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Sympatric *Dreissena* species in the Meuse River: towards a dominance shift from zebra to quagga mussels

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Abstract

The rapid spread of the quagga mussel, *Dreissena rostriformis*, in Western Europe is of particular concern since the species is known to have serious ecological and economic impacts, similar to those of the well-established zebra mussel, *Dreissena polymorpha*. This study aimed (1) to provide an update on the quagga mussel distribution in several Belgian inland waterways, and (2) to check if a shift in dominance between *Dreissena* species is occurring. Using density measurements and artificial substrate samplers, we compared population dynamics for both species at different time-points based on size-frequency distribution. Our results show that quagga mussels are spreading rapidly throughout Belgium via a number of possible invasion fronts based around large rivers and canals. The quagga mussel became the dominant dreissenid species in both the Meuse River and a number of Belgian canals. In just three years, quagga mussel's relative abundance increased from 2.9% (±2.9) to 52.6% (±43.1) of the total dreissenid population in the Meuse River. The most rapid increase in abundance has occurred in the Albert Canal, where quagga mussels achieved a mean relative abundance of 80% two years after the first observation. In the Meuse River, the quagga mussel displays a faster growth rate and/or earlier reproduction than the zebra mussel. We discuss different mechanisms that could explain the quagga mussel's apparent competitive advantage over the zebra mussel.

Key words: aquatic invasive species, competition, *Dreissena polymorpha*, *Dreissena rostriformis*, population dynamics, range expansion, dominance shift

Introduction

North American and European freshwater ecosystems have been greatly affected by anthropogenic factors over the twentieth century, resulting in profound ecological changes (e.g. habitat degradation, water pollution, community change) and the promotion of biological invasions (Naiman and Turner 2000; Dudgeon et al. 2006; Boets et al. 2011). Among the most notorious fresh- and brackish water invaders is the zebra mussel, *Dreissena polymorpha* (Pallas, 1771), which has had a wide range of physical, chemical, biological and socio-economic impacts (reviewed in Sousa et al. 2013; Higgins 2014). The recent expansion of its close relative (Bij de Vaate et al. 2014), the quagga mussel (*D. rostriformis* Deshayes 1838, [formerly known as *D. rostriformis bugensis* Andrusov 1897; see Stepien et al. 2014 for taxonomic revision]), in Western Europe is of particular concern as its ecological and economic impacts are assumed to be as, or even more pronounced than those of the zebra mussel (Karatayev et al. 2014; Roy et al. 2014; Wong et al. 2014).

Introduction of zebra and quagga mussels can result in alterations to the food web with resultant

energy/nutrient fluxes (Higgins 2014). By filtering suspended particles from the water column and depositing them into the sediment, they increase water clarity, allowing the growth of benthic algae and macrophytes (Sousa et al. 2013). Modification of the phytoplankton community, however, may also have a bottom-up effect on the whole food chain (e.g. a decline in planktivorous fishes). As ecosystem engineers, dreissenids also induce profound changes in the benthic macroinvertebrate assemblage (Ward and Ricciardi 2007). It has been shown that mussel beds provide both shelter and food to detritivorous invertebrates, leading to an increase in species richness (Ward and Ricciardi 2007). Furthermore, dreissenids can directly impact native bivalves by fouling the posterior end of unionid shells, disrupting the valve occlusion with resultant suffocation (Lucy et al. 2014). Both the zebra and quagga mussel are considered the most serious biofouling pest species ever introduced into North American and European waters (Pimentel et al. 2005). Mussel beds and associated accumulations of dead shells clog pipelines in industrial facilities; disrupt water flow; affect the integrity of iron and steel pipes; encrust the hulls of boats, thereby altering their sailing efficiency; and contaminate potable water supplies (reviewed in Mackie and Claudi 2010). The impacts of *Dreissena* species, however, are highly density dependent and, therefore, may vary during the invasion process (Karatayev et al. 2015).

Replacement of zebra mussels by quagga mussels has been observed at several locations in the Laurentian Great Lakes area (e.g. Stoeckmann 2003; Wilson et al. 2006; Ram et al. 2011; Stewart 2014). Despite this, there have been few studies on quagga and zebra mussel interaction in Western Europe. Based on 13 sites in Germany and The Netherlands, Heiler et al. (2013) calculated that the relative abundance of quagga mussels in the total dreissenid population increased 26% each year in Western Europe. Bij de Vaate et al. (2014) also reported a dominance shift from zebra to quagga mussels in Lake Ijsselmeer (The Netherlands), with the quagga mussel's relative abundance increasing from 1% in 2007 to 94% in 2011. Over the same period, average biovolume (the amount of water displaced by living mussels) increased from 33 to 152 mL/m² (Bij de Vaate et al. 2014). With the quagga mussel presently expanding its range in Western Europe, it is to be expected that the total impact of *Dreissena* species on the ecosystem will increase (Diggins 2001; Bij de Vaate 2014).

The Meuse River is a topical location to study interactions between zebra and quagga mussels as the river is connected, via a series of canals, to the Rhine and Danube Rivers, a situation that could facilitate wider introduction of these invasive species. The quagga mussel was observed in the Meuse River (Dutch section) for the first time in 2007 (Marescaux et al. 2012), whereas the zebra mussel has been part of this ecosystem since 1835 (reviewed in Pollux et al. 2010). The first record of the quagga mussels in Belgium was in 2009 in the Albert Canal (Sablon et al. 2010), which connects the Meuse River to the port of Antwerp. As the species has a recent invasion into Western Europe compared to the zebra mussel, it is important to establish the current distribution of *D. rostriformis* in Belgium and determine whether the quagga mussel could become the dominant dreissenid species in Belgian waterways, or whether the species might colonise additional habitats, leading to additive ecological and economic effects. As such, this study aims (i) to provide an update on the distribution of the quagga mussel in several Belgian inland waterways, (ii) to assess the density of dreissenid populations in the Meuse River, and (iii) to compare population dynamics of both species in order to evaluate any potential shift from zebra mussels to quagga mussels.

Materials and methods

Dreissenids spatial distribution within Belgian waterways

Dreissena were collected once during lock maintenance in three different canals: at the Ham Kwaad Mechelen lock on the Albert Canal in November 2011, the Havré lock on the Canal du Centre in February 2013 and at the Ronquières inclined plane on the Canal Charleroi-Bruxelles in August 2013 (Figure 1; Table 1). In the Albert Canal and the Canal Charleroi-Bruxelles, density measurements were taken using a surber sampler (500 cm², 0.35 mm mesh) at four randomly selected sites. At the Havré lock, mussels were collected from the upstream and downstream gates after they have been removed for maintenance (no density measurements). In addition, 138 samples containing *Dreissena* specimens taken from 2009–2013 by the Flemish Environment Agency (VMM) and the Royal Belgian Institute of Natural Sciences (RBINS) were also examined in order to determine the occurrence of quagga mussels in waterways situated mainly in the northern part of

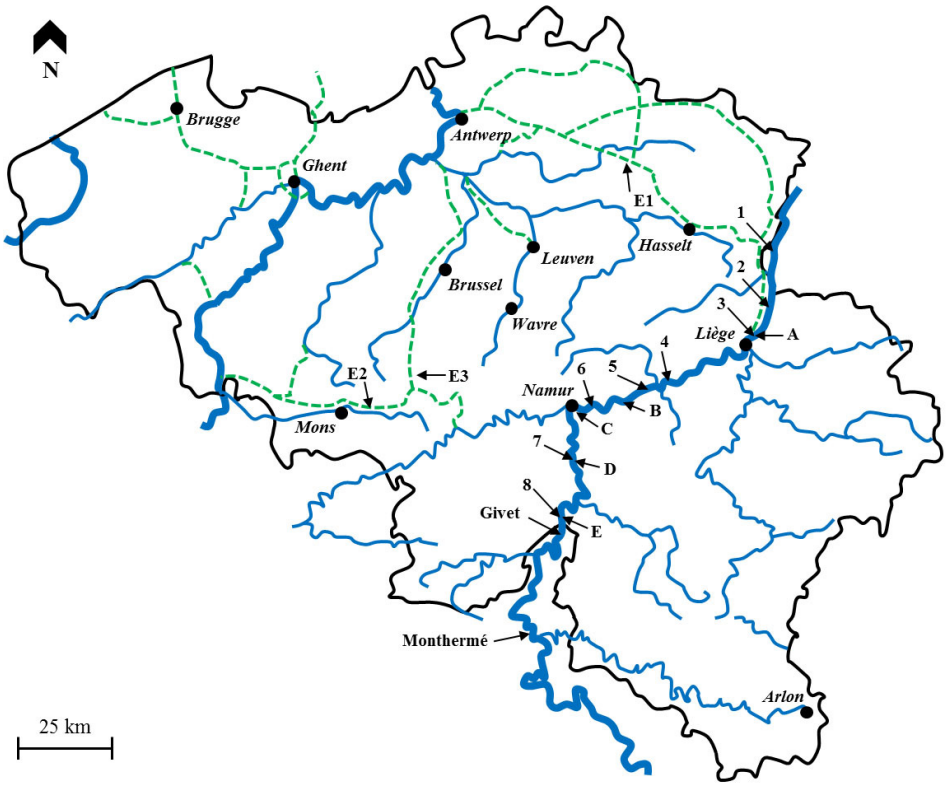

Figure 1. Map showing the location of quagga mussel sampling sites in this study (i) canals (E1 = Albert Canal; E2 = Canal du Centre; and E3 = Canal Charleroi-Bruxelles), (ii) natural substrata for the density study on the Meuse River (1 to 8), and (iii) fish ladders (A to E). The site on the Meuse River (Givet) where artificial case substrata were installed is also indicated. See Table 1 for coordinates. Black dots indicate major Belgian cities. Codes are as follow: bold blue = major rivers; blue = minor rivers; green = artificial waterways (canals).

Table 1. Quagga mussel sampling site details: (E1 to E3) canals, density study on (1 to 8) natural substrata and (A to E) fish ladders, and (AS) Givet station where artificial substrata were placed. The codes in the first column are in accordance with Figure 1.

	Waterway	Location	Coordinates of the sampling site		Depth	Sampling date
			Latitude, N	Longitude, E		
E1	Albert Canal	Ham Kwaad Mechelen	51°05'53.35"	5°06'29.21"	10m	25/11/2011
E1	Canal du Centre	Havré	50°28'15.52"	4°01'29.40"	3-4m	12/02/2013
E3	Canal Charleroi-Bruxelles	Ronquières inclined plane	50°35'19.27"	4°13'09.50"	3-4m	21/08/2013
1	Meuse River	Petit Lanaye	50°48'39.08"	5°41'30.33"	30-40cm	2011-2014
2	Meuse River	Lixhe	50°45'18.29"	5°41'00.62"	30-40cm	2011-2014
3	Meuse River	Monsin	50°39'11.18"	5°38'19.98"	30-40cm	2011-2014
4	Meuse River	Huy	50°30'58.76"	5°14'00.06"	30-40cm	2011-2014
5	Meuse River	Gives	50°30'20.44"	5°08'47.50"	30-40cm	2011-2014
6	Meuse River	Namêche	50°28'07.61"	4°59'43.85"	30-40cm	2011-2014
7	Meuse River	Godinne	50°21'13.24"	4°52'45.28"	30-40cm	2011-2014
8	Meuse River	Hastière	50°12'51.46"	4°49'33.80"	30-40cm	2011-2014
A	Meuse River – fish ladder	Monsin	50°39'09.68"	5°37'54.98"	2-3m	2011-2014
B	Meuse River – fish ladder	Andenne	50°29'36.05"	5°04'12.58"	2-3m	2011-2014
C	Meuse River – fish ladder	Namur	50°27'01.37"	4°51'44.28"	2-3m	2011-2014
D	Meuse River – fish ladder	Hun	50°20'10.46"	4°52'23.53"	2-3-m	2011-2014
E	Meuse River – fish ladder	Waulsort	50°12'05.36"	4°51'10.30"	2-3m	2011-2014
AS	Meuse River	Givet (Fr)	50°08'42.26"	4°49'52.65"	50cm	2013-2014

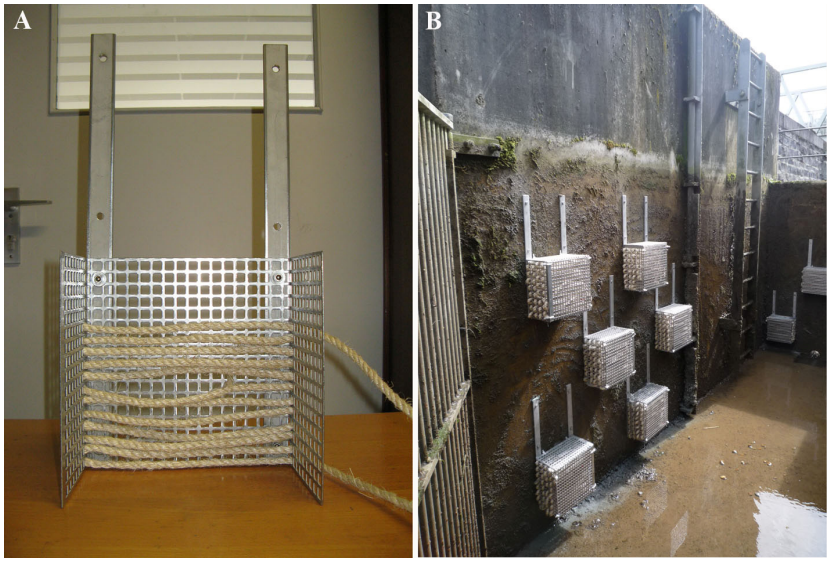

Figure 2. Artificial substrate used to compare the population dynamics of zebra and quagga mussels. (A) Stainless steel cage during construction and prior to deployment, and (B) stainless steel cages attached to the concrete wall of a fish ladder on the Meuse River. Photographs by J. Marescaux.

the country (Flanders). *Dreissena* species were identified based on shell characteristics (Pathy and Mackie 1993; Mills et al. 1996; Sablon et al. 2010).

Density evaluation in the Meuse River

Dreissenid samples were collected at eight natural sites and at five fish ladders on the Meuse River (Figure 1; Table 1) every three months from November 2011 to February 2014. An additional sampling occurred in October 2014. Densities at natural sites were estimated by counting all dreissenid mussels on five randomly selected stones collected in the littoral zone of the river at a depth of 30–40 cm. All individuals were detached, identified to species level and counted directly in the field. Densities on the concrete walls of fish ladders were ascertained using a surber sampler (500 cm², 0.35 mm mesh) at two randomly selected sites at the bottom of the wall. All dreissenid mussels in the surber sampler were detached from the wall and transported to the laboratory for identification and counting.

Artificial substrates to compare population dynamics in the Meuse River

Nine artificial substrates (25 cm × 25 cm × 14 cm stainless steel cages with 0.8 cm² holes and a 20 m rope wound inside; Figure 2) were placed directly on the sheet pile wall at Givet (France) in May 2012 (Figure 1; Table 1). One third of the cage substrates were randomly selected and removed after one year (May 2013), another third after a year and a half (November 2013) and the last cages after two years (May 2014). All *Dreissena* specimens present on each artificial substrate were counted. For each 'time-point' the shell length of 1200 zebra mussels randomly chosen from the sample, and all quagga mussels present, was measured to the nearest 0.1 mm using an electronic digital calliper. The *Dreissena* individuals were then divided into 0.5 mm size classes. Size frequency distribution was analysed using Bhattacharya's graphical method (Bhattacharya 1967), with the aim of separating the length frequencies into cohorts. For each cohort, the mean size, standard deviation and number of individuals was determined. All analyses were conducted using a Microsoft Excel macro developed by the authors.

Results

Distribution of quagga mussels in Belgian waterways

Both zebra and quagga mussels were recorded in the three canals sampled (Table 2). In the Albert Canal, we recorded maximum densities of 2,720 and 45,900 ind/m² for zebra and quagga mussels, respectively. The quagga mussel's mean relative abundance (i.e. number of quagga mussels divided by total number of *Dreissena*) in the Albert Canal was estimated at 82% ± 16.2. The quagga mussel was more abundant in the Canal du Centre, with a mean relative abundance of

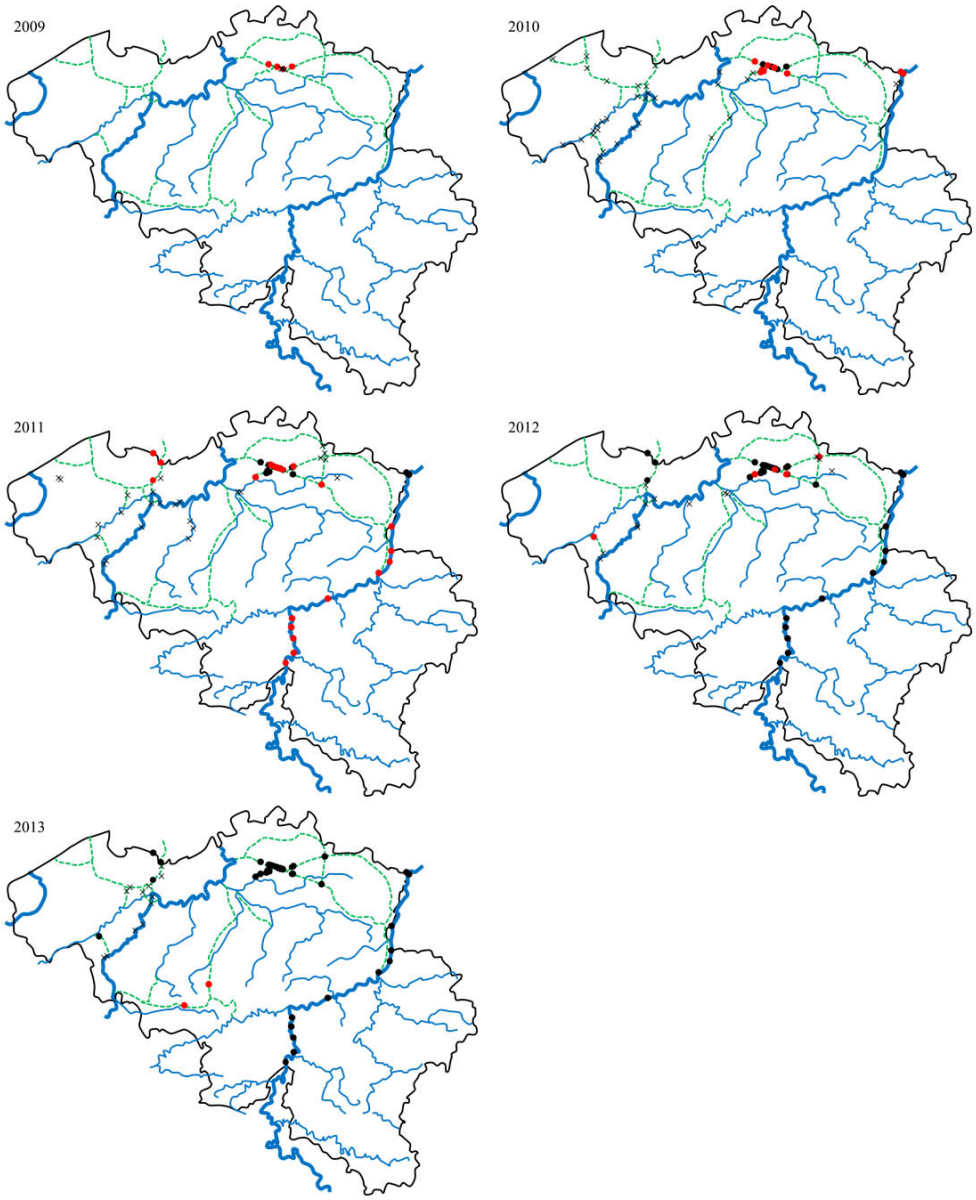

Figure 3. Range expansion of the quagga mussel along several Belgian waterways from 2009 to 2013. Codes are as follow: bold blue = major rivers; blue = minor rivers; green = artificial waterways (canals); red dots = quagga mussel observations; black dots = previous observations; black cross = samples without quagga mussels.

98% ± 0.004. Conversely, a very low abundance of quagga mussel was recorded in the Canal Charleroi-Bruxelles, with less than 0.1% ± 0.001 of total dreissenids.

Of the 138 samples examined from the VMM and RBINS collections, 45 contained quagga mussels (summarised in Figure 3). Based on this sampling collection, quagga mussels were first recorded in Belgium in the Albert Canal in 2009. By 2010, the species was found east of its first observation, in the Meuse River at the Belgian-Dutch border. One year later, the species had extended its range along a large section of the Albert Canal and of the Meuse River, and reached the Canal Gent-Terneuzen in the north of Belgium, at its border with The Netherlands.

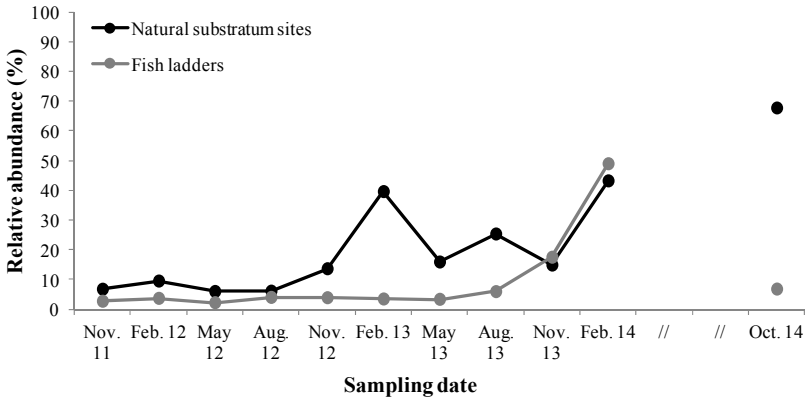

Figure 4. Quagga mussel relative abundance (%) in the Meuse River from November 2011 to October 2014 at sites with natural substrata and on fish ladders.

By 2012, the species was found at one site on the Canal Kortrijk-Bossuit, in the northwest of Belgium, and, by 2013, it had been found in the Canal du Centre and Canal Charleroi-Bruxelles (see above).

Dominance shift from zebra to quagga mussels in the Meuse River

We observed a large variation in *Dreissena* density along the Meuse River (Figure 4; Appendix 1). Maximum quagga mussel density on natural substrata (Gives – October 2014) was 448 ind/m² and 1,440 ind/m² on the fish ladders (Hun – February 2012). Zebra mussel densities were much higher than those of quagga mussels, with maximum values of 1,208 ind/m² on natural substrata (Huy – May 2013) and 40,320 ind/m² on the fish ladders (Hun – February 2012). In September 2012, the nine weirs regulating water flow between Givet (France) and Namur (Belgium) were opened to allow technical maintenance, which results in a dramatic drop in water level along the Meuse River. This river drainage caused 100% dreissenid mortality between the cities of Givet and Namur and re-colonisation by zebra and quagga mussels took approximately one year.

The relative abundance of quagga mussels fluctuated over time, but showed a tendency to increase at both natural sites and sites situated on fish ladders (Figure 4). When considering the natural sites, quagga mussels represented 6.8% ± 5.1 of the total dreissenid population along the Meuse River in November 2011 and 67.8% ± 35.9 by October 2014. We, however, observed a sharp decline in relative abundance on fish ladders at the end of this study (6.8% in October 2014 vs 49.0% in February 2014).

Population dynamics of Dreissena species

In May 2013, 7,121 dreissenids were collected from the three artificial cage substrata situated at Givet. From these, 175 were identified as quagga mussels, indicating a relative abundance of 2.46% ± 0.53. In November 2013, quagga mussel relative abundance was similar to that in 2013 at 2.44% ± 0.36 (154 individuals out of 6,301). Again, in May 2014, 160 quagga mussels were collected from a total of 5,826 *Dreissena*, indicating a relative abundance of 2.73% ±0.34. Overall, quagga mussel relative abundance remained constant over time in these artificial cages.

In all cases, length frequency distributions for both *Dreissena* species showed clear cohort overlap over the three different time-points (Figure 5). This suggests a continuous period of reproduction and high variability in individual shell growth, making further interpretation difficult. In The Netherlands, it was found that zebra mussels start to grow at a minimum temperature of 3°C (Smit et al. 1992). In 2013, the water temperature at Hastière on the Meuse River (located 10km downstream of Givet) was always ≥ 3°C (Aquapol website), indicating that the zebra mussel growing season is continuous, even if only 'ticking-over' in winter. Despite this, the length-frequency distributions do allow differentiation of several peaks corresponding to major reproduction events.

Use of Bhattacharya's method allowed separation of zebra mussel length frequency distributions into five cohorts in May 2013, six in November 2013 and six in May 2014 (Figure 5; mean shell length and number of individuals in each cohort in Table 3). The smaller zebra mussel cohort observed in May 2013 corresponded to newly settled mussels

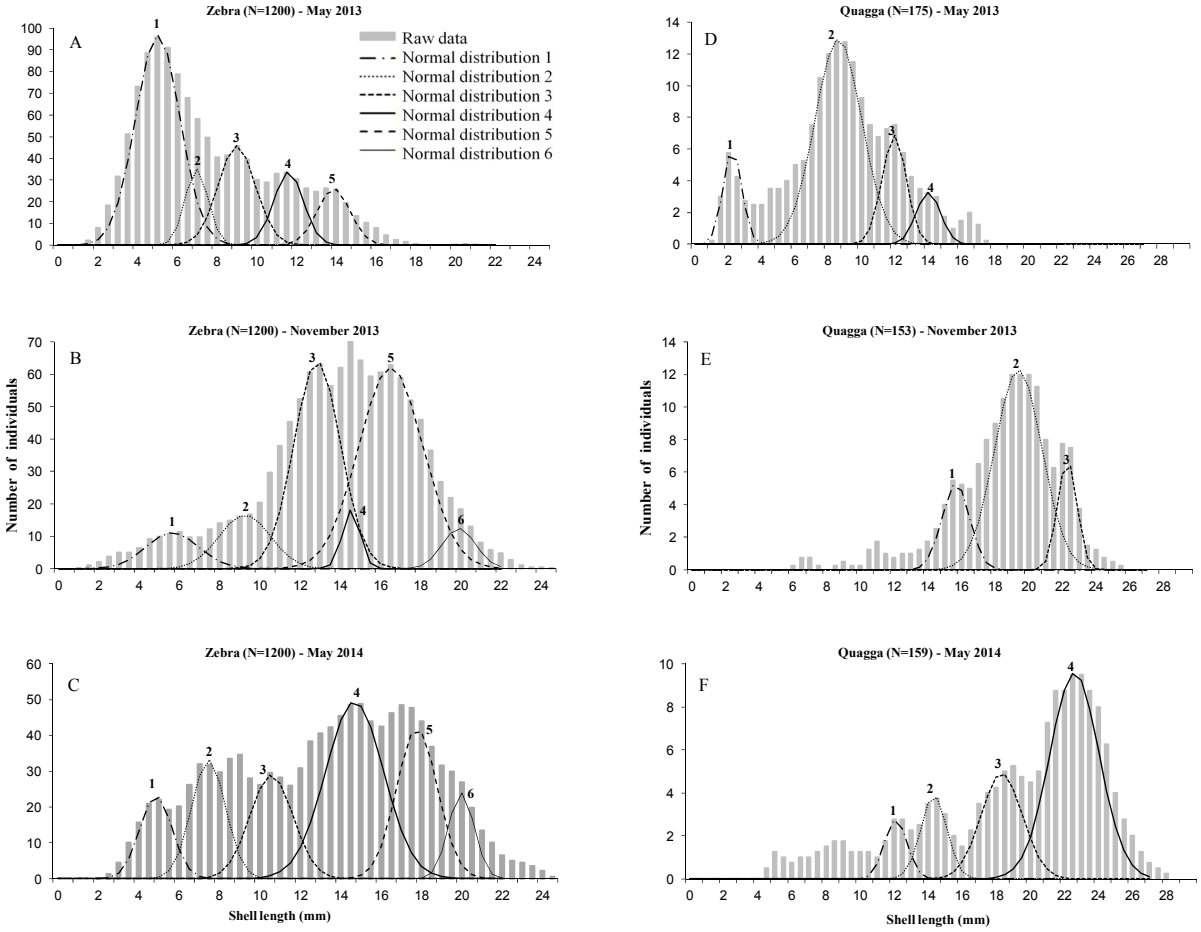

Figure 5. Size distribution based on mean cohort shell length for zebra (left) and quagga (right) mussels sampled at Givet on the Meuse River. Each normalised distribution was calculated using the Bhattacharya method.

Table 2. Number of *Dreissena* collected at different sampling sites studied for quagga mussel expansion and their inferred densities. The codes in the first column are in accordance with Figure 1. n.a. = not-available.

	Waterway	Location	Samples	Collected individuals		Individuals/m²	
				Zebra	Quagga	Zebra	Quagga
E1	Albert Canal	Ham Kwaad Mechelen	a	121	2295	2420	45900
			b	21	766	420	15320
			c	136	259	2720	5180
			d	134	327	2680	6540
E2	Canal du Centre	Havré	a	5	287	n.a.	n.a.
			b	13	1132	n.a.	n.a.
E3	Canal Charleroi-Bruxelles	Ronquières inclined plane	a	871	2	17420	40
			b	1217	1	24340	20
			c	1382	2	27640	40
			d	851	0	17020	0

Table 3. Mean shell length (± standard deviation) and number of individuals estimated (Ne) for each zebra and quagga mussel cohort, determined using the Bhattacharya method.

	Zebra mussels					
Model size	May 2013		Nov 2013		May 2014	
	SL (± sd)	Ne	SL (± sd)	Ne	SL (± sd)	Ne
1	5.51 ± 1.11	545.30	6.16 ± 1.31	72.98	5.34 ± 0.79	92.86
2	7.47 ± 0.56	102.46	9.75 ± 1.25	104.59	7.96 ± 0.83	140.03
3	9.50 ± 0.93	215.37	13.35 ± 1.16	372.84	11.07 ± 1.0	153.472
4	12.09 ± 0.73	126.33	15.05 ± 0.42	40.50	15.18 ± 1.44	357.32
5	14.36 ± 0.82	108.42	17.03 ± 1.60	499.22	18.29 ± 1.00	213.19
6	/	/	20.42 ± 0.83	52.07	20.47 ± 0.62	76.66
	Quagga mussels					
	May 2013		Nov 2013		May 2014	
	SL (± sd)	Ne	SL (± sd)	Ne	SL (± sd)	Ne
1	2.72 ± 0.55	17.0	16.17 ± 0.80	21.7	12.61 ± 0.65	9.2
2	9.10 ± 1.41	91.6	19.89 ± 1.40	86.6	14.83 ± 0.75	14.8
3	12.45 ± 0.72	25.2	22.80 ± 0.55	19.5	18.83 ± 1.20	29.7
4	14.51 ± 0.72	12.0	/	/	23.10 ± 1.45	69.8

born earlier the same year, while the second comprised individuals attached early in 2013 and/or autumn 2012. Individuals of the third cohort were attached in autumn 2012. Cohort four consisted of individuals attached in the autumn and/or spring of 2012, while the largest cohort corresponded to individuals probably settled in spring 2012. Individuals attaching in spring 2013 (cohorts one and two in Figure 5A) achieved a shell size between 9 and 16 mm (cohorts three, four and five in Figure 5B) by November 2013, while those settled in 2012 (cohorts four and five in Figure 5A) reached between 14 and 22 mm (cohorts four, five and six in Figure 5B). Cohorts one and two in November 2013 consisted of individuals attaching in the summer. A similar pattern was observed in May 2014 (Figure 5C), with cohorts one and two corresponding to newly attached mussels, while cohorts three and four corresponded with attachment in summer 2013. The large cohorts observed in May 2014 represented individuals born in 2012 and 2013. Based on the estimated number of individuals (Table 3), it can be inferred that recruitment was lower in 2014 than 2013, but that the growth rate was high in both years. Indeed, previous studies have shown that zebra mussels can reach a shell length of 15 to 17 mm during their first year (Dermott et al. 1993; Araujo et al. 2010).

Despite the relatively low number of individuals measured, several cohorts could also be distinguished for quagga mussels, with four confirmed in May 2013, three in November 2013 and four in May 2014 (Figure 5; mean shell length and number of individuals in each cohort in Table 3). The smaller cohort observed in May 2013 corresponded with newly attached mussels born that year, while the second cohort comprised individuals attached in early 2013 and/or individuals attached in autumn 2012. There was a large gap in mean shell length between cohorts one and two suggesting the possible presence of another cohort that was missed by the Bhattacharya method due to the low number of individuals collected. Individuals in the third and fourth cohorts were attached in autumn and spring 2012, respectively. The three cohorts observed for November 2013 were all derived from the four observed in May 2013. In November 2013, an early cohort probably became established with a shell size ranging between 6 and 12 mm; however, too few individuals were measured for the Bhattacharya method to take it into account. The two first cohorts observed in May 2014 corresponded with newly attached individuals born in November 2013. Cohort number three and four consisted of individuals attaching in autumn 2011 and/or spring 2012, while the larger individuals corresponded with individuals attaching in spring 2012. Once again, an early cohort could be distinguished with a shell size ranging between 4 and 10 mm (corresponding with new recruitment); however, too few individuals were collected to be taken into account.

The principal cohorts for zebra and quagga mussels had a mean shell length of 5.5 mm and 9.1 mm, respectively, in May 2013; 13.3 mm and 19.9 mm, respectively, in November 2013; and 18.3 mm and 23.1 mm, respectively, in May 2014. At each time-point, quagga mussels achieved larger shell sizes for the same age than zebra mussels.

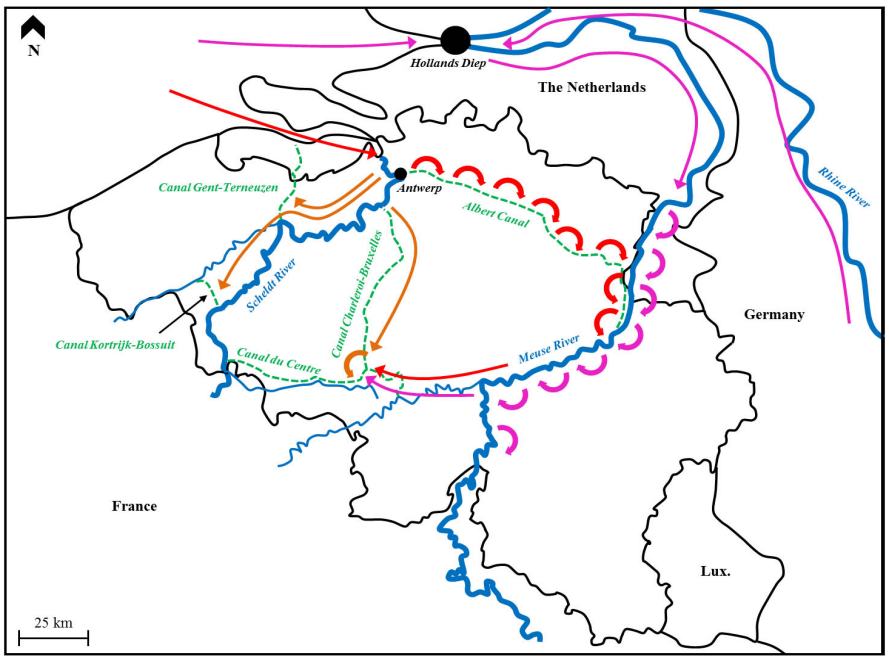

Figure 6. Map showing the different hypothetical invasion fronts for the quagga mussel in Belgium. Codes are as follow: bold blue = major rivers; blue = minor rivers; green = artificial waterways (canals). Red = discharge of ballast water in the port of Antwerp and subsequent stepwise spread along the Albert Canal and the Meuse River; Pink = discharge of ballast water in Hollands Diep or introduction through the Danube and Rhine rivers, and subsequent upstream migration along the Meuse River; Orange = jump dispersal from the port of Antwerp and colonization of the Canal Gent-Terneuzen; the Canal Kortrijk-Bossuit, the Canal du Centre and the Canal Charleroi-Bruxelles.

Discussion

Quagga mussel expansion and dominance shift

The observed discrepancy in quagga mussel's relative abundance in the Belgian waterways examined (i.e. dominant in the Albert Canal, Canal du Centre and River Meuse but only a few individuals present in the Canal Charleroi-Bruxelles) may be the result of arrival by different invasion fronts. The species was probably firstly introduced into Belgium via discharge of ballast water in the port of Antwerp, subsequently spreading stepwise (see Müller et al. 2001 for terminology) along the Albert Canal (Figure 6). The observation of the species in the Meuse River at the Belgian-Dutch border in 2010, and its subsequent rapid upstream migration along the river, could indicate introduction via ballast water discharge at Hollands Diep or introduction via the Danube and Rhine Rivers, with subsequent upstream migration along the Meuse River (Figure 6). Moreover, the Meuse River could have been invaded through a second invasion front through its connection to the Albert Canal, which carries commercial shipping. The Albert Canal is also connected to the Scheldt River, which may explain the quagga mussel observations in the Gent-Terneuzen and Kortrijk-Bossuit canals to the west, having moved there by jump dispersal (see Müller et al. 2001 for terminology; Figure 6). Furthermore, the presence of quagga mussels in the Canal du Centre and Canal Charleroi-Bruxelles are also probably the result of jump dispersal (Figure 6).

Our data, therefore, provide strong evidence for the spread of quagga mussels via shipping and reveal a number of potential canal-based corridor routes for dispersal of the species. Indeed, these canals are already known to have enhanced transport of drifting planktonic veliger in Western Europe (Bij de Vaate et al. 2014). This dispersal is further promoted by transportation of larvae in barge ballast water (Ricciardi and MacIsaac 2000) and by attachment of juveniles and adults to boat hulls, thereby allowing jump dispersal (Carlton 1993; Müller et al. 2001).

Our results show that the quagga mussel has spread rapidly in Belgian waterways, and that the species tends to dominate over other dreissenids in the Albert Canal and Meuse River. The first record of quagga mussels in the Albert Canal was made in 2009 at Grobbendonk (Sablon et al.

2010), a period when zebra mussels dominated the dreissenid community. Our results indicate a rapid increase in quagga mussel abundance with a mean relative abundance of more than 80% in the Albert Canal two years after its first observation. The quagga mussel was also the dominant dreissenid in the Canal du Centre, though only a few individuals were collected from the Canal Charleroi-Bruxelles. Although densities fluctuated over time, leading to large variations in quagga mussel relative abundance, the consistently increasing trend observed in the Albert Canal was also observed in the Meuse River, though at a lower rate of increase. Despite the quagga mussel being first recorded in the Belgian section of the Meuse River in 2011 (Marescaux et al. 2012), the species now makes up 50% of the total dreissenid population (in terms of abundance).

Based on 13 sampling sites in Germany and The Netherlands, Heiler et al. (2013) estimated that quagga mussel's relative abundance in Europe was increasing by 26% per year and Stoeckmann (2003), Wilson et al. (2006), Stewart (2014) have all made similar observations in North America. Quagga mussel's relative abundance in the western basin of Lake Erie, for example, increased from 20% in 1998 to 80% in 2001 (Stoeckmann 2003). Karatayev et al. (2015), however, showed that this species shift varied greatly depending on a range of parameters, including collection depth and waterbody morphometry. Zhulidov et al. (2010) also observed large fluctuations in the ratio of quagga/zebra mussel densities, with quagga mussels eventually displacing zebra mussels in the Dnieper River (Ukraine). The mechanisms underpinning this shift are currently unknown; however, several authors have hypothesised that reproductive or physiological factors may provide the quagga mussel with greater bioenergetic efficiency, giving them a competitive advantage over the zebra mussel (Stoeckmann 2003; Ram et al. 2011). Zuhlidov et al. (2006; 2010) noted, however, the opposite pattern in the Don River system (Russia), with *D. rostriformis* (designated as *D. bugensis* by the authors) declining over time in 14 out of 15 study sites. The authors suggested that, since the quagga mussel has a thinner shell than the zebra mussel, selective predation by fish could potentially explain this unusual result. Indeed, unlike North America, dreissenids can represent an important food resource for cyprinids, whitefish species and the round goby, *Neogobius melanostomus*, in Eurasia (Zhulidov et al. 2006). The round goby was first reported in Belgium in 2010 and is now found in both the Scheldt and Meuse Rivers, which are connected by the Albert Canal (Jacobs and Hoedemakers 2013) where the species can reach extremely high densities (Verreycken 2013).

Population dynamics as a potential explanation for the shift in dominance

Several studies have highlighted the possible competitive advantages of quagga mussels over zebra mussels in deeper and cooler habitats (Dermott and Munawar 1993; Spidle et al. 1994; Wilson et al. 2006; Nalepa et al. 2010). Any such an advantage, however, may not apply in shallow and thermally homogeneous ecosystems (Jones and Ricciardi 2005) such as the Meuse River. While Baldwin et al. (2002) has shown that quagga mussels displays a better assimilation efficiency (81%) at low seston levels than zebra mussel (63%), our previous work does not support this hypothesis (Marescaux, in preparation). For example, we were able to show that, in the Meuse River, the seasonal filtration rate of both the zebra and quagga mussel (expressed per unit of body mass) did not differ significantly at five different algal concentrations. Our results clearly showed that the quagga mussel displayed a faster growth rate and/or earlier spawning than the zebra mussel at our study sites (Figure 5; Table 3). These features allow the quagga mussel to achieve a larger shell size and body mass than zebra mussels, which may also help them survive winter stress better.

In conclusion, the quagga mussel is spreading rapidly in Belgium, mainly via large rivers and canals. It rapidly increases in abundance and quickly becomes the dominant dreissenid species at locations where the zebra mussel was previously well-established.

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The following supplementary material is available for this article:

Table S1. Density of zebra and quagga mussels observed at different sampling locations on the Meuse River.

This material is available as part of online article from:
http://www.aquaticinvasions.net/2015/Supplements/AI_2015_Marescaux_etal_Supplement.xls