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Research Article

Mass mortality of invasive zebra and quagga mussels by desiccation during severe winter conditions

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Abstract

Within impounded sections of the rivers Rhine and Meuse, epibenthic macroinvertebrate communities are impoverished and dominated by non-native invasive species such as the zebra mussel (*Dreissena polymorpha*) and quagga mussel (*Dreissena rostriformis bugensis*). In the winter of 2012 management of the water-level resulted in a low-water event in the River Nederrijn, but not in the River Meuse. Low-water levels persisted for five days with average daily air temperatures ranging from -3.6 to -7.2°C. We assessed the effects of this low-water event on settled dreissenid mussel populations using a before-after-control-impact (BACI) design. Desiccation had a negative effect on the overall density of dreissenids. Six months after the water level recovered, mussel density had increased slightly. After 18 months, mussel density had recovered to pre-event level. Mussels collected after the event were smaller than specimens collected before the event, indicating re-colonization originating from upstream river sections. At the control site, the dreissenid populations showed no significant change in density or shell size distribution. In total, 99.4% of empty shells washed up and sampled directly after the low-water event consisted of invasive bivalves, including zebra mussel, quagga mussel and Asian clams (*Corbicula fluminea* and *Corbicula fluminalis*). The high number of empty dreissenid shells stranded on the river banks directly after the event coincided with a mass mortality of mussels in the littoral zone. Imposing a sudden water-level drawdown during severe winter conditions could be a tool for the temporary reduction of invasive mollusc density in impounded river sections. Full recovery of the population structure likely may require a period of two to three years. Therefore, we recommend that the long-term effects of recurrent water-level drawdowns on the diversity of invasive and native species be assessed.

Key words: desiccation, invasive molluscs, impoundments, rivers, temperature, weir management

Introduction

Biodiversity has decreased strongly in the rivers Rhine and Meuse due to river regulation and environmental deterioration (Nienhuis et al. 2002). In spite of ambitious ecological rehabilitation programmes, riverine biodiversity has recovered only partly (Bij de Vaate et al. 2006; Leuven et al. 2011). The aquatic macroinvertebrate communities in impounded sections in the rivers Rhine and Meuse are still impoverished and dominated by non-native species (Leuven et al. 2009). Hard substrates in the littoral zones are dominated by non-native invasive dreissenid mussels, viz. the zebra mussel *Dreissena polymorpha* (Pallas, 1771) and quagga mussel *Dreissena rostriformis bugensis* Andrusov, 1897 (Bij de Vaate et al. 2014; Matthews et al. 2014).

Late-stage larval, juvenile, and adult dreissenid mussels produce byssal threads that are secreted by the byssus gland in their foot (Rajagopal et al. 2005; Brazee and Carrington 2006; Grutters et al. 2012). These mussels use byssal threads to attach to hard substratum such as rock, wood, other mussels, hydraulic engineering structures, water craft, pontoons and water intake facilities (e.g., water purification plants and power stations).

Figure 1. Locations of the study sites in The Netherlands.

Therefore, sessile mussels cannot move rapidly and may not remain immersed after decreases in water levels. As a result, mortality of dreissenid mussels can occur due to desiccation in littoral zones of rivers and lakes during periods of low river flow or drought (Collas et al. 2014).

Several authors have reported the mass mortality of invasive mollusc species during harsh environmental conditions (Grazio and Montz 2002; Haag and Warren 2008; Werner and Rothhaupt 2008; Weitere et al. 2009; Vohmann et al. 2010; Firth et al. 2011; Ilarri et al. 2011; Churchill 2013; Bódis et al. 2014) (Table 1). However, most research concerning the impacts of extreme weather events on invasive molluscs in freshwater ecosystems has focused on the mass mortality of the Asian clam *Corbicula fluminea* (O.F. Müller, 1774) induced by severe low flows or drought, associated with extremes in temperature. Werner and Rothhaupt (2008) hypothesized that a rapid fall in water level during harsh winter conditions could be used as a management tool to control invasive, non-native aquatic species. During the severe winter of 2012, an unintended large-scale field experiment took place in the River Nederrijn and created conditions under which this hypothesis could be validated for dreissenid mussels using a before-after-control-impact (BACI) design. Data from fauna surveys in the River Nederrijn (extreme event site) and River Meuse (control site) allowed assessment of the effects of desiccation on settled dreissenid mussels in the littoral zone during a low-water event associated with severe winter conditions.

Material and methods

Sampling sites

Density and relative abundance of dreissenid mussels on stones in the main channel and washed-up on the banks of the rivers Rhine and Meuse in The Netherlands were determined (Figure 1). The low-water event site was located on the left bank of the River Nederrijn at Lexkesveer (N 51° 57'28.943"; E 5°40'43.115"). The control site was was located on the right bank of the River Meuse near Mook (N 51°44'23.362"; E 5°52'47.841").

Both sampling locations were positioned on the downstream side of a groyne in an impounded river section. These sites were included in a monitoring programme examining dispersal and impacts of

Table 1. Records of mass mortality of invasive bivalves during extreme weather events.

Water body	State	Species	Extreme event	Year(s)	Reference
Small streams					
Streams in Bankhead National Forest	Alabama and Mississippi (USA)	*Corbicula fluminea*	Severe drought	2000	Haag and Warren (2008)
Large rivers					
River Danube (and its tributary River Ipoly)	Hungary	*Corbicula fluminea* *Sinanodonta woodiana*	Low river flows and thermal pollution during autumn	2011	Bódis et al. (2014)
River Douro	Portugal	*Corbicula fluminea*	High river flow during winter period	2009/2010	Sousa et al. (2012)
River Meuse	The Netherlands	*Corbicula fluminea*	Low river discharges during summer periods associated with high water temperature, low oxygen contents and low food availability	2003 and 2006	Foekema et al. (2008)
River Meuse	Belgium	*Corbicula fluminea* *Dreissena polymorpha* *Dreissena r. bugensis*	Low-water event during summer caused by opening of weirs for maintenance of river bed, banks and hydraulic infrastructure	2012	Personal observation F.P.L. Collas
River Minho	Portugal	*Corbicula fluminea*	Strong heat waves associated with low river flow, high temperature, low dissolved oxygen and lower redox potential	2005 and 2009	Ilarri et al. (2011)
River New	Virginia (USA)	*Corbicula fluminea*	Summer drought conditions	Not mentioned	Cooper et al. (2005)
River Rhine	Germany	*Corbicula fluminea*	Heat waves during summers	2003 and 2006	Westermann and Wendling (2003), Weitere et al. (2009), Vohmann et al. (2010)
River Rhine	The Netherlands	*Corbicula fluminea* *Corbicula fluminalis*	Locomotion of clams to avoid desiccation of littoral zone during extremely low river flow. However, strong shipping induced currents stranded them on the banks resulting in mass mortality	2008	Personal observation R.S.E.W. Leuven & J. Matthews
Lakes					
Lake Constance	Germany, Switzerland and Austria	*Corbicula fluminea*	Severe low-water event and associated low water temperatures during harsh winter conditions	2005/2006	Werner and Rothhaupt (2008)
Lake Texoma	Texas (USA)	*Dreissena polymorpha*	Thermal stress and extremely low lake elevation during summer	2011	Churchill (2013)
Lakes Zumbro and Edinboro	Minnesota and Pennsylvania (USA)	*Dreissena polymorpha*	1.5 m drawdowns during winter and fall conditions	2000/2001	Grazio and Montz (2002)

invasive dreissenid mussels in The Netherlands (Le et al. 2011; Matthews et al. 2014).

Severe low-water event

On February 8, 2012, the weirs in the River Nederrijn at Driel, Amerongen and Hagestein were opened to break up ice in the river, preventing damage to hydraulic infrastructure. The opening of weirs caused a sudden decrease in water level at the impounded sections of the river (Figure 2). The water level in the main river channel, downstream of the upper weir, dropped by 0.5 to 3.4 m below the target level of 6 m above average sea level. Severe low-water conditions were observed for at least five days. Weirs remained closed at the control site in the River Meuse because drifting ice was less problematic at this location. During the extreme event period, water temperature of the rivers Nederrijn and Meuse at a depth of 10 cm ranged between 0 and 1.8°C (Netherlands Directorate-General for Public Works and Water Management 2014). The air temperature at the closest weather station (Volkel) ranged between a daily minimum of

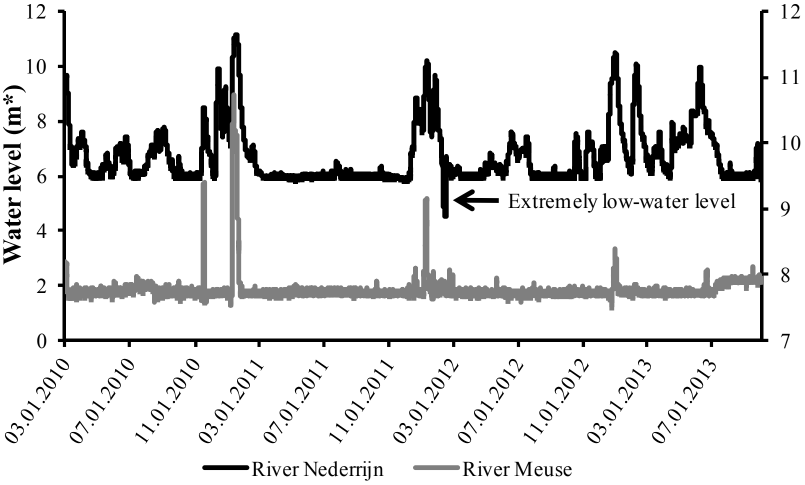

Figure 2. Water levels of the River Nederrijn (left axis) and River Meuse (right axis) during the period March 2010 – October 2013 at gauging stations Driel and Mook, respectively (*: above average sea level).

-8.3 and -12.6°C, a daily average of -3.6 and -7.2°C and a daily maximum of -0.5 and -2.4°C (Koninklijk Nederlands Meteorologisch Instituut 2014). The daily relative humidity ranged between 70 and 86% (Koninklijk Nederlands Meteorologisch Instituut 2014). The distance between sampling sites was circa 30 km, ruling out regional differences in air temperature.

Mussel sampling

Mussel samples were taken at the extreme event and control site before and 1.5, 2, 6 and 18 months after the low-water event. All post-event mussel samples of both sites were collected from five groyne stones that were retrieved at a water depth of 30 to 60 cm. Pre-event data of the rivers Nederrijn and Meuse were based on samples from ten and eight groyne stones, respectively. The sampled groynes were constructed from polygonal basalt stones whose total surface area was calculated by adding up the surface areas of all flat sides. All mussel samples were preserved in ethanol (70%) and transported to the laboratory where they were identified to species level and analysed to determine species density, relative abundance, and shell length.

Mussel densities at the low-water event and control site were always calculated per groyne stone and subsequently averaged per sampling date. Unfortunately, the pre-event samples of stones in the River Nederrijn were pooled (Le et al. 2011), which limited density calculations per stone and statistical comparisons with our post-event data. Therefore, pre-event mussel densities on individual stones at this site were estimated using counts of byssus remnants and dead mussels attached to stones that were collected directly after the event (retrospective approach).

In addition, the density of empty mussel shells washed up on the river bank at the low-water event site was determined 2, 6 and 18 months after the event. For this purpose, all empty shells were collected from the surface of sediment in five quadrants along the high-water line. Quadrants of different surface areas were used depending on rough estimates of mussel density (i.e. 0.075, 0.125 or 0.250 m^2 in case of high, intermediate or low density of shells stranded, respectively). All shells were identified to species level in the laboratory. The density of stranded mussels was determined by calculating per quadrant the number of complete doublets and the number of half shells divided by two, and converting these numbers to individuals per m^2.

Statistical analyses

Mussel density data from groyne stones and river banks were tested for normality and homogeneity of variances with a Kolmogorov-Smirnov test and Levene's test respectively, using the statistics package SPSS 19.0. Subsequently, the Scheirer-

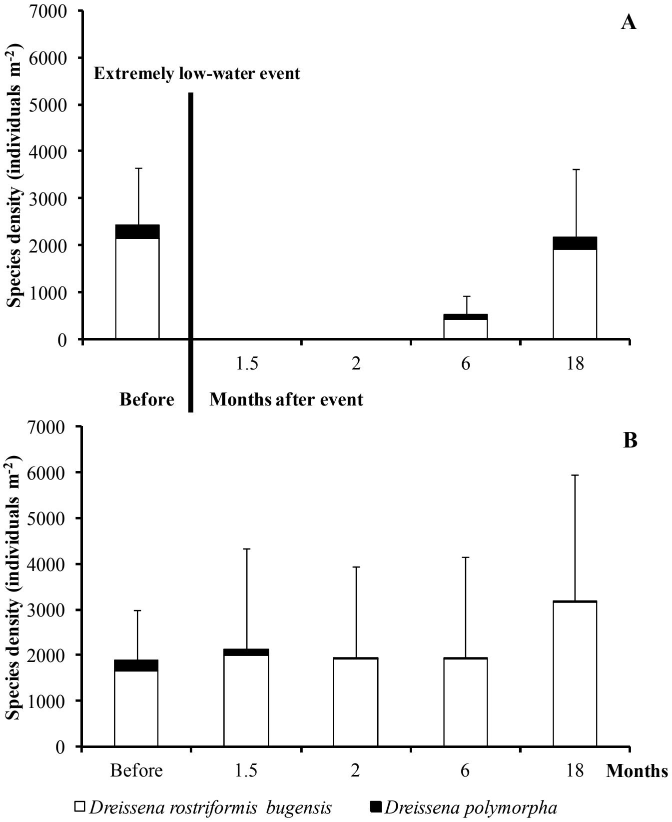

Figure 3. Zebra and quagga mussel densities (± standard deviation) at the extreme low-water event site in the River Nederrijn at Lexkesveer (A) and the control site in the River Meuse at Mook (B).

Ray-Hare test was used for the analyses of ranked density data since our data did not fulfil the assumption of a two-way parametric ANOVA due to absence of homogeneity of variances (P = 0.001) and a marginal normality (P = 0.078). Location and time were used as fixed factors in the analyses. The Scheirer-Ray-Hare rank test is a conservative non-parametric equivalent of a two-way ANOVA with replication (Dytham 2003).

Data concerning mussel shells washed up on the river banks were normally distributed (P = 0.768) but the variances were not homogeneous (P = 0.015). Therefore, samples from river banks were analysed using a one-way ANOVA with a Games-Howell post hoc test. All statistical tests were regarded to be significant at $P < 0.05$.

Results

The actual mussel density in the littoral zone of the River Nederrijn before the low-water event was 2807 individuals per m^2 (pooled pre-event sample of Le et al. 2011). Our retrospective estimation yielded an average pre-event mussel density (± standard deviation) of 2423 ± 1223 individuals per m^2 (Figure 3A). The low-water event and coinciding low air temperature caused mass mortality of dreissenid mussels in the littoral zone of the River Nederrijn. Shortly after this event, all observed zebra and quagga mussel shells attached to groyne stones were empty. The number of byssus remnants indicated that 1.5 and 2 months after the event many mussels were detached. During the 18 months post-event monitoring period, the densities of living mussels gradually increased to pre-event levels (Figure 3AB). At the control site in the River Meuse mussel densities did not show changes. The Scheirer-Ray-Hare test of before-after-control-impact data showed that time and location significantly explained the variability in densities of dreissenid mussels on groyne stones in the rivers Nederrijn and Meuse (P = 0.003 and P = 0.005, respectively; Table 2). The interaction between time and location was not significant (P = 0.054; Table 2).

Table 2. The Scheirer-Ray-Hare rank test results of 'before-after-control-impact' data on densities of dreissenid mussels on groyne stones in the rivers Nederrijn and Meuse.

	SS	SS/MStotal	df	P-value
Location (factor)	2428.985	8.56149	1	0.003*
Time (factor)	4233.348	14.92137	4	0.005*
Location x Time (interaction)	2643.880	9.318936	4	0.054

*: statistically significant

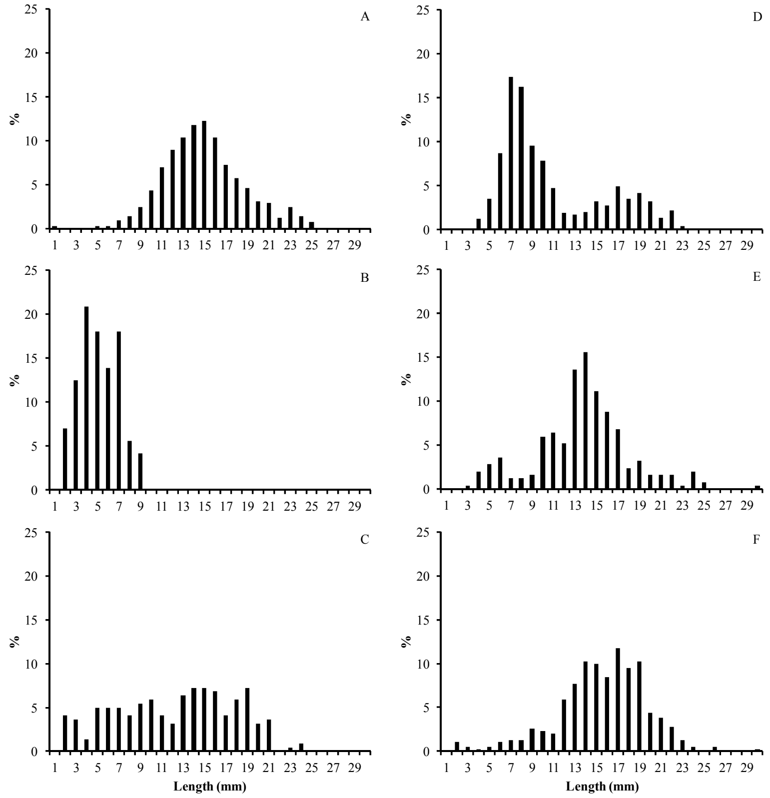

Figure 4. Proportion of quagga mussels per size class at the extreme low-water event site in the River Nederrijn (A-C) and the control site in the River Meuse (D-F), before, and 6 and 18 months after the event date.

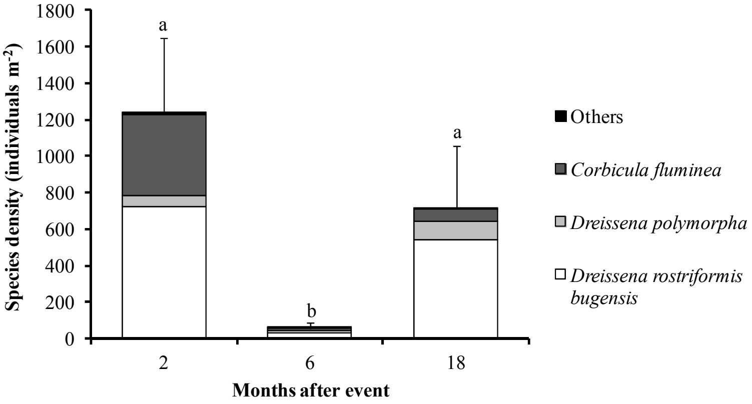

Figure 5. Empty shell density of bivalve species stranded on river banks at the extreme low-water event site in the River Nederrijn at Lexkesveer (number of individuals ± standard deviation per m^2). Different letters indicate significantly different shell densities ($P < 0.05$).

Shell lengths of quagga mussels that were collected in the River Nederrijn before the extreme low-water event were between 1 and 25 mm (Figure 4A). The average and maximum shell length before the event (Figure 4A) were larger than those of mussels collected 6 and 18 months after the event (Figure 4B and 4C, respectively). Shell lengths of mussels that were collected 6 months after the event were between 2 and 9 mm (0+ cohort), indicating re-colonization of this site from upstream populations by veligers or mussel brood drift. However, 18 months after the event shell lengths of mussels were between 2 and 23 mm, indicating on-going colonization as well as aging of the mussel population that recruited in the summer of 2012, following the low-water event. The shell length of quagga mussels at the control site in the River Meuse on all sampling dates ranged from 2 to 30 mm (Figure 4D-F), indicating that this population consisted of at least three annual cohorts (2011–2013) during the monitoring period.

Densities of empty mollusc shells washed up on the river banks of the low-water event site significantly differed over time (Figure 5; one-way ANOVA df = 2; F = 18.503; P < 0.001). After 6 months, the shell densities were significantly lower than 2 months after the event (Games-Howell post hoc test for pair wise comparisons: P = 0.006). After 18 months the density of stranded shells was significantly higher than after 6 months (*P* = 0.028) but did not significantly differ from values recorded 2 months after the event (*P* = 0.130). The quantitative ranking of species in order of high to low densities was quagga mussel, Asian clam, zebra mussel and other species such as the painter's mussel *Unio pictorum* (L., 1758) and the swollen river mussel *Unio tumidus* Philipsson, 1788.

Discussion

Our data indicate that the sudden decrease in water level during severe winter conditions caused mass mortality of dreissenid mussels in the littoral zone of the River Nederrijn. The extreme low-water level in the River Nederrijn lasted for five days with an average daily air temperature ranging between -3.6 and -7.2 °C. Desiccation under such harsh winter conditions can cause high mortality rates in dreissenid mussels (Clarke and McMahon 1993; McMahon et al. 1993). The tolerance of dreissenid mussels to desiccation is temperature and humidity dependent (Collas et al. 2014). Zebra mussels can survive for more than 10 days in cool (15°C), humid conditions (McMahon et al. 1992). At higher temperatures, such as 25°C, zebra mussels can survive independently of humidity for less than 150 hours (McMahon et al. 1993). Clarke and McMahon (1993) found that after dewatering, freezing temperatures resulted in quicker mortality of zebra mussels than when they were exposed to higher temperatures. Clustered mussels survived twice as long as isolated mussels. Time to death decreased exponentially when mussels were exposed to temperatures below -3 °C. The water level was maintained in the impounded section of the River Meuse and at this control site dreissenid mussel density did not change significantly over the monitoring period. Available data on water temperature tolerance confirm that river temperatures recorded during our monitoring period should not cause mortality in immersed zebra and quagga mussels (Verbrugge et al. 2012; Verhofstad et al. 2013; Matthews et al. 2014).

Uncertainties in our assessment concern the retrospective estimation of pre-event mussel densities, rate of background mortality and pseudo-replication in time. On the one hand, our retrospective approach may overestimate the pre-event mussel density, because byssal remnants can persist for a long period of time after dislodgement or predation. On the other hand, the population size may be underestimated because newly recruited mussels may attach to earlier colonizers (clumping) and these individuals will be lost when clumps of shells become dislodged. However, it is likely that our retrospective approach slightly underestimates the pre-event mussel density, because the 'pooled mussel sample' yields a higher density. Moreover, Le et al. (2011) did not observe byssal remnants or dead mussels during pre-event sampling. The number of individuals attached to other mussels was always low, possibly because hard substrate was sufficiently available for colonization. Although background mortality of mussels was not assessed in our study, observations on other locations in the River Nederrijn did not indicate increased mortality before the event (Le et al. 2011; Matthews et al. 2014). Finally, the interval between two post-event samples was short in comparison with intervals between other samples. Pseudo-replication in time could be a possible limitation in the interpretation of our statistical results.

Several other studies report mass mortality of invasive bivalves during extreme climatic events, including die-offs of dreissenids (Table 1). However, most observations concern Asian clams. Mass mortality is often caused by extreme low-water flow at high temperatures, associated with low dissolved oxygen and food quantity. In addition, die-offs of invasive bivalves are also reported after extreme winter or spring flooding associated with increased silt loads.

Water drawdown is a well-accepted management tool for controlling invasive aquatic plants, especially in lakes and reservoirs (Barrat-Segretain and Cellot 2007; Barnes et al. 2013). Tucker et al. (1997) suggest that system-wide drawdowns during warm summer conditions can also have a profound negative impact on zebra mussel demography. Grazio and Montz (2002) reported on winter lake drawdown as a strategy for zebra mussel control. Recently, Werner and Rothhaupt (2008) hypothesized that water-level drawdown during severe winter conditions can be an effective tool for controlling the population densities of invasive molluscs. Mackie and Claudi (2010) also suggest that the exposure of otherwise submerged structures at times of low air temperature is a viable and expedient way of controlling dreissenid mussel infestations. Our data on mass mortality of dreissenid mussels in the River Nederrijn support their hypothesis. In impounded river sections, manipulation of the water level is facilitated by weir management. Shipping traffic and recreational sailing will not be impeded by low-water levels, if interventions occur during severe winter periods, because navigation is limited by (floating) ice on the river at this time.

The gradual increase in density and the small shell size of zebra and quagga mussels in the River Nederrijn after the extreme low-water event indicate that re-colonization mainly occurred as a result of juvenile settlement from this river section or alternatively originating from populations upstream (Lucy et al. 2008 and references therein). Although the population recovered, the shell length distribution of mussels still differed from the pre-event measurements and size distributions at the control site which had at least three year cohorts. Consequently, it could take two to three years before a full recovery of the mussel population structure is achieved. Matthews et al. (2014) observed a shift in species dominance from zebra mussel to quagga mussel in the River Meuse. The increasing relative abundance of quagga mussels and the decreasing density of zebra mussels indicate that this shift in species dominance is continuing.

Empty shells washed up on the river banks may reflect spatial distribution pattern and mortality rates of bivalve species (Sousa et al. 2012; Bódis et al. 2014). Densities of stranded shells on the banks of the River Nederrijn do not allow conclusions on causality of low-water level and bivalve mortality. The fluctuating densities indicate that several other environmental factors may contribute to stranding of shells (e.g., combined effects of shipping induced waves and river flow). Moreover, data on the community composition of benthic bivalves at the low-water event site are not available, limiting comparisons with densities of stranded shells. However, the species composition of empty mussel shells washed up on the banks directly after the low-water conditions indicated that this event also affected bivalve species living in and on sediments in the littoral zone of the river, including Asian clams and native species such as painter’s mussel and swollen river mussel. Asian clams, zebra mussel and native unionids do not necessarily respond to low-water events in the same way due to different physiological adaptations (Tucker et al. 1997; McMahon 2002). According to Haag and Warren (2008), the effects of severe drought on invasive Asian clams at small-stream sites in North America appeared to be stronger than on native mussel species. Therefore, the assessment of long-term effects of recurrent weir management interventions on abundance of invasive and non-target species is recommended.

Invasions of dreissenid mussels affect biodiversity and ecosystem functioning in Northwestern Europe and North America (Van der Velde et al. 2010; Matthews et al. 2014; Nalepa and Schloesser 2014). Mass mortality of dreissenid mussel populations is expected to cause both positive and negative ecological effects. Positive effects resulting from population declines could include a reduction in their competitive influence on resources. In addition, population die-offs of invasive mussels and the resulting sloughing of dead organic matter onto river banks could provide an important resource subsidy for the adjacent terrestrial food web (Bódis et al. 2014). However, a decrease in dreissenid mussel stocks at the wintering sites of waterfowl could also impact diving duck populations, such as the tufted duck *Aythya fuligula* (L., 1758) and pochard *Aythya farina* (L., 1758), which are dependent on zebra and quagga mussels as food resource (Suter and Van Eerden 1992). Moreover, filter-feeding dreissenids can be used to combat eutrophication (Reeders and Bij de Vaate 1990). Therefore, the potential loss of positive as well as negative effects of dreissenids should be considered in impact assessments of water-level drawdowns.

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