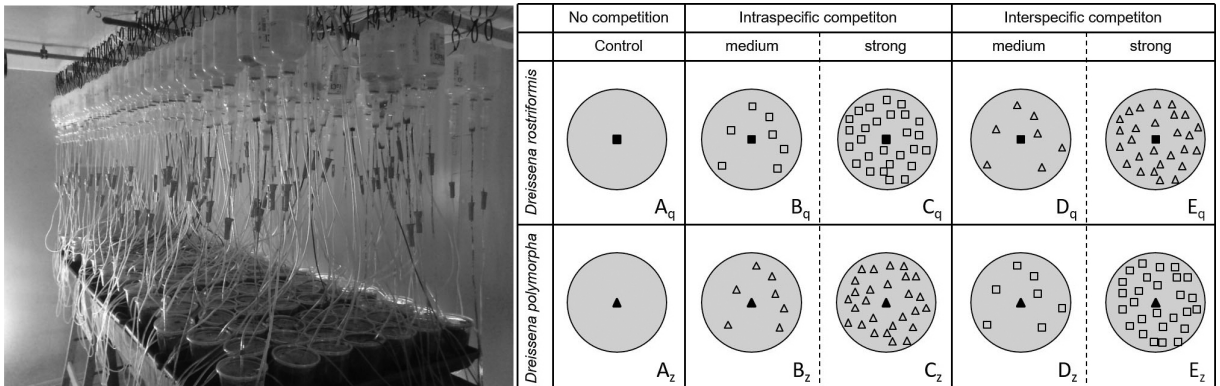
Figure 1. Closed microcosm setup for competition experiments in quagga and zebra mussels. Left: Climate chamber setup. Right: Experimental design for the competition experiments. The growth of focal individuals (■ = quagga mussel; ▲ = zebra mussel) was measured under five competition treatments (A_q–E_q: focal individual = quagga mussel; A_z–E_z: focal individual = zebra mussel). Each treatment was replicated twelve times. □ = quagga mussel individual, Δ = zebra mussel individual. Photograph by K. C. M. v. Oheimb.

Competition treatments

For each species, five intra- and interspecific competition scenarios were studied (Figure 1):

A) no competition; solitary focal individual as "control" (equivalent to 36 individuals m^{-2}),

B) medium intraspecific competition with 1 focal individual and 7 conspecific individuals (equivalent to 288 individuals m^{-2}),

C) strong intraspecific competition with 1 focal individual and 27 conspecific individuals (equivalent to 1009 individuals m^{-2}),

D) medium interspecific competition with 1 focal individual and 7 congeneric individuals, and

E) strong interspecific competition with 1 focal individual and 27 congeneric individuals.

These densities were chosen to represent low, medium and high population densities that are known from natural settings (Heiler et al. 2011, 2012). Mussels of roughly the same size were used as focal individuals and marked with a small dot of non-irritating nail polish for identification purposes. Twelve replicates were set up for each treatment and the positions of the containers in the climate chamber were randomized to minimize possible differences in inner chamber temperature. Deceased focal individuals and focal individuals with lost markings were excluded from the analyses. Other deceased mussels were replaced with individuals of a similar size to keep the competition pressure at a constant level throughout the experiment. Prior and after the experiments (i.e., after 82 days) the wet weight of each focal individual was measured with a high-resolution balance and the differences between start and end weights were recorded as "growth rates".

Statistics

All statistical analyses were done using the R statistical environment version 3.4.1 (R Core Team 2017). Normality and variance were assessed with the Shapiro-Wilk test and the Bartlett's test, respectively. As the samples did not meet the normality or the equal variance assumptions, the two-sided test for the nonparametric Behrens-Fisher problem (Konietschke et al. 2015) was used to compare the overall reactions of the zebra and quagga mussels.

To determine significant differences among the treatments, a linear mixed-effects model was generated using the package lme4 version 1.1-15 (Bates et al. 2015). The growth data was logarithmized (base 10) after adding 0.07 to eliminate negative values that likely resulted from weight loss during the experiment. In the model, treatment was set as fixed effect and the start weight was included as random effect to account for its potential influence on growth rates during the experiment. Outlier residuals were removed from the model with the package LMERConvenienceFunctions version 2.10 (Trembley and Ransijn 2015). A Tukey multiple comparison test (package multcomp version 1.4-8 (Hothorn et al. 2008)) was used to determine the differences between individual treatments.

Results

After excluding deceased individuals and individuals with lost marking from the dataset, the number of focal individuals at the end of the experiment was 55 for the quagga mussel in setups A_q–E_q and 50 for the zebra mussel in setups A_z–E_z, resulting in replicate numbers ranging from 6 to 12 (see Figures 1 and 2).
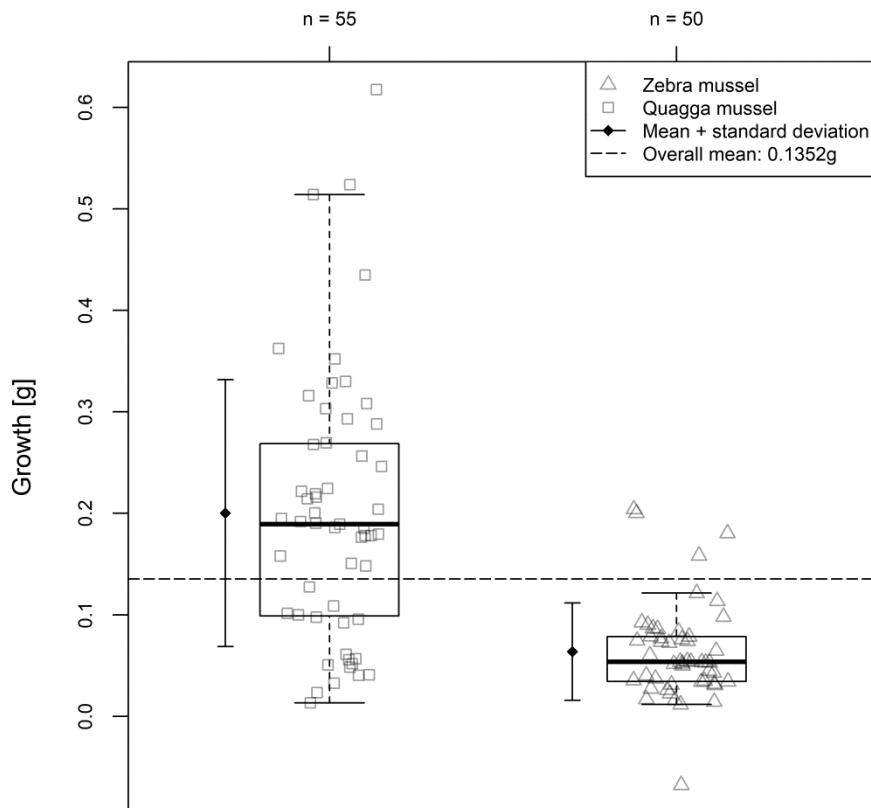
Figure 2. Boxplots of overall growth rates for quagga and zebra mussel focal individuals after 82 days. Symbols indicate the species identity of the focal individual. n = number of focal individuals for each species.

Table 1. Weight distributions of zebra and quagga mussel focal individuals at the beginning and end of the experiment (start/end weights in g; total duration 82 days).

Species	Minimum	1-st quartile	Median	Mean	3-rd quartile	Maximum
Zebra mussel	0.1459 / 0.1962	0.2576 / 0.3020	0.3456 / 0.4158	0.3404 / 0.4041	0.4140 / 0.4749	0.5174 / 0.7166
Quagga mussel	0.1062 / 0.1927	0.1694 / 0.3328	0.2136 / 0.4146	0.2358 / 0.4361	0.2998 / 0.5200	0.3844 / 0.8588

Start weights of the quagga and zebra mussel focal individuals were 0.11 g to 0.38 g and 0.15 g to 0.52 g, respectively. End weights after 82 days were 0.19 g to 0.86 g in quagga mussel focal individuals and 0.20 g to 0.72 g in zebra mussel focal individuals (Table 1 and Supplementary material Table S1).

The quagga mussel showed an overall higher mean and median growth rate as well as a greater range of growth rates in response to the different treatments (Figure 2). The two-sided test for the nonparametric Behrens-Fisher problem showed that the overall growth rate for all quagga mussels tested tended to be greater than for zebra mussels (estimator: 0.16, 95% C.I.: 0.09–0.25, p < 0.01).

A pairwise comparison indicated that for all treatments, growth rates and ranges of growth rates were substantially larger for the quagga mussel (Figure 3, boxplots A_q–E_q) than for the zebra mussel (Figure 3, boxplots A_z–E_z). This finding is largely confirmed by the linear mixed-effects model. Accordingly, the Tukey multiple comparison test (Table S2) revealed significant differences between the two species for all treatments (p = 0.0169 (A_q and A_z), p < 0.01 (B_q and B_z), p < 0.001 (D_q and D_z, E_q and E_z)) except for the strong intraspecific competition treatment (C_q and C_z: p = 0.8976).

When comparing the treatment-specific growth rates within species, no significant differences could be found for the zebra mussel (p > 0.1, see Table S2). In contrast, the growth rates of the quagga mussel were significantly lower under strong intraspecific competition compared to all other treatments (p < 0.001 (C_q and A_q, C_q and D_q), p < 0.01 (C_q and B_q); E_q and C_q: significant at the 10% level (p = 0.0514)). Moreover, quagga mussels showed higher growth rates under interspecific than under intraspecific competition, while the zebra mussel reacted to inter- and intraspecific competition in a similar way (Figure 4).
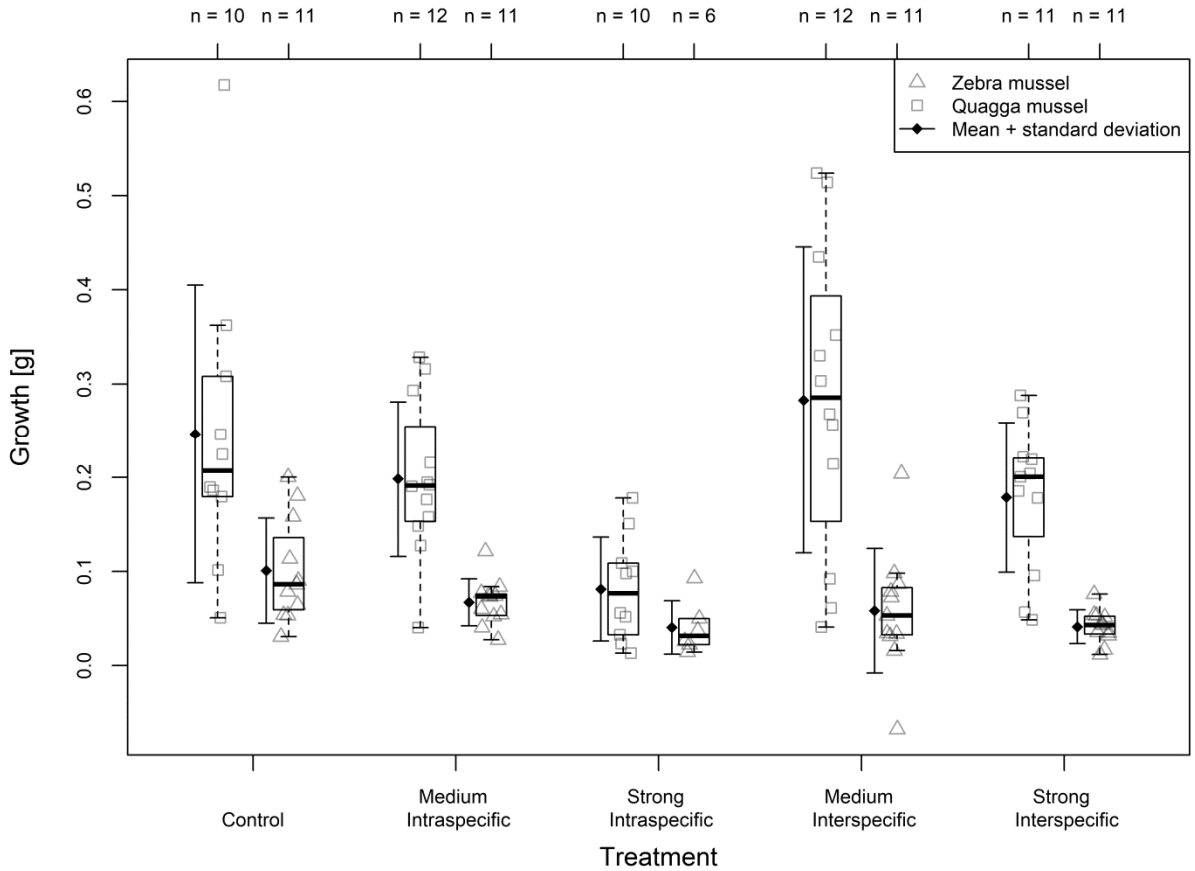
Figure 3. Boxplots of treatment-specific growth rates of quagga (treatments A_q–E_q) and zebra (treatments A_z–E_z) mussel focal individuals after 82 days of treatment. Symbols indicate the species identity of the focal individual. n = number of focal individuals for each species/treatment. Treatments according to Figure 1. (control = no competition, medium intraspecific competition = 7 conspecific individuals, strong intraspecific competition = 27 conspecific individuals, medium interspecific competition = 7 congeneric individuals, strong interspecific competition = 27 congeneric individuals).
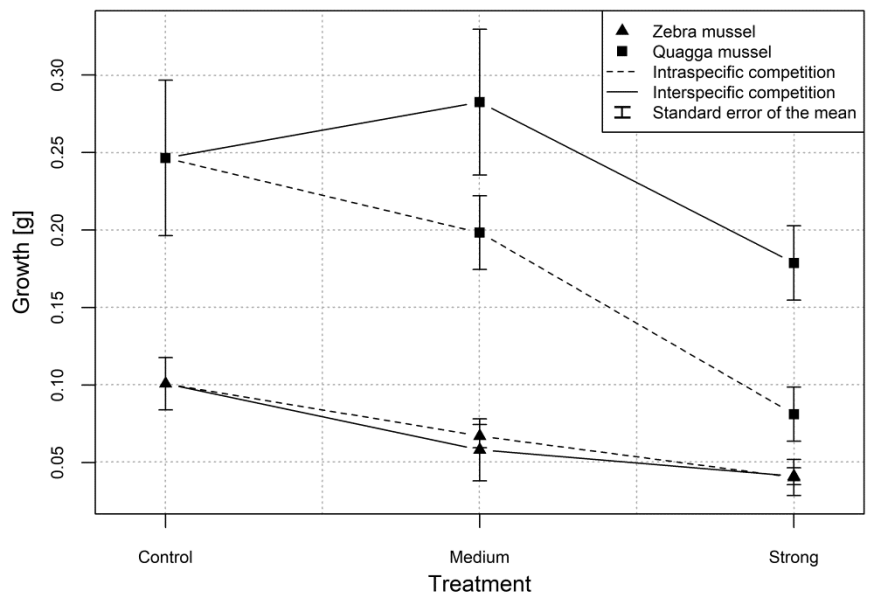

Figure 4. Plot of competition-specific growth rates of quagga and zebra mussel focal individuals after 82 days under different competition treatments (control = no competition, medium = 7 competing individuals, strong = 27 competing individuals). Symbols indicate the species identity of the focal individual and line types the competition treatment (intraspecific = conspecific individuals as competitors, interspecific = congeneric individuals as competitors).

Discussion

Understanding the complex invasion mechanisms of the highly invasive zebra and quagga mussels is fundamental for maintaining native biodiversity and avoiding further losses to ecosystem services (*sensu* Pejchar and Mooney 2009). Typically, mechanisms of invasion are difficult to infer due to the complex interactions in multi-species competition systems. Here, the zebra-quagga-mussel-system has the advantage that the two congeners are ecologically similar, both invasive, and exert a strong competitive pressure on each other. This, in turn, enables the testing of selected species-based mechanisms.

Our study, which mainly aimed at testing whether the quagga mussel derives its competitive advantage from higher growth rates under different competition scenarios, showed that both species reacted qualitatively similar to different intensities of intra- and interspecific competition. However, in four of the five treatments, the quagga mussel showed overall higher growth rates as well as greater growth ranges (see Figures 2, 3 and 4). Interestingly, growth rates of the zebra mussel were not substantially influenced by the presence of conspecifics or congeners, while the growth of the quagga mussel was affected by the presence of other dreissenids (Figure 4). Although not significant, the quagga mussel showed the highest growth rate and also the greatest range of growth rates under medium interspecific competition (Figures 3 and 4). For all other competition treatments, their growth was slightly lower, with growth under high intraspecific competition being significantly lower than under all other treatments.

When alien species invade a new habitat with new environmental conditions, two mechanisms predominantly enable a population to persist: genetic adaptation and phenotypic plasticity (Chevin et al. 2010). As plasticity, in contrast to genetic changes, does not depend on favorable mutations, a population can almost instantaneously respond to new challenges (for a review see Pfennig et al. 2010). This has led to the assumption that greater plasticity provides a fitness advantage to invasive species (e.g., Richards et al. 2006). Recent studies have substantiated this claim by showing that invading species do generally have greater phenotypic plasticity than co-occurring non-invasive species (e.g., Davidson et al. 2011), and thus directly linked plasticity with the potential for invasiveness. Although not specifically tested here, the notable differences observed in the growth ranges of the two species during our study point towards differential degrees of phenotypic plasticity, not only between native and invasive but also within these two invasive species.

Higher growth rates allow a competitor to reach adult size earlier, consequently being comparatively less prone to, for example, parasite pressure or other biological constraints during growth (Dillon 2000). In combination with potentially higher phenotypic plasticity and the observed varying growth rates under different competition pressures, higher growth rates might provide the quagga mussel with greater flexibility in a fluctuating environment (Davis 2009). Quagga mussels potentially benefit from higher growth rates in situations where space (i.e., hard substrate) is limited, and greater growth ranges can provide more flexibility when hard substrate is more heterogeneous or when only less suitable substrate is available. Additionally, higher growth rates might influence filtering activities. When comparing larger mussels, filtration rates of quagga mussels are higher than those of zebra mussels (Diggins 2001). This difference might be further enhanced when quagga mussels reach larger sizes earlier than zebra mussels of the same age, increasing the competitive advantage of the former species.

The competition scenarios analysed in the present paper constitute an ecological snapshot tailored to the given laboratory conditions. Given that temperature ranges do have an important impact on adaptive physiological processes such as consumption, excretion, and filtration (Aldridge et al. 1995; Matthews et al. 2014; Marescaux et al. 2016a), an important question for further investigations will be to what extent the identified reaction patterns of quagga and zebra mussels are valid for broader ranges of temperatures. This is particularly relevant in the light of the continuing range expansion of both species (e.g., Naranjo-García and Castillo-Rodríguez 2017; Prié and Fruget 2017) and the Europe-wide changing water temperature regimes caused by global change (Floury et al. 2013).

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Supplementary material

The following supplementary material is available for this article:

Table S1. Start and end weights of all focal individuals (excluding deceased individuals and individuals with lost markings).

Table S2. Results of general linear mixed-effects model and Tukey multiple comparison test for differences between individual treatments.

This material is available as part of online article from:
http://www.aquaticinvasions.net/2018/Supplements/AI_2018_Metz_etal_SupplementaryTables.xlsx