

Research Article

Drivers of dominance shifts between invasive Ponto-Caspian dreissenids *Dreissena polymorpha* (Pallas, 1771) and *Dreissena rostriformis bugensis* (Andrusov, 1897)Anouk D'Hont^{1,5,*}, Adriaan Gittenberger^{1,2,3}, A. Jan Hendriks⁴ and Rob S.E.W. Leuven^{5,6}¹*GiMaRIS, Marine Research Inventory & Strategy Solutions, Rijkswaterstaat, Rijkswaterweg 75, 2171 AK Sassenheim, The Netherlands*²*Department of Marine Zoology, Naturalis Biodiversity Center, Pesthuislaan 7, 2333 BA Leiden, The Netherlands*³*Centre for Environmental Studies (CML) and Institute of Biology Leiden (IBL), University, Leiden, Sylviusweg 72, 2333 BE Leiden, The Netherlands*⁴*Department of Environmental Science, Institute for Water and Wetland Research, Radboud University, Heyendaalseweg 135, 6525 AJ Nijmegen, The Netherlands*⁵*Department of Animal Ecology and Physiology, Institute for Water and Wetland Research, Radboud University, Heyendaalseweg 135, 6525 AJ Nijmegen, The Netherlands*⁶*Netherlands Centre of Expertise on Exotic Species (NEC-E), Nature Plaza, P.O. Box 9010, 6500GL Nijmegen, The Netherlands*Author e-mails: dhont@gimaris.com (AD), gittenberger@gimaris.com (AG), a.j.hendriks@science.ru.nl (AJH), r.leuven@science.ru.nl (RSEWL)

*Corresponding author

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Abstract

Two of the most invasive freshwater bivalve species in temperate regions worldwide are the Ponto-Caspian dreissenids *Dreissena polymorpha* and *Dreissena rostriformis bugensis*. Throughout their range, observations have been made of a dominance shift favouring *D. r. bugensis* where the two species co-occur. Although both dreissenids have been widely studied, the mechanisms driving this dominance shift are not completely understood. Our long-term and short-term field experiments assessed a selection of species traits related to growth and settlement, which may be linked to a competitive benefit for either of both species. We assessed relative population densities in time and space, mortality, and inter- and intraspecific interactions in relation to environmental factors like temperature, salinity, and light intensity, using 14 × 14 cm PVC settlement plates. Dreissenids were identified, counted and measured over 11 years in the waterbody where *D. r. bugensis* was first discovered in Western Europe. *Dreissena polymorpha* appeared to have a competitive benefit over *D. r. bugensis* by being able to settle earlier, i.e. in spring, while other studies indicate the opposite. As salinities in the study region were relatively high in spring, this discrepancy may be explained by a higher salinity tolerance of *D. polymorpha*, as is known from the literature. In addition, Common Coots predated *D. r. bugensis* clusters. *Dreissena polymorpha* were not usually found in such clusters. Regardless of these competitive benefits for *D. polymorpha*, *D. r. bugensis* is the dominant species in the region. One possible explanation could be the fact that *D. r. bugensis* was found in similar densities on both light exposed and shaded fouling plates. *Dreissena polymorpha* on the other hand, was practically absent on light-exposed plates after 12 months. Therefore, a wider range of habitats seems to be suitable for the settlement of *D. r. bugensis*. Another driver of the dominance shift can be linked to it having faster growth than *D. polymorpha*, especially during spring. More generally, *D. r. bugensis* occurred in higher population densities on plates with *D. polymorpha* than on plates with only *D. r. bugensis*. *Dreissena polymorpha* individuals may thus induce the settlement of additional individuals of *D. r. bugensis*. A final reason for the dominance of *D. r. bugensis* concerns its low winter mortality. While the number of *D. polymorpha* individuals more than halved over the winter 2016–2017, no significant decrease in numbers of *D. r. bugensis* was recorded.

Key words: density, growth, interspecific competition, light, mortality, salinity, settlement

Introduction

Both the zebra mussel, *Dreissena polymorpha* (Pallas, 1771), and the quagga mussel, *Dreissena rostriformis bugensis* (Andrusov, 1897), are notorious for dominating hard freshwater substrates throughout most of the Northern hemisphere. Both species cause extensive ecological and economic damage in their native area (Grigorovich and Shevtsova 1995) and introduced regions (Binimelis et al. 2007; Fahnenstiel et al. 2010). *Dreissena polymorpha* started spreading out of its native area (the Black Sea, Caspian Sea, Azov Sea and Aral lake) to Europe and to countries of the former Soviet Union at the beginning of the 19th century (Van der Velde et al. 2010; Sousa et al. 2011). *Dreissena rostriformis bugensis* was restricted to Ukrainian river estuaries in the Northern Black Sea area until the mid-20th century (Therriault et al. 2005). Within about 20 years, *D. r. bugensis* colonized Europe and Russia and both *D. r. bugensis* and *D. polymorpha* simultaneously colonized Northern America (Molloy et al. 2007; Van der Velde and Platvoet 2007; Matthews et al. 2014). The first population of *D. r. bugensis* in Western Europe was discovered in 2006 in the estuary Haringvliet – Hollands Diep in the Netherlands (Figure 1: Location C) (Molloy et al. 2007; Schonenberg and Gittenberger 2008). The Haringvliet is a part of the Rhine-Meuse river delta which since 1970 has been separated from the North Sea by sluices. As a result, this waterbody became a freshwater system with minimal saltwater influences.

During the last decade, there have been observations of a dominance shift from *D. polymorpha* to *D. r. bugensis*, both in their introduced regions (Europe, Eurasia i.e. Russia and North America) and in their native area (the Ponto-Caspian region) (Stoeckmann 2003; Therriault et al. 2005; Matthews et al. 2014). However, the mechanisms driving this dominance shift are still not completely known. Therefore, research was initiated to disentangle drivers causing competitive benefits for either of the dreissenid species. Some of these drivers have already been assessed during short-term studies. For example, *D. polymorpha* is known to have a higher salinity tolerance and a wider salinity range than *D. r. bugensis* (Mills et al. 1996), possibly leading to a higher prevalence of this species in more saline systems. Additionally, *D. polymorpha* is able to produce more gametes during reproduction (Stoeckmann 2003). Nevertheless, *D. r. bugensis* is the dominant species in most habitats. *Dreissena rostriformis bugensis* is known to be able to persist at greater depths and in lower nutrition environments (Ram et al. 2012). Moreover, *D. r. bugensis* has a higher temperature tolerance and a wider temperature range, permitting

D. r. bugensis to reproduce and settle earlier than *D. polymorpha* (Claxton and Mackie 1998; Gerstenberger et al. 2011). This allows for a faster colonization time of *D. r. bugensis* and potentially leads to a priority effect (Young et al. 2001). *Dreissena rostriformis bugensis* is also known to have a faster growth rate and reach a larger size than *D. polymorpha* (Neumann et al. 1993; Stoeckmann 2003). Moreover, *D. r. bugensis* is known to have a higher assimilation efficiency, a higher activity of certain enzymes (e.g. thiaminase), higher filtration rates and lower respiration rates giving it additional advantages over *D. polymorpha* (Ram et al. 2012). Despite these findings, the current body of knowledge on potential drivers of the dreissenid dominance shift has mostly been based on short-term studies and laboratory experiments. The present study assessed the impact of some of these drivers in a long-term field experiment, leading to a more complete understanding of the observed patterns. SETLement (SETL) monitoring in the river estuary Haringvliet started in 2006 just before *D. r. bugensis* was first recorded. This was also the first record of this species in Western Europe (Bij de Vaate 2008; Schonenberg and Gittenberger 2008). Consequently, the SETL monitoring project enables the documentation of the introduction, population establishment and succession of the *D. r. bugensis* population just after its initial introduction in Western Europe. In addition, this study gives more insight into the interspecific competition of this species with *D. polymorpha* which already occurred commonly in the Haringvliet. The present study uses the data derived from the SETL project to assess 1) the long-term effects of species traits (settlement period and growth rate), environmental factors (temperature, salinity and light intensity), and 2) processes underlying competitive benefits (population density, interspecific competition, winter mortality and predation mortality) to estimate their importance for the dreissenid dominance shift (Figure 2).

Of the known drivers, we have assessed the impact of salinity and temperature on species traits like settlement and growth. Both dreissenid species are known to favour shaded sites for settlement (Kobak 2001; Kobak and Nowacki 2007). This was assessed during the present study. Additionally, we hypothesised that light intensity may also have an impact on population density later on in the succession. The latter appears to be unknown in the literature. Other unknown drivers that may give a competitive benefit for one of the two dreissenid species concern differences in winter mortality and potential interspecific competition. Marescaux et al. (2015) hypothesize that *D. r. bugensis* may have a higher growth rate, causing it to have a larger shell size and

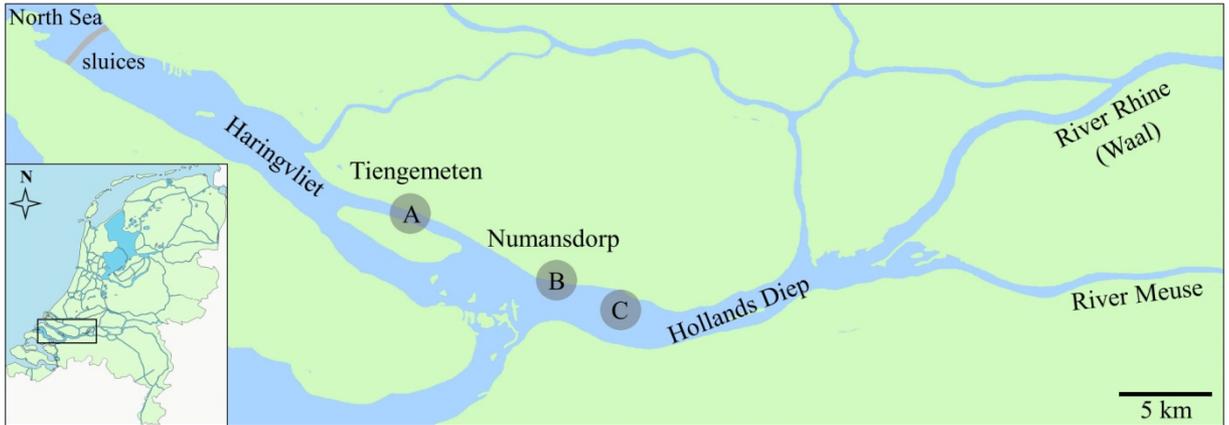


Figure 1. Locations of field experiments in the Rhine-Meuse river estuary in the Netherlands. (A) Tiengemeten ferry dock, (B) Numansdorp, (C) the first record location of *Dreissena rostriformis bugensis* in Western Europe (Molloy et al. 2007) (modified after Figure 1 in Schonenberg and Gittenberger 2008).

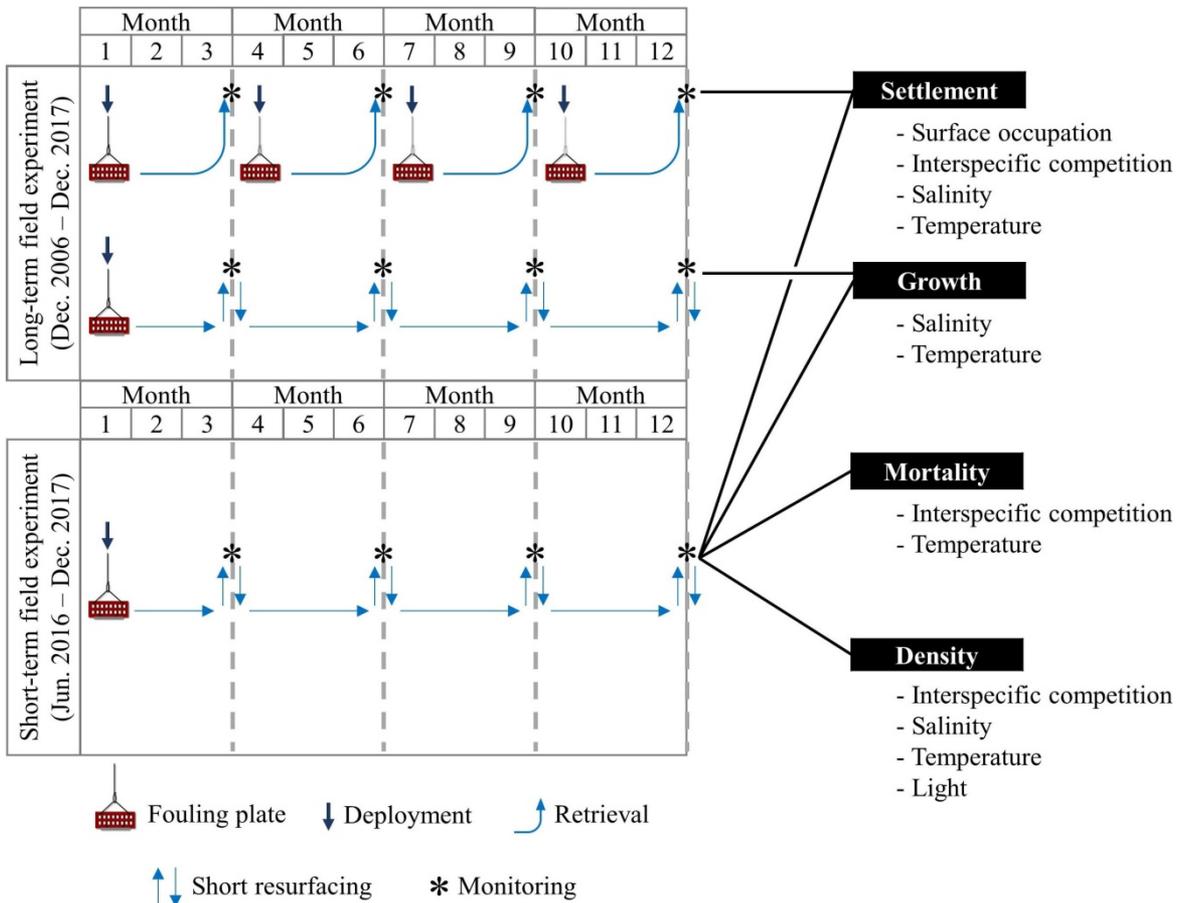


Figure 2. Summary of SETL fouling plate experiment setup concerning the long-term (11 years) and short-term (1.5 years) field experiment. The bricks represent the deployment of a new plate. The * represent the monitoring of the SETL plates, which happened every 3 months. During the long-term field experiment, some fouling plates were deployed for only 3 months and replaced by a new set. Other fouling plates were deployed continuously. During the short-term field experiment, all fouling plates were deployed continuously throughout the experiment. These “continuous” plates got shortly lifted out of the water for monitoring and redeployed in the same place. The assessed parameters were represented in the black boxes. Further details on the setup of the experiment can be found in the material and method section.

body mass, which may help them survive winter stress better. Finally, it was tested to what degree the presence of one species may have an impact on the settlement of the other species. Interspecific competition is known to give a competitive benefit to some invasive species, for example, the invasive tunicate *Botrylloides violaceus* over the native *Botryllus schlosseri* (Gittenberger and Moons 2011).

Material and methods

Study sites

Panmictic populations of *D. polymorpha* and *D. r. bugensis* were studied in Western Europe, in the Netherlands, in Tiengemeten (Figure 1: Location A) and Numansdorp (Figure 1: Location B) in the freshwater Haringvliet. Within the Tiengemeten ferry harbour, SETL fouling plates were attached to a large floating dock near the Haringvliet connection (51°45.250'N; 4°19.050'E) and a smaller floating dock close to the control lock (51°45.261'N; 4°19.046'E). In Numansdorp the SETL fouling plates were deployed onto one large floating dock at the entrance of the village harbour (51°43.037'N; 4°26.211'E). At both locations, there was a subdivision between fouling plates deployed on the southern edge of the floating dock (fully exposed to sunlight), the long western edge (alternately exposed to light and shade) and the northern edge (completely shaded). At these locations, two field experiments were performed: 1) an ongoing long-term experiment which ran from 2006 until the present day of which the data from December 2006 to December 2017 were used, and 2) a short-term experiment running from June 2016 until December 2017 (Figure 2).

Field experiments

SETL

Each SETL plate consists of a 14 by 14 cm sanded PVC plate and a brick stone attached to a rope and deployed 1 meter below the water surface (Figure 3). This setup follows the standardized method developed by the Smithsonian Environmental Research Center (SERC) (Hines and Ruiz 2001). A total of 98 SETL fouling plate structures were deployed for the Haringvliet field experiment (Table 1). Of these, 18 were already deployed during the long-term SETL project in the area and 80 were deployed for the short-term field experiment.

From the start of the short-term field experiment in June 2016, all fouling plates were monitored every 3 months: intervals here referred to as “summer” (July, August, September), “autumn” (October, November,

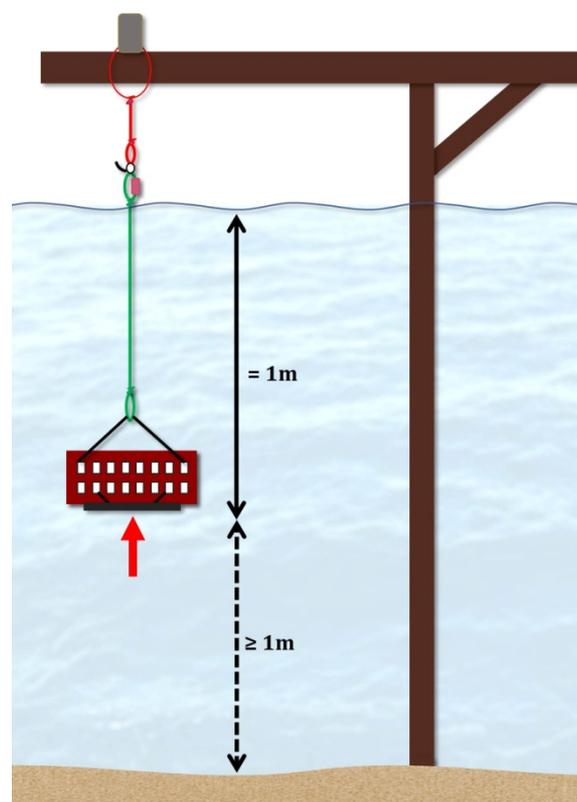


Figure 3. Schematic overview of the construction and deployment of a SETL fouling plate. Sanded 14 by 14 cm PVC fouling plates (indicated with the red arrow) are weighted down by a brick stone. The fouling plate is deployed 1 m below the water surface and preferably at least 1 m above the bottom.

Table 1. The number and date of SETL fouling plates deployed at the two study sites for the long-term and short-term field experiment. The total number indicates the total amount of fouling plates deployed in the long-term experiment (18), the short-term experiment (80) in Tiengemeten (56) and Numansdorp (42).

| Experiment | Deployment date | Tiengemeten | Numansdorp |
|------------|-----------------|-------------|------------|
| Long-term | | | |
| 18 | Summer 2012 | 3 | 1 |
| | Autumn 2012 | 2 | 3 |
| | Winter 2012 | 1 | 0 |
| | Summer 2014 | 2 | 3 |
| Short-term | Summer 2015 | 3 | 0 |
| | Summer 2016 | 33 | 23 |
| | Autumn 2016 | 3 | 3 |
| | Winter 2016 | 3 | 3 |
| | Spring 2017 | 3 | 3 |
| Total | Summer 2017 | 3 | 3 |
| | | 56 | 42 |

December), “winter” (January, February, March), and “spring” (April, May, June) as they approximately correspond with the 4 seasons. Each monitoring

period, the fouling plates were lifted out of the water and placed in a bucket filled with water (Figure 2). Each plate was photographed by taking one overview picture of the whole plate and about 25 detailed pictures of the fouling plate surface.

Dreissenid identification

The fouling plates were lifted out of the water for circa 15 minutes to identify and count all *D. polymorpha* and *D. r. bugensis* individuals on the plate. Both species were identified based on characteristics described in the literature (Domm et al. 1993; Pathy and Mackie 1993; Ram et al. 2012). Both living and dead individuals were recorded.

When measuring *D. polymorpha* and *D. r. bugensis*, all individuals were categorised into one of 9 size classes based on their length, each class representing 0.5 cm (A = 0–0.5 cm, B = 0.5–1 cm, C = 1–1.5 cm, D = 1.5–2 cm, E = 2–2.5 cm, F = 2.5–3 cm, G = 3–3.5 cm, H = 3.5–4 cm, I = 4–4.5 cm). Class I corresponds to the maximal size of *D. r. bugensis* based on the size range stated in the literature (Bij de Vaate 2008; Marescaux et al. 2012).

Data sources and tested parameters

Settlement period

During the long-term field experiment on settlement timing of both species, new sets, each with 3 fouling plates, were deployed at the end of autumn (December), winter (March), spring (June) and summer (September). These plates were retrieved after 3 months. The presence of young individuals (size class A–B) of *D. polymorpha* and *D. r. bugensis* on these plates were recorded to determine and compare their settlement timing and period.

Growth rate

Over the experiment, the length of dreissenids on 54 fouling plates was measured for one year. The shell length of dreissenids on plates deployed at the end of winter and the end of spring was measured every three months during the following year. In 2009–2010, three and four plates deployed in Numansdorp at the end of winter and the end of spring, respectively, were checked. In 2012–2013, dreissenids growing on three plates in Numansdorp deployed both at the end of winter and the end of spring were measured. In 2016–2017 during the short-term field experiment, 41 plates deployed at the end of spring were assessed of which 18 plates were from Tiengemeten and 23 plates from Numansdorp. These years were selected based on the availability of pictures taken during the long-term experiment involving the same plates throughout the year. In 2011–2012 *D. r. bugensis*

gradually became dominant over *D. polymorpha* in the Haringvliet (*unpublished data*). Therefore, the selection of the assessed years for dreissenid growth rate revolved around this “year of shift” 2011–2012. Dreissenids measured in 2009–2010 predate the dominance shift from *D. polymorpha* to *D. r. bugensis*, while dreissenids in 2012–2013 were measured after this shift. The measurements from 2016–2017 were also included in the size curve, as these data represent the short-term extensive experiment. A correction was made for the measurements from fouling plates deployed at the end of winter 2009 for *D. polymorpha* by setting the size to 0 at the beginning of summer. This was needed as there had already been settlement and growth of *D. polymorpha* in spring. To test whether the assigned categorical sizes were comparable to real dreissenid size evolution, the categorical sizes were subtracted by the average deviation of the categorical size from the real size during the first measurement period ($= x - 0.176$ cm). Individuals known to originate from external sources were eliminated from the growth experiment. We thereby ensured that the size evolution curve (Figure 4) represented the growth rate of a similar cohort. Mussels originating from external sources were too large to have settled and grown on the fouling plate itself. They were identified by comparing the maximum size of a certain dreissenid age group known from the literature, to the size of the individuals found in the field (Allen et al. 1999; Orlova and Panov 2004; Pollux et al. 2010; Wong et al. 2011). The external dreissenids exceeding the maximum size had settled on surrounding structures before fouling plate deployment in 2009, 2012 or 2016. Throughout both the long- and short-term field experiment, 6 new empty fouling plates were deployed during each control period. Therefore, we could check for settling individuals, identify them, and exclude them from the growth curve as well.

Relative dreissenid densities

To assess relative densities, only data from the large dock in Tiengemeten was considered, as for the last measurements in summer and autumn 2017 only data from this dock were available. However, population density patterns of both locations were compared to take location effects into account. The mean density and relative abundance on fouling plates populated by both species were assessed on 15, 15, 13, 8, 11 and 8 plates from summer 2016, autumn 2016, winter 2017, spring 2017, summer 2017 and autumn 2017, respectively. The density of both species was expressed in individuals per square meter to facilitate comparisons with existing literature (Stewart et al. 1998). As the bivalves were counted on 14×14 cm ($= 196$ cm²) fouling plates, all values were thus multiplied by 51.

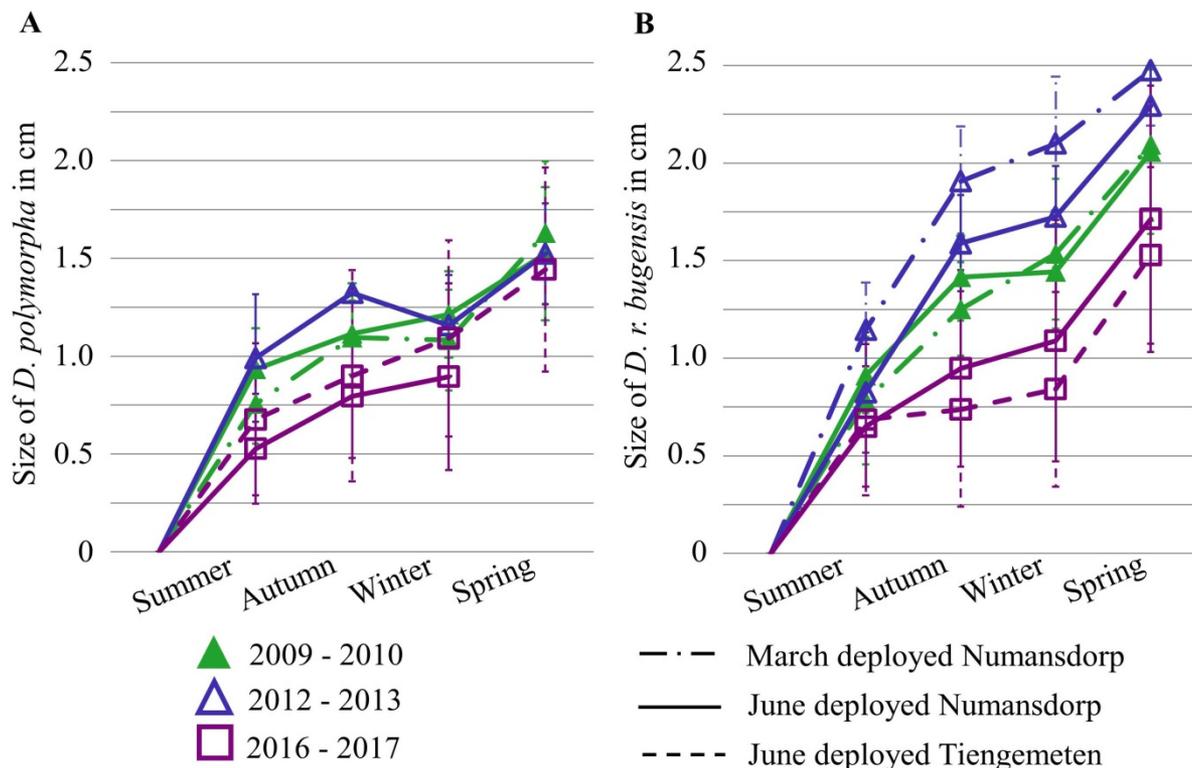


Figure 4. Mean categorical size of (A) *Dreissena polymorpha* and (B) *Dreissena rostriformis bugensis* on fouling plates deployed at the end of winter and/or the end of spring of 2009, 2012 and 2016. The size was measured at four occasions throughout the course of one year at the end of summer (September), autumn (December), winter (March) and spring (June). A correction was made for the measurements of the March deployed fouling plates in 2009 for *D. polymorpha* to set the size to 0 at the beginning of summer, as there had already been settlement and growth in spring.

Light, temperature and salinity impacts

The effect of light intensity was studied by monitoring dreissenid settlement and density on 10 plates deployed from the large dock of Tiengemeten during the first year after settlement. Of these, 6 were deployed on the southern edge of the dock and exposed to sunlight (addressed as “half-shaded”, since settle plates hang upside down in the water (Figure 3)). The other 4 plates were deployed on the northern side of the dock in a shaded area. These 10 plates were the only plates strictly exposed to sunlight or shade and were therefore the only plates used for assessing light impact on settlement and density.

Data on temperature and salinity of the Haringvliet were acquired from the Dutch Ministry of Infrastructure and Water Management (Rijkswaterstaat 2018) (Figure 5). Both parameters were measured at mid-month in surface water near the Haringvliet sluice during both the long- and short-term field experiments between 2006 and 2017. Due to the unavailability of

salinity data in 2017 at the time of analyses, salinity values were derived from chloride concentrations (salinity (‰) = $0.0018066 * [Cl^-]$ ($mg \cdot L^{-1}$)) measured mid-month in surface water near the Haringvliet sluice by the Dutch Ministry of Infrastructure and Water Management (Rijkswaterstaat 2018).

Mortality

During the short-term field experiment, we kept track of empty shells on the fouling plates indicating the mortality of dreissenids. The relative number of empty shells for each period was compared to the total amount of dreissenids found during that time. Data was gathered from autumn 2016 until autumn 2017.

Interspecific competition

To assess whether the presence of *D. polymorpha* affected the density of *D. r. bugensis*, the densities of the latter on fouling plates with syntopic populations (both *D. polymorpha* and *D. r. bugensis*)

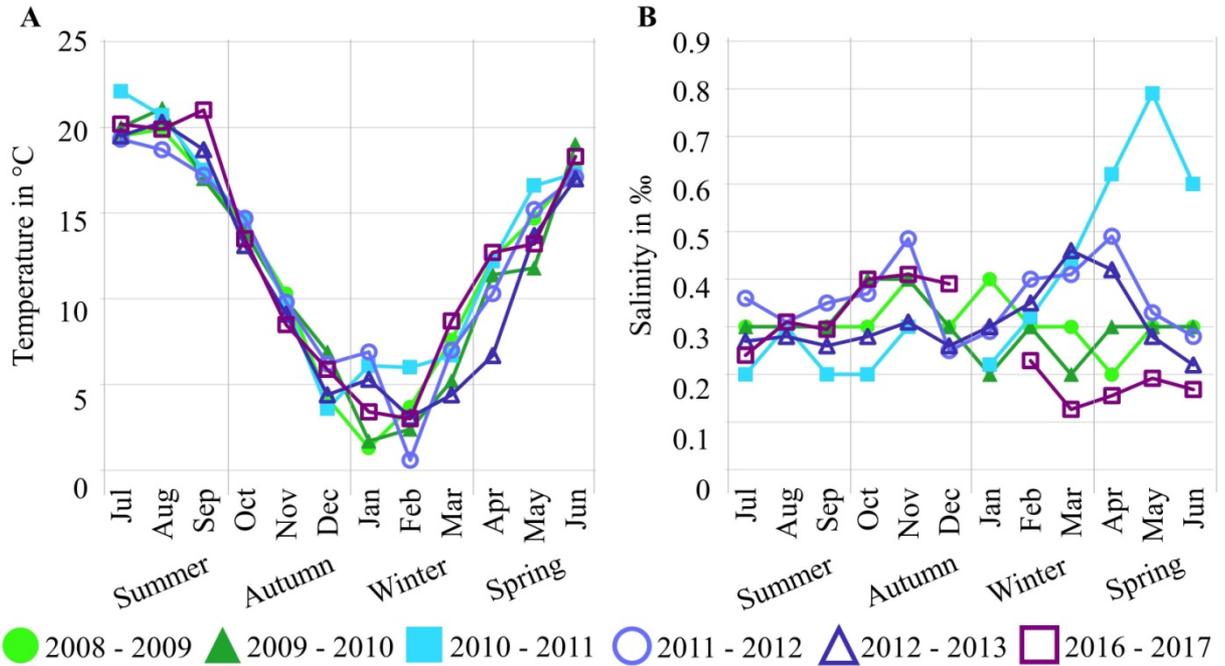


Figure 5. (A) Water temperature and (B) salinity in the Haringvliet measured mid-month in surface water near the Haringvliet sluice before (2008–2010), during (2011–2012) and after (2013) the dominance shift from *Dreissena polymorpha* to *Dreissena rostriformis bugensis*. Additionally, measurements during the short-term field experiment between June 2016 and May 2017 have been plotted. Gaps in the graph are due to lack of data (Rijkswaterstaat 2018).

and allotopic populations (only *D. r. bugensis*) were compared. The term “syntopic populations” is used to describe two species that occur together, while “allotopic populations” is used to indicate a species that occurs by itself, without the second species (Gittenberger and Moons 2011). A similar analysis for *D. polymorpha* was not possible as there were no fouling plates with allotopic *D. polymorpha* populations.

Impact of one-year-old mussels on settlement

The impact of one-year-old mussels on dreissenid settlement was assessed using a subset of the short-term experiment. The relative abundance and density of settling individuals were compared between 15-month-old fouling plates (June 2016–September 2017; containing +/- one-year-old mussels) and 3-month-old empty fouling plates (June–September 2017).

Statistical analyses

A one-tailed Chi-square (χ^2) test was performed to test for differences in winter mortalities based on the absolute numbers of individuals in the winter 2017. Additionally, a one-tailed Chi-square (χ^2) test was used for assessing differences in the relative and absolute abundances of recently settled individuals

of both species on 3-month-old and 15-month-old fouling plates.

A two-tailed Mann-Whitney U test was used to assess whether the abundances of *D. r. bugensis* individuals on the plates in Tiengemeten and Numansdorp were linked to the presence of *D. polymorpha* individuals on those plates. In addition, this test was used to assess whether densities of both species differed significantly for the two levels of shading, i.e. “shade” and “half shade”, during the four seasons from June 2016 to June 2017.

A linear mixed model regression was performed to determine the main factors related to variation in “shell size” between *D. polymorpha* and *D. r. bugensis* and between different years and seasons for each species. This linear mixed model regression was performed using “shell size” as independent variable, and “mussel species”, “year” and “season” as fixed response variables and “SETL plate ID” as a random effect variable. The analysis was performed using the software R (version 1.0.153, package nlme) with a statistical significance level of $P < 0.05$ (Pinheiro et al. 2017). As the H0 for this test, we assumed there was no difference in “shell size” for the fixed variables (“mussel species”, “years” and “seasons”). Subsequently, pairwise post-hoc comparisons were

carried out using Tukey HSD tests to assess within the response variables, which “mussel species”, “years” and/or “seasons” corresponded with significant differences in “shell sizes”. To validate the assumptions of normality and homogeneity of variance within the models, a histogram of the residuals was plotted, and the residuals were assessed against the fitted values (Supplementary material Figure S1).

Results

Settlement period

During the long-term field experiment over 2006–2017 both species were found to settle during summer (Table 2). *Dreissena polymorpha* showed earlier settlement starting in spring between 2006 and 2010. This changed in 2011–2012 when the settlement of *D. polymorpha* was delayed until summer. *Dreissena rostriformis bugensis* only started settling in the summer, with an exception of the early spring settlement in 2017, when both species settled in spring and summer. In conclusion, both species could settle in spring, however *D. polymorpha* did so more frequently. In the winter 2012, a one-time settlement event of dreissenids was recorded, however, the observed individuals were too small for species identification.

Growth rate

Size differed significantly between seasons, with continuous growth throughout the year (linear mixed model: $F = 91.12$; d.f. = 3, 138; $N = 264$; $P < 0.0001$) (Figure 4). The largest increases in size (0.25 and 0.26 cm per month) were measured during summer, while the lowest increase in size (0.03 and 0.05 cm per month) was found during winter for *D. polymorpha* and *D. r. bugensis*, respectively. The increase in *D. polymorpha* size (Figure 4A) showed no significant difference over the years. On the other hand, *D. r. bugensis* showed a significantly different size evolution over time (Figure 4B) (linear mixed model regression: $F = 19.98$; d.f. = 2, 27; $P < 0.0001$). The size evolution curves of *D. r. bugensis* on plates deployed in the same year clustered together. For *D. r. bugensis* the increase in size was significantly smaller in 2016–2017 compared to 2012–2013 (Tukey HSD: $t = 3.472$; d.f. = 27; $P = 0.005$) and to 2009–2010 (Tukey HSD: $t = 3.292$; d.f. = 27; $P = 0.008$). There was no significant difference in size between 2009–2010 and 2012–2013. These differences were usually due to a larger or smaller size increase during autumn of the respective years. When comparing the size evolution of both species with each other, *D. r. bugensis* grew faster than *D. polymorpha*,

Table 2. Settlement period of *Dreissena rostriformis bugensis* and *Dreissena polymorpha* with a size up to 1 cm recorded over the period 2006–2017. P: *D. polymorpha* present; B: *D. r. bugensis* present; –: No dreissenids present; V: Dreissenids present, but too small for species identification; ?: No data.

| Year | Winter | Spring | Summer | Autumn |
|------|--------|--------|--------|--------|
| 2006 | ? | P | ? | ? |
| 2007 | – | P | P&B | ? |
| 2008 | ? | P | P&B | – |
| 2009 | – | P | P&B | – |
| 2010 | – | P | ? | ? |
| 2011 | ? | ? | P&B | ? |
| 2012 | V | – | P&B | – |
| 2013 | – | – | P&B | – |
| 2014 | – | – | ? | ? |
| 2015 | ? | – | P&B | – |
| 2016 | – | – | P&B | – |
| 2017 | – | P&B | P&B | – |

however, the difference was only significant during spring (Tukey HSD: $t = 3.71$; d.f. = 138; $P = 0.007$). These results were based on categorical size measurements, which were not significantly different from the real size evolution of dreissenids (Tukey HSD: summer $t = 0.353$; d.f. = 38; $P = 0.726$, autumn $t = 0.699$; d.f. = 32; $P = 0.490$, winter $t = 0.001$; d.f. = 38; $P = 0.999$, spring $t = 0.438$; d.f. = 60; $P = 0.876$). Therefore, we used the categorical sizes as a representation of real dreissenid size evolution.

Relative dreissenid densities

During the short-term field experiment in summer 2016, right after settlement, we observed the highest relative *D. polymorpha* abundance throughout the whole first year with a 40%–60% ratio for *D. polymorpha* and *D. r. bugensis* (Figure 6). During other periods of this experiment, there was a relative increase in *D. r. bugensis*. The highest relative abundance of *D. r. bugensis* was found in spring 2017 with a 5%–95% *D. polymorpha* : *D. r. bugensis* ratio. The new settlement period had already started in spring 2017, however, the *D. polymorpha* proportion did not increase. *Dreissena polymorpha* showed later settlement as the relative amount of this species increased to about 25% of total dreissenids in summer 2017. In autumn 2017 the relative amount of *D. polymorpha* increased even further to 29%.

Between summer and autumn 2017 there was a drop in the density of dreissenids when nearly three-quarters of the individuals disappeared and the number of individuals reduced from 10464 to 2749 per m². This decrease was stronger for *D. r. bugensis* than for *D. polymorpha* (Figure 6).

Figure 6. Percentage of *Dreissena rostriformis bugensis* and *Dreissena polymorpha* on fouling plates between summer 2016 and autumn 2017 measured on the large dock in Tiengemeten. The mean density of both species per square meter is indicated in the columns.

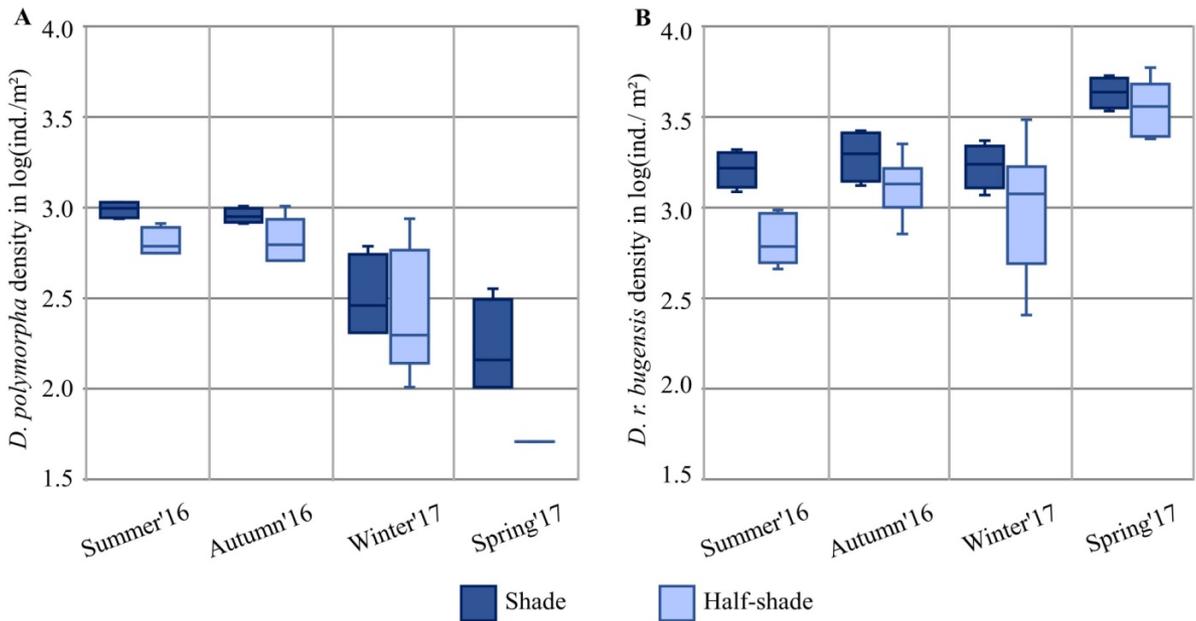
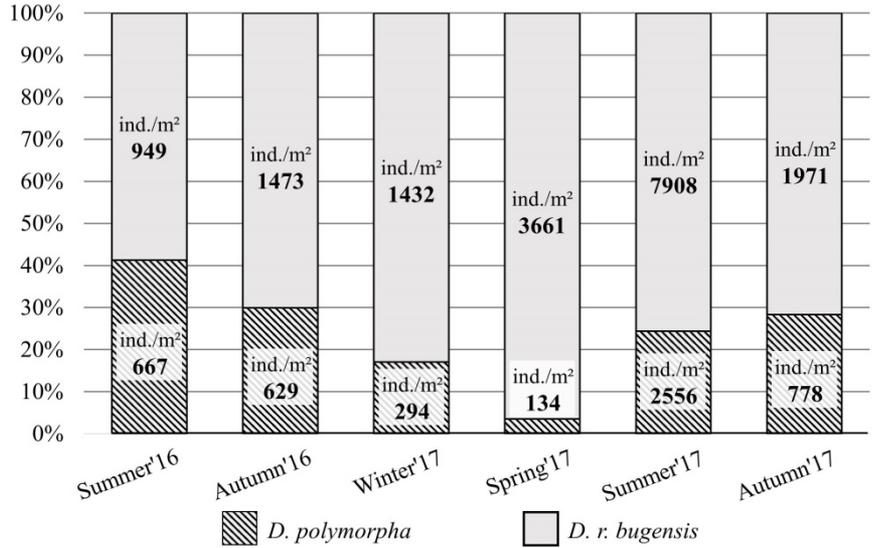


Figure 7. Density (log-transformed) of dreissenids (individuals per square meter, ind./m²) of (A) *Dreissena polymorpha* and (B) *Dreissena rostriformis bugensis* on fouling plates shortly after settlement (summer; July–September 2016), after 6 months (autumn; October–December 2016), after 9 months (winter; January–March 2017) and one year after settlement (spring; April–June 2017). Six fouling plates were exposed to half-shade and four fouling plates were deployed in shade. The box-and-whisker plots represent the minimum, first quartile, median, third quartile and maximum density per sampling date.

Light effect on density

Figure 7 depicts the density of dreissenids per square meter on a subset of the short-term field experiment representing shaded and half-shaded plates. Both species had a higher settlement rate during summer 2016 on fouling plates deployed in shaded areas (Mann-Whitney U test: *D. polymorpha* $W = 24$; d.f. = 8;

$P = 0.01$, *D. r. bugensis* $W = 24$; d.f. = 8; $P = 0.01$). However, the differences in densities on plates deployed in shaded and half-shaded areas minimized over time. When comparing the density in relation to light intensity throughout the year, both species showed the same pattern except for spring 2017. During this period *D. polymorpha* almost completely disappeared on half-shaded plates but remained

present in low numbers on shaded plates. *Dreissena rostriformis bugensis*, on the other hand, had an equal density on both shaded and half-shaded plates.

Mortality

During the long-term SETL project, predation of dreissenids by Common Coots (*Fulica atra*) was recorded for the first time in our study area at the end of autumn 2017. The Common Coots were seen diving and resurfacing carrying clusters of dreissenids. Thereafter, they shook the clusters in the water or banged them on a rock to break up the clusters and swallow the shells. Additionally, a high number of remnants of byssal threads were present, up to a 10:8 ratio of remnants of byssal threads to living dreissenids during autumn 2017 (D'Hont, *pers. obs.*).

The relative contribution of empty, dead shells to the total number of dreissenids on all fouling plates was 3%, 9%, 1%, 2%, 0% for autumn 2016, winter 2017, spring 2017, summer 2017 and autumn 2017, respectively. Natural mortality appeared to be highest during winter (Supplementary material Figure S2). Additionally, the observed winter mortality was mostly due to the death of *D. polymorpha* as it significantly halved in number going from 629 individuals per m² in autumn 2016 to 294 individuals per m² in winter 2017 (Chi-square test: $\chi^2 = 78.724$; d.f. = 12; $P < 0.001$). The number of *D. r. bugensis* remained more or less stable going from 1473 individuals per m² in autumn 2016, to 1432 individuals per m² in winter 2017 (Chi-square test: $\chi^2 = 0.865$; d.f. = 12; $P = 0.352$) (Figure 6).

Interspecific competition

Dreissena rostriformis bugensis was found to have higher abundance in syntopic populations on fouling plates than in allotopic populations (Supplementary material Figure S3). This trend was recorded for both the small and large dock in Tiengemeten and the dock in Numansdorp. We found a significant difference for autumn 2016 in Numansdorp (Mann-Whitney U test: $W = 9$; d.f. = 4; $P = 0.014$).

Impact of one-year-old mussels on settlement

When comparing the young dreissenid ratio on 3-month-old fouling plates (22–78%; *D. polymorpha* – *D. r. bugensis*) with the young dreissenid ratio on 15-month-old fouling plates already containing one-year-old *D. polymorpha* and *D. r. bugensis* (11–89%; *D. polymorpha* – *D. r. bugensis*), we found a significant difference between both ratios (Chi-square

test: $\chi^2 = 80.909$; d.f. = 4; $P = 0.0027$). However, the absolute number of young individuals settling per plate was for both species still higher on the 3-month-old plates (Chi-square test: $\chi^2 = 6.579$; d.f. = 4; $P = 0.01$) (Supplementary material Figure S4).

Discussion

Settlement period

Studies suggest that temperature is the main factor in determining the timing of settlement of both mussel species (Gerstenberger et al. 2011; Ram et al. 2012) (Table 2) which seems to correspond with our data. In winter 2012, the water temperature was close to 7 °C in January, cooled down to ± 0 °C in February and warmed up to 7 °C again in March (Figure 5A). This was the most extreme shift in winter temperature observed over the duration of the experiment since 2006. The extreme temperature shift was probably the reason for the settlement of dreissenids during that winter (Table 2). Settlement was only recorded during spring and summer in all other years. This agrees with Ram et al. (1996) who stated that changes in absolute temperature can trigger settlement. Due to their small size, it was impossible to provide certain identification based on pictures. If these were *D. polymorpha*, this temperature shift may explain the dominance shift to *D. r. bugensis* in the region recorded after 2011–2012 (*unpublished data*). In this case, *D. polymorpha* individuals who settled during winter may not have survived (see “Relative dreissenid densities and mortality” below).

In the American Great Lakes *D. r. bugensis* is able to settle at greater depths, and thus in cooler habitats, than *D. polymorpha* (Mills et al. 1993). Other studies also show earlier settlement onset for *D. r. bugensis* compared to *D. polymorpha* (Claxton and Mackie 1998; Gerstenberger et al. 2011; Ram et al. 2012). However, we found the opposite (Table 2). This earlier settlement onset for *D. polymorpha* may be related to salinity levels in the Haringvliet which were clearly higher in spring 2010–2013 than in summer (Figure 5B): *D. r. bugensis* has a lower salinity tolerance (Mills et al. 1996). In 2017, when salinities were relatively low, *D. r. bugensis* settled in spring for the first time (together with *D. polymorpha*). Such settlement patterns, possibly linked to salinities varying over the years, can only be explained based on long-term studies.

Growth rate

The highest growth rate of *D. polymorpha* was measured during summer (Figure 4) in agreement

with Pollux et al. (2010), but in contrast to Allen et al. (1999) who recorded the highest growth rate during spring. Based on our study it is clear that growth rates can significantly differ between years, which may explain why a relatively fast growth rate was measured in spring over a study lasting just one year (Allen et al. 1999).

We observed *D. polymorpha* having a constant growth rate pattern over several years, in contrast to *D. r. bugensis*. For *D. r. bugensis* the growth rate can be almost twice as high in the same season of different years (Figure 4B). These yearly differences for *D. r. bugensis* may be explained by variations in temperature and salinity as these parameters showed strong annual variation in the Haringvliet (Figure 5). The observed variation in growth (Figure 4B) for *D. r. bugensis* did not seem to coincide with the differences in seasonal water temperatures in those years (Figure 5A), but was connected with salinity (Figure 5B). *Dreissena rostriformis bugensis* seems to adjust its growth rate to salinity concentrations measured in the Haringvliet, growing faster when salinity is lower: salinity in autumn 2012 was low while *D. r. bugensis* showed a remarkably high growth rate (Figure 5B). Additionally, salinity at the end of the autumn in December 2017 was high compared to the average salinity during that season. This might explain the low growth during autumn 2017. During winter, *D. r. bugensis* growth rate is generally low, so this likely explains why the correlation between growth rate and salinity was not very clear during winter. Dreissenids are known to have a decreased growth rate with increasing water salinity (Wright et al. 1996). This effect may be stronger for *D. r. bugensis*, as it is known that this species has a lower salinity tolerance than *D. polymorpha* (Mills et al. 1996). This lower salinity tolerance and the slightly brackish water (on average 0.3–0.4‰) may explain why *D. polymorpha* is still commonly present in the Haringvliet. *Dreissena rostriformis bugensis* is known to dominate at salinities between 0.00–0.02‰ (Mills et al. 1996).

Relative dreissenid densities and mortality

The relative dreissenid densities indicated that *D. r. bugensis* is the dominant species in the Haringvliet. Throughout the experiment, 60% to 95% of all dreissenids were *D. r. bugensis* (Figure 6). This may partly be explained by winter mortalities. For example, *D. polymorpha* density more than halved over winter 2016–2017, while densities of *D. r. bugensis* remained stable (Figure 6). This may be explained by higher growth rates for *D. r. bugensis*,

permitting a large shell size and body mass by winter, which probably gives this species a better chance at surviving the winter (Marescaux et al. 2015).

During the secondary settlement event one year after deployment, in spring and summer 2017, *D. polymorpha* started to increase again in relative and absolute number (Figure 6). In autumn 2017 there was an even further increase in relative abundance of *D. polymorpha* giving an unexpectedly high relative abundance of *D. polymorpha* compared to *D. r. bugensis*, deviating from previous years. Based on observations in 2016, we would expect the relative *D. polymorpha* abundance to decrease again after the secondary settlement (Figure 6). This event co-occurred with a strong drop in the density of dreissenids in general on the fouling plates, losing almost three-quarters of the individuals, and a high number of empty byssal threads. This sudden unexpected drop in dreissenid densities may be related to predation by Common Coots which is well known in the literature (Cavé et al. 1989; Hamilton and Ankney 1994; Werner et al. 2005). For the first time in our study area, one Common Coot was observed feeding on dreissenids, which it picked from the fouling plates, in autumn 2017. The predation by Common Coots might even be selective for *D. r. bugensis*, as it preferably predated on clusters. *Dreissena polymorpha* individuals are usually not found in such clusters. Another potential explanation for the recorded sudden drop of *D. r. bugensis* may be that *D. r. bugensis* individuals died because of a change in the environment, for example in salinity. If that had happened, we would have expected to record empty dreissenid shells on the plates after winter. As such empty shells were not found, predation by Common Coots remains the most likely explanation.

In the Haringvliet, both species preferred shaded habitats as their initial density was higher on those fouling plates (Figure 7), which corresponds to results of other studies (Kobak 2001; Kobak and Nowacki 2007; Marsden and Lansky 2000). The shading preference was higher in settling individuals than at later stages during succession (Figure 7), in contrast to the findings of Kobak and Nowacki (2007). This might be due to spatial competition during later stages of succession causing individuals to migrate to, or settle on, half-shaded plates with a higher light intensity. One year after settlement the densities of *D. r. bugensis* on half-shaded fouling plates were equal to that on shaded fouling plates (Figure 7). Most likely *D. r. bugensis* is better at coping with higher light intensities giving it a competitive advantage over *D. polymorpha* in our study area. This suggests that *D. r. bugensis* can settle in a wider range of habitats (Mills et al. 1993).

Interspecific competition and the impact of one-year-old mussels on settlement

Dreissena rostriformis bugensis was more abundant in syntopic populations than in allotopic populations for settling individuals, 6 and 12-month-old individuals (Supplementary material Figure S3) thus showing a greater increase in abundance in syntopic populations compared to *D. polymorpha*. The capacity of an invasive species to increase its abundance in the presence of competitors is a known trait for some invasive species, such as the invasive tunicate *Botrylloides violaceus* and the native *Botryllus schlosseri* (Gittenberger and Moons 2011). It may be that the presence of *D. polymorpha* causes *D. r. bugensis* to increase in abundance by somehow promoting settlement of the latter. A similar phenomenon was observed when comparing 3-month-old fouling plates to 15-month-old plates: *D. r. bugensis* showed higher relative abundance on 15-month-old plates where one-year-old *D. polymorpha* were already present (Supplementary material Figure S4). This interspecific relationship provides an advantage for *D. r. bugensis* in the competition for space against *D. polymorpha* (Connell and Slatyer 1977; Jackson 1979).

Conclusions

Dreissena polymorpha appeared to have a competitive benefit over *D. r. bugensis* through earlier settlement onset, settling in spring in 2006–2010. *Dreissena rostriformis bugensis* on the other hand was only found to settle in summer except for 2017. This may be linked to relatively high Haringvliet salinities in the spring of those years as *Dreissena polymorpha* has a higher salinity tolerance. Our results support this hypothesis as in 2017, when salinities were relatively low, settlement of *D. r. bugensis* was also recorded in spring. In the Haringvliet the Common Coot preferred to predate *D. r. bugensis* clusters over *D. polymorpha* individuals, as the latter are usually not found in clusters. Despite these competitive advantages for *D. polymorpha*, *D. r. bugensis* is the dominant species in the region. One explanation is that *D. r. bugensis* is more light tolerant while *D. polymorpha* was practically absent on light-exposed fouling plates. This suggests that *D. r. bugensis* can settle in a wider range of habitats than *D. polymorpha*. Higher growth rate, especially during spring, may also contribute to the dominance of *D. r. bugensis*, despite the negative impact of salinity on growth rate. Generally, *D. r. bugensis* occurred in higher densities on fouling plates than *D. polymorpha*. A striking new finding is that

D. polymorpha may induce the settlement of *D. r. bugensis* individuals: the density of *D. r. bugensis* was significantly higher in syntopic populations in comparison to allotopic populations. A final potential reason for the dominance of *D. r. bugensis* concerns winter mortalities. While the absolute number of *D. polymorpha* individuals on the plates more than halved over the winter 2016–2017, no significant decrease in numbers of mussels was recorded that winter for *D. r. bugensis*.

In summary, although *D. polymorpha* is able to settle earlier, is more salinity tolerant, and is predated less than *D. r. bugensis*, *D. r. bugensis* remains the dominant species in the region. This may be explained by being able to settle in a wider range of habitats, adjusting growth and settlement better to seasonally and annually varying salinities and temperatures, having lower winter mortality, and settling in higher numbers when *D. polymorpha* individuals are already present on the substrate.

This study shows the importance of long-term data to assess competitive benefits like settlement, growth and interactions between *D. polymorpha* and *D. r. bugensis*. The impact of drivers such as movement speed and duration, grouping and clustering behaviour, small-scale location preferences, interactions with other species and fouling plate coverage on this dominance shift is still not completely understood, especially related to long-term data.

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Supplementary material

The following supplementary material is available for this article:

Figure S1. Validation of normality assumptions and homogeneity of variance within the statistical models.

Figure S2. The percentage of dead dreissenid mussels in various seasons.

Figure S3. The relative abundance of *Dreissena rostriformis bugensis* in syntopic populations

Figure S4. The relative abundance of newly settled *Dreissena polymorpha* and *Dreissena rostriformis bugensis*.

This material is available as part of online article from:

http://www.aquaticinvasions.net/2018/Supplements/AI_2018_D'Hont_etal_SupplementaryMaterial.pdf