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Research Article

Reconstruction of the early invasion history of the quagga mussel (*Dreissena rostriformis bugensis*) in Western Europe

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Abstract

The recent introduction of the quagga mussel into Western European freshwaters marked the beginning of one of the most successful biological invasions during the past years in this region. However, the spatial and temporal origin of the first invasive population(s) in Western Europe as well as subsequent spreading routes still remain under discussion. In this study, we therefore aim at reconstructing the early invasion history of the quagga mussel in Western Europe based on an age-corrected temporally and spatially explicit spread model. Data were derived from time-series studies at selected sites as well as from a broad spatial survey in Western Europe. According to our spread model, the first successful introduction into Western Europe occurred in the Main-Danube Canal in early 2004, probably via inland navigation. Once populations were established, subsequent spread of the quagga mussel was characterized by a combination of jump dispersal and diffusive spread. This study gives insights into the very early invasion history of the quagga mussel and stresses the importance of the Main-Danube Canal for the introduction of non-native freshwater species into Western Europe.

Key words: introduction dates; Main-Danube Canal; phases of invasion; spread characteristics; time-series studies; vectors

Introduction

Man-made hydrological structures such as the international ports at the Rhine Delta and the Main-Danube Canal are known to play a significant role for the introduction of aquatic non-native species into Western Europe (Reinhold and Tittizer 1997; Bij de Vaate et al. 2002). Vessels that use these water-ways and ports can serve as efficient vectors for aquatic organisms and thus enable species exchange between regions and even continents (Reinhold and Tittizer 1997; Hulme 2009). One of the arguably most important freshwater invasion events into Europe during the recent past was the introduction of the quagga mussel (*Dreissena rostriformis bugensis* Andrusov, 1897) (Van der Velde et al. 2010; Zhulidov et al. 2010). The earliest published record of this taxon in Western Europe goes back to 2005 in the Main River in Germany (Imo et al. 2010). However, in 2006 adult specimens were also found in the Rhine Delta in the Netherlands (Hollands Diep), roughly 1,000 km north-west of the before mentioned site (Molloy et al. 2007). As the precise age of these populations was not known at the time of discovery, it continues to remain unclear when and how this new invader reached Western Europe. The two hypotheses are: first introduction into the Main River through the Main-Danube Canal via inland water transport (Molloy et al. 2007) or first introduction into the Dutch Rhine Delta (Bij de Vaate 2010), perhaps via ocean transport.

Information on place of first occurrence and routes of initial spread are very important for understanding basic invasion processes and for predicting patterns of future spreading. We therefore aim at reconstructing the early invasion history of the quagga mussel in Western Europe based on an age-corrected temporally and spatially explicit spread model.

Methods

Materials

Two general sampling strategies were used: i) time-series studies at selected sites to obtain a correction factor for calculating the date of local quagga mussel introduction and ii) a broad spatial survey for the actual spread model. Altogether, 13 representative sites in Germany and the Netherlands with different ecological characteristics (river, side arm, canal, river delta, coastal lake) were selected for the time-series studies. The broad spatial survey comprised 99 localities from Germany, Austria, Hungary, France and the Netherlands (own sampling and literature data; Appendix 1).

Population age correction

Previous studies have shown that when the quagga mussel invades areas that are occupied by its congener, the zebra mussel *Dreissena polymorpha* (Pallas, 1771), the latter is typically outcompeted over time (Wilson et al. 2006; Nalepa et al. 2010). It has also been shown that the degree of displacement of the zebra mussel by the quagga mussel (measured as the percentage of quagga mussels to zebra mussels; herein referred to as relative abundance) follows a common rate over time across localities in Western Europe. Thus, in principle, it can be used to estimate the time since introduction of a given quagga mussel population (referred to as correction factor) (Heiler et al. 2012). To calculate a common rate of displacement for all localities, we used linear regression to fit sampling date to relative abundance from all localities simultaneously by assuming the same slope over time (= rate of displacement) for each locality, while allowing for different intercepts (= dates of local quagga mussel introduction) for different localities. Simple linear regression was chosen to avoid overfitting of the short time-series with only few points in time available. If the regression resulted in only small residuals, we interpreted this as a confirmation of the assumption of a common rate of displacement. To illustrate adequacy of the regression, time was normalized (see Figure 1, in which the x-axis is displaying the normalized time and the y-axis the relative abundance). Standard errors were then calculated from the normalized data.

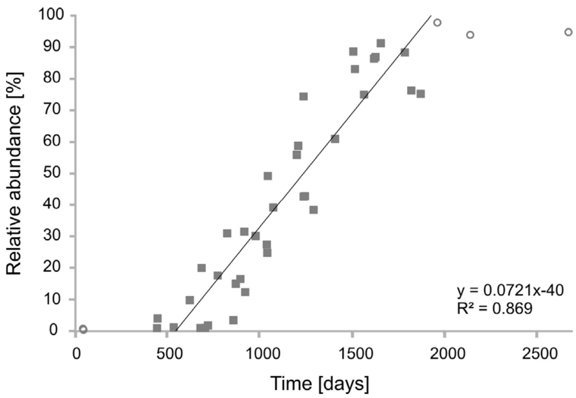

Figure 1. Time-series data of relative quagga mussel abundances (percentage of quagga mussels to zebra mussels) for 13 selected sites. The regression line indicates the common rate of increase (26% per year) for obtaining a correction factor (time since introduction of a quagga mussel population). Outliers are labeled with open circles.

Modeling

For each locality, the date of local quagga mussel introduction was estimated by back-calculation from the relative abundance at the sampling date to intersection with the x-axis using the respective correction factor. Note that we only used data-points representing the phase of linear increase, if available (see Result section; also see Appendix 1 for details). The resulting dates of local quagga mussel introductions were spatially interpolated using the inverse distance weighting algorithm of ArcMAP 10.0 (ESRI, Redlands, CA, USA). Interpolations were carried out according to the method used in Heiler et al. (2012).

Results

Our data show that the increase of relative abundance of the quagga mussel was linear between 1% and 95% relative abundance with only small residuals ($R^2 = 0.87$, $p = < 0.001$). Note that four extreme data-points from outside this range were excluded from regression analyses (Figure 1). Displacement occurred with a rate of 26% per year. Uncertainty of the correction factor of local quagga mussel introduction was ±149 days (standard error of estimate).

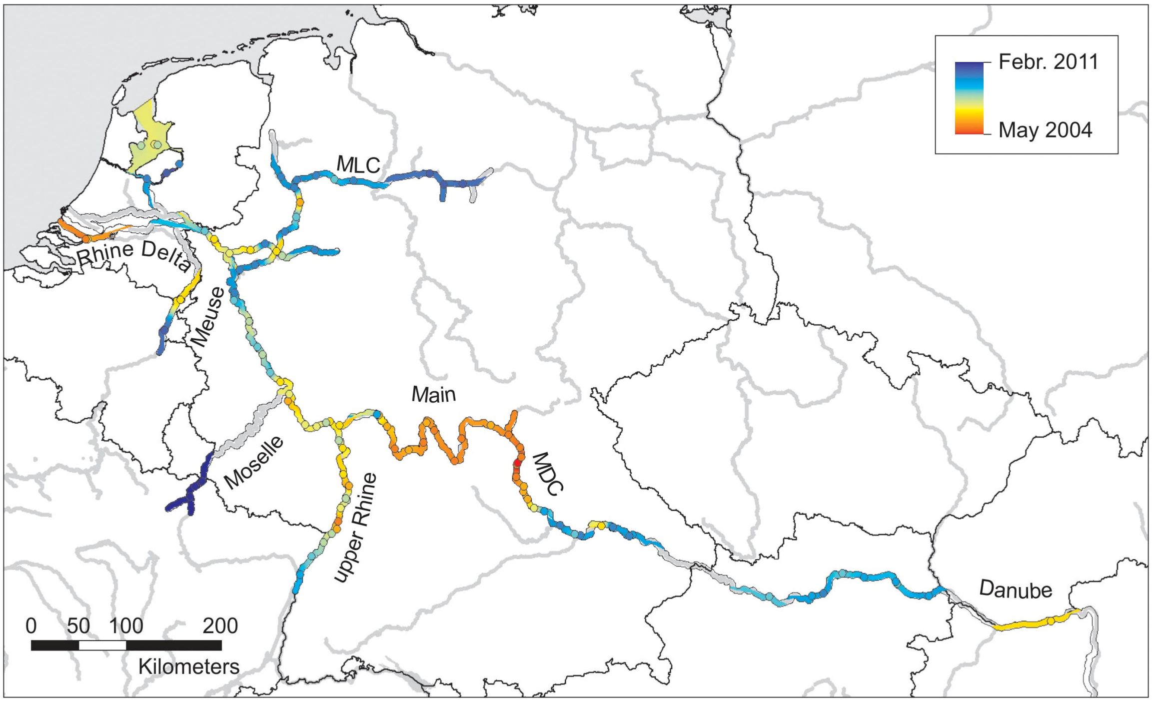

Figure 2. Spread model of the quagga mussel in Western Europe. Data are interpolated with an inverse distance weighting operation. Estimated dates of local quagga mussel introductions are coded from dark red (oldest date) to dark violet (youngest date). Jump dispersal is indicated by spots of the same color at spatially distant places (e.g. reddish spots at the Main-Danube Canal/Main River-region as well as at the Rhine Delta). Diffusive spread is indicated by color gradients radiating for example from the Main-Danube canal to the Main River and to the Danube River.

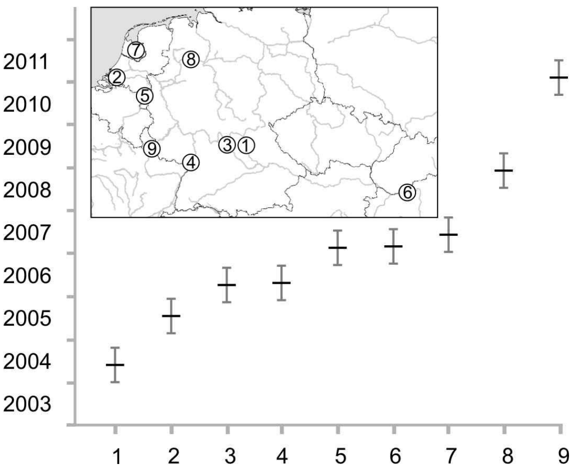

Figure 3. Estimations of the earliest dates of local quagga mussel introductions into selected Western European water bodies. Standard errors of estimates are included. Positions of localities (1-9) are shown on the upper map. 1: Main-Danube Canal, 2: Rhine Delta, 3: Main River, 4: Upper Rhine River, 5: Meuse River, 6: Danube River, 7: coastal lakes that are separated from the former Zuiderzee estuary (IJsselmeer, Markermeer, Drontermeer, Veluwemeer, Eemmeer), 8: Mittelland Canal, 9: Moselle River.

According to our spread model (Figure 2), the first introduction event into Western Europe happened in early 2004 in the upper Main-Danube Canal (Locality 1 in Figure 3). Displacement already reached the saturation phase in March 2008 (100% quagga mussels). The first introduction event of the quagga mussel into the Rhine Delta (Locality 2 in Figure 3) occurred in mid 2005. No saturation was reached in November 2008 (87%). The first introduction event into the Main River (Locality 3 in Figure 3) happened in spring 2006. Nearly simultaneously, the first introduction event in the upper Rhine (oil harbor) took place (Locality 4 in Figure 3). In early 2007 the quagga mussel arrived in the Meuse River (Locality 5 in Figure 3) and shortly thereafter in the middle Danube River (Locality 6 in Figure 3; note that the first record in the lower Danube River in Eastern Europe was already in 2004; Micu and Telembici 2004). The first introduction event into Dutch coastal lakes (e.g., IJsselmeer, Markermeer, Drontermeer, Veluwemeer, Eemmeer; Locality 7 in Figure 3) took place in mid 2007. In late 2008, the quagga mussel arrived in the Mittelland Canal (Locality 8 in Figure 3) and only in spring 2011 in the Moselle River (Locality 9 in Figure 3).

Discussion

Population age estimation

Population dynamics of Western European quagga mussel populations in sympatric occurrence with zebra mussels are characterized by three phases: a phase of establishment with a low and non-linear rate of displacement (indicated by data points below 1%), a phase of linear increase in relative abundance, and a phase of saturation (indicated by data points above 95%).

In a previous methodological study, the general principle of a time depended displacement was shown (Heiler et al. 2012). Based on time-series studies at four sites, a preliminary rate of displacement of 36% per year was proposed. The rate of 26% per year presented in this study is based on a spatially extended data set with 13 localities.

As our model does not take into account the phase of establishment, the estimated correction factors always represent minimum values (see Figure 1). Populations in the establishment phase are difficult to detect as numbers of individuals are extremely low. However, as it is uncertain whether such individuals will survive and successfully establish viable populations (Jones and Gomulkiewicz 2012), they are probably of minor importance for invasion history reconstruction.

Ocean- versus inland water transport

Our spread model indicates that the earliest successful introduction event of the quagga mussel in the Main-Danube Canal (hypothesis 1, see Introduction) occurred no later than spring 2004, whereas the Rhine Delta (hypothesis 2) was not occupied before summer 2005. Even when considering the standard error of our model, the Rhine Delta population appears to be younger than the Main-Danube Canal population (Figure 3; see, however, the shell-based estimate of Molloy et al. 2007, which suggests a first colonization of the Rhine Delta in 2004). The initial introduction of the quagga mussel into Western Europe most likely took place through the Main-Danube Canal via inland navigation. This canal is important for the westward spread of aquatic species from the Ponto-Caspian region as it is part of one of the three presumed major inland migration corridors into Western Europe (e.g. Bij de Vaate et al. 2002). Populations in the Rhine Delta might either result from an independent introduction (via ocean transporttation) or they might have been founded by specimens from the Main-Danube Canal populations that had reached the Rhine Delta via inland water transport.

A preliminary phylogeographical analysis of DNA sequences from the mitochondrial COI gene supports our hypothesis of a first quagga mussel introduction into the Main-Danube Canal. In populations from the Main-Danube Canal/ Main River-region three different haplotypes were found, whereas Rhine Delta populations lack any genetic variability (Albrecht and Heiler, unpublished data).

Spread of the quagga mussel

Our data suggest that the spread of the quagga mussel in Western Europe was characterized by two processes: jump dispersal (e.g., human-mediated passive transport) and diffusive spread (active and passive dispersal of adults and/or larvae) (Figure 2). This combination of jump dispersal and diffusive spread has also been shown for North American quagga mussel populations (e.g. Wilson et al. 1999; Brown and Stepien 2010).

As of 2010/2011, the invasion front has reached the Mittelland Canal, the Moselle River and the Meuse River. This is also in concordance with estimates of population age based on shell sizes or sampling dates (Bij de Vaate and Beisel 2011; Heiler et al. 2012; Marescaux et al. 2012).

Concluding remarks

We here propose that the first introduction of the quagga mussel into Western Europe occurred in the Main-Danube Canal via inland navigation.

Once viable population(s) were established, both, jump dispersal and diffusive spread characterized the subsequent expansion of the quagga mussel in Western Europe.

Moreover, our study stresses the importance of the Main-Danube Canal for the introduction of non-native freshwater species into Western Europe. Finally our analyses confirm the usefulness of correction factors for reconstructing invasion histories based on time-series studies.

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Supplementary material

The following supplementary material is available for this article.

Appendix 1. Sampling information including water body, longitude and latitude, relative abundance of quagga mussels (as percentage to zebra mussels), reference, sampling date, calculated date of local quagga mussel introduction as well as minimum and maximum dates of introduction (according to the standard error of the model).

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