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Research Article

Demographic and genetic structure of the quagga mussel, *Dreissena rostriformis bugensis*, in the Moselle River ten years after first observation

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Abstract

The quagga mussel (*Dreissena rostriformis bugensis*) was first recorded in France in the Moselle River in 2011. The objective of this study was to obtain a better understanding of the species' demographic and genetic structure ten years after its first observation. To do this, we examined quagga mussel (i) relative abundance/biomass (compared with the zebra mussel (*Dreissena polymorpha*), (ii) population structure, and (iii) genetic structure along the navigable stretch of the Moselle during four sampling events conducted between May 2021 and May 2022. The results indicate that, while zebra mussels are still the dominant species (ca. 2/3 of all dreissenid species), quagga mussels represent, on average, 60% of dreissenid biomass. A typical quagga population was composed of five different cohorts with wide, overlapping size ranges, suggesting that the mussels breed for much of the year. Growth in quagga mussel shell length was at least 1.4× greater than that for zebra mussels, regardless of season, with no interruption in growth observed during winter. Unlike zebra mussels, we failed to record any small quagga individuals (4–14 mm shell length) in our samples, possibly indicating high mortality induced by selective predation by invasive round gobies *Neogobius melanostomus*. Genetically, the three Moselle quagga mussel populations examined were highly homogeneous among themselves (based on microsatellite analysis), and very similar to those found elsewhere in Europe (diversity of CO1 haplotypes). A comparison with previous data suggests that the Moselle quagga population comprises haplotypes introduced over several successive introduction waves, a process that may continue in the future.

Key words: CO1 haplotypes, growth-at-length, invasive species, population structure, zebra-quagga coexistence

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Introduction

Dreissenid mussels, freshwater bivalves native to the Ponto-Caspian region of Europe (Mills et al. 1996; Van der Velde et al. 2010), are now considered to be invasive species, especially in North America and Western Europe (Karatayev et al. 2015). The zebra mussel (*D. polymorpha*), which began colonising non-native areas of Europe at the beginning of the 18th century (Van der Velde et al. 2010; Karatayev et al. 2011), was detected in France as early as the beginning of the 19th century (in the Marne Canal in 1854; Testard 1991) and is now found in all major French rivers (Van der Velde et al. 2010). In contrast, the quagga mussel (*D. rostriformis bugensis*) invasion process in Europe only began in the 1940s (Van der Velde 2010; Karatayev et al. 2011). In France, the species was first observed in 2011 in the Moselle River (bij de Vaate and Beisel 2011) and has now spread into the Seine and Rhône River basins (Prié et al. 2021). Latest reports show the species as having invaded perialpine lakes (Haltiner et al. 2022), with the first observation of adults in Lake Geneva in 2015 (Lods-Crozet and Chevalley 2018; Lods-Crozet 2020).

Though zebra and quagga mussels can invade the same types of aquatic ecosystems (i.e. temperate rivers and lakes), they have distinct biological characteristics and ecological preferences that induce a range of processes, from dynamic cohabitation to competitive exclusion, when they are both present in the same ecosystem (Mills et al. 1996; Wilson et al. 2006; Nalepa et al. 2010; Karatayev et al. 2015; 2011). Water temperature (Mackie and Claudi 2010; Zhulidov et al. 2010; Garton et al. 2013), dissolved oxygen (Karatayev 1995; Karatayev et al. 1998; Mackie and Claudi 2010; Garton et al. 2013) and water velocity (Dermott and Munawar 1993; Khalanski 1997; Peyer et al. 2009; Karatayev et al. 2015) are common ecological factors that can also explain cohabitation or exclusion scenarios between the two species. Typically, the quagga mussel has an advantage in deep and cold areas where dissolved oxygen and water velocity are lower, such as in deep lake ecosystems (Lods-Crozet and Chevalley 2018; Haltiner et al. 2022), with numerous studies having shown that quagga mussels come to dominate dreissenid communities within just a few years, especially in the Great Lakes region of North America (Mills et al. 1996; Wilson et al. 2006; Nalepa et al. 2010). The zebra mussel, on the other hand, displays a stronger attachment force than quagga mussels (Peyer et al. 2009; Grutters et al. 2012) and prefers more oxygenated waters (Khalanski 1997; Karatayev et al. 1998, 2007; Mackie and Claudi 2010; Ventura et al. 2016), meaning that this species often remains dominant in streams and rivers. Nevertheless, quagga mussels have also been recorded as becoming the dominant species over a short period in flowing waters, such as the Meuse River in Belgium (Marescaux et al. 2015).

Dreissenid mussels that are established in an ecosystem can then modify its structure and function, acting as ecosystem engineers (Karatayev et al. 2002; Cuhel and Aguilar 2013). This ability to modify their environment is mainly due to their high filtration rate and ability to attach to any hard substrate in high densities. In such cases, the shells of dreissenids can provide a substrate for other organisms to attach to, or a shelter for invertebrates such as Gammaridae (Karatayev et al. 2002). By filtering high volumes of water, dreissenids can also alter elemental cycles and material fluxes by reducing phytoplankton biomass (Karatayev et al. 2002; Evariste 2016) and increasing deposition of organic matter from the water column to the bottom (Karatayev et al. 2002, 2015; Wilson et al. 2006). Quagga mussels are generally larger than zebra mussels of the same age (Mills et al. 1996; Stoeckmann 2003; Garton et al. 2013; Marescaux et al. 2015) and a bivalve filtering capacity will be positively correlated with its biomass

(Marescaux et al. 2016b). Consequently, many studies recommend estimating the biomass of zebra and quagga mussels in invaded ecosystems rather than using abundance only (Nalepa et al. 2010; Boeckman and Bidwell 2013; Locklin et al. 2020; Coughlan et al. 2021).

The quagga mussel was first observed in France in the Moselle River in 2011 (bij de Vaate and Beisel 2011). At that time, the species was only present at a few sites and at very low abundances (i.e. 1–3 mussels per site, representing < 1.5% of the dreissenid populations sampled). The present study assesses quagga mussel dominance, abundance and biomass, 10 years after its first observation in the Moselle, and provides an assessment of its demographic structure since that time. A comparison between the quagga and zebra mussel populations allows for the identification of key demographic parameters in a comparative framework (growth in size, growth period, number of cohorts). Finally, the genetic structure of three adjacent populations of quagga mussel was analysed to determine their diversity and specificity compared to other European populations.

Materials and methods

Sampling protocol

To characterise abundance, biomass and demographic structure, samples of zebra and quagga mussels were collected at eight locations on the Moselle River (Fig. 1). The first sampling event was carried out between 4th and 21st May 2021 at all eight locations. Thereafter, the sampling events were limited to three stations in the downstream stretch of the Moselle (Thionville, Cattenom-upstream and Sierck-les-Bains; Fig. 1), with four sampling events taking place over a period of 12 months, i.e. 4th May 2021, 5th July 2021, 22nd November 2021 and 5th May 2022.

On each sampling date at each site, mussels were carefully collected from all submerged substrata (e.g. rocks and stones) close to the shoreline at ca. 1m depth until a minimum of 300 mussels had been collected. All mussel samples were then preserved in 96% ethanol for further analysis in the laboratory, where they were morphologically identified to species using key identification characteristics such as flatness of the ventral face, shape of the carina, shape of the ventral junction and position of the byssus (May and Marsden 1992; bij de Vaate and Jansen 2007; Sablon et al. 2010; Teubner et al. 2016). All individuals were then measured using an electronic calliper (± 0.01 mm). and separated into size classes of 1mm for further analysis.

Abundance, biomass, and biovolume of quagga and zebra mussels

The number of individual zebra and quagga mussels was evaluated for each sample, whereupon the biomass and biovolume of quagga mussels in each sample was calculated based on regression models between length and biomass and length and biovolume.

To assess the relationship between length and biomass, ca. 100 mussels of each species were sampled in the Moselle River at Sierck-les-Bains on 23rd January 2022 and kept alive in a plastic container with an air bubbler for the duration of the experiment. To feed the mussels, around 1/3 of the water was changed every two to three days, using water from the Rhine River. In the laboratory, each mussel was placed in hot water for a few minutes to open the valves. Once opened, the mussels were identified to species, their shells cleaned with a scalpel and their length measured with an electronic calliper. The shell and soft bodies were then stamped in

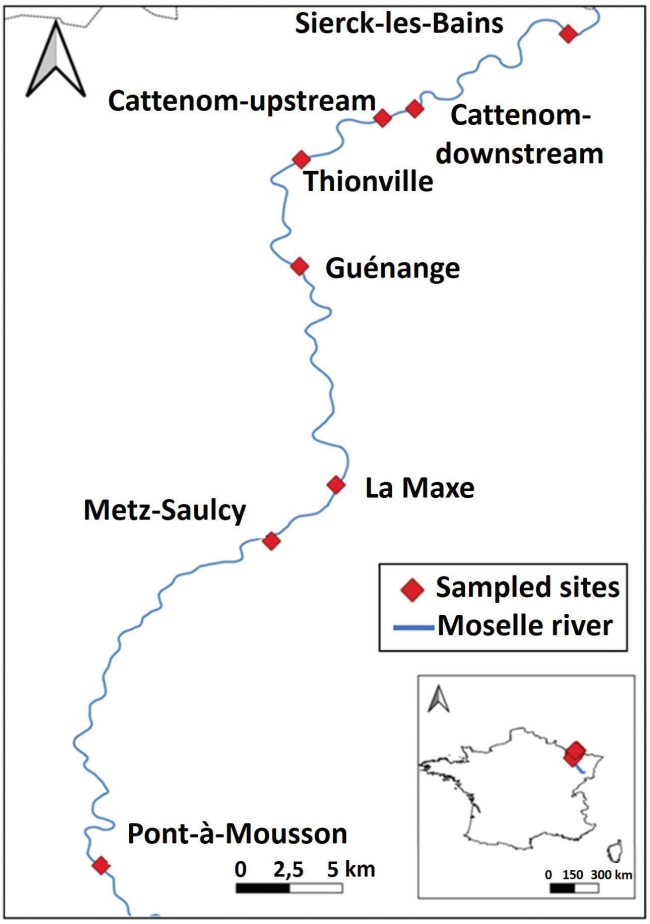

Figure 1. Location of the eight sampling sites along the Moselle River. The Thionville, Cattenom-upstream and Sierck-les-Bains locations were sampled four times from May 2021 to May 2022.

an absorbent cloth, following which the wet weight of soft tissue ($WW_{soft\ tissue}$) and wet weight of the shell (WW_{shell}) were immediately measured using a pre-weighed aluminium cup and a microbalance (± 0.0001 g). After 24h at 105 °C in a stream room, the aluminium cups were re-weighed on the same microbalance to obtain the dry weight of soft tissue ($DW_{soft\ tissue}$) and dry weight of the shell (DW_{shell}). Finally, the aluminium cups containing the dried soft tissue were placed in an oven at 450 °C for 2h to obtain the ash-free-dry-weight (AFDW) of the tissue, with AFDW representing the organism's biomass. To prevent rewetting of the dried material, the aluminium cups were stored in a desiccator before weighing.

To assess the relationship between mussel length and biovolume, 100 zebra and quagga mussels were selected from the sample taken at Sierck-les-Bains on 22nd November 2021 and the shell length of each mussel measured using an electronic calliper. The biovolume of each individual was then calculated by immersing each mussel into a 25ml graduated cylinder half-filled with water, with the change in volume after immersion representing mussel biovolume.

Population structure and dynamics

To determine the number of cohorts present, the size-frequency-distributions for zebra and quagga mussels were analysed separately for each combination of site (Thionville, Cattenom-upstream, Sierck-les-bains) and sampling period (4th May 2021, 5th July 2021, 22nd November 2021, and 5th May 2022), using the graphical

method of Bhattacharya (Bhattacharya 1967), giving a total of 12 size-frequency-distributions for each species. All analyses were conducted using a Microsoft Excel macro developed by one of the co-authors (Jean-Nicolas BEISEL). Despite our efforts to sample the widest range of sizes, some cohorts obtained from a site were based on < 10 individuals. Thus, decided to combine the observations of Thionville, Cattenom-upstream and Sierck-les-Bains into a single dataset for each sampling event and each species to ensure we had a statistically relevant number of individuals and mitigate potential sampling bias. While it is possible there may be ecological differences between stations that could influence growth rate or timing of reproduction, the three stations are spatially close and are all located in the navigable stretch of the Moselle, i.e. they have the same channel width and substrate. Furthermore, the cohorts identified for these three stations separately appeared to be very similar in length (i.e. ± 1.5 mm).

Once all cohorts had been identified for each sampling period, we used a growth-at-length model specific to the Moselle (Beisel et al. 2010) to match zebra mussels cohorts across sampling events. Hypothetical growth rates were then calculated by dividing the difference in length between two sampling periods by the number of days between them.

As there is no known growth-at-length model for the quagga mussel as yet, it was not possible to calculate the age of each cohort. Consequently, for each sampling event, we considered that the growth rate of a cohort was negatively correlated with its age. Using the little data available in European ecosystems (i.e. D'Hont et al. 2018; Haringvliet River, the Netherlands), we calculated an assumed growth rate by dividing the length difference of a cohort between two sampling periods in $mm.d^{-1}$. For both species, cohorts with < 20 individuals were not considered significant enough to be included in the analysis.

DNA extraction, amplification, and sequencing

Genomic DNA was extracted from a subsample of 20 randomly picked quagga mussels from each site to evaluate genetic diversity and structure. DNA extraction was performed using the DNeasy Blood and Tissue kit (QIAGEN, Netherlands), following the manufacturer's instructions, and stored at -20 °C for further analysis.

Each mussel was then genotyped for the 700bp-long cytochrome c oxidase subunit I mitochondrial region (COI) using the universal primers LCO-1490 and HCO-2198 (Folmer et al. 1994). Amplifications were performed in 25 µL reaction mixtures containing 1X GoTaq reaction buffer (1.5 mM $MgCl_2$), 0.2 mM of each dNTP, 0.5 µM of each primer, 0.5 U of GoTaq DNA Polymerase (Promega) and 2 µL (ca. 10 ng) of genomic DNA. The samples were then subjected to a polymerase chain reaction (PCR), with conditions comprising an initial denaturation at 94 °C for 4 min, followed by 30 cycles of 45 s denaturation at 94 °C, 45 s annealing at 40 °C, and 50 s elongation at 72 °C, with a final elongation step of 10 min at 72 °C. PCR products were Sanger-sequenced with the same primers used for amplification (Genewiz, Leipzig, Germany). Chromatograms were visualised and edited in Geneious R9.1.8.

In addition, each mussel was genotyped using the 10 microsatellite (µsat) loci developed by Wilson et al. (1999) (Dbug) and Feldheim et al. (2011) (Dbu). PCR amplifications were performed as in Marescaux et al. (2016b), with 1 µl of PCR product being mixed with 10 µl of Hi-Di formamide and 0.1 µl of GeneScan-500 (LIZ) (Applied Biosystems) for genotyping using a ABI3730 48 capillary DNA Analyser (IPG, Gosselie, Belgium). Peak Scanner v2.0 (Applied Biosystems) was then used to score alleles and genotype individuals.

Genetic analysis and population structure

To illustrate mitochondrial diversity, the COI dataset was aligned with previously published sequences (GenBank accession number DQ840132, DQ840133 – EF080861, EF080862, EU484436, JN133734–JN133747, JQ756297, JQ756298, KJ881409–KJ881415, KP057252, MF469063–MF469065, MK358469, MK358470, U47650) in MAFFT (E-INS-i method; Katoh and Standley 2013) and a Median-Joining Network (Bandelt et al. 1999) calculated (HaplowebMaker; Spöri and Flot 2020).

The Moselle microsatellite dataset was checked for the presence of null alleles using MICROCHECKER v.2.2.3 (Van Oosterhout et al. 2004). For each combination of locus and site, linkage disequilibrium (LD) and Hardy–Weinberg equilibrium (HWE) was tested with GENEPOP (Markov chain parameters set to 1000 for dememorisations, batches and iterations per batch; Raymond and Rousset 1995). Levels of significance for all multiple tests were adjusted using Bonferroni correction (Rice 1989). Molecular variance (AMOVA) was also analysed to assess the degree of genetic diversity within and among populations using Arlequin. In addition, Bayesian clustering of microsatellite genotypes was performed using STRUCTURE v.2.1 (Pritchard et al. 2000), with the optimal number of clusters (K) inferred as in Marescaux et al. (2016b).

Results

Abundance, biomass, and biovolume of quagga mussel

We found that zebra mussel largely dominated the dreissenid populations of the Moselle River, with quagga mussels representing between 28 and 51% in our samples, with no clear upstream/downstream pattern (Fig. 2). On the other hand, the percentage of quagga mussels varied between sampling events, especially at the Thionville site, where we harvested 48, 10, 49 and 40%, respectively, over four successive sampling events. Despite this, the variation in abundance had no effect on the dominance of zebra mussels for all sites and sampling events, with percentages at Cattenom-upstream being 36, 29, 31 and 45%, respectively, and 32, 28, 41 and 45%, respectively, at Sierck-les-Bains, during successive sampling events.

While we recorded significant positive relationships between length and biomass, and between length and biovolume, for both zebra and quagga mussels, there was no significant differences between species (ANCOVA tests; $p > 0.05$; Table 1). Based on these relationships, we were able to convert the data for individual size frequencies into biomass and biovolume. The results for biomass differed greatly from those for density, with quagga mussels having around twice the biomass of zebra mussels, ranging between 29 and 81% of total biomass (Fig. 2). Maximum biomass was achieved at the La Maxe site, where quagga mussels represented 81% of total dreissenid biomass during the first sampling event. At Thionville, quagga mussels, represented just 29% of dreissenid biomass and 10% by population abundance during the second sampling event. The quagga biovolume results were similar to those for biomass, with values ranging from 24 to 75% of total biovolume (Fig. 2), indicating that quagga mussels often represent more than twice the biovolume of zebra mussels, despite them being the dominant species at a site.

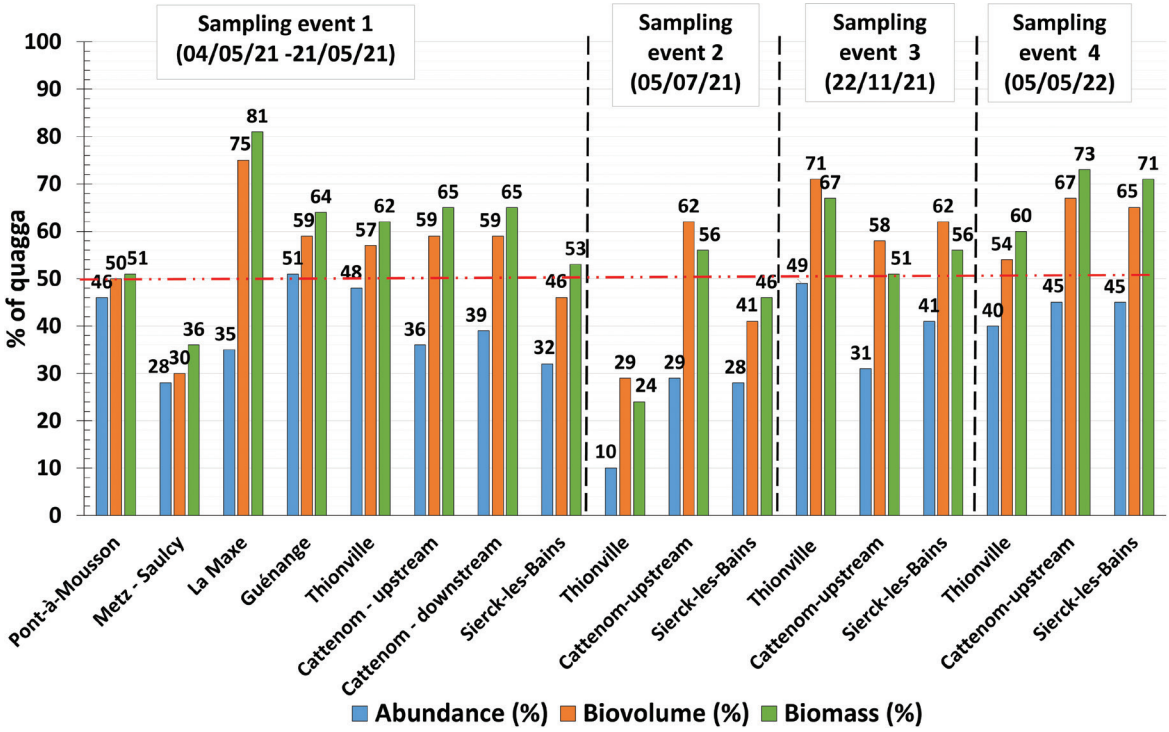

Figure 2. Relative percentage of abundance, biovolume and biomass for quagga mussels compared against all dreissenids along the Moselle River for all sampling events.

Table 1. Relationships between length (in mm) and biomass (in g) and length and biovolume (in mm³) for zebra and quagga mussels.

Relationship	Length (L, in mm) vs biomass (Bm, in g)	Length (L, in mm) vs biovolume (Bv, in mm³)
Zebra mussel		
Equation	ln (Bm) = 2.9871*ln (L) – 5.4568	ln (Bv) = 2.7075*ln (L) – 1.3534
R^2	0.85	0.92
p-value	< 0.01	< 0.01
Quagga mussel		
Equation	ln (Bm) = 2.9091 *ln(L)– 5.0746	ln (Bv) = 2.7122*ln (L) – 1
R^2	0.72	0.95
p-value	< 0.01	< 0.01
Difference between the two species (ANCOVA test)		
p-value	> 0.05	> 0.05

Population structure and dynamics

Analysis of the different cohorts on each sampling event provided us with a comparative framework for population structure. The size structure of the two species differed greatly (Fig. 3). For example, young individuals with a shell length < 15 mm were dominant in the zebra mussel population, representing ca. 70% of the population, with 33% being made up of individuals with a shell length < 10–11 mm (i.e. < 1 yr). In contrast, the quagga mussel population was dominated by larger individuals, with just 22% of the population being < 15 mm in length, with those measuring < 10–11 mm representing just 7%. Unlike zebra mussels, where a large proportion of small individuals survived after attachment, quagga mussels of < 15 mm length appear to have undergone large-scale mortality.

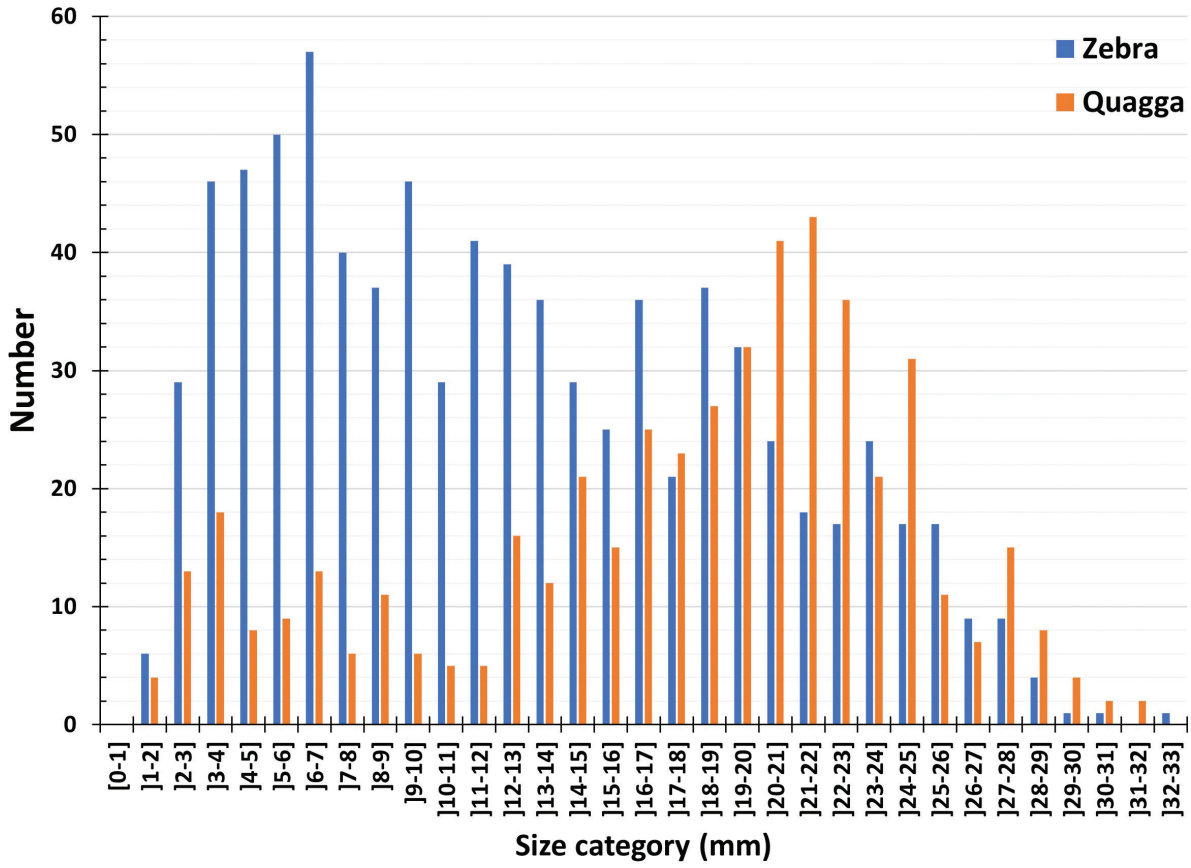

Figure 3. Size class distribution of zebra and quagga mussels during the second sampling event (July 2021), i.e. after the first peak of reproduction. The data sets were obtained by pooling the Cattenom-upstream, Thionville and Sierck-les-Bains sampling locations.

Size-frequency analysis for zebra mussels using Bhattacharya's method revealed seven cohorts between the first (May 2021) and final (May 2022) sampling events (Table 2, cohorts A, B, C, D E, F, G). The theoretical lengths of these cohorts, calculated using a previous growth-at-length model for the Moselle (Beisel et al. 2010), were very close to the observed cohort lengths (< 1 mm difference, yellow square, Table 2). Thus, our model provided theoretical results that were consistent with the observed growth of a cohort between different sampling events, supporting the hypothesis that the zebra mussel growth rate was indeed maximal in spring, with a maximum of 0.081 mm/day between May and June, and almost nil in winter, at between 0.007 and 0.002 mm/day between November and March.

For the quagga mussel, we identified five cohorts for the first and second sampling events, and three for the third and fourth sampling events (Fig. 4). While very few individuals of < 15mm were found during the third and the fourth sampling events (22nd November 2021 and 5th May 2022), the data suggests the presence of two additional cohorts for the third sampling events at ca. 3 and 11 mm); however, these were not included in the analysis due to the low number of individuals. Assuming that (i) the growth rate of a cohort is proportional to its age (Stoeckmann 2003), (ii) the growth rate of the quagga mussel is greater than that of the zebra mussel at the same age (Neumann et al. 1993; Stoeckmann 2003; D'hont et al. 2018), and (iii) the quagga mussel grows throughout the year, even in winter (D'hont et al. 2018), we linked the cohorts observed during the different sampling events. This suggests that five different cohorts occured between the first sampling event in May 2021 and the fourth in May 2022 (i.e. A, B, C, D and E in Fig. 4).

Table 2. Mean length of zebra mussel cohorts identified during the four sampling events. For cohorts that could be tracked over time, observed growth-rates were systematically calculated between two successive dates. Yellow boxes indicate the theoretical length of a cohort across different sampling events, calculated using a growth-at-length model.

Sampling event n°1 04/05/2021	Observed growth rate	Sampling event n°2 05/07/2021	Observed growth rate	Sampling event n°3 22/11/2021	Observed growth rate	Sampling event n°4 05/05/2022
				Cohort G : 5.3 +/- 1.4 mm n= 29	0.007 mm/day	Cohort G : 7.2 +/- 1.3 mm n= 44
						7.0 mm (+0.2)
		Cohort F : 5.9 +/- 1.5 mm n= 73	0.03 mm/day	Cohort F : 10.2 +/- 1.9 mm n= 139	0.003 mm/day	Cohort F : 11.0 +/- 1 mm n= 54
				11.3 mm (- 1.2)		***11.6 mm (-0.6)***
Cohort E : 6.2 +/- 2.3 mm n= 303	0.081 mm/day	Cohort E : 11.2 +/- 3.1 mm n= 643	0.027 mm/day	Cohort E : 15.1 +/- 1.5 mm n= 165	0.002 mm/day	Cohort E : 15.7 +/- 2 mm n= 253
		10.8 mm (+ 0.4)		***15.2 mm (- 0.2)***		***16.2 mm (-0.5)***
Cohort D : 12.8 +/- 2.2 mm n= 216	0.040 mm/day	Cohort D : 15.3 +/- 1.2 mm n= 75	0.027 mm/day	Cohort D : 18.3 +/- 1.4 mm n= 103	0.004 mm/day	Cohort D : 19.4 +/- 1.3 mm n= 208
		16.2 mm (- 0.8)		***19.4 mm (-0.2)***		***19.2 mm (-0.2)***
Cohort C : 16.7 +/- 0.9 mm n= 49	0.023 mm/day	Cohort C : 18.1 +/- 0.8 mm n= 76	0.021 mm/day	Cohort C : 21.5 +/- 1.2 mm n= 234	0.003 mm/day	Cohort C : 22.2 +/- 2.7 mm n= 360
		19.4 mm (-1.3)		***22 mm (+0.8)***		***22.2 mm (-0.2)***
Cohort B : 19.3 +/- 1.1 mm n= 91	0.036 mm/day	Cohort B : 21.5 +/- 1.1 mm n= 73				
		21.6 mm (- 0.1)				
Cohort A : 23.9 +/- 2.5 mm n= 127	0.023 mm/day	Cohort A : 25.3 +/- 1.5 mm n= 67				
		25.3 mm (0)				

During the fourth sampling event, two cohorts (i.e. cohorts F and G, Fig. 4) could not be linked to those identified during the previous sampling events, while a third cohort almost certainly links with cohort B as its growth rate was close to that recorded in D'Hont et al. (2018) for the winter period (i.e. 0.02 mm/day). Quagga mussels achieved their highest growth rate between the first and second sampling campaigns, i.e. between May and July, with a maximum rate of 0.104 mm/day in cohort B (Fig. 4).

To effectively compare the growth of quagga and zebra mussels in 2021, we chose to analyse the small quagga mussels represented by cohorts A, B and C (3.9, 7.3 and 15.5 mm, respectively) sampled during the first sampling event. We then used the growth model specific to zebra mussels from the Moselle to calculate the projected length of the three cohorts during the three other sampling events. This model has proved effective in predicting zebra mussel length in previous analyses and thus provides a useful comparison with the length of quagga mussels in cohorts A, B and C observed during the first three sampling events.

Between the first and second sampling event (May to July 2021), cohort A had the smallest difference in length between the two species, with zebra mussels being 8.9 mm and quagga mussels 9.7mm (Fig. 5). The associated growth rate for this period was 0.081 mm/day for zebra mussels and 0.093 mm/day for quagga mussels. For cohorts B and C, however, quagga mussels were much larger (in average about 2 mm) than the zebra mussels, with cohort B showing the greatest difference in growth rate between the two species at 0.10 mm/day (mean) for quagga mussels and 0.071 mm/day for zebra mussels (Table 3). Between the second and third sampling events (July to November 2021), the mean

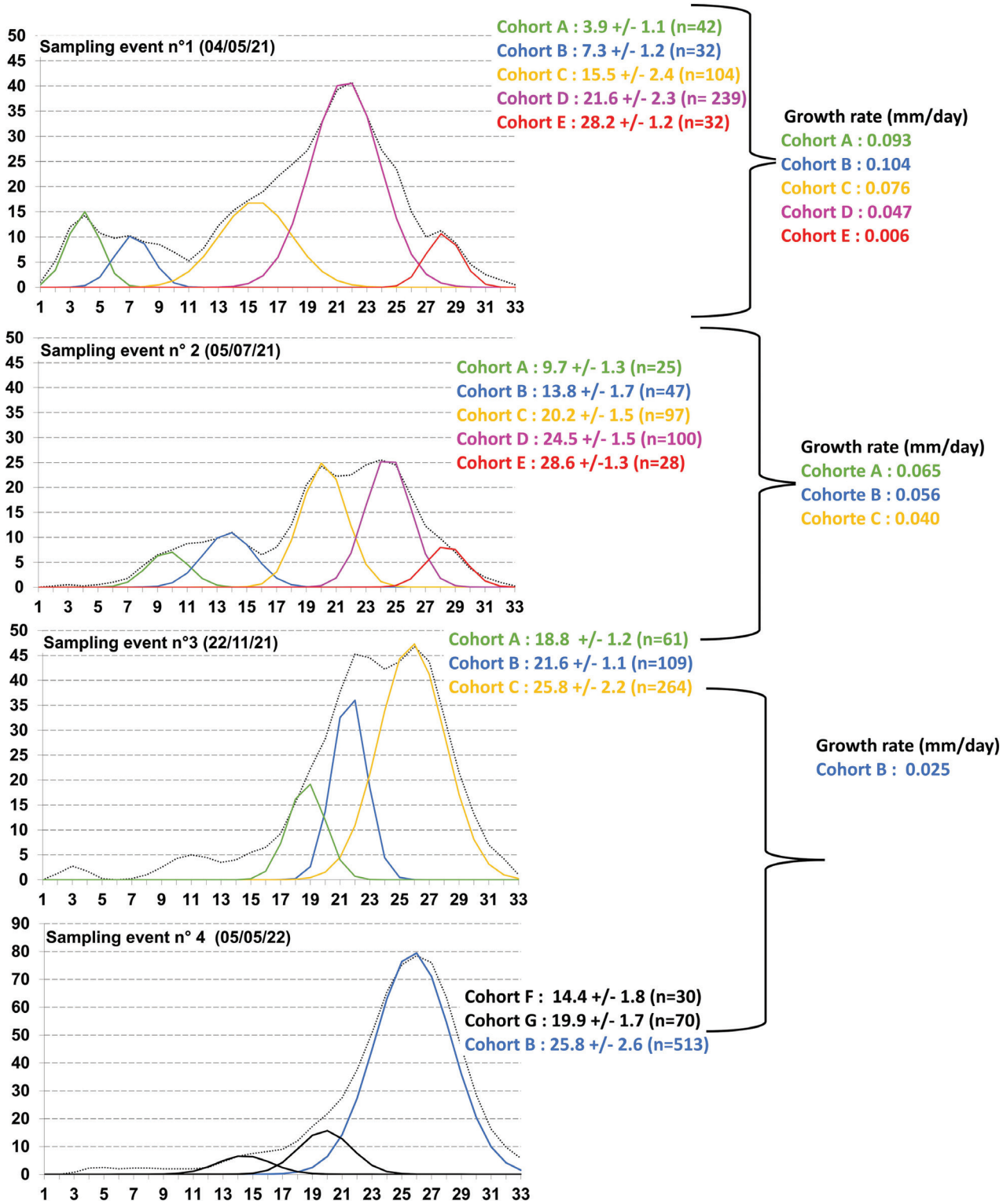

Figure 4. Cohorts of quagga mussels identified during the four sampling events carried out between May 2021 and May 2022, along with growth rates calculated between two sampling events, with standard deviation and number of individuals for each cohort.

length zebra mussels in cohorts A, B and C stabilised rapidly, reaching 13.7, 15.9 and 21.2 mm, respectively, during the third sampling event (Fig. 5). In contrast, quagga mussel cohorts A, B and C continued to grow to a length of 18.8, 21.6 and 25.8 mm, respectively. Overall, the zebra mussel cohorts displayed a slower

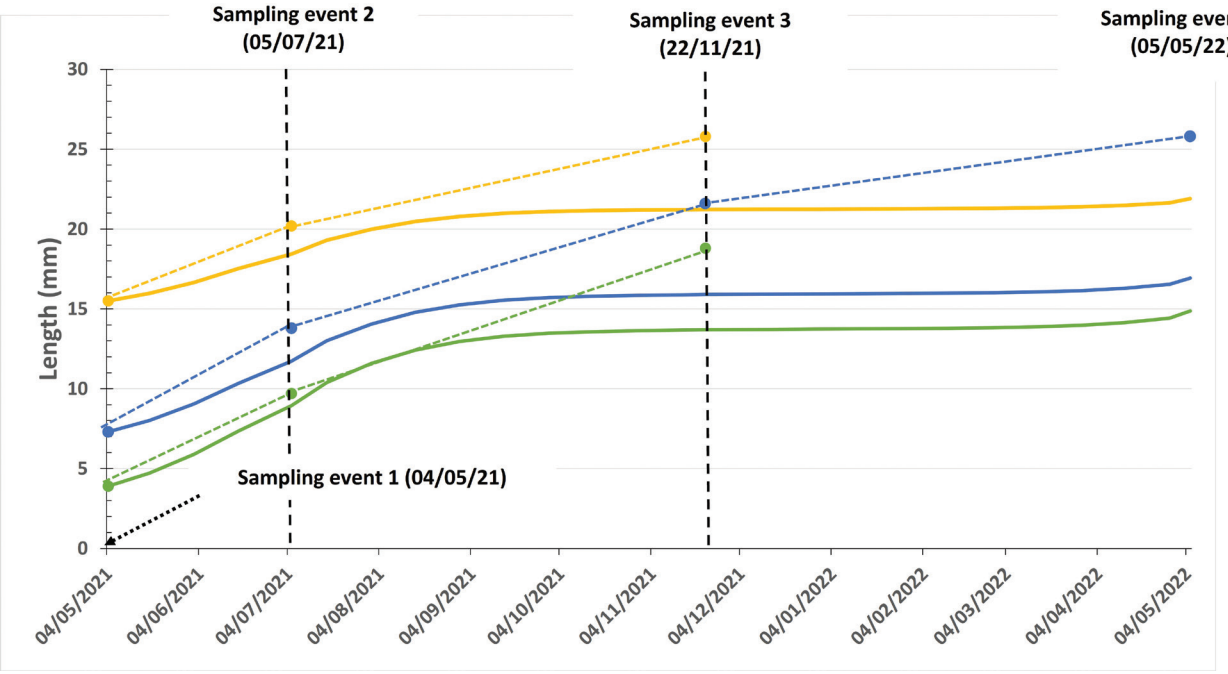

Figure 5. Theoretical growth of three zebra mussel (solid line) cohorts (**A–C**), compared with the observed growth of three quagga mussel (dotted lines) cohorts (**A–C**) for the four sampling events from May 2021 to May 2022. The initial theoretical sizes of the three zebra mussel cohorts correspond with the observed sizes of the three quagga mussel cohorts during the first sampling event. Theoretical growth of the zebra mussel cohorts was calculated with a species-specific growth-at-length model for the Moselle River (Beisel et al. 2010). For a summary of the length and growth rate data associated with this model, see Table 3.

Table 3. Mean length (in mm) of each cohort of each species for all sampling events, with associated growth rate (in mm/day) between two sampling events. Quagga cohort lengths were determined for each sampling period from different samples (see Fig. 3). The length of each zebra mussel cohort was calculated using a species-specific growth-at-length model. The initial cohort length for both species was taken as the mean length of the first three quagga mussel cohorts from the first sampling event.

		1st sampling event (04/05/21)		2nd sampling event (05/07/21)		3rd sampling event (22/11/21)		4th sampling event (05/05/22)
Cohorts	**Species**	**Mean length (mm)**	**Growth rate (mm/day)**	**Mean length (mm)**	**Growth rate (mm/day)**	**Mean length (mm)**	**Growth rate (mm/day)**	**Mean length (mm)**
A	*Zebra*	3.9	0.081	8.9	0.034	13.7	0.007	14.9
	Quagga	3.9	0.093	9.7	0.065	18.8		
B	*Zebra*	7.3	0.071	11.7	0.030	15.9	0.006	16.9
	Quagga	7.3	0.104	13.8	0.056	21.6	0.025	25.8
C	*Zebra*	15.5	0.047	18.4	0.020	21.2	0.004	21.9
	Quagga	15.5	0.076	20.2	0.040	25.8		

growth rate than quagga mussels, with cohort A having growth rates of 0.034 and 0.065 mm/day, cohort B 0.030 and 0.056 mm/day, and cohort C 0.020 and 0.040 mm/day for zebra mussels and quagga mussels, respectively (Table 3). In autumn, quagga mussel growth rates were almost twice as high as those for zebra mussels, with zebra mussel growth rates in cohorts A, B and C being very low (0.004–0.007 mm/day) between the third and fourth sampling event (November 2021 to May 2022), while the maximum length of the only known quagga mussel cohort (B) during the final survey (May 2022) reached 25.8 mm, with a mean growth rate of 0.025 mm/day.

Quagga mussel genetic diversity and population structure

Four distinct haplotypes were identified among the 60 quagga mussels genotyped for the Moselle River (Fig. 6, Q1, Q2, Q4 and Q5), all of which have been retrieved in previous studies (see Marescaux et al. 2016b), including Q1, the most widespread haplotype historically, which was dominant at all sites. At each of the three sites sampled, the Q1 haplotype represented between 70 and 95% of all individuals sampled, while the other three haplotypes corresponded to variants found at lower frequencies in other European rivers in 2016 (haplotype Q2 in the Ijsselmeer, Markemeer, Meuse, Rhine, Main and Danube rivers; haplotype Q5 in the Danube River and Datteln-Hamm canal; haplotype Q4 has also been recorded in North America) (Fig. 6). Interestingly, haplotypes Q1 and Q4 were previously detected in the Moselle at similar frequencies between 2011 and 2013 (Marescaux et al. 2016b).

STRUCTURE analysis performed on the entire microsatellite dataset, which included all sequences observed in this study alongside those of Marescaux et al. (2016b), failed to distinguish genetic clusters (data not shown). This was corroborated by the AMOVA analysis, which indicated that just 0.59% of genetic variation found in the quagga mussel population was retrieved when comparing worldwide groups (Table 4).

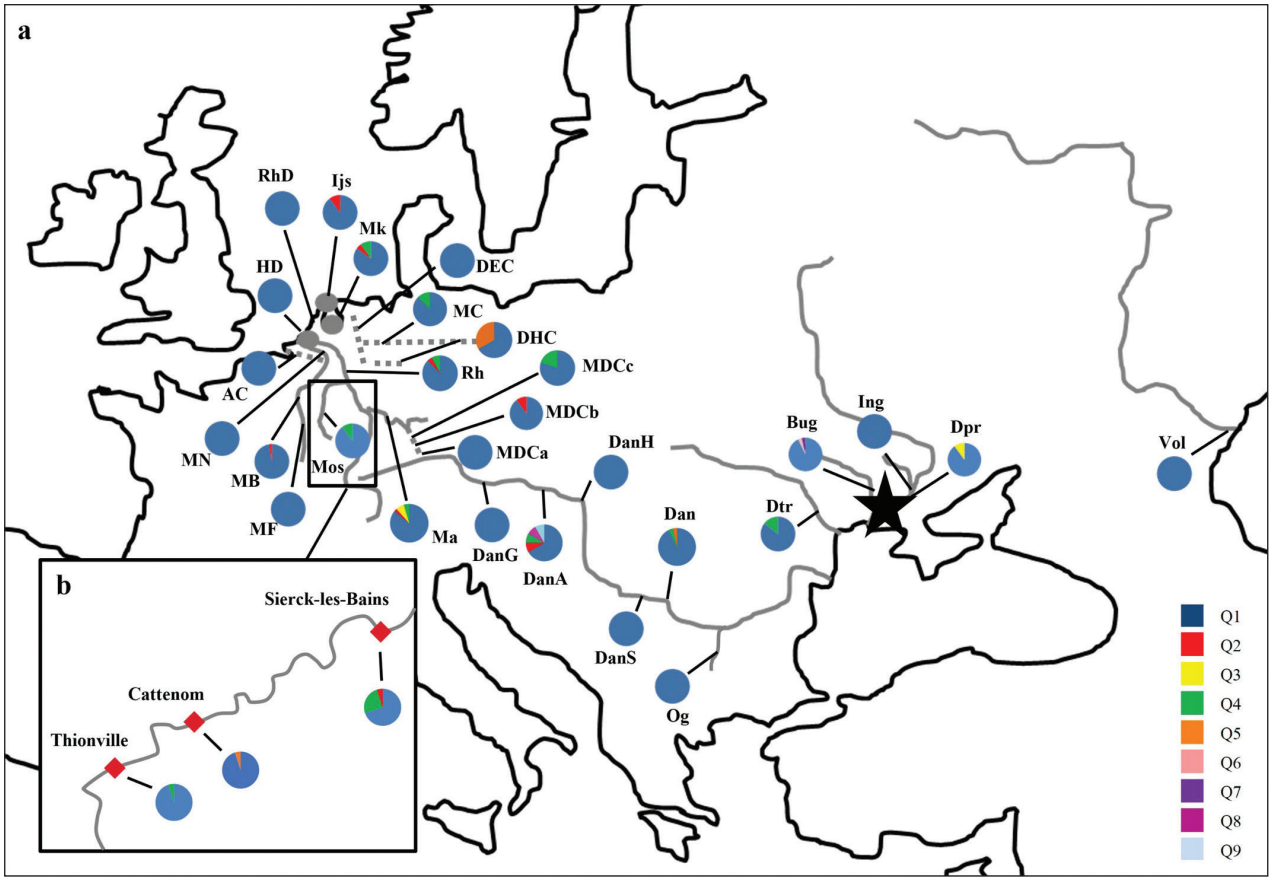

Figure 6. (**a**) European quagga mussel populations, with a haplogroup distribution map of the mitochondrial COI gene (haplotypes Q1 to Q9) sequenced for 519 individuals (adapted from Marescaux et al. 2016b), with the results of the present study inset (**b**). The black star indicates the species' native area, solid grey lines represent rivers, grey circles represent lakes and dotted grey lines represent canals.

Table 4. Analysis of MOlecular VAriance (AMOVA) for the quagga mussel microsatellites, including the dataset published in Marescaux et al. (2016b). Distinct groups were defined as follows: Moselle, Western Europe, Central Europe, Eastern Europe, Eastern North America and Western North America.

Source of variation	DF	Sum of squares	Variances	% of variation	Significance
Between groups	5	55.881	0.02482	0.59	0.00[1]
Among populations within groups	29	183.902	0.05934	1.42	0.00[1]
Within populations	1283	5270.612	4.10804	97.99	0.00[1]
Total	1317	5510.395	4.19220	100	–

[1]Significant based on 1023 permutations.

Discussion

Quagga mussels have lower relative abundance than zebra mussels but higher biomass

Ten years after its first observation in the Moselle River, our results show that the quagga mussel represents between 28 and 51% of all dreissenids sampled, compared with just 0–1.5% (i.e. 0–3 individuals per site) at the same locations in 2011 (bij de Vaate and Beisel 2011). Though the percentages observed between 2021 and 2022 varied between sites, there was no clear upstream-downstream distribution pattern along the river, suggesting that the variation determinant may be linked to variations in flow rate through the year.

While our findings indicate a 30-fold increase in the quagga mussel population in ten years, such an increase is not always observed in running waters. In the USA for example, quagga mussels made up only 1% of dreissenids after 12 years of coexistence on the Mississippi and Ohio rivers (Grigorovich et al. 2008). In the Albert Canal (Meuse River, Belgium), quagga mussels accounted for 80% of all dreissenids in 2014, just three years after its first observation (Marescaux et al. 2015). Heiler et al. (2013) also showed a dominance of quagga mussels in rivers and canals in Germany, including the Main-Danube Canal (76–100% at some sites), the Main River (> 80%) and the Upper Rhine (80–90%). In Belgium (Meuse River; Marescaux et al. 2015) and Germany (Heiler et al. 2013), quagga mussel dominance was achieved in less than three years following its first observation/introduction (date of introduction modelled in Heiler et al. 2013). In the Moselle, however, quagga and zebra mussels have been coexisting for at least 10 years (bij de Vaate and Beisel 2011) with quagga mussels still not dominant. While Strayer et al. (2019) noted a wide range of temporal dynamics in their analysis of long-term (>10 years) dreissenid population datasets from 47 lakes and three rivers in Europe and North America, a general pattern that applied across many populations was that quagga mussels arrived later than zebra mussels and usually caused large declines in the zebra mussel population over a relatively short period. After 10 years, they felt it unlikely that zebra mussels would continue to decline any further due to the presence of quagga mussels.

Our results showed that, locally, quagga mussels could represent more than twice the biomass or biovolume of zebra mussels in the Moselle, with biomass ranging between 29 and 81% and biovolume between 24 and 75% of the dreissenid population.

As filtration rate is dependent on the size/biomass of individuals, the ecological impacts of invasive species such as dreissenid mussels tends to be dependent on biomass rather than density (Marescaux et al. 2016a; Strayer et al. 2019). Even where quagga mussels are less numerous than zebra mussels, therefore, they can still cause a greater ecological impact. At present, assuming equal sampling effort throughout the year,

we are unable to explain the 10% of quagga mussels found at Thionville during the second sampling event. The sites of Thionville, Cattenom-upstream, and Sierck-les-Bains are all located in the same navigated sector and very similar.

The relationship between biomass and length was more variable for quagga mussels (Table 1; $R^2 = 0.72$) than zebra mussels ($R^2 = 0.85$). Burlakova et al. (2006) has shown that the biomass of a bivalve can vary greatly over the course of a year, especially during the reproduction period when the gonads make up a greater proportion of overall weight. While some studies have shown that quagga mussels are able to reproduce continuously throughout the year (Marescaux et al. 2015; Hesselschwerdt and Teiber-Siesseger 2021), which may account for this difference in biomass between the species, we did not specifically investigate whether quagga mussels could reproduce during the winter months in this study.

Quagga mussel population structure suggests high mortality of young and year-round growth

In this study, at a given date, the zebra mussel population was composed of five different cohorts, resulting in demographic dynamics of seven cohorts over one year (Table 2). Overall growth rate was highest in spring, reaching 0.081 mm/day between May and July, and very low in winter, at just 0.007–0.002 mm/day between November and March. These results are in accordance with those of D'Hont et al. (2018) for the Haringvliet River (The Netherlands), where highest growth rates occurred during the summer (0.08 mm/day) and lowest during winter (0.01 mm/day). A previous study in the Moselle also recorded a maximum growth rate of between 0.087 and 0.135 mm/day between June and August, though only for mussels < 3 months old (Beisel et al. 2010). In the Lower Rhine (Germany), a similar study found a maximum growth rate of 0.095 mm/day in June, though also for individuals < 3 months of age (Neumann et al. 1993; Jantz and Neumann 1998). Finally, in Lake Maarsseven (The Netherlands), Dorgelo and Smeenk (1988) reported that zebra mussels of 5.2 mm length grew at an average rate of 0.046 mm/day between June and November. In our study, we recorded zebra mussels of 6 mm length at the beginning of July having a mean growth rate of 0.03 mm/day between July and November (Table 2). Compared to previous studies, therefore, the growth rate of zebra mussels in the Moselle is similar to that reported in other European ecosystems, confirming that optimal growth clearly takes place during spring.

As with Zebra mussels, we recorded five separate quagga mussel cohorts at any given time, with seven cohorts observed over the course of the year (Fig. 3). The quagga mussel growth rate was also highest in spring, at 0.104 mm/day between May and July; however, unlike zebra mussels, the growth rate remained relatively high in winter at 0.025 mm/day. While there have been few exhaustive studies on the growth of quagga mussels in running waters in Europe, there have been several in the Laurentian Great Lakes of the USA (Malkin et al. 2012; Casper et al. 2014; Karatayev et al. 2018; Elgin et al. 2021). For example, a study done by Karatayev et al. (2018) in the Lake Erie have shown that a 12 mm quagga mussel have a mean growth rate of 0.018 mm/day at 15m water depth, between May and December (mean value recalculated by us). Another study by Elgin et al. (2021) in Lake Ontario showed that a 12 mm quagga mussel gained 10.2 mm in one year at 15m depth. However, comparing our values to those obtained in Laurentian Great Lakes is not an easy task as these environments are far too different from the Moselle, especially regarding their thermal regime. D'Hont et al. (2018), however, in their study on growth of quagga mussels in the Haringvliet River, found a maximum growth rate of 0.09 mm/day in summer, and an average growth rate in

winter of 0.02 mm/day (recalculated by us), which are close to our own values. It should also be noted that the cohorts identified were often overlapping, suggesting that quagga mussels may be reproducing continuously throughout the year.

Our comparison between zebra and quagga mussels (Fig. 4, Table 3) showed that quagga mussels always displayed a higher growth rate than zebra mussels at any time of the year, with the quagga mussel growth rate being 1.4× greater between May and July, 1.5× greater between July and November and 4× greater in winter (zebra mussel = 0.006 mm/day, quagga mussel = 0.025 mm/day, cohort B, Fig. 4). Note, however, as we were only able to follow one cohort for quagga mussels through winter, and as there is only one reference in the literature to compare with (D'Hont et al. 2018), we recommend that further studies are needed to better define quagga mussel growth over the winter period. As a comparison, Casper et al (2014) observed in the St-Lawrence River that quagga mussel had a growth rate almost twice that zebra mussel, between July and September with water temperature between 19 and 27 °C.

Our analysis also showed a significant difference in the size structure of the two species, with very few quagga mussels < 15 mm found, especially during the third and fourth sampling events. A similar lack of smaller size classes was also observed in the Meuse River by Marescaux et al. (2015). One potential explanation is predation by the round goby, *Neogobius melanostomus*, which is known to occur at high abundances in both the Moselle and Meuse (Verreycken et al. 2011; Manné et al. 2013). Round gobies in the USA are known to feed on dreissenids (Houghton and Jansen 2013), with up to 90% of its food potentially consisting of mussels (Andraso et al. 2011), particularly dreissenids of between 5 and 13–14 mm (Djuricich and Jansen 2001; Andraso et al. 2011; Naddafi and Rudstam 2014), though the zebra mussel's position on or within the substrate and their shell shape can make it more difficult to predate (Houghton and Jansen 2014). Quagga mussels are also believed to have greater attachment strength than zebra mussels (Peyer et al. 2009), which could also result in differential predation between the two species, and the very particular quagga mussel population structure observed in this study.

Genetic data suggest panmixis and successive events of invasions

Our genetic results appear to confirm that most individuals sampled worldwide correspond to a single haplotype (Q1) originating from the species' native area in the Pontic region (Marescaux et al. 2016b). This well-established haplotype suggests a first, or a single massive, dispersion event, followed by successive additional invasions by other haplotypes thereafter. Interestingly, our data highlighted two recent dispersions of haplotypes Q2 and Q5, these being retrieved during one sampling event but not before (see Marescaux et al. 2016b). Though haplotype Q2 has previously been detected on the Meuse River, and could have been transported downstream and then upstream again by boat traffic, the Q5 haplotype is mainly restricted to the Danube River and the Datteln-Hamm canal, both of which are directly connected to the Moselle via the Main-Danube canal and thereafter the Main and Rhine Rivers. These results could potentially indicate either new invasion corridors, considerable changes in haplotype distribution since the last comprehensive study or an undervaluation by Marescaux et al. (2016b) due to under-sampling. Given the results obtained from the microsatellite data, one might expect that genetic exchanges are frequent between distinct populations in rivers/canals, and even between groups from different continents. This observation appears to support our hypothesis that new invasion events have occurred repeatedly since the last comprehensive study and that more haplotypes might also be observed in populations from other rivers.

Conclusions

In this study, we showed that the quagga mussel now represents around one third of the dreissenid population in the Moselle, and at least 60% of dreissenid biomass, 10 years after its first observation in the Moselle River. This appears to have been due to distinct differences in life history dynamics between quagga and zebra mussels. Specifically, the reproduction process of quagga mussels is much more spread out in time, it has a much faster growth rate and, while it slows down it does not stop during the winter period. Size structure analysis revealed a lack of individuals of 4–14 mm in length, possibly due to differential predation by the invasive round goby, though high mortality of young quagga mussels due to other factors cannot be excluded. Quagga mussel population at our sampling locations on the Moselle had a homogeneous genetic structure that was similar to that observed at other sites throughout Europe. A comparison with previous data suggests that several successive introduction waves may have built up the existing population, contributing to the high degree of homogeneity within invaded ecosystems. The rate of veliger production, winter growth and, potentially, predation by gobies, appear to be the main determinants of quagga mussel life history dynamics on the Moselle, though all three factors deserve further investigation.

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Authors contribution

NT: sample design and methodology; investigation and data collection; data analysis and interpretation; writing - original draft; writing - review & editing. TB: sample design and methodology; investigation and data collection; writing - original draft. ND: sample design and methodology; data analysis and interpretation; writing - original draft. JM: sample design and methodology; data analysis and interpretation; writing - original draft. GN: research conceptualization; sample design and methodology; data analysis and interpretation; funding provision; writing - original draft; writing - review & editing. JNB: research conceptualization; sample design and methodology; investigation and data collection; data analysis and interpretation; writing - original draft; writing - review & editing.

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