Rapid range expansion of the invasive quagga mussel in relation to zebra mussel presence in The Netherlands and Western Europe

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ORIGINAL PAPER

Rapid range expansion of the invasive quagga mussel in relation to zebra mussel presence in The Netherlands and Western Europe

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Abstract Since its appearance in 2006 in a freshwater section of the Rhine–Meuse estuary (Hollandsch Diep, The Netherlands), the non-indigenous quagga mussel has displayed a rapid range expansion in Western Europe. However, an overview characterising the spread and impacts of the quagga mussel in this area is currently lacking. A literature study, supplemented with field data, was performed to gather all available data and information relating to quagga mussel dispersal. Dispersal characteristics were analysed for rate and direction and in relation to hydrological connectivity and dispersal vectors. To determine ranges of conditions suitable for quagga mussel colonisation, physico-chemical characteristics of their habitats were analysed. After its initial arrival in the freshwater section of the Rhine-Meuse estuary and River Danube, the quagga mussel demonstrated a rapid and continued range expansion in Western Europe. Quagga mussels have extended their non-native range to the network of major waterways in The Netherlands and in an upstream direction in the River Rhine (Germany), its tributaries (rivers Main and Moselle) and the River Meuse (Belgium and France). The calculated average quagga mussel dispersal rate

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in Europe was 120 km year^{-1} (range 23–383 km year^{-1}). Hydrological connectivity is important in determining the speed with which colonisation occurs. Dispersal to water bodies disconnected from the freshwater network requires the presence of a suitable vector e.g. pleasure boats transferred over land. Upstream dispersal is primarily human mediated through the attachment of mussels to watercraft. The relative abundance of quagga mussel to zebra mussel has greatly increased in a number of areas sampled in the major Dutch rivers and lakes and the rivers Main and Rhine and the Rhine–Danube Canal leading to a dominance shift from zebra mussels to quagga mussels. However, evidence for displacement of the zebra mussel is limited due to the lack of temporal trends relating to the overall density of zebra and quagga mussel.

Keywords Dispersal · Distribution · Dominance shift · *Dreissena polymorpha* · *Dreissena rostriformis bugensis* · Invasiveness · Species displacement

Introduction

The recent appearance and rapid range expansion of the non-indigenous quagga mussel, *Dreissena rostriformis bugensis* Andrusov, 1897 in Western Europe highlights the need for assessment of its colonisation and dispersal mechanisms in European freshwater ecosystems.

Until the 1940s, the quagga mussel only occurred in the mouth of two rivers discharging into the Black Sea, viz. the Southern Bug and Dnieper in the Ukraine (Son 2007; Van der Velde et al. 2010b). Since then it has extended its range in Russia considerably, reaching the River Volga via the River Don and the Volga-Don Canal (Orlova et al. 2003, 2004; Son 2007; Zhulidov et al. 2004, 2005). The quagga mussel was first recorded in North America in 1991, possibly arriving simultaneously with the zebra mussel, *Dreissena polymorpha* (Pallas, 1771) around 1986. This introduction probably occurred at the larval stage via ballast water discharge (May and Marsden 1992). By 2004 the quagga mussel had expanded its range to the Romanian section of the River Danube, Eastern Europe (Micu and Telembici 2004; Popa and Popa 2006). The first observation in Western Europe was made in 2006 in the Hollandsch Diep, a dammed, freshwater section of the Rhine and Meuse estuary in The Netherlands (Molloy et al. 2007). Subsequently, the species spread rapidly and it is now classified as invasive in Western Europe (Matthews et al. 2012). Certain records indicate that quagga mussel density is higher than that of the earlier invader, the zebra mussel (Bonhof et al. 2009; De Rooij et al. 2009; Bij de Vaate 2010a; Matthews et al. 2012; Heiler et al. 2012).

Besides exhibiting a planktonic larval stage, unique for dreissenids among freshwater bivalves in Europe and North America, the adults secrete proteinaceous byssal threads allowing attachment to hard substrata (Bonner and Rockhill 1994; Clarke and McMahon 1996). Dreissenids byssally attach to vectors e.g. recreational boats or shipping and are subsequently transported upstream or overland to hydrologically disconnected, uninfested water bodies (Johnson and Carlton 1996).

A review exclusively based on North American studies, identified excretion rate and heavy metal accumulation as the only impacts that differed between quagga and zebra mussels (Kelly et al. 2010). Dreissenids negatively impact unionid mussels and certain fish populations, alter macroinvertebrate composition, reduce plankton abundance and increase macrophyte and benthic algal growth (Kelly et al. 2010). However, dreissenids provide food for certain water birds, fish, zoobenthic detritivores, crayfish and crabs. Moreover, increase in benthic invertebrate abundance after dreissenid invasion benefits invertebrate predators (Kelly et al. 2010; Mitchell et al. 1996; Mörtl et al. 2010; Van Eerden and De Leeuw 2010).

An overview characterising the spread and impacts of the quagga mussel in Western Europe is currently lacking. Additionally, insight into controllable environmental factors that influence quagga mussel distribution and population establishment is required. This paper characterises the current spread of the quagga mussel in The Netherlands and Western Europe and describes dispersal mechanisms and factors that influence quagga mussel distribution. Additionally, dominance shifts due to quagga mussel colonization within established zebra mussel habitats are analysed.

Materials and methods

Data acquisition and analyses of current distribution

A literature study was carried out to derive information on the current distribution, colonisation vectors and dispersal mechanisms of dreissenids in The Netherlands and Western Europe. Search terms included the Latin names: *Dreissena bugensis* and *D. rostriformis bugensis* which produced search results written in languages other than English and Dutch. English terms and their Dutch equivalents included: quagga, zebra, exotic, dispersal, colonisation, abundance, invasive, connectivity, vectors, physiological, tolerance, replacement, demographics, population, dynamics, Netherlands. Scientific papers, (grey) publications and websites were searched systematically, ensuring the quality of the data obtained, using several academic search engines (the Zoological Record, Web of Knowledge, Scopus, Google Scholar, www.science.gov, SCIRUS, Grey Literature in The Netherlands (GLIN), The Dutch Central Catalogue (PiCarta) and Greynet). Records taken from grey literature were only included if they were associated with a named specialist and/or governmental or non-governmental organisation.

Field surveys were carried out in The Netherlands with supplementary data obtained from co-authors who collected samples in Belgium, Germany and France. In The Netherlands, previously unexamined water bodies were identified for sampling. Sites were chosen to increase the representativeness of different levels of hydrological connectivity and water types. Sites were added at previously sampled locations to explore trends in abundance and species replacement. Sampling in The Netherlands occurred between March and September in the years 2011 (59 samples) and 2012 (26 samples) at different locations, primarily in the littoral zones of large rivers, tributaries, canals and lakes (Fig. 1). The major substrata (soft substratum, stone and vegetation) were sampled. If stones were sampled, five were removed at random along a 10–20 m stretch from depths of up to 75 cm. Groynes were sampled from their downstream side. All mussels were removed from the most densely colonised side of each stone. Five samples were scraped from vegetation, soft substrates, ship hulls and immovable substrates using a sieve or dip net. Mussel samples were preserved in ethanol (70 %), identified in the laboratory and analysed for relative abundance and density. The water-type (river, stream, canal etc.), colonisation vectors present (shipping, driftwood etc.) were recorded. Data on mussel abundance, sampling location, sampling methodology and sampling date derived from the literature study and field notes were entered into a database.

Analysis of dispersal rate and vectors

Dispersal rates (km year^{-1}) were calculated using the shortest distance of continuous waterway located between the point of initial quagga mussel colonisation in The Netherlands (Molloy et al. 2007; Bij de Vaate 2006), and the farthest known Dutch records to the north, south and east and the time delay occurring between the establishment of these records. This method has been used previously by Voelz et al. (1998), Leuven et al. (2009) and Kappes and Haase (2012). Arrival time was determined using a calculation of maximum age, derived from shell length, where sample populations were divided into length classes that represented age classes: 0+, 1+ and 2+ years at an average length of 5.6, 16.1 and 25.6 mm, respectively (Bij de Vaate 2008). The rates obtained were averaged and compared to rates for Western Europe found in literature. Dispersal maps

Fig. 1 Locations sampled during field surveys in The Netherlands

illustrating a different time period during quagga mussel colonisation in The Netherlands were created using the mapping programme Stipt (Frigge 2012). The yearly cumulative totals of Dutch quagga mussel locations were calculated. Vector types and modes of dispersal (active, passive, upstream, downstream, overland) used by quagga mussels were identified from literature and during field sampling.

Distribution in relation to connectivity and physico-chemical characteristics of water bodies

Dutch sampling locations were divided into hydrological connectivity classes (permanently connected, disconnected and seasonally connected water bodies) to analyse the effect of hydrological connectivity on quagga dispersal. Permanently connected water bodies are located downstream of quagga populations allowing colonisation by passive drift. A disconnected water body is defined where no quagga population exists upstream of the sampled location and where colonisation is facilitated by vectors (includes land-locked water bodies). Seasonally connected water bodies are connected discontinuously, depending on water level. Sampling locations were only included in the analysis when accurate information was available detailing the hydrological connectivity of the sampled water-body. Subsequently, the number of samples containing quagga mussels within each connectivity class was calculated and the results compared. The same methodology was applied in a separate analysis of water-type where sampling locations were assigned to the categories of river/stream, canal, lake and harbour. For the statistical analysis, categories were defined according to the abundance of individual mussel species. Potential pseudo-replication was avoided as data used were obtained from spatially differentiated sampling locations and sampling was not repeated at the same location. Differences between the categories were tested for statistical significance using the Kruskal–Wallis test (SPSS 17, IBM, version 17.0.0). The results were judged to be significant at a level of $P = <0.05$.

Physiological tolerance limits obtained from literature were validated by comparing them with water quality data collected from monitoring stations coinciding with quagga mussel presence in The Netherlands. Where tolerance limits for the quagga mussel were not available, data for the zebra mussel, indicative for quagga mussel tolerance, were used. Data on calcium, cadmium, copper, lead, nitrate, dissolved oxygen, pH, salinity, temperature, total phosphate and zinc were sourced from Waterbase.nl, a validated online database of the Dutch Ministry of Infrastructure and the Environment. Data was collected from the monitoring stations: River Meuse at Eijsden (N 48°16′19.86″, E 5°40′59.67″) and Belfeld (N 51°19′6.97″, E 6°6′47.97′), River Waal at Lobith (N 51°51′15.14″, E 6°5′28.24″), River IJssel at Kampen (N 52°33′13.74″, E 5°55′26.07″), Amsterdam-Rhine Canal at Nieuwegein (N 52°1′21.83″, E 5°6′46.83″), Twente Canal at Eefde (N 52°9′37.54″, E 6°14′15.81″), Lake IJsselmeer at Vrouwezand (N 52°48′37.26″, E 5°23′35.30″) and Lake Markermeer (N 52°31′36.09″, E 5°13′9.72″). Minimum and maximum values were calculated and compared with the established physiological tolerance data. Flow velocity data were obtained from 10 sampling points within quagga mussel microhabitats in the rivers Waal, Meuse, Nederrijn and IJssel using a TAD-micro flow meter (Van Vugt Instrumentation) that measures multi-directional flow rate with a small propeller. Reference and extreme values were measured during monitoring (e.g. before and directly following the passage of large vessels).

Analysis of species dominance shifts

Mussel abundances and total density data were derived for quagga and zebra mussels from Dutch sampling locations and literature. The criteria for inclusion were that both species were present and that sampling had occurred repeatedly at the same location. Species replacement was said to be occurring in the presence of a positive trend in quagga relative abundance in association with a positive or neutral trend in density of both species. A reduction in overall mussel density accompanied by an increase in quagga mussel density suggests that factors unrelated to interspecific competition may have resulted in reductions in zebra mussel density. Therefore, situations where an overall reduction in mussel density occurred were not defined as species replacement. Density trends of both species derived from consistent sampling approaches are necessary to conduct a sound analysis of species replacement.

In a separate analysis, Dutch sampling locations were divided into three classes: (1) only quagga mussels found, (2), only zebra mussels found, (3), both quagga and zebra mussels found. This identified the level of coexistence of quagga and zebra mussels at the sampled sites. Coexistence of mussel species suggests that quagga and zebra mussels require similar habitat and introduces the possibility that species replacement may occur when quagga mussels colonise sites shared by zebra mussels.

Results

Current European distribution

The first observation of the quagga mussel in Western Europe was made in 2006 in the Hollandsch Diep, a former estuary of the rivers Rhine and Meuse in The Netherlands (Bij de Vaate 2006; Molloy et al. 2007; Bij de Vaate and Jansen 2007; Schonenberg and Gittenberger 2008). Figures 2 and 3 illustrate the range expansion of the quagga mussel in The Netherlands and Western Europe. Bij de Vaate et al. (2010, 2013) argued that quagga mussel introduction into Western Europe was not the result of a continuous range expansion through the River Danube and the Main-Danube Canal and River Rhine, as previously suggested by Molloy et al. (2007). Ballast water transport and release in the Hollandsch Diep or transport after attachment to inland shipping have been suggested as potential dispersal mechanisms (Bij de Vaate 2010b; Bij de Vaate and Beisel 2011; Bij de Vaate et al. 2013; Heiler et al. 2013). Ballast water may have originated from the Black sea area or North America in the Port of Rotterdam or Hollandsch Diep (Van der Velde et al. 2010b).

In 2007 Van der Velde and Platvoet (2007) discovered quagga mussels in the River Main (Germany), a tributary of the River Rhine, but not in the Danube near the Main-Danube canal or the Main-Danube canal itself. This led to further observations in Germany. Martens et al. (2007) discovered the species in a series of Upper Rhine harbours, while Haybach and Christmann (2009) found them in the Lower Rhine in 2008 between Dormagen and Bimmen. In 2008 quagga mussels were found in the northern part of the Main-Danube Canal (Bij de Vaate 2010b). Mayer et al. (2009) found quagga mussels on ship's hulls on the slipway of a shipyard at Speyer, along the Upper Rhine.

Quagga mussels found near Karlsruhe an Mannheim in the River Rhine were smaller than in the River Main (Imo et al. 2010). However, genetic analysis ruled out the presence of founder effects. Based on non-continuous distribution and shell size, it was concluded that range expansion in Germany involved at least two independent settling events. The first event occurred before 2005, probably caused by jump dispersal, while the second event was due to continuous range expansion. Heiler et al. (2012) observed range expansion in Germany in an easterly direction through canals of which the Mittelland Canal is most important, connecting the river basins of the Weser, Elbe and Oder. Bij de Vaate and Beisel (2011) are responsible for the first French record in the River Moselle, another tributary of the River Rhine. In 2009 Sablon et al. (2010) recorded the quagga mussel for the first time in Belgium (Albert Canal, in the vicinity of Grobbendonk), while Marescaux et al. (2012) observed upstream migration of the species in the Belgian section of the River Meuse beginning in 2010. This pattern of records demonstrates the rapid range extension of the quagga mussel in Western Europe after its establishment in The Netherlands.

Rate and direction of colonisation in The Netherlands

Initially, quagga mussel records were limited to the Hollandsch Diep, lakes IJsselmeer and Markermeer, and the rivers Meuse and Waal. Spatial analysis shows the rapid range expansion of the quagga mussel to all the major rivers and canals in The Netherlands since 2006 (Fig. 3). Records exist for the rivers Nederrijn, IJssel and Bovenrijn, and large canals and lakes connected to the European network of waterways e.g. the Frisian lakes, Lake Volkerak-Zoommeer, the Pannerdensch Canal, the Amsterdam-Rhine Canal, the Rhine-Scheldt Canal, the Wilhelmina Canal, the Bathse Spui Canal and the Meuse-Waal canal (Soes 2008; Bij de Vaate and Jansen 2009, 2011; Bij de Vaate 2009, 2010a; Raad 2010; Bij de Vaate et al. 2011; Matthews et al. 2012). Recently, quagga mussel records have extended as far south as the River Meuse at the mouth of the Juliana Canal at the Dutch-Belgian border, South Limburg and as far North as the Van Harinxma Canal to the West of Leeuwarden in Friesland and the Van Starkenborgh Canal in the Province of Groningen.

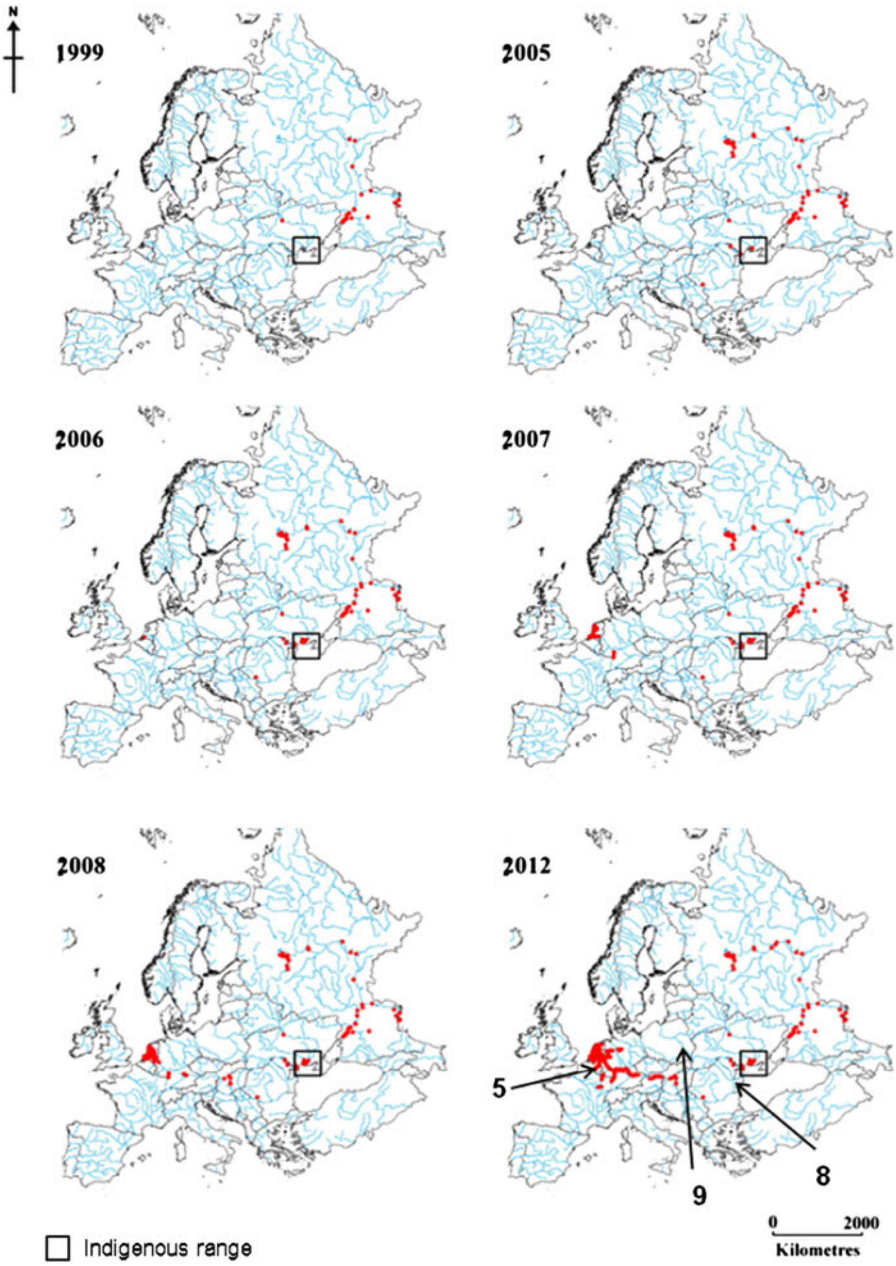

Fig. 2 Available records demonstrating the rapid range expansion of the quagga mussel in Europe; numbers refer to locations used to calculate dispersal rates in table 1

The number of quagga mussel records has been increasing in The Netherlands since 2006 (Figs. 3, 4). The cumulative number of records sharply increased between 2006 and 2008. Since 2008 the rate of increase has reduced, however the overall number of records continues to rise.

The dispersal rate for the quagga mussel in Europe was found to range between 23 and 383 km year^{-1} with an average of 120 $\pm$ SE 53.8 km year^{-1} (Table 1). Dispersal rates calculated for major Dutch rivers, lakes and canals varied between 23 and 105 km year^{-1}. Rates calculated within The Netherlands were for upstream dispersal in lotic water bodies apart from the lentic water bodies Lake IJsselmeer and the Prinses Margriet Canal (Province of Friesland).

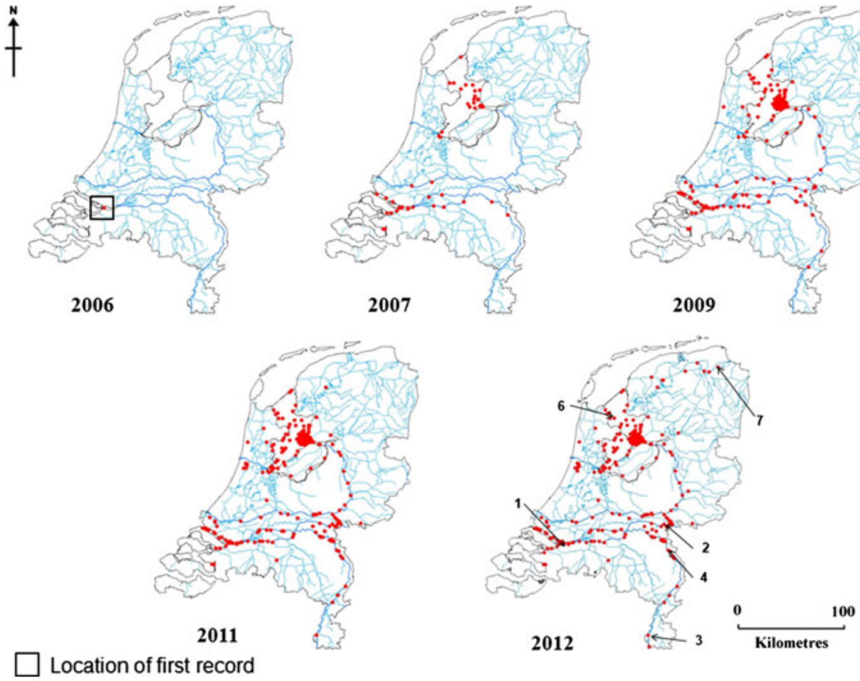

Fig. 3 Rapid range expansion of the quagga mussel through the waterway network after its first record in the freshwater section of the Dutch Rhine–Meuse river estuary, Hollandsch Diep in 2006; numbers refer to locations used to calculate dispersal rates in table 1

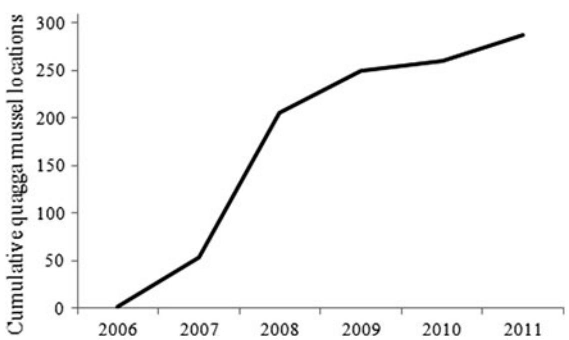

Fig. 4 Cumulative number of locations where quagga mussels were identified in The Netherlands

Distribution in relation to the connectivity of water bodies, substrates and watertypes

While both quagga and zebra mussels occurred at a similar frequency in permanently connected water bodies, limited hydrological connectivity reduces quagga mussel occurrence to a greater degree (Fig. 5). In seasonally connected water bodies, quagga mussels occurred at 20 % of locations whereas the zebra mussel occurred at 40 % of locations. In disconnected water bodies the quagga mussel occurred at no locations whereas the zebra mussel occurred at 35 % of locations. Hydrological connectivity was found to have a statistically significant effect on the distribution of the quagga mussel ($\chi^2 = 24.667$, $df = 2$, $P = <0.001$) but not the zebra mussel ($\chi^2 = 5.702$, $df = 2$, $P = 0.058$). These observations must be viewed with caution, however, as only five samples were included in the analysis of seasonal connectivity.

The quagga mussel was found to attach to a number of different hard substrates. These included stone, metal and concrete (Table 2). Moreover, quagga mussels were observed to attach to the empty shells of dead native mussels. Of the 18 soft substrate samples taken at four locations, one sample contained seven quagga mussels that were attached to each other. At no other locations were quagga mussels observed on soft substrate. Moreover, of the 15 samples taken of vegetation (3 locations), none contained specimens of either quagga or zebra mussels.

Quagga and zebra mussels were present in all sampled water-types: rivers/streams, canals, lakes and harbours (Fig. 6). Quagga mussels occurred most frequently in canals and harbours followed by rivers/streams and lakes. Zebra mussels occurred most frequently in harbours followed by lakes, rivers and

Table 1 Dispersal rate of the quagga mussel in The Netherlands and Western Europe

Dispersal route	Coordinates	Distance (km)	Duration (years)	Dispersal rate (km $year^{-1}$)	Dispersal attributes	References
From Hollandsch Diep to the Lake Kaliwaal, via the River Waal (The Netherlands)	N 51°41′34.38″, E 4°25′57.45″ (1) to N 51°51′18.82″, E 5°59′17.28″ (2)	116	5	23	Upstream	Matthews et al. (2012)
From Hollandsch Diep to the entrance of the Juliana Canal, via the River Meuse[a] (The Netherlands)	N 51°41′34.38″, E 4°25′57.45″ (1) to N 50°52′11.10″, E 5°41′57.95″ (3)	265	4	66	Upstream	Bij de Vaate, unpublished data
River Meuse from Sambeek (The Netherlands) to Gives (Belgium)[a]	N 51°38′12″, E 5°59′24″ (4) to N 50°30′33″, E 5°08′55″ (5)	260	3	87	Upstream	Bij de Vaate et al. (2013)
From Hollandsch Diep via Dordtsche Kil, River Oude Maas, Noord, River Lek, Amsterdam-Rhine Canal to Oude Zeug in Lake IJsselmeer (The Netherlands)	N 51°41′34.38″, E 4°25′57.45″ (1) to N 52°52′9.76″, E 5°7′38.33″ (6)	211	2	105	Upstream and via lentic water bodies (lakes) and water bodies with low flow velocity (canals)	Bij de Vaate (2009)
From Hollandsch Diep via Dordtsche Kil, River Oude Maas, Noord, River Lek, Amsterdam-Rhine Canal, Lake IJsselmeer, Prinses Margriet Canal to Eemskanaal (The Netherlands)	N 51°41′34.38″, E 4°25′57.45″ (1) to N 53°16′37.7″, E 6°45′28.4″ (7)	339	6	57	Upstream and via lentic water bodies (lakes) and water bodies with low flow velocity (canals)	Bij de Vaate, unpublished data
River Danube, from Cernavodă (Romania) to Komarum (Hungary)[a]	N 44°21′, E 28°01′(8) to N 47°44′, E 18°08′(9)	1,450	4	383	Upstream	Bij de Vaate et al. (2013)

Numbers in brackets refer to coordinates of locations identified in Figs. 2 and 3

[a] Dispersal rate determined using sampled years

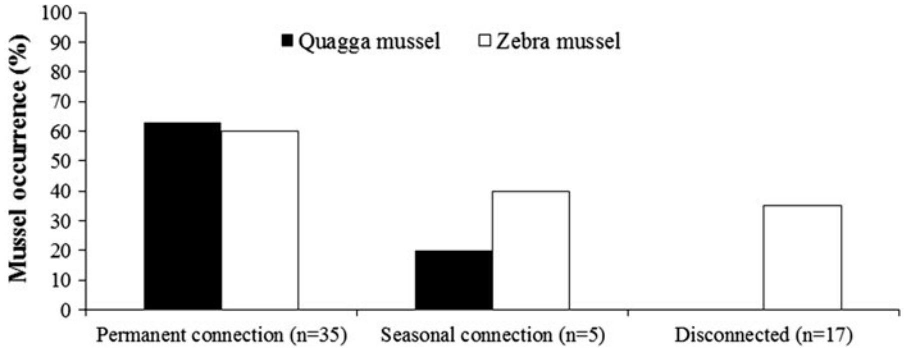

Fig. 5 The influence of the level of hydrological connectivity on quagga and zebra mussel occurrence in The Netherlands

Table 2 Presence of quagga mussels on sampled substrates

Substrate	Number of quagga mussel locations (n)	Total number of locations sampled (n)
Stone	21	44
Concrete	1	8
Soft (e.g. sand)	1	4
Metal	3	5
Rubber	1	1
Wood	1	8
Vegetation	0	3

streams and canals, however this trend was not statistically significant. The largest difference in occurrence between zebra and quagga mussels was between the harbour and lake water-types. However, this result should be treated with caution as only four harbour locations were sampled. Water-type was found to have a statistically significant effect on the distribution of the quagga mussel ($\chi^2 = 19.677$, $df = 3$, $P = <0.001$), but not on the distribution of the zebra mussel ($\chi^2 = 2.190$, $df = 3$, $P = 0.534$).

Identification of dispersal vectors

An overview of dispersal vectors utilised by dreissenid mussels is given in Table 3. The quagga mussel was observed attached to driftwood and boat hulls and it was present in high abundance inside a discarded car tyre on the banks of a floodplain lake. The literature survey revealed a number of human mediated vectors that facilitate dreissenid mussel dispersal. Attachment to watercraft was the most frequently cited mode of human mediated dispersal (Keevin et al. 1992; Allen and Ramcharan 2001; Johnson et al. 2001). Additionally, transport upstream, downstream and overland is facilitated by animals or manmade structures such as pontoons, buoys, floats or the overland transfer of pleasure boats (Pollux et al. 2010; Therriault and Orlova 2010). Zebra mussel specimens were attached to a metal pontoon and buoys in an inland lake indicating that human mediated transport may play a role in the colonisation of hydrologically isolated water bodies by dreissenids.

Analysis of physico-chemical characteristics of colonised water bodies

Water quality data indicate that most measurements lay within the physiological limits of the quagga mussel (Table 4). Temperature measurements did not exceed the maximum physiological tolerance for the quagga mussel. The overall minimum temperature was 1.1 °C, however, measurements were taken at the water surface and relatively warm, deeper water may provide refuges for mussels (Leuven et al. 2011). Data for pH tolerance were only available for the zebra mussel. pH remained within physiological tolerances in lake habitats but minimum pHs measured in canals and rivers were 7.2 and 7.3, respectively, and below the minimum tolerance of 7.4. However, this minimum represents one in 24 measurements recorded in the Twente canal (2010–2011) and one in 260 measurements recorded in the river Meuse (2007–2011). pH was measured at relatively high frequencies in the Twente canal and river Meuse, and could only have resulted in unsuitable conditions for relatively short periods. Dissolved oxygen was measured above the minimum tolerance for zebra mussels at all locations. Peak flow velocities measured in

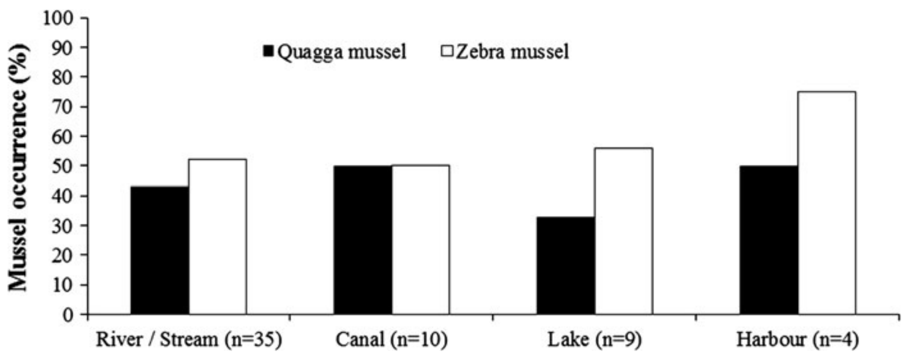

Fig. 6 Presence of dreissenids species per water-type

Table 3 Overview of dispersal vectors relevant to the spread of dreissenids

Vector/mechanism	Mode of transport	Examples and relevant information	References
Water-flow	Downstream, lateral	In the presence of upstream populations	1, 2
Foot and shell movement	Active up- and down-stream, lateral	Triggered by change in habitat	3
Wind driven water flow	Multi-directional	Most relevant in lentic water bodies	
Vegetation, wood[a], detached floats, buoys, plastic rubbish, rubber tyres[a]	Downstream, lateral and overland	Longitudinal with water-flow and lateral with flooding or attached to other vectors e.g. watercraft	4, 5, 6, 7
Commercial shipping	Up- and down-stream	Barges	4, 8, 9, 10, 11, 12
Watercraft[a]	Up- and down-stream	Recreational vessels	7, 13
Ballast water	Sea going	Sea going vessels	14, 15, 16
Watercraft overland	Overland	Canoes, sailing/rowing/motor boats. dependant on resistance to desiccation	4, 11, 13, 17, 18, 19, 20, 21, 22, 23, 24
Other overland	Overland	Metal pontoon, floats, entangled vegetation	7, 21, 25
Several animal species	Up- and down-stream, lateral and overland	Predatory animals such as aquatic birds, muskrats and brown rats, and attached to Chinese mitten crabs, crayfish and turtles	26, 27, 28

1: Johnson and Padilla (1996), 2: Stoeckel et al. (1997), 3: Kappes and Haase (2012), 4: Carlton (1993), 5: Horvath and Lamberti (1997), 6: Wilson et al. (1999), 7: Matthews et al. (2012), 8: Keevin et al. (1992), 9: Nehring (2002), 10: Slynko et al. (2002), 11: Bij de Vaate et al. (2002), 12: Olenin (2002), 13: Minchin et al. (2003), 14: Carlton and Geller (1993), 15: Endreson et al. (2004), 16: Holeck et al. (2004), 17: Padilla et al. (1996), 18: Buchan and Padilla (1999), 19: Kraft and Johnson (2000), 20: Allen and Ramcharan (2001), 21: Johnson et al. (2001), 22: Kraft et al. (2002), 23: Minchin et al. (2002), 24: Pollux et al. (2003), 25: Bidwell (2010), 26: Johnson and Carlton (1996), 27: Bossenbroek et al. (2001), 28: Karatayev et al. (2003)

[a] Quagga mussel dispersal vectors observed during this study

quagga mussel microhabitats far exceeded physiological tolerances. However, these measurements were transient, resulting from turbulence created by passing ships. Moreover, at the location of maximum water velocity, only a single live quagga mussel was found. When the effect of shipping was removed, the maximum flow velocity was far lower (Table 4). 50 % effect concentrations for filtration of metals ($EC_{50\ filt}$) were available for the zebra mussel only. EC_{50} values for lead, cadmium and copper were higher than environmental concentrations found in quagga mussel habitats. A single zinc measurement in the river Meuse at Eijsden exceeded the EC_{50}. Due to the sampling frequency, this condition could only have persisted for a maximum of 14 days within the 5 year period that quagga mussels have been recorded in the river Meuse. All other measurements for metal concentrations lay below the maximum tolerance values.

Shifts to quagga mussel dominance

When ordered chronologically, samples taken from Dutch and German water bodies, where both species occurred together, indicate that the quagga mussel increased in abundance relative to the zebra mussel (Fig. 7). Data from 2011 indicates that the quagga population represented 95 % of the dreissenid population in Lake IJsselmeer and Hollandsch Diep. However, in recent years in the rivers IJssel and Nederrijn, the quagga mussel relative abundance has reduced by as much as 66 %.

Twelve locations were identified where temporal trends could be used to establish if species replacement was occurring, some within the same water body (Table 5). Zebra mussels were present in the most recent samples at all locations. In total, seven out of 12 locations lacked mussel density data or data that could be used to calculate density. Of the remaining five

Table 4 Ranges of physico-chemical properties per water-type where the quagga mussel has colonised in The Netherlands in comparison with physiological tolerances

Physico-chemical property	Large rivers	Canals	Lakes	Combined	Physiological tolerances
Calcium (mg l^{-1})	35.0–92.1	39.2–105.0	39.7–99.0	35.0–105.0	>12[1]
Cadmium (μg l^{-1})	0.05–2.27	0.05–0.45	0.05–0.20	0.05–2.27	<27[2,c,d]
Copper (μg l^{-1})	1.38–39.4	1.89–20.1	1.34–6.63	1.34–20.1	<43[2,c,d]
Lead (μg l^{-1})	0.17–37.0	0.1–10.0	0.1–4.7	0.1–37.0	<91[2,c,d]
Zinc (μg l^{-1})	6.2–330	2.24–67	1–37	1–330	<131[2,c,d]
Nitrate (mg l^{-1})	1.09–4.4	0.789–8.72	0.01–0.48	0.01–8.72	No data
Total phosphate (mg l^{-1})	0.04–1.9	0.02–1.3	0.02–0.48	0.02–1.9	No data
Oxygen saturation (mg l^{-1})	3.2–14.8	5.18–12.8	8.7–15.9	3.2–15.9	>1.8–2.4[3,c]
pH	7.3–8.48	7.2–8.33	8.3–10.4	7.2–10.4	7.4[4,5]–(9.3–9.6[6])[c]
Salinity (psu)	0.0–0.4	0.2–0.6	0.3–0.44	0.0–0.6	<5[7,8]
Temperature (°C)	1.1–26.8	0.6–24.1	0.2–2	0.2–26.8	9 for reproduction[9]–(25–34[7,10,11])
Flow velocity (cm s^{-1})	1–2.2[a]/117[b]	3–7	No data	1–117[b]	<(9–20[12, 13])

[a] Maximum velocity under no influence of shipping

[b] One live quagga mussel found at this location, maximum velocity caused by passing shipping

[c] Data only available for zebra mussel

[d] Fifty percentage effect concentration for filtration, 10 week exposure

[1] Jones and Ricciardi (2005), [2] Kraak et al. (1994), [3] Karatayev et al. (2007), [4] Ramcharan et al. (1992), [5] Neary and Leach (1992), [6] Bowman and Bailey (1998), [7] Karatayev et al. (1998), [8] Spidle et al. (1995), [9] Bij de Vaate (2008), [10] Mills et al. (1996), [11] Verbrugge et al. (2012), [12] Ackerman (1999), [13] Eckman et al. (1989)

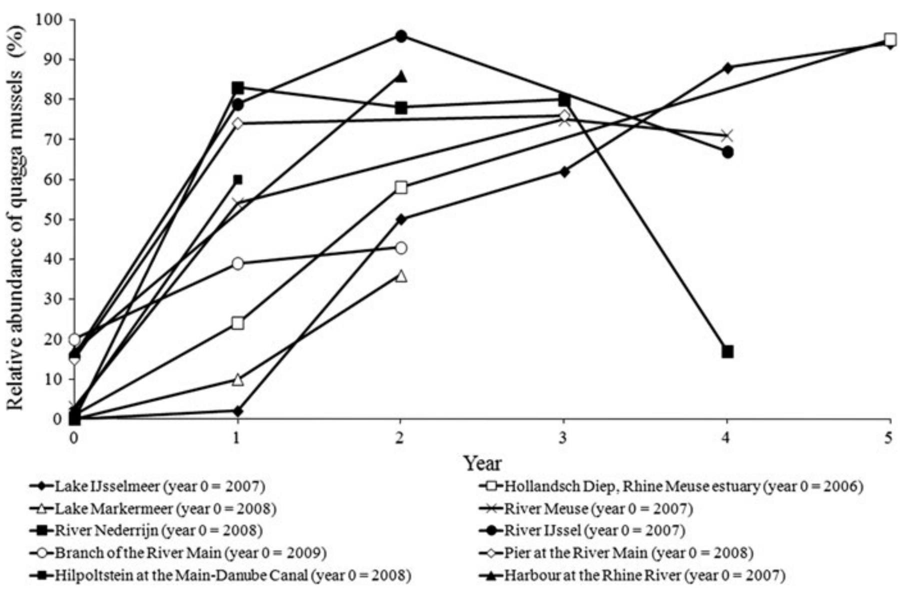

Fig. 7 Percentage contribution of quagga mussel to the overall quagga and zebra mussel population in major European water bodies (Bij de Vaate 2008, 2010a; Bij de Vaate et al. 2012; Heiler et al. 2012; Matthews et al. 2012; unpublished data A. bij de Vaate)

locations, three demonstrated an increasing trend in total mussel density and two showed a decreasing trend in total mussel density. The density ratio of quagga to zebra mussels increased in four out of the five locations where density data were available. None of the locations identified in table 5 showed a

Table 5 Available zebra and quagga mussel density and relative abundance data used to analyze the occurrence of species replacement in The Netherlands

Water body	GPS coordinates	Period	Δ quagga to zebra density ratio (%)[a]	Δ total mussel density (ind/m^2)[a]	Δ quagga relative abundance (%)[a]	Possible species replacement?	References
River Nederrijn	N 51°57′30.3″ E 5°56′0.6″	2009–2011	64 → 85 (+)	14 → 53 (+)	84 → 86 (+)	Yes	This study
River Nederrijn	N 51°57′35.2″ E 5° 40′46.7″	2007–2011	99 → 83 (−)	24,191 → 98 (−)	0 → 83 (+)	No	This study
River Meuse	N 51° 43′47.5″ E 5°53′6.5″	2009–2011	87 → 90 (+)	1,893 → 297 (−)	35 → 90 (+)	No	This study
River Meuse	N 51°45′57″ E 5°44′12.9″	2007–2011	nd	nd	0 → 91 (+)	?	This study
Meuse-Waal Canal	N 51°48′23.6″ E 5°48′59″	2008–2011	28 → 88 (+)	939 → 1020 (+)	72 → 88 (+)	Yes	This study
Lake IJsselmeer	N 52°38′12.8″ E 5°24′47″	2006–2010	nd	nd	0 → 88 (+)	?	Bij de Vaate (2010a) and unpublished results
Lake IJsselmeer	N 52°29′28.7″ E 5°23′19.2″	2008–2008	nd	nd	0 → 41 (+)	?	Bij de Vaate (2009)
Lake IJsselmeer	N 52°38′58.1″ E 5°27′50.6″	2009–2009	nd	nd	53 → 65 (+)	?	Bij de Vaate (2010a)
Lake IJsselmeer	N 52°38′58.1″ E 5°27′55.9″	2009–2009	nd	nd	36 → 72 (+)	?	Bij de Vaate (2010a)
Lake Markermeer	N 52°29′ 28.7″ E 5°23′19.2″	2008–2008	nd	nd	1 → 24 (+)	?	Bij de Vaate (2009)
Lake Markermeer	N 52°37′30.3″ E 5°12′20″	2009–2012	nd	nd	9 → 81 (+)	?	Bij de Vaate and Jansen (2012)
Hollandsch Diep	Several locations (mean average)	2004–2008	26 → 76 (+)	35 → 90 (+)	0 → 44 (+)	Yes	Bij de Vaate (2009)

+: Positive trend; −: negative trend; 0: no trend; nd: no data; ?: impossible to assess due to data limitation

[a] The first and last value within the series

decreasing trend in quagga relative abundance. Species replacement could be happening at three locations, in the River Nederrijn in the side channel at Bakenhof, the Meuse-Waal canal at Dukenburg and in the Hollandsch Diep. Eighty percent of samples containing dreissenids in the years 2011 and 2012 included both mussel species. Only 15 and 5 % of locations contained only zebra and quagga mussels, respectively.

Discussion

The number of quagga mussel locations in The Netherlands has increased rapidly since it was first identified in the Rhine-Meuse estuary in 2006 (Fig. 3). Dispersal in an easterly and northerly direction rules out the possibility of naturally occurring modes of dispersal, e.g. downstream drift in the River Rhine, and supports the hypothesis that initial establishment of quagga in The Netherlands occurred in the Hollandsch Diep (Molloy et al. 2007; Bij de Vaate 2006). In the absence of upstream source populations, colonisation via jump dispersal facilitated primarily by watercraft must occur first, followed by passive 'natural' dispersal on the water current originating from the newly established upstream population. A number of authors have emphasised the primary importance of watercraft as a vector for dreissenid dispersal (Keevin et al. 1992; Allen and Ramcharan 2001; Johnson et al. 2001; Heiler et al. 2013). During our field research, quagga mussels were found attached to ship hulls. This combined with the presence of quagga mussels in navigable water bodies suggests that watercraft may be the primary mode of dispersal for quagga mussels in The Netherlands. Inland vessels do not feature ballast tanks, however, they often feature equipment for hull decontamination that contains residual water that may provide a vector for mussel larval transfer. Moreover, sludge that may contain mussels is transferred via inland waterways by dredgers. Passive 'natural' dispersal of larvae is largely accomplished by movement of water, including lake currents driven by wind and water density differences and/or uni-directional flow associated with rivers, streams and slow flowing canals (Johnson and Padilla 1996; Stoeckel et al. 1997). Moreover, mussels have the ability to move over short distances using foot and shell movement. Active upstream movement may be well below 0.1 km year^{-1} for bivalves, however (Kappes and Haase 2012). Attachment to floating debris such as plant material, plastic and wood facilitates the transport of adult mussels downstream (Pollux et al. 2010). In The Netherlands, various modes of dispersal allow the quagga mussel to disperse rapidly. Quagga mussels are able to attach to wood, rubber and ship hulls. In Western Europe, available records for the quagga mussel demonstrate its rapid expansion into the rivers Main and Rhine in Germany, the River Meuse and the Albert canal in Belgium and the French section of the River Moselle (Bij de Vaate and Beisel 2011; Imo et al. 2010; Sablon et al. 2010; Van der Velde and Platvoet 2007).

Calculated dispersal rates in The Netherlands were lower than those in the Danube (Table 1). Dispersal occurred in a primarily upstream direction and shipping is likely to be a major mode of dispersal. The Danube dispersal rate was calculated over a significantly longer distance (between Romania, Germany and Austria) than those calculated within The Netherlands. The length of the dispersal route and mode of dispersal may influence the calculated dispersal rate. Commercial shipping can traverse large distances within a few days. Theoretically, quagga mussels may begin colonisation 1,000s of kilometres away from the original colonisation source after a single ship passage. Moreover, dispersal rates may be underestimated due to the time lag between dispersal, establishment of populations and the first recorded observation of each non-indigenous species (Leuven et al. 2009). However, other authors have used a similar method to calculate dispersal rates (Voelz et al. 1998; Leuven et al. 2009; Kappes and Haase 2012) and the extensive governmental sampling network and large number of amateur observers in The Netherlands increases the probability that quagga mussels will be recorded close to their time of arrival.

Quagga and zebra mussels use similar vectors of dispersal (Table 3). Dispersal of both dreissenid mussels is hindered by a lack of hydrological connectivity (Fig. 5), and facilitated by dispersal vectors such as watercraft, moveable pontoons and floats. Samples taken from the tributaries of large rivers and hydrologically disconnected water bodies in The Netherlands contained no quagga mussels, however, zebra mussels were sometimes present. The delayed dispersal of the quagga mussel to disconnected water bodies may be explained by the time needed for source populations to develop in downstream reaches. The quagga mussel was first recorded in Western Europe in 2006 whereas the zebra mussel colonised at least 200 years ago also with delayed initial dispersal to more isolated water bodies (Bidwell 2010; Van der Velde et al. 2010a).

Transient recreational boating is commonly perceived as the primary means by which dreissenids are transported between disconnected water bodies (Johnson et al. 2001). However, a relative intolerance to drying (Ricciardi et al. 1995; Allen and Ramcharan 2001) may reduce the probability of quagga dispersal overland. Macrophytes, however, may provide a refuge against desiccation. Attachment to macrophytes has been implicated in the spread of zebra mussels by overland transport on boats (Wilson et al. 1999; Johnson et al. 2001). However, quagga mussels exhibit a lesser ability to attach to macrophytes than zebra mussels (Diggins et al. 2004) and no quagga mussels were found attached to macrophytes during our field surveys (Table 2). Moreover, higher byssal thread synthesis rate in zebra mussels will likely minimize their dislodgment in flow and increase short-term attachment strength (Peyer et al. 2009; Grutters et al. 2012). However, another study found no significant difference in attachment strength measured between dreissenid species (Ackerman et al. 1995). As both the quagga and zebra mussel use byssal threads to attach to dispersal vectors and despite issues relating to desiccation and attachment strength, it may only be a matter of time before quagga mussels colonise hydrologically isolated water bodies.

The analysis of environmental conditions indicates that physiological tolerance ranges obtained from literature are representative of quagga mussel populations found in The Netherlands (Table 4). Tolerances relating to nutrients and feeding conditions were not found in the literature, however, the quagga mussel is generally more tolerant of high silt levels than the zebra mussel and prefers more oligotrophic conditions (Karatayev et al. 1998; Orlova et al. 2005). Total phosphorus and nitrate data ranges give examples of conditions suitable for quagga mussel colonisation as nutrient levels will impact on plankton and seston food sources and mussel filter feeding. In experiments examining the impact of temperature, salinity and light on substrate attachment, it was found that both species were similar in their initial re-attachment ability (Grutters et al. 2012). Byssal threads were not produced by either species at salinities of 4 psu or higher. Byssogenesis was similar in both species below 25 °C, a value that was not exceeded at our sampling locations. The maximum flow velocity in the littoral zone of major rivers and canals lay outside the physiological tolerances of both dreissenid species. However, if peak values created by passing shipping are removed, ambient flow velocities are not limiting. The presence of mussels at sites with a pH of between 7.2 and 8 supports the view that pHs below 8 while not ideal, do not rule out dreissenid invasion (Mackie 2005). pH has a greater impact on survival at lower calcium concentrations (Claudi et al. 2012). In general, calcium concentrations in Dutch freshwaters are relatively high and do not limit the colonisation of the quagga mussel (Matthews et al. 2012). Acidified bogs, moorland pools in the southern, central and eastern parts of The Netherlands and locations with seepage of CO_2-rich groundwater are examples of habitats where pH levels exclude quagga and zebra mussels (Leuven et al. 1992). Dreissenids are relatively salinity tolerant and salinity levels at sampling sites lay well within the maximum tolerance of the quagga mussel. Estuaries, coastal lagoons and brackish inland waters featuring salinities above 5 psu are the only areas where the quagga mussel may be limited (Matthews et al. 2012). Temperature will probably present no barrier to quagga mussel colonisation as maximum water temperatures in Dutch freshwaters rarely exceed 25 °C (Matthews et al. 2012). Moreover, mussels may acclimatise to adverse pH, temperature and salinity conditions (Bowman and Bailey 1998; Thorp et al. 1998).

Core samples taken from soft substrates established the presence of quagga mussels in one location only (Table 2). Dreissenids exhibit a preference for the colonisation of hard substrates (Wilson et al. 2006). In areas where hard substrates such as groyne stones are absent, colonisation is restricted to unionid mussel shells and in the case of the IJsselmeer and Markermeer to old empty sea shells such as *Mya arenaria* (Noordhuis et al. 2010) and zebra mussel beds. However, there is some evidence to suggest that a profundal variety of the quagga mussel can establish on soft substrates. The profundal variety of the quagga mussel has recently been recorded in the Cheboksary Reservoir situated in the midstream of the Volga River (Russian Federation) (Pavlova 2012). Moreover, quagga mussels have been recorded in the profundal zones of the Great Lakes of North America and the Volga river basin (Orlova et al. 2005). However, the relatively shallow depth of Dutch water bodies may prevent colonisation by the profundal variety of the quagga mussel in The Netherlands.

A number of factors may explain the more recent range expansion of the quagga mussel relative to the zebra mussel. In general, the quagga mussel originated from a much smaller indigenous range resulting in a much smaller chance of dispersal (Van der Velde et al. 2010b). The quagga mussel has a lower respiration rate, a greater body mass and shell growth than the zebra mussel (Stoeckmann 2003). At 25 °C and a salinity of 0.2 psu the zebra mussel exhibits a significantly higher byssogenesis rate compared to the quagga mussel increasing the likelihood of substrate attachment (Grutters et al. 2012). Moreover, the quagga mussel produces fewer byssal threads in flowing water (Peyer et al. 2009). The quagga mussel may suffer from selective predation as its thinner shell allows even large individuals to be crushed and digested by fish (Zhulidov et al. 2006). The recent increasing abundance of predatory Ponto-Caspian gobies in The Netherlands may have intensified this effect (Matthews et al. 2012). However, the most efficient European dreissenid predator, the roach (*Rutilus rutilus*), is limited by prey size and not by crushing force (Nagelkerke and Sibbing 1996). This suggests that shell thickness will play a less significant role in predation by this species. During reproduction, zebra mussels release more eggs and gametes than quaggas in general (Stoeckmann 2003). As a result, the zebra mussel may demonstrate greater reproductive success and be more likely to colonise new habitats than the quagga mussel. Orlova et al. (2005) suggested that a preference to lentic conditions may have resulted in the quagga mussels delayed range expansion. Quagga mussel invasions started only when newly created ecosystems (i.e. reservoirs) changed from riverine to lacustrine (Orlova et al. 2005). Moreover, quagga mussels prefer more oligotrophic conditions compared to the zebra mussel (Therriault and Orlova 2010). High densities of filter feeding zebra mussels may encourage oligotrophication and so facilitate the colonisation of the quagga mussel.

It is expected that a number of changes in environmental parameters will occur that may affect the establishment of the quagga mussel in Dutch freshwater bodies. A quantitative prediction of the effects of these changes on establishment success of quagga mussels is currently not possible due to a lack of data and predictive models. However, overall it is expected that in large rivers an increase in the abundance of quagga mussels will be limited by bank rehabilitation (e.g. removal of hard substrates) and an increase in peak discharges, wave stress due to expanding shipping activities, water depth fluctuations (desiccation) and increasing abundance of predatory Ponto-Caspian gobies (Matthews et al. 2012). Rehabilitation of floodplain lakes and side channels may, however, increase the likelihood of quagga mussel establishment due to their preference for lentic environments (Zhulidov et al. 2010). Increases in macrophyte populations may lead to an increase in the relative abundance of the zebra mussel over the quagga mussel. The quagga mussel is found in lesser abundance in habitats with a high macrophyte coverage in comparison to the zebra mussel (Diggins et al. 2004; Zhulidov et al. 2010; Karatayev et al. 2011).

It is commonly suggested that the zebra mussel is gradually replaced by the quagga mussel following its establishment, particularly in deeper more oligotrophic habitats (Ricciardi and Whoriskey 2004; Orlova et al. 2005; Zhulidov et al. 2010). Species replacement may have happened in the River Nederrijn at the Bakenhof side channel, the Meuse-Waal canal at Dukenburg and in the Hollandsch Diep in The Netherlands (Table 5). The analysis of coexistence demonstrates the rapidity with which the quagga mussel has made inroads into zebra mussel habitat since its discovery in The Netherlands in 2006. Quagga and zebra mussels have overlapping niches increasing the chance that they will colonise the same water bodies. Once established, increasing mussel density will play an important role in determining possible inter-specific interactions leading to the dominance of the quagga mussel. Evidence of increasing relative abundances was identified (Fig. 7). Dominance shifts from zebra mussels to quagga mussels were reported for the river estuary freshwater remnants Haringvliet and Lake Volkerakmeer, with relative abundances of quagga mussels reaching >95 and 99 %, respectively (Bij de Vaate et al. 2010, 2011). However, analysis of the causes of species dominance is hampered by a lack of consecutive measurements of overall dreissenid density at sampling locations. A consistent approach and a focus on mussel density as-well as relative abundance is required to determine whether the quagga mussel is replacing the zebra mussel in Western European freshwaters or is additional to the zebra mussel, increasing the total numbers of dreissenid mussels. Dominance shifts from zebra mussels to quagga mussels may be caused by interaction (facilitation, competition) or factors not influenced by mussel interaction. Relative abundances give no insight into the mechanism leading to a dominance shift nor do they indicate actual species replacement. Consistent series of density data will be required to unravel the mechanism of species dominance (e.g. by species replacement).

This information becomes important if the impacts of the quagga mussel are different to that of the zebra mussel. Evidence of differing impacts is limited and conflicting. The condition of diving ducks that feed on dreissenids in the Great Lakes of North America, such as the Lesser and Greater Scaup (*Aythya affinis* and *Aythya marila*) is affected by the higher concentrations of selenium found in the quagga mussel (Schummer et al. 2010). A thinner shell allows larger quagga individuals to be crushed and digested leading to selective predation by certain fish species (Zhulidov et al. 2006). Zebra mussels are more likely than quagga mussels to colonise native unionid mussel shells inferring a greater impact from zebra mussel presence (Conn and Conn 1993). Heiler et al. (2011), however, suggest that the impact on European unionids will probably be similar to that of the zebra mussel. Increased levels of toxic cyanobacteria have been linked to quagga mussel invasion alone (Sarnelle et al. 2010) and together with the zebra mussel (Makarewicz et al. 1999; Zhang et al. 2011). However, during a laboratory experiment, Dionisio Pires et al. (2007) observed that zebra mussel grazing reduced the levels of the cyanobacterium *Planktothrix agardhii*.

Coexistence of both species and an increase in the overall dreissenid density will increase the overall impact of dreissenids on the aquatic ecosystem. An increase in overall dreissenid abundance as a result of coexistence may occur due to the quagga's wider depth tolerance and lower respiration rate that decreases metabolic cost and increases tolerance of oligotrophic conditions (Mills et al. 1996; Baldwin et al. 2002; Stoeckmann 2003). Moreover, dreissenids display differences in substrate preferences (Mills et al. 1996; Karatayev et al. 1998; Diggins 2004), exhibit different temperature and silt tolerances and nutrient requirements (Roe and MacIsaac 1997; Karatayev et al. 1998; Orlova et al. 2005).

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