

Research Article

Risks and management of alien freshwater crayfish species in the Rhine-Meuse river districtPim Lemmers^{1,2,3}, Frank P.L. Collas^{1,3}, Ronald Gylstra⁴, Ben H.J.M. Crombaghs^{2,3}, Gerard van der Velde^{1,3,5} and Rob S.E.W. Leuven^{1,3,*}¹Radboud University, Institute for Water and Wetland Research, Department of Animal Ecology and Physiology, P.O. Box 9100, 6500 GL Nijmegen, The Netherlands²Natuurbalans – Limes Divergens, Toernooiveld 1, 6525 ED Nijmegen, The Netherlands³Netherlands Centre of Expertise for Exotic Species (NEC-E), Nature plaza, P.O. Box 9010, 6500 GL Nijmegen, The Netherlands⁴Water Board Rivierenland, De Blomboogerd 1, 4003 BX Tiel, The Netherlands⁵Naturalis Biodiversity Center, P.O. Box 9517, 2300 RA Leiden, The NetherlandsAuthor e-mails: lemmers@natuurbalans.nl (PL), f.collas@science.ru.nl (FPLC), r.gylstra@wsrl.nl (RG), crombaghs@natuurbalans.nl (BHJMC), g.vandervelde@science.ru.nl (GV), r.leuven@science.ru.nl (RSEWL)

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Abstract

Since the 1950s, nine alien crayfish species have been introduced in the Rhine-Meuse river delta. Seven species originate from North America, one from Southeast Europe and one from East Europe/Asia. Currently, at least seven species have well-established populations. Five species are listed as invasive alien species (IAS) of European Union (EU) concern (i.e. *Faxonius limosus*, *Faxonius virilis*, *Pacifastacus leniusculus*, *Procambarus clarkii* and *Procambarus virginialis*). All crayfish species of EU concern are subject to restrictions on keeping, transportation, importing, selling and breeding. Member States are required to take action on pathways of unintentional introduction, to perform measures for early detection and rapid eradication of these species, and to manage species that are already widely spread. The impact of these IAS on biodiversity and functioning of ecosystems mainly results from transmission of the crayfish plague pathogen *Aphanomyces astaci*, predation on native fauna, and fragmentation and consumption of aquatic plants. Moreover, burrowing activities of some IAS cause bank instability, increase risk of dike breaches in peatland areas and enhance sedimentation rates in ditches and canals. First-line risk assessments for the Rhine-Meuse river district with the Harmonia⁺ scheme shows that seven crayfish species have a high risk of impact on biodiversity, water safety and ecological status of water bodies. Four species have already established populations in this area of concern. The risk of spread via interconnected rivers, canals and small watercourses is high for all species of North American origin. Eradication of alien crayfish populations in an extensive and open network of interconnected watercourses is not feasible. Six management strategies for control of alien crayfish species were formulated. These strategies were assessed using various criteria for cost-effectivity and subsequently prioritized using an unweighted Multi Criteria Analysis. Feasible strategies for population control of invasive crayfish species combine a) measures for enhancing robustness and resilience of ecosystems, and b) crayfish trapping by commercial fishermen, water authorities and well-informed citizens.

Key words: decapods, ecosystem resilience, EU Regulation 1143/2014, management strategies, population control, risk assessment

Introduction

The Rhine-Meuse river delta in Northwest Europe harbours only one native freshwater crayfish species, namely the noble crayfish *Astacus astacus* (Linnaeus, 1758). This species mainly occurred in pristine streams and was locally common (Geelen 1978). However, the populations of *A. astacus* severely declined since 1950 due to water pollution, habitat degradation and spread of the crayfish plague pathogen *Aphanomyces astaci* (Schikora, 1906) by the introduction of alien crayfish species (Geelen 1978; Koese and Soes 2011; Tilmans et al. 2014). Currently, the occurrence of *A. astacus* in the Rhine-Meuse river delta is reduced to one isolated location (Koese and Soes 2011).

In 1956, the first alien crayfish species in the Rhine-Meuse river delta was recorded (Koese and Soes 2011). Since then, eight other crayfish species have been reported for this area. Currently, five of these species are listed as invasive alien species (IAS) of European Union (EU) concern (European Commission 2016). These species are the virile crayfish *Faxonius virilis* (Hagen, 1870), spiny-cheek crayfish *Faxonius limosus* (Rafinesque, 1817), signal crayfish *Pacifastacus leniusculus* (Dana, 1852), red swamp crayfish *Procambarus clarkii* (Girard, 1852) and marbled crayfish *Procambarus virginalis* Lyko, 2017. IAS of EU concern are subject to restrictions on possession, transportation, import, trade and breeding. Moreover, member states are required to take action with respect to pathways of unintentional introduction, measures for early detection and rapid eradication of these species, and management of species that are already widely spread.

The number of records and abundance of alien crayfish in the Rhine-Meuse river delta strongly increased during the last decade (NDFFF 2019), likely facilitated by habitat deterioration of crayfish predators, such as birds, fish and mammals (Lemmers et al. 2018, 2019). The increase in spread and density of invasive crayfish species accelerates their impact on aquatic ecosystems (Dickey et al. 2020). This results in adverse ecological impacts, water safety problems and risks for non-compliance of the ecological status of water systems with goals of the European Water Framework Directive. The extent of these effects may differ for various crayfish species, climate zones and habitat types. This possibly limits generalisation of outcomes of risk assessments from other regions (Matthews et al. 2017a). Therefore, the aim of this study is to conduct a risk analysis for nine alien crayfish species in the Rhine-Meuse river district taking into account their potential effects on biodiversity, water safety and ecological status of water bodies. This risk analysis includes the following aspects: a) risks of introduction, establishment, spread and impacts of alien crayfish species, b) identification of feasible management strategies for control, and c) cost-effectivity and public support of these strategies. For this purpose, extensive literature reviews and expert based assessments have been performed.

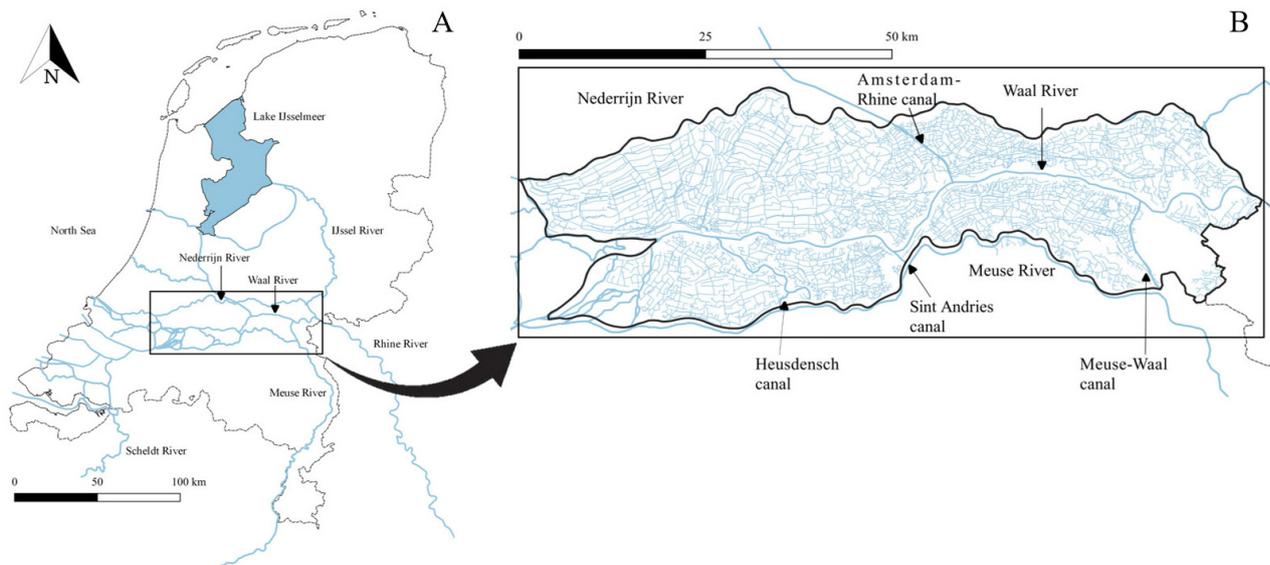


Figure 1. (A) Location of the large rivers Rhine and Meuse (solid blue lines) and lake IJsselmeer (solid blue polygon) in the Netherlands (dashed black line). The area of concern is framed. (B) Map of Rhine-Meuse river district showing the network of watercourses. Large rivers (black lines) demarcate the study area. Blue lines depict the network of rivers, canals and other primary watercourses.

Materials and methods

Area of concern

The area of concern of the risk analysis encompasses the Rhine-Meuse river district in the Netherlands (Figure 1). The northern border of this area is demarcated by distributaries of the rivers Rhine River (Nederrijn/Lek) and the southern border by the Meuse River. This river district is characterized by an extensive network of small watercourses consisting of 4,517 km primary canals and 15,871 km ditches. The large rivers (Meuse, Waal and Nederrijn) in this area are interconnected via the Amsterdam-Rhine canal, Meuse-Waal canal, Sint Andries canal and Heusdensch canal (Leuven et al. 2009). Nearly all watercourses are manmade and often concern heavily modified streams with deteriorated habitats. Alien crayfish can easily spread by natural means within this network of hydrologically connected water bodies. Some crayfish species can also reach isolated water bodies by dispersal over land (Cruz and Rebelo 2007; Roessink et al. 2009; Souty-Grosset et al. 2016).

Data collection

A literature search was conducted by means of Google Scholar and Web of Science (v.5.35) using the scientific species names of all assessed crayfish species in combination with the following representative set of search terms: risk*, “biological control”, burrow*, containment, competition, “density dependence”, effect, “effect mitigation”, eradication, impact, “interspecific competition”, “population control”. The search focussed on the ecology, risks and control mechanisms for alien crayfish species that have been recorded or are expected to be introduced in the Rhine-Meuse

Table 1. Overview of alien crayfish species in the Rhine-Meuse river delta and district (area of concern). Species are ordered according to their first record in the Rhine-Meuse river delta.

Scientific name	English name	Native range	First record in the Rhine-Meuse river delta	Recorded in % grid cell ($5 \times 5 \text{ km}$) ¹ since introduction ²	Current establishment status in Rhine-Meuse river delta	First record in area of concern	Current establishment status in area of concern	Species of European Union concern
<i>Austropotamobius torrentium</i> (Schrank, 1803)	Stone crayfish	Central Europe ¹	1956 ^{b,2}	0.1%	Casual	N.A. ²	Not recorded	No
<i>Faxonius limosus</i> (Rafinesque, 1817)	Spiny-cheek crayfish	North America ¹	1968 ²	39.5%	Established	1971 ²	Established	Yes ³
<i>Pontastacus leptodactylus</i> (Eschscholtz, 1823)	Galician crayfish	Eastern Europe and Asia ¹	1978 ²	2.0%	Established	1980 ²	Casual	No
<i>Procambarus clarkii</i> (Girard, 1852)	Red swamp crayfish	North America ¹	1985 ²	14.5%	Established	2001 ²	Established	Yes ⁴
<i>Procambarus acutus</i> (Girard, 1852)	White river crayfish	North America ⁵	2002 ²	2.7%	Established	2002 ^{6,2}	Established	No
<i>Faxonius virilis</i> (Hagen, 1870)	Virile crayfish	North America ¹	2004 ²	3.0%	Established	2008 ²	Established	Yes ⁶
<i>Procambarus virginalis</i> Lyko, 2017	Marbled crayfish	North America ¹	2004 ²	0.2%	Established ^{7,8}	N.A. ²	Casual ⁷	Yes ⁹
<i>Pacifastacus leniusculus</i> (Dana, 1852)	Signal crayfish	North America ¹	2005 ²	0.7%	Established	N.A. ²	Not recorded	Yes ¹⁰
<i>Faxonius immunis</i> (Hagen, 1870)	Calico crayfish	North America ¹	2019 ¹¹	0.1%	Unknown	2019 ^{a,11}	Unknown	No

^a: total number of grid cells is 1685; ^b: Single record; ^c: First record for the Rhine-Meuse river district, but identification is uncertain; ¹: Souty-Grosset et al. (2006); ²: NDFFF (2019); ³: NNSS (2011a); ⁴: NNSS (2011c); ⁵: Koese and Soes (2011); ⁶: Rogers and Watson (2013); ⁷: Soes (2016); ⁸: Unpublished data April 2020, P. Lemmers; ⁹: Holdich (2011); ¹⁰: NNSS (2011b); ¹¹: Ottburg et al. (2019).

river district. For each species, the first 50 hits were judged on relevance for our study according to the approach used by Matthews et al. (2017a). Additionally, relevant information was obtained from a Dutch database for articles on natural history and ecology of the study area (Natuurtijdschriften 2019). The literature search was expanded by using a backward snowballing technique to acquire relevant literature cited in hits retrieved using the search engines. All this information was used for identifying risks of alien crayfish species, deriving feasible management strategies and assessing cost-effectivity of these strategies. The present paper follows the most recent classification and nomenclature of freshwater crayfish. *Faxonius limosus* and *F. virilis* replace former species names *Orconectes limosus* and *O. virilis*, respectively (Crandall and De Grave 2017; Table 1). Based on different fitness traits, reproductive incompatibility and substantial genetic differences, *Procambarus fallax* forma *virginalis* has been described as a new species named *Procambarus virginalis* (Lyko 2017). Data on crayfish distribution was retrieved from the Dutch National Database Flora and Fauna (NDFFF 2019).

Risk assessment of species

Risks of alien crayfish species for the Rhine-Meuse river district were assessed using the internet-based Harmonia⁺ risk assessment protocol (D'hondt et al. 2015). This protocol took into account environmental risks, impact on human infrastructure, impact on ecosystem services and effects

of climate change on risks (D'hondt et al. 2015; Vanderhoeven et al. 2015). The protocol consisted of 41 questions grouped in the following six categories: 1) context, 2) introduction, 3) establishment, 4) spread, 5) impact categories (environment, plant cultivation, animal production, human health, infrastructural and ecosystem services) and 6) future effect of climate change. Risk scores for crayfish species and confidence levels were assigned to all questions. The Harmonia⁺ risk classification yielded an invasion score, impact score and overall risk score for each species by calculating the arithmetic mean and maximum score for each risk category. The assessment was carried out and discussed by the authors until consensus was reached. In case of data deficiency, risks were assigned based on best professional knowledge of the authors.

Identification and assessment of management strategies

Six strategies for control of the invasive alien crayfish in the Rhine-Meuse river district were agreed at European legislation and regional policies for prevention and management of IAS. Feasibility of these strategies was evaluated using eight criteria: 1) effectivity on the short term, 2) effectivity on the long run, 3) contribution to biodiversity conservation, 4) risk management regarding water safety (e.g. flooding risk, drainage function and bank stability), 5) short term costs, 6) long term costs, 7) expected public acceptance, and 8) estimation of compliance with management goals of water authorities. All management strategies were assessed by best professional judgement of the authors based on consensus. A five-point scale was used for scoring each criterion, where 1 = Very low, 2 = Low, 3 = Medium, 4 = High and 5 = Very high. An unweighted Multi Criteria Analysis (MCA) was performed for prioritizing the management strategies using the sum of scores for all criteria.

Results

Introduction and establishment of crayfish in the Rhine-Meuse river district

The first alien crayfish observation in the Rhine-Meuse delta concerns a single record of a stone crayfish *Austropotamobius torrentium* (Schrank, 1803) in 1956 (Koese and Soes 2011). This species is indigenous to Central Europe and has not been recorded in our area of concern (i.e. the Rhine-Meuse river district). Some *A. torrentium* populations in the Elbe basin have been influenced by translocations in the past (Petrušek et al. 2017; Pârvolescu et al. 2019), which could also have been the case in the Rhine-Meuse delta in 1956. The first North-American species, *F. limosus*, was recorded in the Rhine-Meuse delta in 1968 (Geelen 1978). Three years later, this species was observed in the area of concern. At present, nine invasive alien crayfish species have been reported for the entire Rhine-Meuse river delta and six of these species are recorded in the area of concern

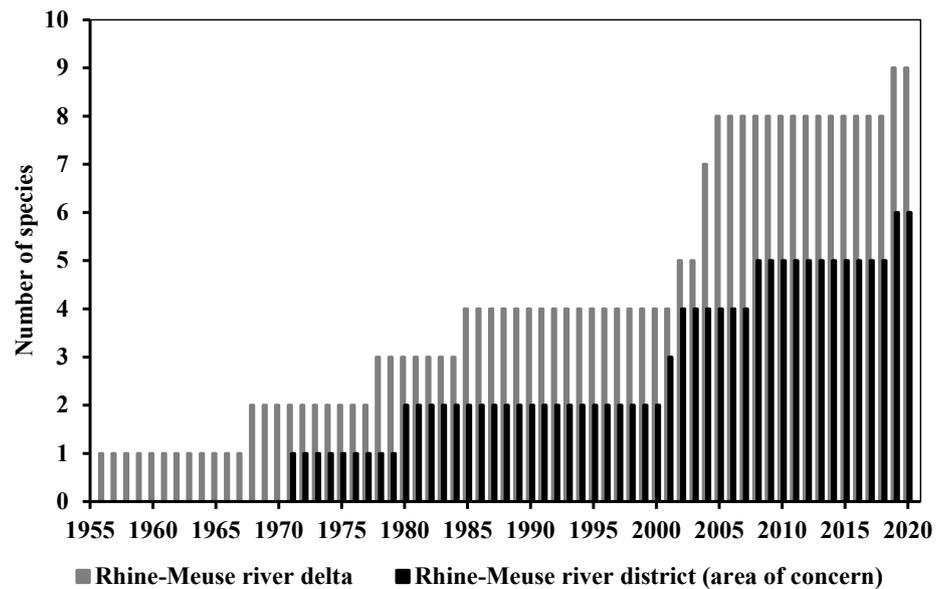


Figure 2. Cumulative number of alien crayfish species recorded for the Rhine-Meuse river delta and district since 1950.

(Figure 2; Table 1). Seven species have established populations in the Rhine-Meuse river delta, viz. *F. limosus*, *F. virilis*, *P. leniusculus*, Galician crayfish *Pontastacus leptodactylus* (Eschscholtz, 1823), white river crayfish *Procambarus acutus* (Girard, 1852), *P. clarkii* and *P. virginialis* (unpublished data April 2020, P. Lemmers). With the exception of *P. leniusculus* and *P. virginialis*, all these species have also been reported in the area of concern. *Faxonius immunis* has been reported from this area in 2019 (Ottburg et al. 2019), but species identification remains uncertain (see the section Risk assessment of species). In the area of concern, *Faxonius limosus* and *P. clarkii* are most wide spread (highest percentage of occupied grid cells). *Faxonius limosus*, *F. virilis*, *P. clarkii* and *P. virginialis* are listed as IAS of EU concern (European Commission 2016).

Risk assessment of species

The most important pathways for introduction of alien crayfish species in the area of concern are aquarium trade, food trade, fish bait and deliberate introductions (Chucholl 2013a; Rogers and Watson 2013; Faulkes 2015; Matthews et al. 2017b). All alien crayfish species with established populations in the Rhine-Meuse river delta will also spread to the river district through human interference and dispersal (viz. through the above-mentioned introduction routes). The success of invasive alien crayfish is attributed to reproductive plasticity on which (facultative) parthenogenesis (*F. limosus*, *P. virginialis*) and storage of sperm in females, high fertility and fecundity, long spawning periods, fast growth rates, an early age of sexual maturity and high degree of environmental tolerance or adaptation with an omnivorous diet (Buřič et al. 2011, 2013; Gherardi et al. 2011; Pârvulescu et al. 2015). The storage of sperm in a ventral body cavity (annulus ventralis) of

Table 2. Overview of assigned risk classifications for alien crayfish that are recorded or expected in the Rhine-Meuse river district. The levels of confidence of these risk classifications are provided in the Supplementary material Tables S1–S10. Species are ordered from high to low risk according to their Harmonia⁺ risk classification (overall risk score; maximum).

Scientific name	English name	Introduction	Establishment	Spread	Ecological effects	Socio-economic effects	Harmonia ⁺ score	References
<i>Procambarus clarkii</i> (Girard, 1852)	Red swamp crayfish	High	High	High	High	High	High	1–22
<i>Faxonius virilis</i> (Hagen, 1870)	Virile crayfish	High	High	High	High	High	High	8, 13, 23–25
<i>Procambarus acutus</i> (Girard, 1852)	White river crayfish	High	High	High	High	High	High	11, 13, 23
<i>Faxonius immunis</i> (Hagen, 1870)	Calico crayfish	High	High	High	High	High	High	8, 26–29
<i>Pacifastacus leniusculus</i> (Dana, 1852)	Signal crayfish	High	High	High	High	Medium	High	8, 13, 26–32
<i>Faxonius limosus</i> (Rafinesque, 1817)	Spiny-cheek crayfish	High	High	High	High	Low	High	8, 13, 22, 23, 37, 38
<i>Procambarus virginialis</i> Lyko, 2017	Marbled crayfish	High	High	High	High	Low	High	8, 22, 39–41
<i>Pontastacus leptodactylus</i> (Eschscholtz, 1823)	Galician crayfish	Medium	High	High	Medium	Low	Medium	8, 11, 23, 42, 43
<i>Austropotamobius torrentium</i> (Schränk, 1803)	Stone crayfish	Low	High	Low	Low	Low	Low	8, 43, 44

Colour scheme: Red, orange and yellow colour indicate that Harmonia⁺ risk scores (RS) were > 0.66 , $0.33 \leq RS \leq 0.66$ and < 0.33 , respectively; ¹: Angeler et al. (2001); ²: Gherardi et al. (2001); ³: Barbaresi et al. (2004); ⁴: Rodríguez et al. (2005); ⁵: Rodríguez et al. (2003); ⁶: Cruz and Rebelo (2005); ⁷: Gherardi (2006); ⁸: Souty-Grosset et al. (2006); ⁹: Gherardi and Acquistapace (2007); ¹⁰: Cruz et al. (2008); ¹¹: Koese and Soes (2011); ¹²: Koese et al. (2011); ¹³: Longshaw (2011); ¹⁴: NNSS (2011c); ¹⁵: Chucholl (2013b); ¹⁶: Koese and Vos (2013); ¹⁷: Brannelly et al. (2015); ¹⁸: Carvalho et al. (2016); ¹⁹: Gylstra et al. (2016); ²⁰: Souty-Grosset et al. (2016); ²¹: Van Dobben et al. (2017); ²²: Kouba et al. (2016); ²³: Lemmers et al. (2018); ²⁴: Rogers and Watson (2013); ²⁵: Roessink et al. (2017); ²⁶: Gelmar et al. (2006); ²⁷: Chucholl (2012); ²⁸: Herrmann et al. (2018); ²⁹: Ottburg et al. (2019); ³⁰: Peay (2001); ³¹: Bubb et al. (2004); ³²: NNSS (2011b); ³³: Vaeßen and Hollert (2015); ³⁴: Westman et al. (2002); ³⁵: Söderbäck (1991); ³⁶: Söderbäck (1995); ³⁷: NNSS (2011a); ³⁸: Pârvulescu et al. (2015); ³⁹: Holdich (2011); ⁴⁰: Soes (2016); ⁴¹: Feria and Faulkes (2011); ⁴²: Stucki and Romer (2001); ⁴³: Expert judgement; ⁴⁴: Pârvulescu et al. (2016).

females may facilitate a) multiple paternity to increase of genetic diversity, b) mate selection, and c) increasing chance of successful mating at low population densities (Yue et al. 2010; Buřič et al. 2013). The absence of natural parasites, pathogens and predators in introduced areas is likely to increase the survival of invasive alien crayfish (Aquiloni et al. 2005; Gherardi 2006; Gherardi and Barbaresi 2008; Hanshew and Garcia 2012). This allows invasive alien crayfish to establish populations in a wide variety of habitats. The probability of establishment of *P. leptodactylus* and *A. torrentium* is assessed to be high in case of introduction of the species (Table 2). However, these species are not expected to establish populations in co-occurrence with North American crayfish species due to their susceptibility to the crayfish plague. Only one population of *P. leptodactylus* is known from the Rhine-Meuse river delta. This population has been established in a reservoir that is isolated from locations where North American species occur (Koese and Soes 2011). *Procambarus virginialis* is a parthenogenetic species (Martin et al. 2010). This implies that large populations can be formed from a single individual (Vogt et al. 2004; Feria and Faulkes 2011). *Procambarus virginialis* is reported almost annually (NDFP 2019), likely due to a high propagule pressure as the species is popular in aquarium trade (Holdich 2011). The risk of establishment in the area of concern for this species is high, since the habitat suitability is

optimal and *P. virginialis* can survive low winter temperatures (Feria and Faulkes 2011; Veselý et al. 2015). The risk of establishment for *F. immunis* is very high, since this species has already established populations in similar habitats in the upstream parts of the Rhine River in Germany, where it is spreading rapidly (Gelmar et al. 2006; Chucholl 2012; Herrmann et al. 2018). The risk of spread of crayfish species by natural means is very high since much suitable habitat is hydrologically interconnected via rivers, canals and smaller watercourses (Figure 1). The risk of spread via human activities has also been estimated to be high as there is a trade in live animals for consumption (e.g. *P. clarkii*) (Lemmers et al. 2018). Temporal distribution maps show that alien crayfish are regularly recorded at locations not linked to earlier-known areas of occurrence (NDFP 2019), which indicates release by humans or long-range migration of crayfish pioneers over land.

Crayfish can behave like ecosystem engineers (Statzner et al. 2000, 2002). At high crayfish densities, ecosystems can change from clear (species-rich) to turbid and nutrient-rich (species-poor) systems (Angeler et al. 2001; Rodríguez et al. 2003, 2005). The strongest impact of invasive crayfish can be observed in ecosystems suffering from anthropogenic disturbance, such as eutrophication or construction of steep banks (Hobbs and Huenneke 1992; Van der Wal et al. 2013; Van Dobben et al. 2017). The impact is mainly related to their burrowing behaviour and generalist feeding habits. Digging by crayfish leads to disturbance in the nutrient balance as nutrients are released from the soil, which induces turbidity, leads to negative effects on biodiversity and limits success of ecological restoration (Gherardi and Acquistapace 2007; Van der Wal et al. 2013; Souty-Grosset et al. 2016). Crayfish are omnivorous and can have negative effects on biodiversity by predation on amphibians (mainly larvae), fish and aquatic macroinvertebrates, and by fragmentation and consumption of aquatic plants (Gherardi et al. 2001; Geiger et al. 2004; Cruz and Rebelo 2005; Gherardi and Barbaresi 2008). Negative effects increase with increasing crayfish density (Gherardi and Acquistapace 2007). North American crayfish species are potential carriers of the crayfish plague pathogen *A. astaci* for which they are resistant. European crayfish species are highly susceptible to *A. astaci* and the spread of this fungus threatens indigenous crayfish populations in Europe (Holdich and Reeve 1991; Pârvulescu et al. 2012; Filipová et al. 2013; Ungureanu et al. 2020). In the area of concern, *A. astaci* contributed to near-extinction of *A. astacus* (Geelen 1978). However, a recent study in Eastern Europe found a *P. leptodactylus* population infected by *A. astaci*, suggesting that this indigenous host and the crayfish plague pathogen can coexist in a natural equilibrium (Panteleit et al. 2018; Ungureanu et al. 2020). Crayfish can also be reservoirs of a wide range of other infectious and non-infectious agents, including bacteria, viruses, fungi and protists as well as parasites (Longshaw 2011; Brannelly et al. 2015).

Interspecific competition is also a key factor for species displacement in the wild. Competition for shelter and food is one of the most important mechanisms for several invasive alien crayfish species to displace native taxa, such as *A. astacus*. *Astacus astacus* co-occurred 30 years in a Finnish lake with *P. leniusculus* without any signs of *Aphanomyces astaci*. However, after 30 years the *A. astacus* population collapsed as a result of interspecific competition and harvesting (Westman et al. 2002). Similarly, an *A. astacus* population in a Swedish lake declined from 40% to 1% in four years due to interspecific competition by *P. leniusculus* (Söderbäck 1995). *Pacifastacus leniusculus* strongly dominates *A. astacus* and the latter species can be excluded when both species compete for resources (Söderbäck 1991). Contrary, laboratory studies found that *A. astacus* was dominant over *F. limosus* (Maiwald et al. 2006) and *F. limosus* had a very low survival rate (Kozák et al. 2007). When these species co-occur in the wild, however, the diurnal activity of *A. astacus* increases which makes the species more vulnerable for predation (Musil et al. 2010). *Pontastacus leptodactylus* can show aggressive interaction with *A. astacus*, potentially resulting in displacement of the latter species (Stucki and Romer 2001). No studies were found that describe competition between *A. astacus* and *F. immunis*, *F. virilis*, *P. acutus*, *P. clarkii* or *P. virginalis*. Several experimental studies show that co-occurring alien crayfish species may also compete with each other, for instance *P. leniusculus* with *F. limosus* (Hudina et al. 2011), *F. limosus* with *P. virginalis* (Linzmaier et al. 2018) and *P. clarkii* with *P. virginalis* (Hossain et al. 2019). Interspecific competition can determine the progression of crayfish invasions and may result in differential impacts on native species and ecosystems.

Seven species, viz. *F. immunis*, *F. limosus*, *F. virilis*, *P. acutus*, *P. clarkii*, *P. leniusculus* and *P. virginalis*, showed a high-risk score for ecological effects and the confidence levels of these scores were high (Table 2; Figure 3; Supplementary material Tables S1–S10). All of these North American species have significant negative impacts on biodiversity and the functioning of ecosystems (Table 2 and supporting references). *Austropotamobius torrentium* showed a low risk score with a high confidence score, as there is no evidence for negative impacts on biodiversity and ecological functioning in the Rhine-Meuse river district. *Pontastacus leptodactylus* scored a medium risk with a medium level of confidence in accordance with some published evidence for aggressive interaction of this species with *A. astacus* (Stucki and Romer 2001).

Socio-economic effects of alien crayfish include instability of dikes in peatlands, acceleration of bank erosion and increase of sedimentation rates, and these effects are mainly related to their burrowing activities (Table 2). However, these effects differ per species and habitat type (Kouba et al. 2016; Pârvulescu et al. 2016). Due to their typical burrowing behaviour, *F. immunis*, *F. virilis*, *P. acutus* and *P. clarkii* scored a high risk for socio-economic effects

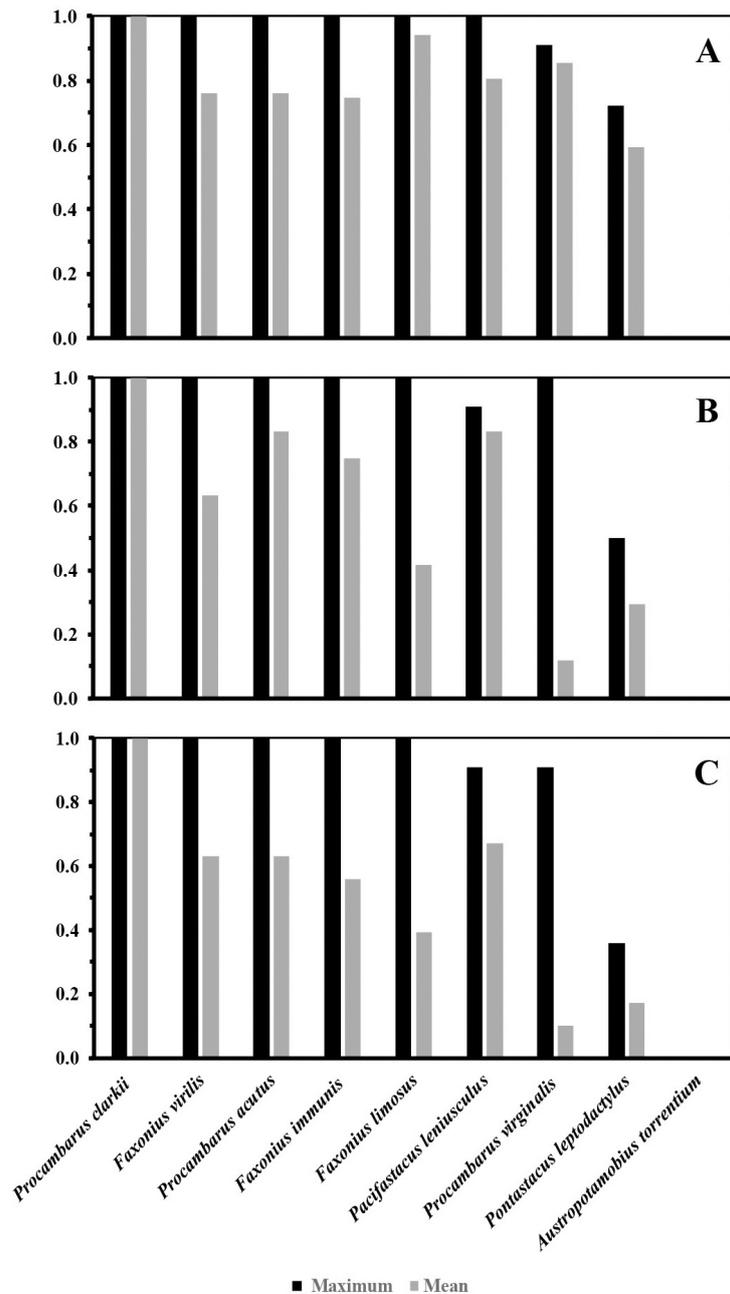


Figure 3. Invasion (A), impact (B) and overall (C) risk scores for alien crayfish species in the Rhine-Meuse river district, using the Harmonia+ scheme for the first-line risk assessment. Ordering of species is from high to low risk according to the maximum values of their overall risk score.

with medium to high confidence levels. Although literature on the risks of *P. acutus* is scarce, it is supposed that this species represents a similar risk as *P. clarkii*. Burrowing damage by crayfish in the river district has increased considerably in recent years (Lemmers et al. 2018), resulting in water safety risks by instability of dikes in peatland areas, erosion of banks and additional sediment dredging to ensure water discharge in drainage ditches and canals. For instance, during maintenance of dikes surrounding the UNESCO World Heritage Site Kinderdijk, an extensive network of burrows of *P. acutus*, together with those of the European mole *Talpa*

europaea (Linnaeus, 1758) and muskrat *Ondatra zibethicus* (Linnaeus, 1766) was detected (Lemmers et al. 2018). Burrowing of *F. virilis*, *P. acutus* and *P. clarkii* has also led to accelerated bank erosion in the area of concern (Lemmers et al. 2018). The sediment release during burrowing activities increases sedimentation rates up to 25% and reduces water discharge capacity of drainage ditches in areas with peaty soils (Gylstra et al. 2016). This entails extra dredging by water authorities to ensure the water discharge. *Pacifastacus leniusculus* scored a medium risk for socio-economic effects. The risk scores of *A. torrentium*, *F. limosus*, *P. leptodactylus* and *P. virginalis* were low with medium to high confidence scores. Scientific evidence for socio-economic effects of these species is not available. The vast majority of publications report on ecological effects of invasive crayfish. These effects may deteriorate the ecological status of water systems and limit compliance with mandatory European Water Framework Directive (WFD) and Natura 2000 objectives. Deterioration of the ecological status of WFD water systems from the baseline in the year 2000 is not allowed. The ecological status is measured using standards for three types of quality elements (European Parliament & Council of the European Union 2000): biological (macroinvertebrates, fishes, phytoplankton, water flora), physico-chemical (e.g. dissolved oxygen, pH and nutrient balance), and hydro-morphological (e.g. alteration of natural watercourses and degree of naturalness). Negative effects caused by crayfish are to be expected on all three WFD quality elements (Van der Meulen et al. 2009), with higher densities potentially increasing the risk of a negative assessment value for the ecological status.

Assessments of seven species resulted in a high overall risk score (invasion \times impact) for the Rhine-Meuse river district, *viz.* *F. immunis*, *F. limosus*, *F. virilis*, *P. acutus*, *P. clarkii*, *P. leniusculus* and *P. virginalis* (Table 2; Figure 3). *Pontastacus leptodactylus* showed a medium risk score and *A. torrentium* had a low risk score. The level of confidence of risk scores for species was medium to high since the severity of their ecological and socio-economic impacts were moderately acknowledged to well-documented in the scientific literature, respectively (Tables S1–S10).

Available management measures

Several measures for management of crayfish populations were examined, *viz.* application of physical barriers, chemical control, use of pheromones, introduction of diseases, commercial trapping, control trapping by governmental bodies, introduction of natural predators and enhancing natural resilience by stimulating robustness of aquatic ecosystems (Table 3). Most measures are not species specific and appeared to be unsuitable for eradication of crayfish.

Table 3. Overview of available management measures for controlling invasive alien crayfish.

Management measure	Species specificity	Elimination successful
Application of physical water barriers ¹⁻⁵	No	No, populations of some species can be controlled
Chemical control ^{6,7}	No	Yes
Use of pheromones ^{8,9}	Yes	No
Introduction of diseases ^{9,10}	No	No
Commercial trapping ^{3,11-13}	No	No
Control fishery by governmental bodies ¹⁴	No	No
Introduction of natural predators ¹⁵⁻¹⁷	No	No, populations of some species might be controlled
Enhancing natural resilience by stimulating robustness of aquatic ecosystems ^{3,7,16,17}	No	No, populations of some species might be controlled

¹: Kerby et al. (2005); ²: Dana et al. (2011); ³: Gherardi et al. (2011); ⁴: Rosewarne et al. (2013); ⁵: Benejam et al. (2015); ⁶: Sandodden and Johnsen (2010); ⁷: De Hoop et al. (2016); ⁸: Aquiloni and Gherardi (2010); ⁹: Freeman et al. (2010); ¹⁰: Davidson et al. (2010); ¹¹: Roessink et al. (2009); ¹²: Van Emmerik (2010); ¹³: Van Tilburg (2010); ¹⁴: Heuts and Van der Wekken (2011); ¹⁵: Rach and Bills (1989); ¹⁶: Hein et al. (2007); ¹⁷: Hansen et al. (2013).

Control strategies

Since eradication of invasive alien crayfish established in a hydrologically connected network of aquatic ecosystems was not regarded feasible (Table 3), six strategies for their population control were identified:

1. No control measures and rely on natural processes;
2. Commercial crayfish trapping;
3. Commercial crayfish trapping combined with additional efforts by water authorities;
4. Biological control;
5. Chemical control;
6. Enhancing ecological robustness and resilience of water systems.

Based on the results of the literature review on management measures, the feasibility of the strategies for population control was assessed using multiple criteria (Table 4). An unweighted MCA revealed that strategies 3 and 6 scored highest and ranked best.

Discussion

Three North American crayfish species with established populations in the Rhine-Meuse river district are mentioned on the List of the 100 worst alien species for Europe. Ranking from high to low, this list includes *P. clarkii* (3), *F. virilis* (68) and *F. limosus* (85) (Nentwig et al. 2017). These species are also listed as IAS of EU concern (European Commission 2016). Their adverse ecological and socio-economic effects have been demonstrated in numerous international studies (Table 2 and supporting references). The North American *P. acutus* has also established populations in the Rhine-Meuse river district but is not included in the abovementioned European top-100

Table 4. Expert-based assessment of impacts and feasibility of the six identified management strategies for population control of invasive alien crayfish in the Rhine-Meuse river district.

Management strategy	Effectivity on the short term	Effectivity on the long term	Biodiversity conservation	Expected risk for water safety	Expected public acceptance	Expected compatibility with the policy and management of water authorities	Expected certainty of risk assessment	Expected short term costs	Expected long term costs	Unweighted Multi Criteria Analysis score	Ranking
1. No control measures and rely on natural processes	Very low ¹⁻⁶	Very low ¹⁻⁷	Very low ^{3,4,7-9}	Very low ¹⁰	Low ¹⁰	Low ¹⁰	High ¹⁰	Very low ¹⁰	Very low ¹⁰	22	6
2. Commercial crayfish trapping	Medium ^{4,11-15}	Medium ^{4,11-15}	Medium ¹⁶	Low ¹⁰	Medium ¹⁰	High ¹⁰	Medium ¹⁰	Low ¹⁰	Low ¹⁰	29	3
3. Commercial crayfish trapping combined with additional efforts by water authorities	High ^{4,11,14,15,17,18}	High ^{4,11,14,15,17,18}	High ¹⁶	Medium ¹⁰	Medium ¹⁰	High ¹⁰	Medium ¹⁰	Medium ¹⁰	Medium ¹⁰	31	2
4. Biological control	High ^{4,12,17,19-21}	Medium ^{4,12,17,19-21}	Medium ^{4,17,21}	Medium ¹⁰	Low ¹⁰	Medium ¹⁰	Low ¹⁰	Medium ¹⁰	Medium ¹⁰	26	4
5. Chemical control	Very high ^{4,21,22}	Medium ^{4,21}	Very low ²²	Very high ¹⁰	Very low ¹⁰	Very low ¹⁰	High ¹⁰	Low ^{10,22}	High ¹⁰	25	5
6. Enhancing ecological robustness and resilience of water systems	Medium ¹²	Very high ^{4,12,14,16,17,21,23-30}	Very high ^{16,17,21,24,26-35}	Medium ¹⁰	High ¹⁰	High ¹⁰	Medium ¹⁰	Very high ¹⁰	Low ¹⁰	32	1

¹: Torchin et al. (2003); ²: Colautti et al. (2004); ³: Gherardi and Acquistapace (2007); ⁴: Freeman et al. (2010); ⁵: Mastitsky et al. (2010); ⁶: Gendron et al. (2012); ⁷: Alcorlo et al. (2009); ⁸: Taugbol and Skurdal (1993); ⁹: Souty-Grosset et al. (2016); ¹⁰: Expert judgement; ¹¹: Peay (2009); ¹²: Roessink et al. (2009); ¹³: Gherardi et al. (2011); ¹⁴: Hansen et al. (2013); ¹⁵: Van Emmerik (2010); ¹⁶: Lemmers et al. (2018); ¹⁷: Gherardi et al. (2011); ¹⁸: Heuts and van der Wekken (2011); ¹⁹: Davidson et al. (2010); ²⁰: Oliveira and Hilker (2010); ²¹: De Hoop et al. (2016); ²²: Sandodden and Johnsen (2010); ²³: Rach and Bills (1989); ²⁴: Czamecki et al. (2003); ²⁵: Hein et al. (2007); ²⁶: Carol et al. (2009); ²⁷: Copp et al. (2009); ²⁸: Musseau et al. (2015); ²⁹: Soes (2018); ³⁰: Lemmers et al. (2019); ³¹: Beja (1996); ³²: Correia (2001); ³³: Neveu (2001); ³⁴: Rodriguez (2006); ³⁵: Amori and Battisti (2008).

nor listed as IAS of EU concern. However, the Harmonia⁺ risk classification for this species is also high (Table 2). Listing of *P. acutus* as a high-risk species at a European level is recommended.

The current Dutch policy regarding management of IAS of EU concern in the Rhine-Meuse river district is covered in a national master plan (Ministry of Economic Affairs 2016). Crayfish species of EU concern are currently widespread (Lemmers et al. 2018; Soes 2018; De Jong et al. 2019; Koese et al. 2019). Their eradication in hydrologically connected aquatic ecosystems is not regarded feasible. The Dutch regulation on trapping alien crayfish states that commercial fishing will be implemented as a measure for population control (Staatssecretaris van EZ 2016). Commercial crayfish trapping in inland waters is exempted from the restrictions of the EU regulations on keeping, transporting, marketing and using or exchanging these species. The exemption is also granted for the subsequent storage, trade, transport, keeping, using or destruction of animals, and all immediate related activities. However, the effectivity of commercial trapping for control of invasive crayfish species of EU concern is not yet scientifically supported. Feasible management strategies aiming at prevention of significant adverse effects by realizing admissible densities of invasive crayfish species should be implemented in the national policy. The

outcomes of our risk assessments allow national and regional prioritisation of species using ecological as well as socio-economic risk categories (Table 2; Figure 3).

In the risk assessment of crayfish species, interspecific competition between the indigenous *A. astacus* and invasive alien crayfish has been assessed. Invasive species displacements are not part of the Harmonia⁺ protocol (D'hondt et al. 2015). Therefore, these effects have not been considered in our risk assessments. However, there is much evidence that invasive alien crayfish species can replace each other (Jimenez and Faulkes 2011; Hanshew and Garcia 2012; Fořt et al. 2019; Hossain et al. 2020). In the case of co-occurring invasive crayfish species, dominance shifts may alter the effects on biodiversity and ecosystems. Field knowledge on invasive crayfish species displacement in the Rhine-Meuse river district is still lacking. As hundreds of freshwater crayfish species are known worldwide (Crandall and De Grave 2017), it is highly likely that more species will be introduced and may establish in the EU and the Rhine-Meuse river district, where they pose potential risks to biodiversity and the functioning of aquatic ecosystems, with potentially high (financial) consequences. Species distribution modelling can be used to identify crayfish species that show a high climate and habitat match with north-western Europe (Faulkes 2015). A generic ban on the import and trade of these species would be an important step forward to prevent introduction of new invaders. Such a ban will be most effective if implementation occurs in cooperation with all neighbouring countries or at EU level. Pending this regulating, increasing public awareness concerning negative impacts of invasive alien crayfish is recommended in order to prevent their introduction and spread.

Available management measures

The overview of management measures shows that a wide range of methods is available to control invasive crayfish populations (Table 3). Chemical control is the only measure that might completely eradicate invasive alien crayfish (Sandodden and Johnsen 2010; Freeman et al. 2010; Gherardi et al. 2011). Some crayfish species might be controlled by application of dispersal barriers, introduction of natural predators or enhancing natural resilience by stimulating robustness of aquatic ecosystems (Table 3). The application of physical barriers in watercourses may prevent invasive crayfish from colonising upstream sites (Kerby et al. 2005; Dana et al. 2011; Rosewarne et al. 2013; Benejam et al. 2015) However, this measure is not desirable in the Rhine-Meuse river district because the European Water Framework Directive (WFD) requires that watercourses are passable for migratory fish species (European Parliament & Council of the European Union 2000).

In the United States of America, native fish is used to control small crayfish, which are difficult to trap. For instance, largemouth bass *Micropterus*

salmoides (Lacépède, 1802) was used to control *F. immunis* and this approach ultimately resulted in a greater reduction of crayfish populations than trapping (Rach and Bills 1989). In another study carried out in an isolated lake (Sparkling Lake) in the United States of America, crayfish traps were set for the capture of rusty crayfish *Faxonius rusticus* (Girard, 1852) during four consecutive years (2001–2005). Intensive crayfish trapping in combination with introduction of predatory sunfish (*Lepomis* sp.) resulted in a 95% reduction in the catch rates (Hein et al. 2007). After four years without trapping, the crayfish abundance was still reduced by 99% as a result of natural control by sunfish (Hansen et al. 2013). According to European and Dutch nature law, it is forbidden to release alien species into the wild. However, introduction of native predators to control crayfish populations is allowed and has been used (Aquiloni et al. 2010; Musseau et al. 2015).

Natural regulation of crayfish populations in unnatural watercourses is not to be expected. Therefore, ecosystems must be made more invasive-resistant by stimulating crayfish consuming species and reducing the carrying capacity of these systems for crayfish. Improving the habitat quality, e.g. by transforming steep banks to nature-friendly banks or restoring brooks to their original state, is a promising measure (Lemmers et al. 2019). Different types of predators can complement each other (e.g., water fowl, fish, and mammals). Predation pressure on alien crayfish populations in healthy ecosystems will be higher than in unnatural and disturbed systems. Relevant crayfish predating water fowl in the Rhine-Meuse river delta are herons (Ardeidae), storks (Ciconiidae), cormorants (Phalacrocoracidae), loons (Gaviidae) and grebes (Podicipedidae) (Carboneras and Bonan 2018; Elliott 2018; Llimona et al. 2018; Martínez-Vilalta and Motis 2018; Orta 2018). Common fish species that prey on crayfish are eel *Anguilla anguilla* (Linnaeus, 1758), European pike *Esox lucius* (Linnaeus, 1758), perch *Perca fluviatilis* (Linnaeus, 1758) and European catfish *Silurus glanis* (Burton, 1836) (Blake and Hart 1993; Söderbäck 1994; Elvira et al. 1996; Neveu 2001; Czarnecki et al. 2003; Aquiloni et al. 2010; Carol et al. 2009; Copp et al. 2009; Dörner et al. 2009; Gherardi et al. 2011; Reynolds 2011; Musseau et al. 2015). The effect of predatory fish on crayfish populations likely depends on habitat type and quality (Freeman et al. 2010). Mammals occurring in the Rhine-Meuse river district that have been observed to prey on crayfish are brown rat *Rattus norvegicus* (Berkenhout, 1759) European otter *Lutra lutra* (Linnaeus, 1778) and red fox *Vulpes vulpes* (Linnaeus, 1758) (Beja 1996; Correia 2001; Amori and Battisti 2008; Heuts 2012).

Lemmers et al. (2018) derived a generic threshold value for preventing significant adverse effects of crayfish using density-effect relationships of ten studies (Rodríguez et al. 2003; Gherardi and Acquistapace 2007; Banha and Anastácio 2011; Chucholl 2013b; Van der Wal et al. 2013; Carvalho et

al. 2016; Jackson et al. 2016; Crombaghs et al. 2017; Roessink et al. 2017; Van Dobben et al. 2017). The maximum threshold density is estimated 0.9 individuals m^{-2} . However, the uncertainty of this value is high because information on density-effect relations for various crayfish species and different types of aquatic ecosystems is scarce. Scientific sound threshold densities for various species and systems are vital for decision making of water authorities due to high costs of population control measures. Moreover, threshold densities will be required to set appropriate goals for (commercial) crayfish trapping.

Management strategies

1. No control measures and rely on natural processes

It is sometimes suggested that taking no control measures is an option because the problems with invasive species will eventually be solved by natural processes (Brown and Sax 2004; Simberloff 2009). This view is based on the “enemy release” and “boom and bust” hypotheses. These hypotheses imply that a population of invasive alien species outside their natural range is not suppressed by diseases, parasites and natural predators. The lack of natural population suppression during the initial invasion phases increases their survival rate and reproductive success (Torchin et al. 2003; Colautti et al. 2004; Mastitsky et al. 2010; Gendron et al. 2012; Strayer et al. 2017). When, over time, native parasites and predators become familiar with invaders or diseases and/or parasites are introduced from their native range, the population of these species will be naturally regulated or may even collapse. However, it is unpredictable within what timeframe this will occur. This makes it difficult or even impossible to predict if, and when, populations of invasive alien species will collapse (Lester and Gruber 2016; Strayer et al. 2017). Moreover, it is likely that these species will be replaced by more harmful species, as is currently the case with alien gobies and gammarids in large rivers (Leuven et al. 2009; Van Kessel et al. 2013; Leuven 2017). The collapse of populations of invasive species is often manifested only on the long run (decades to centuries). In the Lower Danube, long-term coexistence between a native population *P. leptodactylus* and invasive *F. limosus* population is recorded (Pacioglu et al. 2020). However, it comes with a cost for the native species resulting in lower genetic diversity, diminished trophic endpoints and lower growth rates. Adverse impacts and costs for mitigation of ecological and socio-economic effects will be evident during the boom of invasive species populations. Since the densities of *P. clarkii* in Spain are still high 30 years after introduction (Alcorlo et al. 2009), it is not expected that their populations in the Rhine-Meuse river district will decrease in the short term. Implementation costs of this management strategy are very low, however, the ecological damage and socio-economic

costs of invasive alien crayfish will further increase (Gherardi 2010). Therefore, public support for this management strategy is expected to be low. Failure to control the risks of hydraulic damage, deterioration of the water quality or threat to biodiversity by invasive alien crayfish is not compliant with the duty of care and objectives of water authorities.

2. Commercial crayfish trapping

The Dutch government's master plan for managing IAS of EU concern states that effective and proportionate measures to reduce the population size of alien crayfish or to prevent their spread are not available (Ministry of Agriculture, Nature and Food Quality 2018). However, commercial crayfish trapping is implemented as a possible measure limiting their local nuisance to a certain extent (Ministry of Agriculture, Nature and Food Quality 2018). There is no scientific evidence that only extensive (commercial) trapping of crayfish is effective or has led to the prevention of their expansion in connected aquatic ecosystems (Peay 2009; Van Emmerik 2010). Further research is needed for a definite statement about the effectiveness of commercial trapping on population size and impact of alien crayfish. Commercial trapping will mainly be concentrated at locations with high densities (*viz.* large, unnatural watercourses). Moreover, commercial trapping will be ceased if catches become too low in relation with costs and efforts of trapping. The national master plan does not offer sufficient prospects for tackling crayfish problems in small regional watercourses and in aquatic ecosystems of nature reserves. Especially in nature reserves it is crucial to manage crayfish populations to restore the habitat of endangered threatened native species (such as red-listed dragonflies). If it is not feasible to eliminate crayfish populations, their spread and establishment in regional aquatic ecosystems will continue. This does not solve the adverse ecological and socio-economic risks for water safety in regional water systems. Commercial trapping is a low-cost measure for the national government and water authorities, because catching and selling of crayfish for human consumption is the economic driving force behind it. The costs for governments are thereby limited to planning, coordination, monitoring, evaluation of effectiveness and assuring consumer safety. An important concern of this management strategy is that illegal stocking will take place or that crayfish populations will not be sufficiently reduced, since commercial fishermen have a financial interest in conserving crayfish populations at high levels. Public support for this measure will diminish if the problems are not solved or risks increase. Commercial fishermen have permits and resources in various water systems to carry out the management envisaged in the master plan. The management strategy fits in with the policy and intended invasive species management of the national and provincial governments, and also guides the implementation of measures by water authorities. However, for many water systems commercial trapping

permits have not (yet) been issued and water authorities do not always own fishing or trapping rights.

3. Commercial crayfish trapping combined with additional efforts by water authorities

In addition to the management of invasive alien crayfish by commercial trapping as envisaged in the national master plan (Management strategy 2), additional trapping by water authorities and possibly also by well-informed citizens with permits for crayfish trapping is a feasible strategy. Control of muskrats by water authorities in various areas appeared to be very effective (Van Loon et al. 2016). An extension of the remit of muskrat control officers can be considered. The use of professional rat-catchers from water authorities for invasive alien crayfish control fits in well with this management strategy. Heuts and Van der Wekken (2011) investigated opportunities for expansion of tasks of muskrat control officers and concluded that monitoring by these persons already provides valuable information about the distribution and density of alien crayfish. In addition, muskrat catchers enter watercourses that may not be suitable or commercially interesting for commercial fishing, which covers a large control area. However, the remove of invasive alien crayfish has not led to a decrease of their population on the long run (Peay 2009). The effectiveness of this management strategy is assessed to be favourable if it will be combined with measures to reduce the carrying capacity of ecosystems for crayfish (Management strategy 6). Trapping avoids young and small individuals (Figler et al. 1999; Holdich et al. 1999). Therefore, healthy ecosystems with sufficient top-down regulation by predators are necessary for sustainable control of crayfish. This management strategy complies with current policy of water authorities. Public support for this strategy is expected to be high when it will be combined with management strategy 6. The efforts of water authorities must aim at reducing the population sizes or density of crayfish below threshold values for significant adverse effects and may therefore conflict with the interests of sustainable commercial trapping.

4. Biological control

Here, the biological management strategy refers to the use of diseases or pathogens to control invasive crayfish populations. Crayfish species are sensitive to a wide variety of bacteria, fungi and viruses (Longshaw 2011). Davidson et al. (2010) have explored several microbial control agents to control invasive crayfish and suggest that control by these agents is possible. However, the side effects of such biological control agents on native crustaceans (e.g. gammarids and asellids) and other (macro)invertebrates have been poorly investigated. Once effective and species-specific biological methods have been developed, implementation costs are expected to be

lower compared to traditional control methods (such as chemical control and crayfish trapping). Public support for the implementation of this management strategy is expected to be very low. Unforeseen and adverse side effects of natural enemies cannot be ruled out in advance. Potential long-term effects on the ecosystem cannot be predicted with high certainty, taking into account the current body of knowledge about these effects. Applying control measures with unprecedented risks do not fit within the policy of the water authorities. In addition, the native *A. astacus* will very likely be susceptible to such diseases and pathogens. Currently, possibilities for reintroduction of *A. astacus* are explored to reduce the risk of regional extinction and to restore lotic ecosystems (Ottburg and Roessink 2012; Roessink and Ottburg 2012).

5. Chemical control

Only a single study mentions the possible elimination of invasive alien crayfish in five ponds, using a chemical pesticide (Sandodden and Johnsen 2010). The costs of this measure were estimated €19000 for two treatments per pond, which is relatively low compared to the expected costs of other management strategies. However, potentially suitable chemicals for control of crayfish, such as rotenone, are not permitted by law for use in water systems because of environmental risks and effects on native biodiversity (De Hoop et al. 2015, 2016). Therefore, the use of such methods is considered unrealistic. Public and political support for chemical control in aquatic ecosystems is expected to be very low. The use of chemical control in aquatic ecosystems does not comply with current policy of water authorities. Apart from legal bottlenecks, the use of chemicals is not considered effective in an open network of interconnected watercourses.

6. Enhancing ecological robustness and resilience of water systems

The reason why invasive crayfish species reach high densities in various types of interconnected aquatic ecosystems in the Rhine-Meuse river district is the high carrying capacity due to high nutrient loads and low top-down regulation by native predators. On the one hand, these species are probably facilitated by the unnatural manmade habitat and on the other hand, such a habitat is characterized by low densities of native predators and low top-down regulation of crayfish densities. Ecological rehabilitation of watercourses should be focussed on increasing habitat suitability and accessibility for predators of alien crayfish. Thereby, robustness and resilience of these ecosystems are enhanced. This can be achieved by rehabilitation measures such as improving water quality, re-meandering of watercourses and creating natural banks (Lemmers et al. 2019). Promoting the regulation of invasive crayfish on the long run through natural control is considered a feasible and sustainable strategy. This strategy will also benefit native biodiversity. Active trapping of

reproducing crayfish (described in management strategy 3) might have an additional effect on the size of crayfish populations. The costs of implementing this management strategy on a short-term are likely to be very high. Naturalizing of watercourses is expensive and cannot be realised within a few years. However, in the context of the European WFD and Habitat Directive obligations, watercourses are being restored to a good ecological status. Viewed over a longer period, the costs of these measures are low since continuous control measures are not required and other water quality objectives will also be achieved. The public support for this management strategy is expected to be high because biodiversity in general benefits and water safety is likely to increase in problem areas due to suppression of crayfish populations. Enhancing ecological robustness and resilience of watercourses is a main goal of water authorities, which is also pursued in the context of the European WFD.

A promising combination of management strategies

The carrying capacity of aquatic ecosystems for alien crayfish in the Rhine-Meuse river district is currently high. Invasive crayfish species are partially facilitated by unnatural, manmade habitats with low densities of predators. Natural control of crayfish populations by predators will not be sufficient to prevent their adverse ecological effects. Therefore, ecological rehabilitation of water systems at a catchment scale is required for effective and long-term control of crayfish populations. A promising rehabilitation approach combines both highest ranked management strategies according to our MCA (Table 4). This comprises: 1) enhancing the resilience and robustness of aquatic ecosystems, and 2) extensive commercial fishing of crayfish and additional removal by professional trappers commissioned by water authorities for a longer period of time at high-risk sites (e.g. areas with vulnerable dikes and banks) and in watercourses that are not suitable for commercial fishing.

Conclusions

Invasive crayfish species rapidly spread via the network of interconnected watercourses in the Rhine-Meuse river district. Most species disperse over land to hydrologically isolated water systems. There also remains a high risk of spread via deliberate and unintentional releases from aquarium trade (e.g. *P. virginalis*) or live animal trade for consumption (e.g. *P. clarkii*). *Faxonius virilis*, *P. acutus* and *P. clarkii* pose the highest ecological and socio-economic risks and already have established populations in the Rhine-Meuse river district. Establishment of three other high-risk species is expected (*F. immunis*, *P. leniusculus* and *P. virginalis*). Eradication of invasive alien crayfish will not be feasible nor cost-effective in open networks of interconnected watercourses. Enhancement of robustness and resilience of aquatic ecosystems to control population densities of crayfish

is a promising, cost-effective strategy on the long run. This strategy reduces the carrying capacity of crayfish by enhancing naturalness of watercourses and facilitating population recovery of native species that predate on crayfish. These measures can be complemented with active removal of crayfish over a longer period at high-risk sites (e.g. areas with vulnerable dikes and banks). Increase of public awareness and attention for introduction prevention of new potentially invasive alien crayfish species in the entire EU is urgent. It is also important to derive sound limit values for densities of various crayfish species in order to prevent significant adverse environmental effects and socio-economic impacts.

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Supplementary material

The following supplementary material is available for this article:

- Table S1.** Risk scores of alien crayfish species.
- Table S2.** Risk classification of *Austropotamobius torrentium*.
- Table S3.** Risk classification of *Faxonius immunis*.
- Table S4.** Risk classification of *Faxonius limosus*.
- Table S5.** Risk classification of *Faxonius virilis*.
- Table S6.** Risk classification of *Pacifastacus leniusculus*.
- Table S7.** Risk classification of *Pontastacus leptodactylus*.
- Table S8.** Risk classification of *Procambarus acutus*.
- Table S9.** Risk classification of *Procambarus clarkii*.
- Table S10.** Risk classification of *Procambarus virginalis*.

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