HOMAGE TO HENRI DUMONT

Life in a changing environment: dreissenids' feeding response to different temperature

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Abstract Invasive species have far-reaching consequences for whole ecosystems. The two dreissenids zebra and quagga mussels are two of the most successful invaders in aquatic systems. Quagga mussels can colonize deeper parts of a lake while zebra mussels prefer shallow areas. Both species show large variability in shell morphology, but only quagga mussels show a shallow and deep-water morphotype. The aim of this study is to investigate the depth adaptation of quagga mussels and the potential filtration advantage of the quagga mussel compared to the zebra mussel.

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We conducted common garden experiments, where we measured filtration rates at different temperatures of quagga mussels collected from different water depths and compared them to zebra mussel from 1m depth. We found filtration rates to be strongly temperature dependent, and in particular, lower at 4 °C. Overall, zebra mussels fed less than quaggas. Quagga mussels collected from 1 m depth fed more at higher temperature than quaggas from 30 and 60 m. We hypothesize that deep-water quagga mussels are less sensitive to lower temperature and/or constrained to modify filtration rates at higher temperatures.

Introduction

Worldwide, invasive species have far-reaching consequences for ecosystems (Simberloff, 2013). They can lead to extinction of native organisms, reduce biodiversity, compete with native species for resources and alter habitats. Invasive species can have strong negative impacts on the abundance and diversity of native organism, which is particularly pronounced in freshwater systems (Strayer, 2010; Gallardo et al., 2016). The two dreissenids zebra and quagga mussels, *Dreissena polymorpha* (Pallas 1771) and *D. bugensis* (Andrusov 1897, also described as *D. rostriformis bugensis*, Wesselingh et al., 2019), are

two of the most successful invaders in Europe and North America, due to their ability to spread quickly between and within lakes and to achieve high densities. Dreissenids have high filtration rates, so they can cause a decrease in phytoplankton, a reduction in nutrient levels and generally have a strong top-down control over phytoplankton. Usually zebra mussels invade waterbodies first and quagga mussels follow later (Karatayev et al., 2015). In shallow lakes, zebra and quagga mussels can coexist, while in deep lakes, quagga mussels tend to displace zebra mussels (Karatayev et al., 2015).

Quagga mussels can colonize lakes to large depths (> 200 m), while zebra mussels prefer shallow areas and are rarely found deeper than 30–40 m (Karatayev et al., 2015). In deep lakes outside of their native range (Pavlova et al., 2021), quagga mussels express two different morphotypes: a shallow living morphotype with a thick and robust shell, and a deep living morphotype, the so-called profunda morphotype. The profundal morphotype is less pigmented (brighter) and more elongated compared to mussels found in shallow waters (Dermott & Munawar, 1993; Claxton et al., 1998). The profundal morph has physiological advantages to live in the deep: it is able to spawn at lower temperatures (Claxton et al., 1998) and consumes less oxygen (Tyner et al., 2015). Because living in the deep requires coping with different challenges, e.g. higher hydrostatic pressure, less light and oxygen, fewer nutrients and lower but more constant temperatures, this raises the question of whether the changes in morphological and physiological traits of profundal quagga mussels are an adaptation to depth. Here we refer to adaptation as a genetic and heritable process.

At the ecosystem level, a change from zebra mussel to quagga mussel dominance can have different top-down effects. Top-down control means that mussels affect the food web on lower trophic levels, i.e. they reduce or change primary production (phytoplankton in lake ecosystems). In North American lakes, quagga mussels decreased the spring bloom of phytoplankton in deep (Lake Michigan) and shallow lakes (Lake Oneida). This effect was observed after quagga mussels invaded these lakes, but not at the time zebra mussels were present (Vanderploeg et al., 2010; Karatayev et al., 2021b). In deep lakes such as Lake Michigan, quagga mussels occupy a larger niche than zebra mussels (> 40 m, where zebra mussels are less

likely to occur). Therefore, quagga mussels can reach greater biomass in deep lakes and have the potential of more top-down control. In polymictic lakes where both species co-occur, zebra mussels reduced nutrients and phytoplankton, and increased water clarity in summer as much as quagga mussels did (Mei et al., 2016). However, studies comparing water quality and food web changes between zebra and quagga mussel dominating lakes are rare. Usually, the only comparison that exist are observations when a lake changes from zebra to quagga mussel dominance (Pothoven & Fahnenstiel, 2014; Karatayev et al., 2021b).

Do quagga mussels only outcompete zebra mussels in deep lakes because of their sheer higher abundance or are there other reasons? One hypothesis is that zebra mussels invest more into predator defence while quagga mussels invest more in growth (Rudstam & Gandino, 2020). Studies on growth have found that quagga mussels grow significantly faster than zebra mussels (Baldwin et al., 2002; Zhang, 2022). A possible explanation for this could be that the difference in growth is coupled with higher feeding rates of quagga mussels. However, studies comparing feeding rates of quagga and zebra mussels have found contradicting results. Some showed that quagga mussels filter more than zebra mussels (Diggins, 2001), while others observed the opposite (Baldwin et al., 2002; Marescaux et al., 2016). In some studies filtration rates were similar for both species (Vanderploeg et al., 2010; Mei et al., 2016). Contradicting results might arise due to different experimental set ups (flow-through systems vs standing water). It is known that filtration rates depend on various factors: seasonal differences (mussels collected in different seasons, Vaughn and Hakenkamp 2001; Baldwin et al. 2002; Vanderploeg et al. 2010), different ecosystems (Lorenz & Pusch, 2013), food amount (Vaughn & Hakenkamp, 2001; Baldwin et al., 2002; Marescaux et al., 2016), flow velocity (Xia et al., 2021), presence of predator kairomones (Naddafi & Rudstam, 2013), and the most important: different food sources (from natural seston to lab cultured single-cell cultures, toxic and non-toxic algae, Vanderploeg et al., 2001; Dionisio Pires and Van Donk 2002). Furthermore, algal species composition strongly influences filtration rates (Tang et al., 2014). Contradicting results might also arise because the filter feeding mechanism of dreissenids is a complex system that is still not entirely understood. Therefore, in our opinion more standardized studies

should be done, preferably fully factorial so that the influence of different factors on filtration rate as well as their interaction can be studied.

The aim of this study is to measure filtration rates of both species of dreissenid mussels collected from the same lake and interpret those results in the context of adaptation to depth. We collected mussels of both species from the littoral of the same lake (1 m) and quagga mussels from depths of 30 and 60 m (zebra mussels were not found deeper than the littoral). We performed common garden experiments, where we measured filtration rates at different temperatures (4, 12 and 20 °C). We chose these temperatures because in our study system, Lake Constance (border lake between Switzerland, Austria and Germany), mussels that occur in water depths < 10 m cope with temperatures below 7 °C for about 128 days a year. They also experience temperatures over 18 °C on 58 days a year and temperatures above 10 °C for around 205 days a year. Because of their dominance in deep lakes, we hypothesize that quagga mussels have higher filtration rates than zebra mussels, especially at lower temperatures. Further, we expect at lower temperatures deepwater morphotypes will have higher filtration rates compared to shallow-water mussels. We hypothesize that mussels from deep-water sites will perform better at cold temperatures than mussels collected from shallow-water sites, and vice versa, which indicate s adaptation to depth.

Materials and methods

Mussel collection

In August 2021, we collected zebra mussels by snorkelling in Lower Lake Constance on the shore of the island of Reichenau (N: 47° 41′ 26.9″ E: 9° 03′ 11.4″), Germany. Quagga mussels were collected off Konstanz (N: 47° 41′ 43.7″ E: 9 °11′ 37.3″). Quagga mussels from shallow habitats were collected at about 1–3 m (pelagial water temperature at 1 m on 02.09.2021: 18.1°C, approx. 9 km from sampling location, data from Zhang et al., 2023) depth by snorkelling and quagga mussels from 30 and 60 m with a bottom trawl (mesh size: 7 mm, pelagial water temperature at 30 m: 6.6°C and at 60 m: 5.9°C, data from Zhang et al., 2023). Mussels from 30 and 60 m were

all of the deep morphotype (for a visual impression of the two morphotypes see Fig. S1).

After collection, mussels were transported in lake water to the laboratory within four hours and transferred to six 18 L-aquaria with unfiltered lake water in three different temperature chambers (4, 12 and 20 °C, two aquaria each). We used three different temperatures to simulate the origin temperature of the mussels in Lake Constance (IGKB, 2018). Usually, mussels taken from two depths shared an aquarium, but were separated with a mesh (mesh size 1.4 mm) so that they could not mix. We let the mussels acclimatize to the different temperatures for seven days before we started the experiment (as done by Horgan & Mills, 1997). We fed the mussels with 8 ml *Scenedesmus obliquus* solution (approx. 7.9×10^6 cells/ml) at the beginning (day 3) and on the day before the feeding experiment (days 6, 9, 13). This food amount is based on own experiences while culturing the mussels with this algae to prevent overfeeding. We fed the mussels before the experiment to avoid starving the animals, which could influence the outcome of the experiment (Roditi et al., 1996; Bastviken et al., 1998).

We changed the water (filtered Lake Constance water, pore size: 0.045 mm) on days 4, 9 and 13 to remove food residues and excretions (see Fig. 1 for a schematic schedule).

Experimental setup

The feeding rate of the mussels was estimated using the green algae *S. obliquus* as food source. The algae were cultivated at 18–22 °C in aerated 2-L flasks (WC medium after Guillard 1975) near constant fluorescent light and harvested in the early stationary phase.

The experimental schedule is shown in Fig. 1. The experiment was repeated (replicated) on days 8, 11 and 15 after collection and was conducted always with mussels that had not been used in an earlier experiment. The day before the experiment, we selected 20 mussels from each origin (zebra mussels from 1 m, quagga mussels from 1 m, 30 m and 60 m) and temperature treatment (4, 12 and 20 °C). The mussels were measured with a digital calliper (length, width, height) and the wet weight recorded. After the measurements, the mussels were carefully glued to a plastic stick with a two-component glue (UHU-Plus Sofortfest, see Fig. 1b) and we tried to
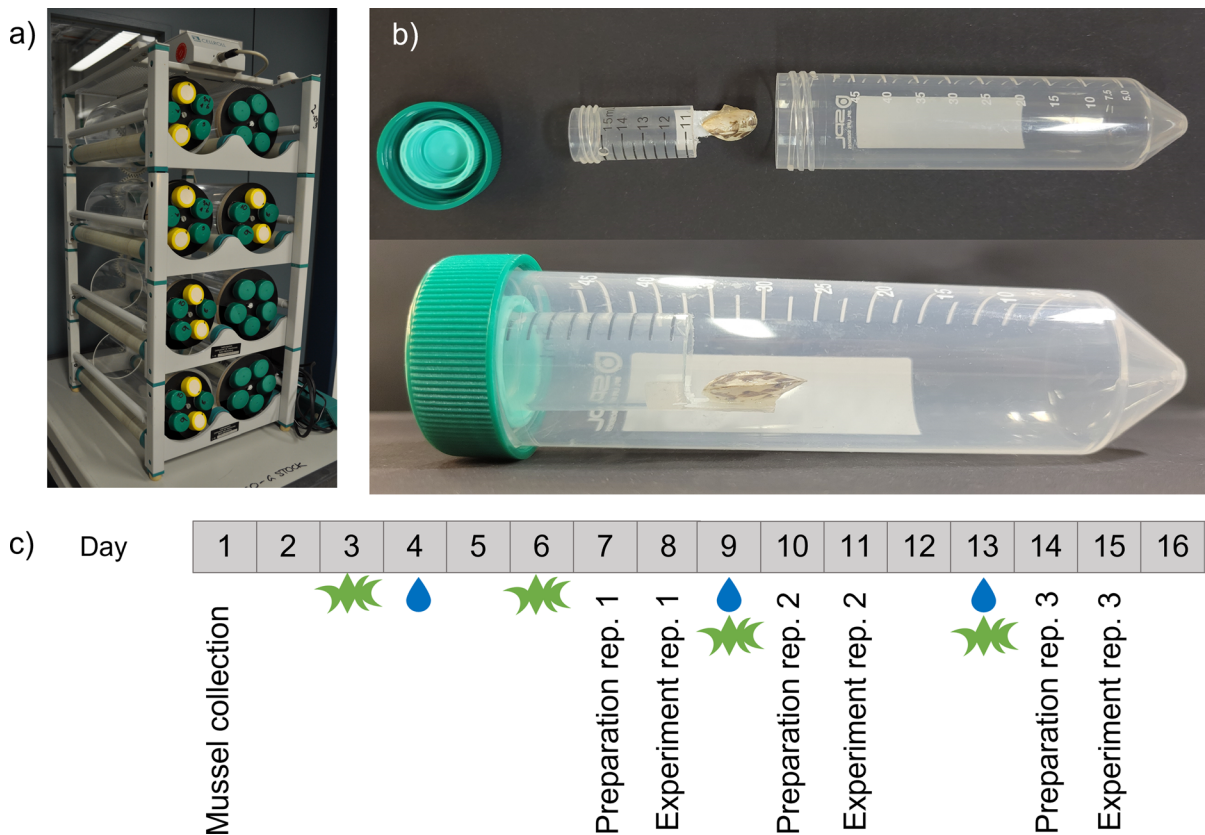
Fig. 1 Experimental setup of the filtration experiment. **a** The plankton wheel is designed for 80 replicate vessels of 50 ml (16×4 mussel origin treatments plus 16 control vessels). **b** Mussels were glued to the plastic stick and screwed into the lid of the vessel. **c** Replicate experiments were conducted on days 8, 11 and 15 according to the schedule. We collected the mus-

sels on day 1 in Lake Constance. Green symbols indicate when we fed the mussels (with *S. obliquus*) in the aquaria. Blue drops show the days when the water was changed. Preparation days (7, 10, 15) included mussel measurements (length, width, height, wet weight) and gluing to sticks as shown in **b**

prevent the shells from sticking together. After drying for max. 5 min, the mussels were returned to their temperature chambers to settle down.

On the day of the experiment, 16 (out of 20) mussels per treatment were screwed into the lid of a 50 ml falcon tube (see Fig. 2b for picture of the stick and tube and Figs. S2 and S3 to compare mussel sizes of the experimental animals between treatments). One mussel was placed per 50 ml tube. The tube contained 50 ml filtered lake water (pore size: 0.045 mm) from Lake Constance with a standard *S. obliquus* solution (appr. 523'000 cells/ml). The tubes with mussels were placed in a plankton wheel that rotates the tubes (1.5 rotations per minute) to keep the algae constantly in suspension (Fig. 1a).

The mussels were checked after 30 min in the experiment to see if they were open and feeding. Closed shells, which were the results of either stress or careless gluing, were excluded from the experiment. After one hour, the mussels were separated from the algal solution, removed from the stick, frozen and later weighed (shell-free dry weight: soft tissue dried at 60 °C for at least 48 h). The algal solution (1 ml) was immediately fixed with a fixative solution to a final concentration of 0.01% paraformaldehyde and 0.1% glutaraldehyde. Duration and volume of the experiment was determined through a series of pre-experiments, so that quagga mussels feeding at 20° consumed ~40–60% of the available algae.

Fig. 2 Filtration rates of quagga and zebra mussels sampled from 1 m depth (raw data mean ± SE, ml per *Dreissena* dry weight in mg per hour). Quagga mussels overall fed more on *S. obliquus* than zebra mussels. At 12 °C and 20 °C, both dreissenids were able to feed more than at 4 °C. Grey points indicate filtration rates of single individuals. Data points are slightly jittered to avoid overlaps and to allow for better visualization. The results of the post hoc tests between the compared groups are indicated with brackets and the corresponding significance levels (**$P < 0.01$, * $P < 0.05$)
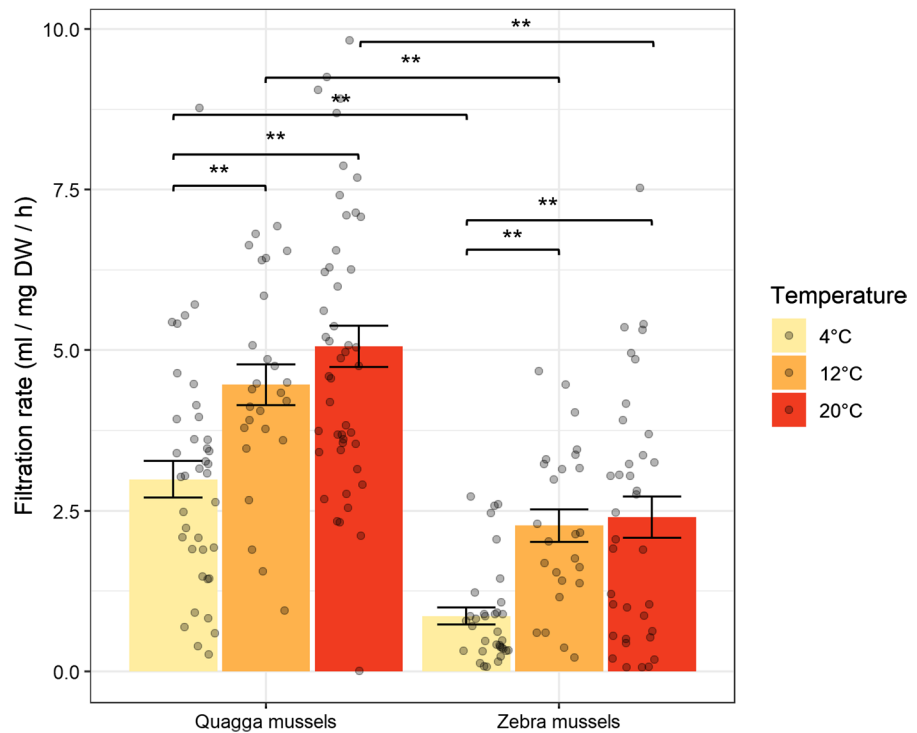
On the day after the experiment, the fixed algal solution was measured (three technical replicates of 200 μl) as chlorophyll-*a* relative fluorescence unit (RFU) in a plate reader (Biotek Cytation5). RFU were used to calculate filtration rates, or clearance rates, according to Coughlan (1969) adjusted per mussel dry weight:

$$FR = \frac{V}{DW * t} * \left\{ \left(\ln C_0 - \ln C_t \right) - \left(\ln C_0\prime - \ln C_t\prime \right) \right\}$$

where *FR* filtration rate in ml/DW mussel/ h, *V* total volume in ml, *DW* shell-free dry weight in mg, *t* duration of the experiment in *h*, C_0 and C_t RFU of beginning and end of the experiment with mussels, $C_0\prime$ and $C_t\prime$ = RFU of beginning and end of control vessels without mussels. We also calculated filtration rates corrected per individual, as well as corrected for shell-on wet weight and for shell length (in mm) instead of shell-free dry weight (see supplementary material).

In general, in the literature, different ways of calculating filtration rates are reported. Other studies corrected filtration rates per mussel (Diggins, 2001), per mussel length or for biomass as dry weight (Dionisio Pires et al., 2005), ash-free dry weight or relative filter

area (Vanderploeg et al., 2010). We decided to correct for dry weight (without shell) because we could not provide enough mussels of the same size from all depths and from all species. The main difference in weight between mussels from different depths and species results from the weight of the shell. Therefore, we consider the difference between ash-free dry weight and shell-free dry weight as negligible. Shell weight or size increases the shallower the mussel lives (Elgin et al., 2021), and shell thickness increases when exposed to predator cues (Naddafi & Rudstam, 2013). We tried to avoid these plastic changes in shell thickness by using shell-free dry weight.

Differences between zebra and quagga mussel filtration rates

To analyse the effects of temperature on filtration rates (transformed as: $\sqrt{FR}$) of quagga and zebra mussels, we run a mixed model for the subset of the dataset containing only zebra and quagga mussels from 1 m. We run the model with temperature, species and their interaction as fixed factors and block (= replicated on different days) as a random factor.

Filtration rates of quagga mussels from different depths

To analyse the effect of depth of origin on filtration rates (transformed as: $\sqrt{FR}$), we run another mixed model with the dataset consisting only of quagga mussels sampled from different depths. Temperature, depth and their interaction were included as fixed factors and block (=replicated on different days) as a random factor. All model assumptions were checked, and all analyses were run in R (R Core Team, 2017).

Results

Differences between zebra and quagga mussel filtration rates

Zebra mussels had lower filtration rates (corrected for shell-free dry weight) than quagga mussels at all temperatures (see Fig. 2, X^2 (1) = 86.45, $P < 0.001$, $b = -0.80$, t (198) = -6.43, $P < 0.001$). Quagga mussels had 57% higher filtration rates (4.21 ± 0.20 ml/mg DW/h, raw data mean ± SE) than zebra mussels (1.81 ± 0.16 ml/mg DW/h). Both quagga and zebra mussels had higher filtration rates at higher temperatures (i.e. 12 and 20 °C) compared to the low temperature treatment (X^2 (2) = 31.34, $P < 0.001$, 12 °C: $b = 0.43$, t (198) = 3.18, $P = 0.0017$, 20 °C: $b = 0.54$, t (198) = 4.67, $P < 0.001$). The interaction between species and temperature was not significant (X^2 (2) = 0.91, $P = 0.636$), meaning that temperatures affect both dreissenid species in the same way. However, quagga mussels seem to feed slightly more at 20 than at 12 °C, while zebra mussels seem to filter the same amount at 12 as at 20 °C (see post hoc results visualized in Fig. 2). We show the same trends for filtration rates corrected for dry weight of mussels as for wet weight, size and per mussel (in Fig. S4).

Filtration rates of quagga mussels from different depths

Quagga mussels from the deeper sites (i.e. 30 and 60 m) tend to filter less than mussels from 1 m (X^2 (2) = 16.98, $P = < 0.001$, 30 m: $b = -0.15$, t (294) = -1.16, $P = 0.24$, 60 m: $b =$ $P < 0.10$, t (294) = -0.79, $P = 0.25$). In general, quagga mussels had higher filtration rates at higher temperatures (X^2

(2) = 35.08, $P < 0.001$, 12 °C: $b = 0.43$, t (249) = 3.06, $P = 0.002$, 20 °C: $b = 0.54$, t (249) = 4.5, $P < 0.001$). At the lowest temperature (4 °C) the mussels filtered the least (2.75 ± 0.18 ml/mg DW/h), but no strong increase could be observed between 12 °C (3.37 ± 0.19 ml/mg DW/h) and 20 °C (4.44 ± 0.20 ml/mg DW/h). The interaction between depth and temperature was not significant (X^2 (4) = 5.43, $P = 0.25$), although we found a tendency for quagga mussel from 30 and 60 m depth to filter-feed the same amount at 4 and 12 °C, while mussels from 1 m depth seem to increase their feeding rate with temperature (see post hoc results visualized in Fig. 3). We show the same trends for filtration rates corrected for dry weight of mussels as for wet weight, size and per mussel (in Fig. S5).

The effective temperature in the climate chambers deviated slightly from the targeted 4 °C (mean: 4.91 ± 0.08 °C), 12 °C (mean: 10.52 ± 0.07 °C) and 20 °C (mean: 18.82 ± 0.04 °C) due to the instability of the chambers (detailed temperature curves in Fig. S6).

Discussion

In the common garden experiment where we measured filtration rates of zebra and quagga mussels from Lake Constance, we show that quagga mussels filter more than zebra mussels at all temperatures investigated. As expected, the filtration rates were temperature dependent, but only weak difference in filtration rates were found between 12 and 20 °C for mussels living in shallow water depths. Deep-water quagga mussels filter less than shallow-water quagga mussels at higher temperatures. We did not find evidence for local adaptation to depth.

Differences between zebra and quagga mussel filtration rates

Our results showed that at all tested temperatures, quagga mussels filtered the green algae *S. obliquus* at a higher rate than zebra mussels. Previous studies examining filtration rate differences between the two species have provided mixed results. Diggins (2001) also found that quagga mussels filter at a higher rate than zebra mussels, although that study used natural seston rather than a monoculture as we

Fig. 3 Filtration rates of quagga mussels (raw data mean ± SE, ml per quagga mussel dry weight in mg per hour). Quagga mussels from 1 m depth overall fed more on *S. obliquus* than mussels from 30 or 60 m depth. Filtration was lower at 4 °C than at 12 °C or 20 °C, but not different between the mussels from different depths. Grey points indicate filtration rates of single individuals. Data points are slightly jittered to avoid overlaps and to allow for better visualization. The results of the post hoc tests between the compared groups are indicated with brackets and the corresponding significance levels (**$P < 0.01$, *$P < 0.05$)
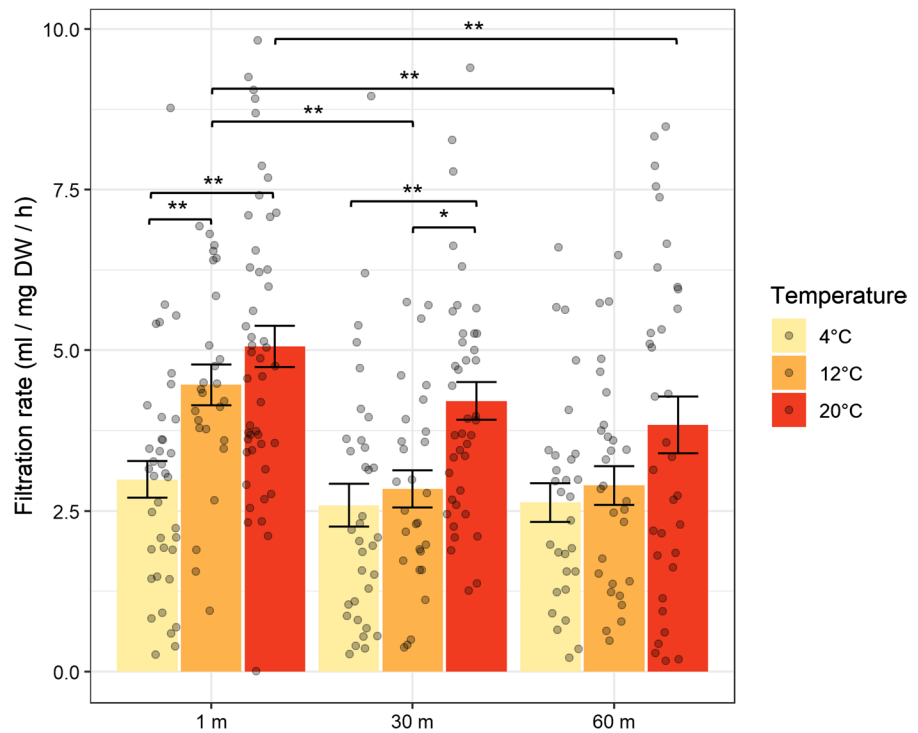
did. In contrast, other studies found that zebra mussels filtered more than quagga mussels—regardless of whether green algae (*Chlamydomonas reinhardtii,* Baldwin et al. 2002) or natural seston (Marescaux et al., 2016) was provided as a food source. Another study did not find a difference in filtration rates between the two species when fed the cryptophyte, *Cryptomonas ozolini* (Vanderploeg et al., 2010).

One of the central issues in reconciling these disparate findings is that there is no consensus on how such studies should be performed. Both Baldwin et al. (2002) and Marescaux et al. (2016) measured filtration rates of population of both species rather than their individuals, while Vanderploeg et al. (2010) compared mussels from a lake and a river at very low temperatures (< 3 °C). When combined with the different food sources and the potential for dreissenids to feed selectively (Tang et al., 2014), it is not surprising that results vary so wildly. Other factors that can alter filtration rates include food concentration (Baldwin et al., 2002; Marescaux et al., 2016), food source and composition (Tang et al., 2014), temperature and season (Baldwin et al., 2002; Vanderploeg et al., 2010), flow velocity (Xia et al., 2021), laboratory acclimatization time (Lei et al., 1996; Horgan & Mills, 1997;

Sylvester et al., 2005; Marescaux et al., 2016; Xia et al., 2021) and probably larger differences including population variation (De Ventura et al., 2016). The food concentration, volume and duration of our experiments were based on pre-experiments as well as on earlier studies. In the study of Xia et al. (2021), for example, the volume of water per mussels was double as in our study. However, their experimental chambers were static, allowing the algae to sink and mussels were placed on the bottom of the container, compared to our experiment algae were kept in suspension, reducing but not excluding effects of refiltration. Mussels in our experiment might have experienced refiltration; therefore, we focus on the discussion of the results on the relative rather than absolute clearance rates.

The differences in techniques make comparing feeding studies using different setups difficult. However, the main goal of this study was not to make the comparison between zebra and quagga mussels, but to investigate their filtration response under different temperatures. Initially, we had hoped to compare individuals of both species collected from different depths under different temperatures, but the absence of zebra mussels at deeper sites did not allow us to

do this. Therefore, we can only compare the performance/relative filtration rates of the two mussel species using individuals collected from shallower water.

While quagga mussels in our study always had a higher filtration rate than zebra mussels, temperature effects were consistent in the two species: filtration rates were lowest at 4 °C and there was no large difference between 12 and 20 °C. Other studies have also found that zebra and quagga mussels show similar filtration rates at temperatures between 12 and 24 °C (Kemp & Aldridge, 2018; Gopalakrishnan & Kashian, 2020; Xia et al., 2021). This suggests that these shallow-depth mussels may be limited in their ability to increase their filtration rate beyond that at which they already achieve at these temperatures. That is, they may be well adapted to maximize their performances at temperatures to which they are most often exposed. In Lake Constance, mussels in the littoral zone (1–5 m) experience an annual mean temperature of 12.8–13 °C which is comparable to the temperature at which they showed their maximized filtration rates and could not increase when it got warmer. Indeed, for other mussel species (van Ee et al., 2022), increasing water temperatures are beginning to have adverse effects on a range of measurable biological endpoints such as respiration rates or phosphorus excretion.

Filtration rates of quagga mussels from different depths

In deep lakes, not only zebra and shallow-water quagga mussels have recognizable impact on filtration, but the deep living quaggas might have an even stronger effect. We analysed filtration of quagga mussels from different depths at multiple temperatures and found that shallow living quagga mussels filter more than quagga mussels from greater depths (30 and 60 m). However, mussels filtered similar amounts at low temperatures (4 °C) irrespective of their depth of origin. While mussels from the deep show no increase in filtration between 4 and 12 °C, shallow living mussels increase their filtration between 4 and 12 °C, but not between 12 and 20 °C.

While all mussels filtered the same amount at 4 °C, that could be an indication that mussels reached their lower thermal limit. This suggests that at 4 °C, quagga mussels from Lake Constance filter as much as they can in order to balance their food requirements

and maintain optimal metabolism. They maybe cannot filter any faster at this temperature irrespective of their depth of origin. The mussels' metabolism is known to be temperature dependent (Clarke & Fraser, 2004; Paolucci et al., 2022). Temperature is also limiting multiple other life history processes, e.g. zebra mussels only reproduce above 12 °C in polymictic lakes (Borcherding, 1991). That all mussels in Lake Constance reach the lower thermal limit at 4 °C is not a surprise as all mussels need to cope with low temperatures, i.e. shallow-water mussels during winter months and deep-water mussels constantly.

At higher temperature, we showed different filtration rates between mussels' depth of origin: shallow-water mussels show similar filtration rates between 12 and 20 °C, but in contrast, deep-water mussels show similar filtration between 4 and 12 °C. As in our experiment mussels from 30 and 60 m were all the deep morphotype, both showed the same filtration responses to temperatures. Vanderploeg et al. (2010) also investigated filtration of mussels of the two morphotypes: but showed no clear differences between them at 1 °C. However, at 2 °C, the shallow morph filtered more. In contrast to our study, they used very low temperatures, but the relative differences are similar: deep-water mussels did not react to the temperature increase at low temperatures, while shallow-water mussels did. It seems that deep-water mussels are less sensitive to lower temperature changes and have a higher temperature threshold to increase their filtration, i.e. > 12 °C, they start to increase their filtration rate significantly. Maybe the deep-water morphotype has weakened the ability to filter much at higher temperatures. Deep-water morphotypes in Lake Constance never expect to filter at high temperatures, i.e. they never experience temperatures above 13 °C. In contrast, shallow-water mussels in Lake Constance can cope with a wide range of temperatures as the yearly mean temperature is 11–13 °C (> 15m), and in winter, they cope with 4–5 °C, while in summer, they experience temperatures over 20 °C (based on mean temperature data in 2021 of Lake Constance, Zhang et al., 2023). In other words, mussels from the deep never experience higher temperatures while mussels from the shallows live at all the temperatures tested (data from Zhang et al., 2023).

To test our suggestions of different thermal sensitivity, we propose that future studies investigate thermal performance curves between zebra and quagga

mussels and in particular between the different morphotypes. Tests should include measurements of different performance traits at multiple temperatures at a higher resolution to characterize the shape. Further, different acclimatization to experimental conditions should be tested. However, all those results are only comparable with other studies if experiments follow a standard testing framework which would make them comparable between species.

Although we found difference in filtration rates between mussels of different depths of origin, we could not show signals for local adaptation. Other studies have already investigated if the morphotypes are an adaptation to depth or a result of plasticity, but they used different approaches or measured different traits. They mostly found indices for phenotypic plasticity rather than genetic adaptation. Genetic studies found no difference between shallow and deep-water mussels (Spidle et al., 1994; Claxton et al., 1998; Stepien et al., 1999, 2002, 2003; Pavlova et al., 2021). Also in a detailed study using ddRAD sequencing combined with a local transplant experiment, we did not find evidence for local adaptation (Haltiner et al., submitted). Other studies investigating local adaptation found that shell morphologies seems to be a plastic trait which changes when juvenile mussels from different depths are raised in a common garden (Peyer et al., 2010). However, the different morphotypes seem to be irreversible in adulthood. Consequently, this type of plasticity is referred to as developmental plasticity: the genotype produces different phenotypes under different environmental conditions during an animals' development and the phenotype is irreversible during adulthood (reviewed in Lafuente and Beldade 2019).

Based on our results and previous studies, we hypothesize that quagga mussels show highly plastic responses to the life in the deep, which brings them advantages when living in deep lakes compared to zebra mussels. Also zebra mussels are known to show plastic responses to different habitats in shell morphology and colour (Pathy & Mackie, 1993; Lajtner et al., 2004). However, zebra mussels did not show a plastic response to depth (Claxton & Boulding, 1998; Lajtner et al., 2004). High plasticity is a characteristic of other successful invasive species (Richards et al., 2006; Davidson et al., 2011; Liao et al., 2016). The overall better filtration performance of quagga mussels compared to zebra mussels in our experiment is probably an important factor for their dominance in Lake Constance.

In a deep lake, in which average biomass is higher for quagga than for zebra mussels (Karatayev et al., 2021a), we would expect increased filtration pressure on phytoplankton by quagga mussels. In addition, the impact of filtration also increases because quagga mussels seem to generally filter more than zebra mussels. For future models of dreissenid filtration impacts in lakes, temperature-dependent filtration rates should be considered, and filtration experiments should be expanded. We think, that the deep-water morphotype might be induced by developmental plasticity and that they maybe have lost the ability to filter at higher temperatures and show less sensitivity to higher water temperatures as a cost of living in the deep.

Data availability Data and scripts generated and analysed during the current study are publicly available on the Eawag data repository ERIC https://doi.org/10.25678/0007DF.

Declarations

Conflict of interest The authors have no competing interests to declare that are relevant to the content of this article.

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