Dreissenid’s need for speed: mobility as a driver of the dominance shift between two invasive Ponto-Caspian mussel species

Anouk D’Hont1,2*, Adriaan Gittenberger1,3,4, A. Jan Hendriks5 and Rob S.E.W. Leuven2,6

1GimMarIS, Marine Research Inventory & Strategy Solutions, Rijkstraatweg 75, 2171 AK Sassenheim, The Netherlands
2Department of Animal Ecology and Physiology, Institute for Water and Wetland Research, Radboud University, Heijendaalseweg 135, 6525 AJ Nijmegen, The Netherlands
3Department of Marine Zoology, Naturalis Biodiversity Center, Pesthuislaan 7, 2333 BA Leiden, The Netherlands
4Institute of Biology Leiden (IBL), University, Leiden, Sylviusweg 72, 2333 BE Leiden, The Netherlands
5Department of Environmental Science, Institute for Water and Wetland Research, Radboud University, Heijendaalseweg 135, 6525 AJ Nijmegen, The Netherlands
6Netherlands Centre of Expertise on Exotic Species (NEC-E), Nature Plaza, P.O. Box 9010, 6500 GL Nijmegen, The Netherlands

Author e-mails: anouk.dhont91@gmail.com (AD), gittenberger@gimaris.com (AG), a.j.hendriks@science.ru.nl (AJH), r.leuven@science.ru.nl (RSEWL)

*Corresponding author

Research Article

Abstract

Both the quagga mussel (Dreissena bugensis) and the zebra mussel (Dreissena polymorpha) are notorious for dominating hard substrates in freshwater ecosystems throughout most of the Northern hemisphere. Despite widespread observations of a dominance shift favouring D. bugensis, where both Ponto-Caspian dreissenids co-occur, mechanisms driving this shift are still largely unknown. This study assessed whether movement behaviour differs between these two mussel species. That way we aimed at assessing whether mobility might be a contributing driver to the observed dominance shift. The mobility of dreissenids was assessed in an experimental set-up consisting of polyethylene tanks marked with squares and concentric circles facilitating location tracking of the dreissenids by time-lapse photography. Specimens were collected at the Haringvliet and Hollands Diep in the Rhine-Meuse river delta. The experiments mimicked unfavourable habitat conditions by drying, cleaning, tagging and placing mussels in a new environment. After these disturbances, the movement rate, duration, distance, pattern and speed of 299 individuals were monitored. For both species, most individuals moved in more or less circular patterns, causing their actual movement distance to be twice as high as their displacement distance. The average movement duration within 24 hours after the start of each experiment was 65 min, with an average speed of 28 cm/h and an average distance of 29 cm. Hereby no significant differences were found between D. polymorpha and D. bugensis. However, a higher top speed was observed for D. bugensis than for D. polymorpha. The fastest individuals of these two species moved at 90 cm/h and 60 cm/h, respectively. Moreover, about twice as many D. bugensis individuals moved during the experiments in comparison to D. polymorpha individuals. Hereby it was recorded that any point in time close to 10% more D. bugensis specimens were moving around. The results support our hypothesis that D. bugensis could have a competitive benefit over D. polymorpha by having a higher top speed and a significantly higher number of individuals moving after a disturbance of their population. Detachment and mobility of sessile mussel species are supposed to be avoidance mechanisms during unfavourable environmental conditions. Therefore, mobility might be one of the contributing drivers of the observed dominance shift between both species.

Key words: distance, Dreissena bugensis, Dreissena polymorpha, duration, motility, movement, size

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Introduction

The zebra mussel (*Dreissena polymorpha* Pallas, 1771) and the quagga mussel (*Dreissena bugensis*, also described as *Dreissena rostriformis bugensis* auct. Andrusov, 1897) are notorious freshwater invaders. Both dreissenid species cause extensive ecological effects (Grigorovich and Shevtsova 1995) and economic damage in their native area (Popa and Murariu 2009) as well as introduced regions (Pimentel et al. 2005; Binimelis et al. 2008; Fahnenstiel et al. 2010). Ecological changes caused by dreissenids include a dramatic increase in water filtration causing a reduction in food and oxygen availability and shifts in species composition, relative abundance and biomass of functional groups within aquatic ecosystems (Binimelis et al. 2008; Fahnenstiel et al. 2010). Economic damages include an increase in maintenance costs of overgrown man-made structures like hydraulic infrastructures, water corridors, boat hulls and pipes in cooling water circuits (Binimelis et al. 2008; Schonenberg and Gittenberger 2008). They originate from the Ponto-Caspian region and have spread to many parts of the Northern hemisphere (Europe, Eurasia and North America) (Therriault et al. 2005; Molloy et al. 2007; Van der Velde et al. 2010; Sousa et al. 2011). *Dreissena polymorpha* started to spread out of its native area at the beginning of the 19th century (Van der Velde et al. 2010; Sousa et al. 2011). *Dreissena bugensis* followed in its footsteps at the end of the 20th century (Therriault et al. 2005). Recently, there have been widespread observations of a shift from *D. polymorpha* to *D. bugensis* as the dominant species in their introduced range as well as in their native area (Karatayev et al. 2011; Matthews et al. 2014; D’Hont et al. 2018). Although *D. polymorpha* is able to settle earlier in the season, is more salinity tolerant, and is predated less upon than *D. bugensis*, *D. bugensis* usually remains the dominant species where both species co-occur (D’Hont et al. 2018). Although *D. polymorpha* is able to settle earlier in the season, is more salinity tolerant, and is predated less upon than *D. bugensis*, *D. bugensis* is known to have a higher assimilation efficiency, a higher activity of certain enzymes, higher filtration rates and lower respiration rates (Ram et al. 2012). Moreover, this species has lower winter mortality and settles in higher numbers when *D. polymorpha* individuals are already present on the substrate (D’Hont et al. 2018). Additionally, a higher attachment strength is found for *D. bugensis* compared to *D. polymorpha* (D’Hont et al. 2021). This may give *D. bugensis* an advantage over *D. polymorpha* when it comes to withstanding predators and disturbances such as currents (Hunt and Scheibling 2001; Kobak 2001; Czarnołęski et al. 2010) and navigation-induced changes in flow velocity (Koopman et al. 2018).

Dreissenids are generally considered sessile and sedentary animals (Kobak and Kakareko 2009). However, dispersal and migration are common...
for a dreissenids' larval life stage. The larval settlement is a critical dispersal period in its life cycle (Wilson et al. 1999). Additionally, settled mussels can relocate by detaching their byssus from the substrate and actively moving around using their foot (Toomey et al. 2002). They do so in reaction to changes in environmental factors, like water quality, orientation, presence or absence of conspecifics, oxygen and desiccation during water level drawdown (Kobak 2001; Kobak and Nowacki 2007; Collas et al. 2018). Higher movement ability may thus promote the avoidance of unfavourable environmental conditions.

Most knowledge of the mobility of dreissenids is based on studies with *D. polymorpha*. Light, temperature and water hardness are found to have no effect on the distance travelled by this species (Toomey et al. 2002; Coons et al. 2004). However, the presence of crushed individuals can cause a significant decrease in movement in the remaining individuals (Toomey et al. 2002). The urge to move and the distance moved by *D. polymorpha* individuals is inversely proportional to shell size, as small individuals move more than large ones (Toomey et al. 2002).

We conducted a comparative analysis of the rate, duration, speed and distance moved and the relationship between the movement and shell size of *D. polymorpha* and *D. bugensis*. To assess whether mobility may contribute to the dominance shift from *D. polymorpha* to *D. bugensis*, we studied whether any of these characteristics differed between both species.

**Materials and methods**

**Study sites**

Individuals of *D. bugensis* and *D. polymorpha* were collected in the Haringvliet and Hollands Diep, which are a part of the Rhine-Meuse delta in the Netherlands. They were collected in the ferry harbour of the island Tiengemeten (51°45.261′N; 4°19.046′E) and about 8 km upstream in the same river system in the harbour entrance of Numansdorp (51°43.037′N; 4°26.211′E). *Dreissena bugensis* was observed for the first time in Western Europe in 2006 in this part of the Rhine-Meuse delta (Molloy et al. 2007; Schonenberg and Gittenberger 2008). Dreissenids were collected from bricks deployed for about 1.5 years from the local docks at a depth of 1 m. Individuals of both species were collected at both locations to be able to collect enough specimens. There were no indications for differences in population structure of both species between both locations.

**Experimental setup**

In total 299 dreissenids were collected in three separate batches on 19 December 2017 (water temperature 5.2 °C), 6 March 2018 (1.4 °C) and 9 December 2019 (7.2 °C) (batch 1, 2 and 3, respectively; Figure 1) (Rijkswaterstaat 2020). Batch 1 and 2 consisted each of 40 *D. polymorpha*
individuals and 40 D. bugensis individuals with shell lengths between 1 and 2 cm. To test the potential impact of shell size on the movement rate, duration, speed and distance of dreissenids, batch 3 was collected. This batch was collected from bricks which were deployed for about 1.5 years at a depth of 1 m. Batch 3 consisted of 54 collected individuals with shell lengths between 0.86–2.27 cm of D. polymorpha, and 68 individuals with shell lengths between 1.02–3.04 cm of D. bugensis. As D. bugensis grows faster and larger, the collected individuals of D. bugensis were slightly larger (D’Hont et al. 2018). By specifically searching for the largest individuals present, additionally, eight about 3 cm long D. polymorpha and nine about 4 cm long D. bugensis individuals were found and included in the experiments. Unfortunately, these were the only maximum-sized individuals to be found at that time on the sampled bricks.

Movement experiments were conducted to assess the speed (cm/h), distance (cm), duration (min) and movement rate (%) of both dreissenid species. After collection in the field, the dreissenids were gradually acclimatized to room temperature (± 20 °C) for 24 to 48 hours. This was done by slowly increasing the water temperature from the ambient temperature at the sampling sites (1.4–7.2 °C) to room temperature (± 20 °C). Acclimation of 4–48 hours is common practice in experimental studies with dreissenids (Vanderploeg et al. 2001; Toomey et al. 2002; Juhel et al. 2006a, b; White et al. 2015; Whitten et al. 2018). Subsequently, the mussels were dried, cleaned and tagged by applying a number to both sides of the shell using Tipp-Ex correction fluid and permanent marker. Finally, the byssal threads were cut off using small scissors before placing them in the tanks. The mortality rate throughout this experiment was low (< 1%). The deceased individuals were excluded from the analyses. The experimental setup consisted of four polyethylene containers with 60-litre non-aerated fresh tap water. The surface area of these containers was subdivided into
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152 grid cells (6 cm² squares) and eight concentric circles, to indicate the location of dreissenids (Figure 1). The tap water had a pH of 7.84, and salinity of 0.28 PSU. Within the Haringvliet the pH normally ranges between 7.7 and 8.6, the salinity between 0.2 and 0.8 PSU and the temperature between approximately 0 and 28 °C (Rijkswaterstaat 2020). Dreissenids were added to a tank with tap water of room temperature (± 20 °C). The four containers were stocked with 20 individuals each. All tanks were illuminated with daylight coming in through windows of the laboratory, with a natural photoperiod (batch 1 and 3: 8L:16D, batch 2: 11L:13D; Light:Dark).

In total six repeated runs of a movement experiment were carried out (batch 1: run 1–3; batch 2: run 4–6, Figure 1). The movement of the same individuals was tracked for three consecutive runs because of the limited collection capacity of dreissenids from the bricks at our study sites. Dreissenids were allowed to move within the tanks for 4 to 10 days. The initially selected duration of the experiments was 10 days. However, after noticing that most individuals stopped moving after 24–48 hours, the following experiments were shortened. This way we were able to run more experiments in a shorter amount of time. In between each run, the mussels were allowed to recover for 3 days in aerated and acclimatized Haringvliet water. The particulate organic matter present in this Haringvliet water served as their only food source. An additional experiment was conducted with differentially sized mussels collected in batch 3 to assess whether the size of an individual affected its movement.

Movement rate, duration, speed and distance

To assess the movement rate, data from all runs (1–6) were analysed. The movement rate was measured as the number of moving individuals over the total number of individuals (%) for both dreissenid species during each of the days of the 6 runs. The total number of each dreissenid species used differed between the days as the duration of the experiments varied between 4 and 10 days. The maximum and average movement duration, speed and distance were assessed during runs 4 to 6 with a focus on the first 24 hours of the experiment, as most of the dreissenids moved within this timeframe. These parameters were measured using 2-minute interval time-lapse photography. Once an individual started moving, we recorded this as an “active period” for this specific individual. We defined an active period as the moment at which an individual started to move at a speed higher than 15 cm/h for at least 2 consecutive minutes. The active period came to an end at the moment the individuals remained at the same location in two consecutive photos, which corresponds to 2 minutes. One individual might display multiple active periods throughout the experiment, therefore, the number of active periods was registered for each individual. The maximum and average movement duration of an individual was registered as the duration
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Figure 2. The difference between displacement distance and the actual distance travelled by dreissenids (A: location at the beginning of the movement experiment; B: location after 24 hours).

of all active periods of that individual within the first 24 hours and as the duration of the first active period. The maximum and average speed was measured as the distance travelled by an individual in between two consecutive photos. This distance was noted as the number of centimetres covered in 2 minutes and recalculated to centimetres per hour. The distance moved could be subdivided into two different types: the displacement distance and the actual distance (Figure 2). The displacement distance is the shortest distance between the dreissenids’ location at the beginning of the experiment and its location after 24 hours. The actual distance moved by the dreissenids was calculated as the sum of distances measured between consecutive time-lapse photos. The actual distance was estimated for the first 24 hours and the first active period of each individual.

Statistical analyses

A generalized linear mixed model was performed to determine whether the number of individuals moving for several days, the total number of individuals moving throughout all of the movement experiments and the number of individuals moving each separate day of the experiments, differed between both species. This test was chosen because the data contained repeated measurements, as the movement of each mussel was tracked for three consecutive runs. We used three separate binomial generalized linear mixed models to test for differences between species in the following independent test variables: (i) individuals moved for multiple days (“yes” or “no”), (ii) individuals moved at some point during the experiment runs (“yes” or “no”), (iii) individuals moved each day (“yes” or “no”). The mussel “species” was the fixed response variable, while the “run” number and individual “mussel” number were the random effect variables. The analysis was performed using the package nlme (Pinheiro et al. 2017). As the H₀ for this test, we assumed there was no difference in total individuals moved or individuals that moved for multiple days for the fixed variables (“species”). A one-tailed Chi-square (χ²) test was used to assess whether the movement rate for individuals with different shell sizes differed significantly. The Mann-Whitney U test was used to analyse the statistical significance of differences in movement duration, speed and distance between both species. Additionally, the relationship between shell
Figure 3. The percentage of individuals moving for both dreissenid species throughout the movement runs. The error bars represent the standard error. An equal number of dreissenids of each species was used to calculate the percentage for each day. The total number of each dreissenid species used (=N indicated above dots) differed between the days as the results were based on 2, 1, 1 and 2 experiments, which ran respectively for 4, 5, 7 and 10 days. During one of the experiments of 10 days, the movement was not tracked on day 8 and 9, explaining the lower N on those days.

size and movement rate was assessed using the Mann-Whitney U test. The Kruskal-Wallis test was used to check the effect of the number of days moved on the displacement distance. All analyses were performed using the software R (version 3.6.2) with a statistical significance level of $P < 0.05$.

Results

Movement rate and shell size

*Dreissena bugensis* individuals with a shell size of 1–2 cm moved every day during the experiments (Figure 3). The *D. polymorpha* individuals with the same shell size were found to be moving on each day except day 9 (Figure 3). During the first 24 hours, the percentage of moving individuals of *D. bugensis* was higher than that of *D. polymorpha* (circa 50% vs 40%, respectively; Generalized linear mixed model: $P = 0.003$, Table 1). Throughout all remaining days, i.e. up to the 10th day, the number of moving individuals was also recorded to be higher for *D. bugensis* than for *D. polymorpha*. Apart from the first day, this difference was also found to be significant for day 2 (Generalized linear mixed model: $P < 0.001$, Table 1), while for days 3 to 10 the difference was not significant (Generalized linear mixed model: all $P \geq 0.613$, Table 1) (Figure 3). Throughout the whole experiment, the number of individuals that moved at any point in time was almost two times higher for *D. bugensis* (58%) compared to *D. polymorpha* (39%) (Generalized linear mixed model: $P < 0.001$, Figure 3, Table 1).
Table 1. The movement rate, duration, speed, actual distance, displacement distance and the relationship between movement and shell size for both species in the first 24 hours of the movement experiments. The standard error is represented next to the average values. Where appropriate, a Generalized linear mixed model (Z), Mann-Whitney U test (U), Kruskal-Wallis test (K) or Chi-squared test ($\chi^2$) was performed and represented.

| Statistical test | Dreissenia polymorpha | Dreissenia bugensis | Movement rate same size (1–2 cm) |
|------------------|-----------------------|---------------------|---------------------------------|
| Total number moved (%) | 39 | 58 | $Z = -4.1, N_{1,2} = 240, P < 0.001^*$ |
| Number moved Day 1 (%) | 33 | 46 | $Z = -3.0, N_{1,2} = 240, P = 0.003^*$ |
| Day 2 (%) | 6 | 20 | $Z = -124.7, N_{1,2} = 240, P < 0.001^*$ |
| Day 3 (%) | 7 | 13 | $Z = -0.4, N_{1,2} = 240, P = 0.706$ |
| Day 4 (%) | 5 | 9 | $Z = -0.3, N_{1,2} = 240, P = 0.746$ |
| Day 5 (%) | 4 | 12 | $Z = -0.5, N_{1,2} = 160, P = 0.634$ |
| Day 6 (%) | 4 | 15 | $Z = -0.5, N_{1,2} = 120, P = 0.613$ |
| Day 7 (%) | 4 | 11 | $Z = -0.4, N_{1,2} = 120, P = 0.726$ |
| Day 8 (%) | 3 | 10 | $Z = -0.2, N_{1,2} = 40, P = 0.816$ |
| Day 9 (%) | 0 | 5 | $Z = -0.01, N_{1,2} = 40, P = 0.911$ |
| Day 10 (%) | 3 | 9 | $Z = -0.3, N_{1,2} = 80, P = 0.772$ |
| Movement and shell size | | | |
| Movement rate (%) different sized individuals | 19 | 41 | $\chi^2 = 6.2, N_1 = 54, N_2 = 68, P = 0.013^*$ |
| Relationship between shell size and movement rate | NA | NA | |
| Movement duration | | | |
| Maximum duration (min) | 178 | 126 | NA |
| Average duration (min) | 74 ± 14 | 57 ± 11 | $U = 64.5, N_1 = 14, N_2 = 11, P = 0.511$ |
| Average duration in one active period (min)$^*$ | 55 ± 14 | 35 ± 7 | $U = 66.5, N_1 = 14, N_2 = 11, P = 0.583$ |
| Multiple days moved (%) | 13 | 35 | $Z = -5.4, N_{1,2} = 240, P < 0.001^*$ |
| Speed | | | |
| Maximum speed (cm/h) | 60.0 ± 3.1 | 90.0 ± 6.1 | $U = 99.0, N_1 = 14, N_2 = 11, P = 0.225$ |
| Average speed (cm/h) | 25.4 ± 2.3 | 30.4 ± 3.4 | $U = 97.5, N_1 = 14, N_2 = 11, P = 0.273$ |
| Maintained top speed for | 4.0 cm / 4 min | 3.0 cm / 2 min | NA |
| Actual distance | | | |
| Maximum distance (cm) | 58.0 | 56.2 | NA |
| Average distance (cm) | 31.0 ± 5.5 | 27.4 ± 5.3 | $U = 72.0, N_1 = 14, N_2 = 11, P = 0.809$ |
| Average distance per active period (cm)$^*$ | 24.1 ± 5.9 | 17.9 ± 4.0 | $U = 72.0, N_1 = 14, N_2 = 11, P = 0.809$ |
| Displacement distance | | | |
| Maximum distance (cm) | 24.7 | 19.2 | NA |
| Average distance (cm) | 11.6 ± 2.2 | 11.6 ± 1.9 | $U = 81.0, N_1 = 14, N_2 = 11, P = 0.848$ |
| Distance in relation to number of days moved | NA | NA | $D. polymorpha: K = 4.2, df = 3, P = 0.245$ |

$^*$ Values derived from the first active period instead of the first day

$^*$ Significant p-values

When comparing various sized individuals to each other (1.02–3.04 cm and 0.86–2.27 cm, respectively), D. bugensis (41%) had twice as many moving individuals in comparison to D. polymorpha (19%) (Chi-squared test: $P = 0.013$). No significant relationship was found between the shell size and the movement rate of individuals for either D. polymorpha or D. bugensis (Mann-Whitney U test: $P = 0.193$, $P = 0.172$, respectively, Figure 4). However, for D. polymorpha none of the individuals with a shell size larger than 2 cm moved, while D. bugensis individuals of the whole size range moved. The largest, and thus oldest collected D. bugensis (± 4 cm) had a tendency to move (two out of nine individuals), while none of the large D. polymorpha (± 3 cm) individuals moved (zero out of eight individuals).
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Figure 4. The effect of shell size on the movement of dreissenids after 24 hours. In general, twice as many *D. bugensis* moved in comparison to *D. polymorpha*. For *D. polymorpha* only the small (< 2 cm) individuals moved, while for *D. bugensis* individuals of all sizes moved around in the tank. Photo by Anouk D’Hont.

Figure 5. Average speed, average displacement distance, average actual distance and average movement duration for the two dreissenid species. For each of the parameters, 14 *D. polymorpha* and 11 *D. bugensis* individuals were assessed.

**Movement duration**

The movement duration of dreissenids measured during the first 24 hours was not significantly different between the two species (Mann-Whitney U test: *P* = 0.511, Table 1, Figure 5). Additionally, there was no significant difference found between the duration of the first active period of each species (Mann-Whitney U test: *P* = 0.583, Table 1).

Individuals started moving within 2.5 and 12 hours after the start of the experiment runs. The number of individuals that moved for more than one
day was significantly higher for *D. bugensis* (35%) during each of the six runs compared to *D. polymorpha* (13%) (Generalized linear mixed model: $P < 0.001$, Table 1). *Dreissena bugensis* specimens moved for a maximum of 5 out of 10 days. *Dreissena polymorpha* specimens moved for a maximum of 4 out of 10 days.

**Movement speed**

The average movement speed did not differ significantly between both dreissenid species (Mann-Whitney U test: $P = 0.273$, Table 1, Figure 5). The top speed of *D. bugensis* (90 cm/h for 2 min) was a third higher than the top speed measured for *D. polymorpha* (60 cm/h for 4 min). The maximum speed was estimated for each individual. When comparing this maximum speed of the separate individuals of each species with each other, no significant difference was found between both species (Mann-Whitney U test: $P = 0.225$, Table 1).

**Movement distance**

The average displacement distance within the first 24 hours did not differ significantly between both dreissenid species (Mann-Whitney U test: $P = 0.848$, Table 1, Figure 5). Additionally, the actual distance moved within the first 24 hours and during one active period by either of the dreissenids did not differ significantly (Mann-Whitney U test: $P = 0.809$, Table 1, Figure 5). There was no significant relationship between the number of days moved and the displacement distance for either *D. polymorpha* or *D. bugensis* (Kruskal-Wallis test: $P = 0.245$, $P = 0.643$, respectively).

**Discussion**

**Movement distance**

The displacement and actual distance moved, did not differ significantly between both species (Figure 5). The maximum distance of 58.0 and 56.2 cm and average distance of 31.0 and 27.4 cm measured during this study for *D. polymorpha* and *D. bugensis*, respectively, are comparable to the values measured in literature (Table 1) (Toomey et al. 2002; Coons et al. 2004; Kobak and Nowacki 2007; Kobak and Kakareko 2009; Kobak 2013). In other studies, the maximum distance travelled by *D. polymorpha* was estimated to be between 20.5 and 80.3 cm with an average between 5.9 and 27.5 cm (Toomey et al. 2002; Coons et al. 2004; Kobak and Nowacki 2007; Kobak and Kakareko 2009; Kobak 2013). The maximum distance moved by both species is thus within the range reported by the previously mentioned studies. However, *D. polymorpha* moved up to 10–20 cm further in Kobak and Nowacki (2007) and Kobak and Kakareko (2009) compared to the maximum distance measured during our study. These studies assessed the effect of light and the presence of several predators on
the distance moved by *D. polymorpha*, representing lesser optimal environmental conditions for this species than the ones in our study. This would support the hypothesis that suboptimal environmental conditions promote dreissenid movement.

Both dreissenids species displayed non-linear, corkscrew-like or circular movement paths resulting in a higher actual distance travelled in comparison to the displacement distance. For both species the actual distance travelled was more than two times higher than the displacement distance (Table 1). In case they would be exposed to a directional nuisance, like for example strobe lights, they might have displayed a linear and directional movement path, moving away from the nuisance source (Coons et al. 2004).

**Movement duration**

No significant differences were found for the movement duration within the first 24 hours (65 min) and the duration of one active period (45 min) between individuals of both species (Table 1, Figure 5). However, the number of individuals moving for more than one day (2–5 days) was more than two times higher for *D. bugensis* compared to *D. polymorpha*. Having more than one movement day might have an effect on the distance moved by an individual. Unfortunately, we do not have time-lapse photos throughout the whole experiment, to check whether this is actually true. Therefore, we were not able to assess the relationship between the actual movement distance and number of days moved by an individual. Consequently, we do not know whether having several movement days is beneficial for an individual. We could hypothesize that having several movement days gives *D. bugensis* a higher chance to avoid unfavourable conditions and find optimal environments.

All relocating individuals started moving within 2.5 and 12 hours after the start of the experiments. During this research, none of the individuals moved during the first 2.5 hours of the experiments, whereas Toomey et al. (2002) recorded movement for about half of the assessed *D. polymorpha* during their 2-hour lasting experiment. Toomey et al. (2002) exposed their *D. polymorpha* individuals to several temperature, light and water hardness treatments. These treatments might have provoked the mussels, more than our setup, to start looking for a better environment, mobilising them earlier. Additionally, we acclimatized the dreisseni ds for 24 to 48 hours before starting each experiment, while Toomey et al. (2002) collected their mussels only 4 hours prior to the start of their experiment. Our dreissenids might have moved during the first two hours after placement in the acclimatization tank, however, we did not monitor the dreissenids during acclimatization.
Movement speed

The observed top speed was a third higher for *D. bugensis* (90 cm/h) in comparison to *D. polymorpha* (60 cm/h). These top speeds are higher than the known top speed of 48 cm/h for *D. polymorpha* (Toomey et al. 2002; Czarnołęski et al. 2010). Both dreissenid species moved at more or less the same average speed throughout the experiments (Table 1, Figure 5). However, the average speed measured during this study (25.4 cm/h and 30.4 cm/h for *D. polymorpha* and *D. bugensis*, respectively) was more than two times higher than the average speed known from literature for *D. polymorpha* (between 6 and 12 cm/h) (Toomey et al. 2002; Czarnołęski et al. 2010). The cited articles might have underestimated the movement speed of *D. polymorpha*, as they extrapolated possible speed values from the distance moved over the 2-hour duration of the experiment (Toomey et al. 2002) or with intervals of 15 minutes over 3 hours (Czarnołęski et al. 2010). Individuals probably did not move at a constant speed throughout the experiment, as they might have stopped moving within the 2 hours or 15-minute interval, respectively.

Movement rate and shell size

The shell size and movement rate of individuals were not correlated for either *D. polymorpha* or *D. bugensis*. This result is different than generally reported in literature where, for *D. polymorpha*, the movement rate and the distance moved is inversely proportional to their shell size and thus also to their age (Kobak 2001; Toomey et al. 2002). Even though our study found no significant effect of the shell size on the movement rate of both species, we did observe that none of the individuals of *D. polymorpha* larger than 2 cm moved (Figure 4).

Movement rate

This study exposed that about twice as many *D. bugensis* individuals moved during the movement experiments in comparison to *D. polymorpha* individuals when looking at variously sized specimens (41% and 19%, respectively). This experiment mimicked a natural dreissenid community as *D. bugensis* grows faster and larger than *D. polymorpha* (D’Hont et al. 2018). When comparing individuals with an equal shell size to each other, we obtained a similar result with a significantly higher movement rate for *D. bugensis* (58% and 39%, respectively). Additionally, about 10% more *D. bugensis* specimens were moving around the polyethylene tanks at any point in time during the experiments (Figure 3). This comparison has to our knowledge not been made before in literature. In another experiment by the first author, a significantly lower percentage of *D. bugensis* (69%) individuals were found to be attached to the substrate in comparison to
D. polymorpha (85%) individuals (D’Hont et al. 2021). This lower attachment rate for D. bugensis could correspond to its higher movement rates, as dreissenids will most likely not attach to the containers while moving. Since we assume that our experimental circumstances (drying, cleaning and tagging of mussels and non-aerated, nutrient-poor water) mimicked unfavourable conditions for dreissenids, they were likely triggered to look for a better environment. Examples of such unfavourable environmental conditions in their natural habitat are poor water quality, changes in orientation, presence of conspecifics, low oxygen content or desiccation (Kobak 2001; Alexander and McMahon 2004; Kobak and Nowacki 2007; Collas et al. 2018). These environmental conditions are proven stimuli of detachment and/or movement in dreissenids (Kobak 2001; Kobak and Nowacki 2007; Collas et al. 2018). One could expect that a higher percentage of moving individuals gives D. bugensis a higher chance to find optimal environments.

The results of this research can contribute to assessing the risk of spread and establishment of both dreissenid species (Andersen et al. 2004; Verbrugge et al. 2012). Boat traffic and, to a lesser degree, birds and fish were suggested to be the main (upstream) dispersal vectors for dreissenids (Wilson et al. 1999; Karatayev et al. 2011). This type of dispersal most likely includes passage through unfavourable environmental conditions like overland transport or changes in salinity. Dreissena polymorpha individuals endure these types of e.g. overland transport better than D. bugensis does (Collas et al. 2018). Dreissena bugensis will in such situations probably detach looking for a better environment (D’Hont et al. 2021). Consequently, the risk of introduction is higher for D. polymorpha in comparison to D. bugensis (Baldwin et al. 2002). However, the higher number of moving individuals with the ability to look for better locations allows D. bugensis to become a stronger invader once the population is settled and established. This might give D. bugensis a competitive benefit over D. polymorpha and possibly be a contributing driver to the observed dominance shift between both species. This will mostly be the case in highly fluctuating environments, i.e. with strong water currents, large fluctuations in water level or salinity. As our study site, the Haringvliet, has little to no currents and well-regulated constant water levels, the motivation to move to better environments will be low in this area. This might explain why both species still co-occur in the Haringvliet, 14 years after the introduction of D. bugensis and why D. bugensis was not able to fully outcompete D. polymorpha.

The movement of dreissenids might be influenced by environmental conditions, like e.g. temperature, salinity, light conditions, oxygen and food availability (Kobak 2001; Toomey et al. 2002; Coons et al. 2004; Kobak and Nowacki 2007; Collas et al. 2018). We chose to keep these
environmental conditions constant throughout the experiment while aiming at elucidating the differences in moving behaviour of two dreissenid species. Our study was conducted with a temperature difference of about 15 °C between the temperature at the collection site and the experimental water temperature (using gradual acclimatization). Future research may be focused on unravelling differential effects of various environmental conditions and procedures for acclimatization. Therefore, we recommend future studies to include movement experiments conducted at several temperatures and other environmental conditions.

**Conclusions**

The top speed of *D. bugensis* was higher than that of *D. polymorpha*, moving at maximum 90 cm/h and 60 cm/h respectively, after a disturbance of environmental conditions. Additionally, about twice as many individuals of *D. bugensis* moved during the experiments in comparison to *D. polymorpha*. The same result was found when comparing individuals with various shell sizes to each other. About 10% more *D. bugensis* specimens were moving around the polyethene tanks at any point in time during the experiments. This gives them the capacity to actively move away from unfavourable environmental conditions. Examples of such unfavourable environmental conditions for dreissenids are poor water quality, changes in orientation, presence of conspecifics, low oxygen content and desiccation. The average movement duration, average speed and average distance moved did not differ significantly between *D. polymorpha* and *D. bugensis*. Most individuals moved in more or less circular patterns, causing their actual movement distance to be twice as high as their displacement distance. Consequently, the average movement duration, average speed, average distance moved and general movement pattern of these two mussel species probably do not contribute to the species displacement. However, the results support our hypothesis that *D. bugensis* could have a competitive benefit over *D. polymorpha* by having a higher top speed and a significantly higher number of individuals moving when their populations are disturbed. Therefore, mobility might be one of the contributing drivers of the observed dominance shift between both species.

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