Proceedings of the 18th International Conference on Aquatic Invasive Species (April 21–25, 2013, Niagara Falls, Canada)

Review

The profile of a 'perfect' invader – the case of killer shrimp, *Dikerogammarus villosus*

Tomasz Rewicz[1]*, Michal Grabowski[1], Calum MacNeil[2] and Karolina Bącela-Spychalska[1]

[1]*Department of Invertebrate Zoology and Hydrobiology, University of Lodz, 12/16 Banacha, 90-237 Lodz, Poland*

[2]*Department of Environment, Food and Agriculture, The Isle of Man Government, Thie Slieau Whallian, Foxdale Road, St. Johns IM4 3AS, Isle of Man, The British Isles*

E-mail: tomek.rewicz@gmail.com (TR), michalg@biol.uni.lodz.pl (MG), Calum.MacNeil@gov.im (CML), karolina@biol.uni.lodz.pl (KBS)

*Corresponding author

Abstract

The 'killer shrimp', *Dikerogammarus villosus*, has been recognised as one of the 100 worst alien species in Europe, in terms of negative impacts on the biodiversity and functioning of invaded ecosystems. During the last twenty years, this Ponto-Caspian amphipod crustacean has rapidly spread throughout Europe's freshwaters and its invasion and continued range expansion represents a major conservation management problem. Although a great deal of research has focused on this almost 'perfect' invader as its damaging impacts, realised and potential, have become evident, we now present the first comprehensive review of *D. villosus* taxonomy, morphology, distribution, community impacts, parasites, life history, physiological tolerance and finally, possible eradication methods. We show the direct and indirect ecosystem impacts of this invader can be profound, as it is a top predator, capable of engaging in a diverse array of other feeding modes. It can quickly dominate resident macroinvertebrate communities in terms of numbers and biomass, with subsequent large-scale reductions in local biodiversity and potentially altering energy cycling, such as leaf litter processing. This damaging European invader has the potential to become a key invader on a global scale as it may be capable of reaching North American freshwaters, such as the Great Lakes. One positive aspect of this invader's spread and impact is increased interest in alien species research generally, from decision-makers, stakeholders and the general public. This has resulted in greater financial support to study invasion mechanisms, preventative measures to stop invasion spread and ways to minimise damaging impacts. Our review provides a specific example, that studies identifying management strategies that mitigate against a potential invader's spread should be undertaken at the earliest possible opportunity in order to minimise potentially irreversible ecosystem damage and biodiversity loss.

Key words: biological invasions, non-indigenous species, Amphipoda, Ponto-Caspian, risk assessments, aquatic invasive species (AIS)

Introduction

Alien species represent a major threat to conservation management on both a continental and global scale (Leppäkoski et al. 2002; Chandra and Gerhadt 2008; Richardson and Ricciardi 2013). Invasion by alien species is increasingly recognised as one of the major threats to biodiversity in freshwater ecosystems (Sala et al. 2000; Holdich and Pöckl 2007; SCBD 2010; Lambertini et al. 2011). The 'killer shrimp', *Dikerogammarus villosus* (Sowinsky, 1894), is a euryoecious amphipod crustacean of Ponto-Caspian origin, regarded as one of the worst one hundred invasive species in Europe (DAISIE 2009). It is a highly voracious, physiologically tolerant and adaptable species, threatening freshwater biodiversity and ecosystem functioning on various levels (Bollache et al. 2008; MacNeil et al. 2010; Piscart et al. 2010). Within two decades, it has succeeded in colonising most of the major European inland waterways replacing many resident amphipod 'shrimp' species, including previously successful invaders (Bij de Vaate et al. 2002; Bollache et al. 2004; Grabowski et al. 2007c; Bącela et al. 2008). In 2011 the species was detected outside mainland Europe for the first time, namely in Great Britain, in an English reservoir called Grafham Water (MacNeil et al. 2012). Subsequently, several more populations were detected in quick succession in other parts of England and Wales (Environmental Agency 2012; MacNeil et al. 2012). If *D. villosus* spread follows the pattern of many other aquatic invaders, its range could expand beyond Europe to

Figure 1. The number of publications dealing with various aspects of *Dikerogammarus villosus* invasion, published up to 2013 and registered in the SCOPUS database.
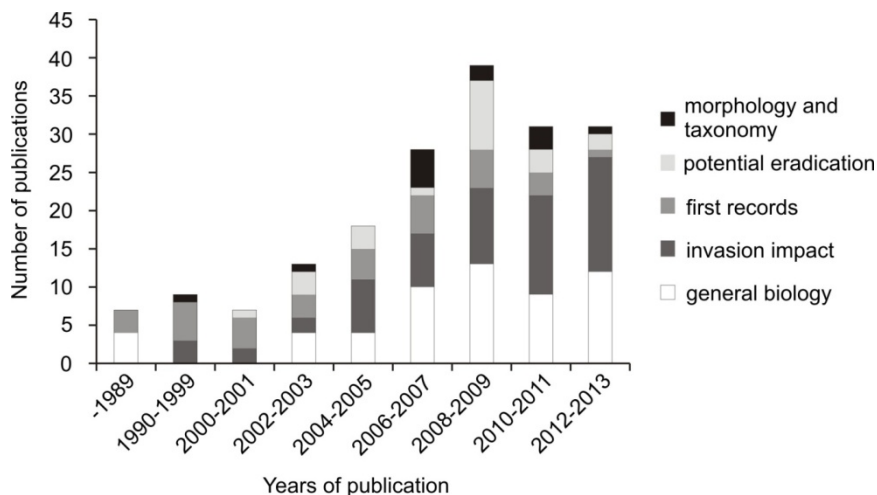
eventually reach North American freshwaters, such as the Great Lakes, as has previously happened with the zebra (*Dreissena polymorpha* (Pallas, 1771)) and quagga mussels (*Dreissena rostriformis bugensis* (Andrusov, 1897)), as well as another amphipod, *Echinogammarus ischnus* (Stebbing, 1899) (Ricciardi and MacIsaac 2000). Taking into account the ever increasing amount of research that the scientific community has focussed on the killer shrimp, we conducted the first comprehensive review of the literature, including searching the Scopus database with the keywords *Dikerogammarus villosus* and 'killer shrimp', as well as sourcing unpublished reports and local Russian literature. We thus aim to both summarise and critically evaluate all the major published studies dealing with this species, its invasion history, ecology, interaction with local communities, its invasion potential and issues of control and eradication (Figure 1).

Taxonomic remarks and potential reasons for the success and range expansion of Ponto-Caspian invaders in European watercourses

According to Bousfield (1977), genera such as *Dikerogammarus*, *Pontogammarus*, and *Obeso-gammarus*, are grouped in the family Ponto-gammaridae and all include species which are invasive to numerous parts of Europe. The taxonomy of the *Dikerogammarus* genus remains a source of both confusion and contention. For instance, some 12 species are ascribed to this genus in various papers (summarised by Grabowski et al. 2011), but as a consequence of weak species

definition and loss of type materials, further taxonomic revisions are required that will probably reduce this number. However, more recent studies have also revealed the presence of cryptic species within the genus (Grabowski and Jażdżewska unpublished data), adding further to the confusion. Fortunately, for this current review, among the *Dikerogammarus* species, *Dikerogammarus villosus* is the most completely defined in morphological terms. An established and comprehensive literature allows for its unambiguous identification among other congeneric species alien in Central and Western Europe, such as *Dikerogammarus haemo-baphes* (Eichwald, 1841) or *Dikerogammarus bispinosus* Martynov, 1925 (Eggers and Martens 2001; Konopacka and Jażdżewski 2002; Mordukhai-Boltovskoi et al. 1969; Özbek and Özkan 2011). Contrary to the singular opinion of Pjatakova and Tarasov (1996) that *D. villosus* should be synonymised with *D. haemobaphes*, other studies have shown the clear differentiation of *D. villosus* from *D. haemobaphes* and also from *D. bispinosus*, both on morphological and molecular bases (Carauşu 1943; Carauşu et al. 1955; Müller et al. 2002; Wattier et al. 2006) (Figure 2).

Dikerogammarus villosus belongs to the 'Ponto-Caspian faunistic complex', which includes predominantly euryoecious animal species, originally endemic to the coastal areas of the Caspian Sea, Azov Sea, Black Sea, their brackish lagoons (limans), and associated lower reaches of rivers which drain to these seas (Mordukhai-Boltovskoi 1964; Stock 1974; Jażdżewski 1980; Barnard and Barnard 1983). The Ponto-Caspian basin resulted from the transformation of the Neogene

Figure 2. Live specimen of *Dikerogammarus villosus* (picture by Michal Grabowski).

epicontinental Sea of Parathetys (Dumont 2000). Tectonic movements followed by sequential regressions/transgressions then transformed the sea into a number of brackish and freshwater lakes. Since the beginning of the Pleistocene (ca. 2.5 Mya), rapid climatic and geological changes resulted in reformation of the Ponto-Caspian basin. This in conjunction with glaciation/deglaciation events, resulted in temporal connections with the Arctic Ocean and changing of the whole salinity regime in the basin. The Caspian Sea eventually became isolated and gradually its waters acquired a unique salt composition, similar to freshwater but more concentrated. The Black Sea was freshwater/slightly brackish during the Holocene but when connected to the Mediterranean Sea (c.a. 7–6 kyrs) (Dumont 2000; Chepalyga 2007), the subsequent inflow of seawater caused serious extinctions of resident biota. The results of this can be seen in the assemblages of present-day 'relic' species now confined to brackish lagoons and river estuaries. Some 80% of this assemblage is endemic, including more than one hundred endemic crustacean species, of which amphipods are the most prominent group. The long and complex chain of events which formed the Ponto-Caspian basin, combined with a harsh continental climate with large annual fluctuations in water temperature and dissolved oxygen levels, have ultimately created an assemblage of euryoecious and euryhaline species highly tolerant of rapid environmental change. Such adaptations have undoubtedly contributed to the success of Ponto-Caspian invaders during their subsequent invasions of Central European waters (Bij de Vaate et al. 2002).

Distribution in native and colonized range

Native range of Dikerogammarus villosus

In its native range, i.e. the Ponto-Caspian area, *Dikerogammarus villosus* inhabits lower courses of big rivers, such as Danube, Dnieper, Dniester, Don and Volga as well as coastal lagoons and limans, however its distribution has not been studied in details, particularly in the Caspian Sea area (eg. Carauşu 1943; Carauşu et al. 1955; Mordukhai-Boltovskoi 1960, 1969; Birstein and Romanova 1968; Mordukhai-Boltovskoi et al. 1969; Pjatakova and Tarasov 1996) (Figure 3). Presumably, it is present in most of the major rivers and limans of the Black, Azov and Caspian sea basins.

Invasion routes of D. villosus *in continental Europe*

Jażdżewski (1980) and Bij de Vaate et al. (2002) distinguished three main aquatic migration corridors: southern, central and northern, which provide access routes through Central Europe for Ponto-Caspian fauna. The southern corridor covers the Danube and Rhine rivers connected by Main–Danube Canal. The central corridor constitutes of the Dnieper and the Pripyat rivers, connected first to the Baltic Sea basin by the Bug and Vistula Rivers and then to the North Sea basin via the Mittelland Canal. The northern corridor is comprised mainly of the Volga River, the Beloye, Onega and Ladoga lakes and of the Neva River that drains to the Baltic Sea. The three above routes were used by numerous Ponto-Caspian species (Bij the Vaate et al. 2002; Panov et al. 2009) to invade the freshwaters of central and western Europe, however the invasion of *D. villosus* presents a unique case (Figure 3).

The *D. villosus* invasion via the southern corridor started as early as in 1926, where the monitoring of macroinvertebrates in the Danube River first revealed the presence of this species in Hungary (Nesemann et al. 1995). Then, in the 1950s, the species was detected in Lake Balaton (Muskó 1989; Muskó 1990; Muskó 1993), shortly after opening of a canal connecting the lake to the Danube. The invader then continued its riverine migration up the Danube, until in 1989 it was detected in Austria and subsequently, in 1995 in Slovakia (Šporka 1999). Amongst the main tributaries of the Danube, an abundant *D. villosus* population was detected in the Croatian section of the River Drava in 2007 (Żganec et al. 2009)

Figure 3. Invasion history and routes of *Dikerogammarus villosus* spread in Europe. Dates indicate the first record in the particular section of the invasion route (citations in the text). Red stars indicate known localities within the native range (for details see Supplementary material - Tables S1 and S2).

Table 1. Presence of *Dikerogammarus villosus* in the Alpine Lakes.

No	Lake	Country	Year of first record of *D. villosus*	Source
1	Leman	France, Switzerland	2002	Bollache 2004
2	Constance / Bodensee	Germany	2003	Mürle et al. 2003
3	Garda	Italy	2003	Casellato et al. 2006
4	Neuchatel	Switzerland	2003	Lods-Crozet and Reymonnd 2006
5	Traun	Austria	2003	Holdich and Pöckl 2007
6	Bienne	Switzerland	2005	Lods-Crozet and Reymonnd 2006
7	Murten = Morat	Switzerland	2006	Lubini et al. 2006
8	Zurich	Switzerland	2006	Steinmann et al. 2006
9	Bourget	France	2007	Grabowski et al. 2007b
10	Greifen	Switzerland	2008	Steinmann 2008
11	Zug	Switzerland	2010	Steinmann 2010
12	Iseo	Italy	2011	Bącela-Spychalska et al. 2013a

and in the lower section of the River Vah in Slovakia in 2001 (Brtek 2001, summarised by Lipták 2013), followed by its spread upstream to the middle section of the river (Hupało et al. 2014). In 1992, reconstruction of the Ludwig Canal connecting the Danube, via the Main River, to the Rhine River was completed (Van der Velde et al. 2000; Nehering 2002) and *D. villosus* quickly penetrated this new waterway, with stable *D. villosus* populations being found both in the upper Rhine (in Bavaria) and the lower Rhine (in the Netherlands) by 1994 (Bij de Vaate and Klink 1995; Bij de Vaate et al. 2002). Further rapid range expansion then occurred, with it being detected

in the River Meuse in 1996 (Josens et al. 2005) and a year later in the River Saone in France (Devin et al. 2001; Bollache et al. 2004). Assessment of monitoring covering the years 1997–2002 showed *D. villosus* had, by the end of that period, spread throughout the entire course of the Rhine, having colonized the Moselle River in 1999, the Seine River in 2000 and the Loire River in 2001–2003 (Bollache et al. 2004). From the Rhine River, *D. villosus* most probably spread eastwards, entering the central corridor *sensu* Bij de Vaate (2002), through the Mittelland Canal to the River Elbe and thence its largest tributary, the Vltava (Berezina and Duris 2008). Continuing this eastward migration, it spread to the Havel, Spree and Oder Rivers in quick succession, arriving in the latter by 1999 (Grabow et al. 1998; Zettler 1999; Rudolph 2000). From the Oder River, *D. villosus* then spread quickly upstream and downstream, reaching the oligohaline Szczecin Lagoon (Jażdżewski et al. 2005; Grabowski et al. 2007c).

Thus far, the final step of this eastward migration from the southern corridor has been to the Warta River, the largest tributary of the Oder. Thus, the species has followed a very long, circuitous route comprising almost 4500 km in length, which commenced in the Black Sea basin, continued through the North Sea basin and ultimately ended in the Baltic Sea basin (Müller et al. 2001; Jażdżewski and Konopacka 2002). Another facet of *D. villosus* range expansion via the southern corridor, was colonization of the Alpine region, with *D. villosus* being detected in 12 Alpine lakes (Table 1), the River Mincio in Italy in 2003 (Casellato et al. 2006) and in 2008 it reached Lake Bilancino near Florence (Tricarico et al. 2010).

Dynamics of the species migration through the Dnieper River system to Central Europe followed a scheme, very different from those described earlier for other invasive species. During the 1950s and 60s the Soviet Union undertook an extensive dam construction program on the Dnieper River system, thereby creating several massive lakes. Ponto-Caspian amphipods, including *D. villosus,* were recognized as an important fish food (Zuravel 1963; Dedju 1967), and deliberately introduced to these newly established water bodies to enhance the resident fish food base and facilitate faster fish production (Zuravel 1965; Ioffe and Maximova 1968). From there, *D. villosus* was able to progress up the Dnieper and then Pripyat River to the Pripyat-Bug Canal, thus

crossing the Black Sea/Baltic watershed, until in 2003 it was reported from the Bug River, a tributary of the Vistula River in eastern Poland (Konopacka 2004). A later record of *D. villosus* in the Belarusian part of the Dnieper in 2006 (Mastitsky and Makarevich 2007) confirmed its spread via the central corridor. After the rapid spread through the Bug River, *D. villosus* then reached the entrance of the Zegrzynski Reservoir (Grabowski et al. 2007c) and here the range expansion seemingly stalled for three years until in 2007, when *D. villosus* was detected in the Vistula, the largest river of the Baltic Sea drainage area (Bącela et al. 2008).

D. villosus has also spread successfully in the Volga River system, migrating out from the deltaic system to reach a distance 4000 km upstream by the middle of the 20th century (Mordukhai-Boltovskoi 1960). In 2000 it was detected for the first time in the Kuybyshev Reservoir, the most northern record of this species in the northern corridor (Yakovleva and Yakovlev 2010). However, surprisingly, this particular range expansion seems to have stalled in recent years (Yakovleva and Yakovlev 2010).

Colonisation of Great Britain

The most recent episode in the European range expansion of *D. villosus* has seen it escape the confines of mainland Europe, to reach Great Britain. Here, in 2010, it was found in the Grafham Water Reservoir in Cambridgeshire, England (MacNeil et al. 2010). The source population for this introduction remains unidentified and requires a molecular approach to reveal it. This British introduction provoked a great deal of press interest and the English and Welsh Environment Agency set about implementing biosecurity precautions and new procedures in an attempt to halt its future spread (Constable and Fielding 2011; Madgwick and Aldridge 2011). However, despite these efforts, *D. villosus* continued to spread rapidly throughout Britain and within a space of a few months was reported at Eglwys Nunydd and in Cardiff Bay in Wales, as well as at several sites in England (Environmental Agency 2012; MacNeil et al. 2012).

Any which way you can – reasons why *D. villosus* has spread so fast

Dikerogammarus villosus possesses several behavioural traits that probably facilitated its extremely rapid dispersal throughout Europe.

Firstly, it has a high tendency to drift in the water column. Van Riel et al. (2011) showed this species is a dominant component of the drifting macroinvertebrate fauna in the River Rhine and thus may easily colonize rivers by downstream drift. The species also has a tendency to hide among zebra mussel *Dreissena polymorpha* beds covering the sides of boats and can survive amongst such mussel bed clusters for at least 6 days even when these boats are out of water (Martens and Grabow 2008). This ability while accelerating upstream migration will also, perhaps more importantly, enable overland transport to isolated waterbodies. For instance, Bącela-Spychalska et al. (2013a) found *D. villosus* occurs most frequently in those Alpine lakes experiencing the highest tourist pressure and presented experimental evidence suggesting this could be due to *D. villosus* being introduced and spread via sailing ropes and diving equipment.

Is the killer shrimp really a killer?

Dikerogammarus villosus has earned the nickname 'killer shrimp', with a body size (30 mm body length) larger than all other European freshwater gammarids (Devin et al. 2003), coupled with massive mouthparts allowing it to overpower and predate large and well-armored prey (Nesemann et al. 1995; Mayer et al. 2008; Mayer et al. 2009). It is a voracious predator, preying upon a wide range of benthic macroinvertebrates, such as chironomid, mayfly and dragonfly larvae, aquatic bugs, leeches, isopods, juvenile crayfish and other amphipods (Dick et al. 2002; Krisp and Maier 2005; MacNeil and Platvoet 2005; Buric et al. 2009; Platvoet et al. 2009a; Boets et al. 2010; Hanfling et al. 2011). *D. villosus* frequently injures and kills other macroinvertebrate taxa without consuming them, which additionally increases this invader's impacts on prey populations (Dick et al. 2002). This predation extends to fish eggs and fry (Casellato et al. 2007; Platvoet et al. 2009b) and *D. villosus* can actually function as a top predator occupying the same trophic level as fish and the largest predatory macroinvertebrates (van Riel et al. 2006). However *D. villosus* could actually have a greater impact than fish predators on resident benthic prey communities, because it occurs at higher abundances and has a body size similar to potential prey. This latter factor allows *D. villosus* to penetrate small refugia, so there is no effective hiding place for prey taxa, as there would be from fish predators (MacNeil et al.

2011). The mere presence of *D. villosus* has also been shown to lead other amphipods to leave previously occupied benthic refugia, swim up in the water column and become more vulnerable to fish predators (Kinzler and Maier 2006).

D. villosus is a voracious predator so obviously it cannot be classified as predominantly a shredder of leaf litter, as are most native amphipods (Mayer et al. 2009; MacNeil et al. 2011). However, it is not a strict predator, feeding as it does on detritus, carrion, and even microalgae (Dick et al. 2002; Kley and Maier 2005; Platvoet et al. 2006a; Mayer et al. 2008). Indeed, juveniles are very efficient consumers of plant material (micro-algae), before they reach maturity and become extreme opportunists (Platvoet et al. 2006a; Maazouzi et al. 2007; Mayer et al. 2008). This is confirmed by ultrastructure studies of its mouthparts, which show a lack of morphological specialization to eat any particular food type (Platvoet et al. 2006a; Mayer et al. 2012). This capability to function mainly as a major predator but also act as an omnivore when other food resources are more plentiful or easier to obtain, confers a huge competitive advantage over many other amphipod species resident in European freshwaters. An indirect effect of *D. villosus* invasion may also be disruption of leaf-litter processing and shredder efficiency, as laboratory studies have shown that predation by and even the mere presence of, *D. villosus*, can curtail the activity of macroinvertebrate taxa engaged in leaf shredding (MacNeil et al. 2011). This could have profound consequences on energy cycling in the invaded ecosystem as leaf litter may cease to be broken down and so remain unavailable to the rest of the resident community who rely on the breakdown products of litter 'shredding' (MacNeil et al. 1997; 2011).

It is unsurprising that the invasion and spread of *D. villosus*, with its high population densities and predatory disposition, has generated many interactions with resident amphipod species, both natives and previously successful invaders (Dick and Platvoet 2000; Dick et al. 2002; Kinzler and Maier 2003; Kley and Maier 2005; Platvoet et al. 2006a; van Riel et al. 2009). One such example is the elimination of the native *Gammarus duebeni* Liljeborg, 1852 from the Ijsselmeer/Markermeer lake in the Netherlands. This lake was previously inhabited by *G. duebeni* coexisting with a North American invader, *Gammarus tigrinus* Sexton, 1939. Both these species inhabited basalt boulders lining the shore-line and there was direct competition between newly arrived *D. villosus*

with these species for this habitat. Subsequent monitoring revealed *D. villosus* had replaced the other species in the boulder zone, with *G. duebeni* completely disappearing and *G. tigrinus* retreating to softer sediments, deeper in the lake (Dick and Platvoet 2000; Dick et al. 2002; Platvoet et al. 2006b). The impact of *D. villosus* on resident amphipod assemblages of the River Rhine has also been drastic. After its arrival, the abundance of the resident *Chelicorophium curvispinum* (G.O. Sars, 1895) was greatly reduced (van Riel et al. 2006) and *G. tigrinus* was displaced from its preferred stony habitat to less favorable ones (van Riel et al. 2006). Such patterns of displacement tend to be repeated in all newly colonized areas and niche partitioning presents itself as the only mechanism allowing resident amphipods to co-exist with *D. villosus*, being confined to macrophytes, weeds or soft sediments, while being eliminated in stony habitats by *D. villosus* (Devin et al. 2003; Kley and Maier 2005; van Riel et al. 2007; Felten et al. 2008b*;* Hesselschwerdt et al. 2008; MacNeil et al. 2008; Kley et al. 2009; Boets et al. 2013a).

Intraguild predation (IGP) or predation between competitors belonging to the same ecological guild (Polis et al. 1989), despite being considered an unstable phenomenon (e.g. Holt and Polis 1997), is a widespread interaction in natural food webs (Arim and Marquet 2004) and is increasingly acknowledged as a major driver of rapid species exclusions during biological invasions (e.g. Snyder et al. 2004; Wang et al. 2013). IGP by *D. villosus* of several amphipod species including *G. duebeni*, *G. tigrinus, Gammarus fossarum* Koch, 1836 and *Gammarus roeselii* Gervais, 1835 has been witnessed in laboratory studies (Dick and Platvoet 2000; Kinzler and Maier 2003). IGP of *Gammarus* spp. by *D. villosus* occurs on both newly moulted (Kinzler and Maier 2003) and intermoult (Dick and Platvoet 2000) individuals, albeit less frequently on the latter. Although Kinzler et al. (2009) found no superior IGP by *D. villosus* upon other similar sized *Dikero-gammarus* species, such results appear counter intuitive when field observations indicate displacement of species such as *D. haemobaphes* by *D. villosus* incursions (Grabowski et al. 2007c*;* Kinzler et al. 2009).

One important factor facilitating *D. villosus* colonization is the presence of the zebra mussel *Dreissena polymorpha*. This globally widespread bivalve lives in colonies and these shell 'beds' provide the heterogeneous, hard structured habitat ideal for *D. villosus* (Devin et al. 2003). *D. villosus* also feeds on the zebra mussel's byssus threads (Platvoet et al. 2009b), faeces and pseudofaeces (Gergs and Rothhaupt 2008a). The biomass accumulating in zebra mussel colonies also forms a perfect food base for chironomid larvae, a major *D. villosus* prey item (Maier et al. 2011) and such very abundant and highly calorific food items promotes the rapid growth and development of *D. villosus* (Gergs and Rothhaupt 2008b). Labora-tory experiments have shown *D. villosus* grows at double the rate when consuming chironomid larvae, rather than biodeposited material or conditioned leaves (Gergs and Rothhaupt 2008a). In comparison, the growth rate of *G. roeselii* is half that of *D. villosus*, when provided with the same number of larvae (Maier et al. 2011).

An approach to assessing the ecological impact of an invading species such as *D. villosus* on a resident community is the comparison of its resource uptake rate or predatory 'capacity' compared with that of a trophically analogous resident species (Dick et al. 2013; Dodd et al. 2013). This predatory 'capacity' can be quantified by measuring the relationship between resource consumption rate (in this case predation rate) and resource density (in this case prey availability) in a 'functional response' (Abrams 1990). A Type II functional response represents a consumption rate which increases with prey density but then declines to an asymptote as prey handling time becomes a limiting factor (Holling 1966). Dodd et al. (2013) compared the functional responses of *D. villosus* to that of *G. pulex* Linnaeus, 1758, in respect of three common prey, *Asellus aquaticus* (Linnaeus, 1758)*, Chironomus* sp. and *Daphnia magna* Straus, 1820. Both large *D. villosus* individuals and those matched for body size with *G. pulex*, showed higher Type II functional responses than *G. pulex* in respect of two prey types and similar for the third. Thus, *D. villosus* showed higher maximum feeding rates than *G. pulex* on both *A. aquaticus* and *D. magna* (similar for *Chironomus* sp.), making it a more efficient predator and consequently likely to have a greater impact on prey populations. In addition, mixed prey type experiments showed that *D. villosus* was signifi-cantly more indiscriminate in prey selection than *G. pulex* and this may be crucial as the ecological impact of an invader possessing indiscriminate feeding habits is likely to be far greater than a more selective one.

As quick and as many as possible

Biological invasion is a combination of stages and barriers that the future invader has to cross (Blackburn et al. 2011). Thus only the species that can be transported, introduced, survive, reproduce and spread may invade new territories successfully. Several biological traits promote invasion of these species and in general species with greater dispersal ability, ecological generalization and greater reproductive rate should be more likely to colonize new areas. Thus detailed knowledge on the life history of an invader is crucial for estimating the likely invasion success of the invader (Olden et al. 2006). *Dikerogammarus villosus* seems to be a model, almost 'perfect' invader in these aspects. Its life cycle and reproductive behaviour has been investigated in both its native and invaded range (Mordukhai-Boltovskoi 1949; Kley and Maier 2003; Piscart et al. 2003; Devin et al. 2004; Kley and Maier 2006; Pöckl 2007; Pöckl 2009). Grabowski et al. (2007a) summarised all available data on the life history traits of amphipods native and invasive to Central Europe, including *D. villosus*, and found that, generally, alien species were characterised by larger brood sizes, higher partial fecundity, earlier maturation and a higher number of generations per year, than native species.

Dikerogammarus villosus grows faster than many freshwater amphipods (Piscart et al. 2003) and reaches sexual maturity earlier, with females as small as 6 mm in length having broods (Mordukhai-Boltovskoi 1949; Piscart et al. 2003; Devin et al. 2004; Pöckl 2007; Pöckl 2009). This size is achieved between the 33rd and 60th day of life, depending on temperature (Piscart et al. 2003; Pöckl 2009). The results from these latter studies contrast with Mordukhai-Boltovskoi (1949) who reported *D. villosus* taking 110 days to achieve sexual maturity but this latter study did not specify the temperature or body size achieved by this time. However, compared to *D. villosus*, other European amphipods lag far behind in the time needed to attain sexual maturity, for example *Gammarus pulex* needs 133 days at 15°C (Welton and Clarke 1980), *Gammarus fossarum* 96 days and *Gammarus roeselii* 85 days at 20.2°C (Pöckl 1992). Once sexual maturity has been reached, the breeding period of *D. villosus* is also relatively long and under European climatic conditions, ranges from 9 to 12 months (Ciolpan 1987; Devin et al. 2004; Pöckl 2007; Pöckl 2009) which contrasts with 4 to 9 months for most other amphipod species inhabiting the same geographic region (summarized in Grabowski et al. (2007a) (Table 2).

In summary, these life history traits make this species an excellent colonizer, with one large female *D. villosus* capable of producing more offspring in one brood than a female *G. fossarum*, *G. pulex*, or *G. roeselii* could do during their entire lives. This means, potentially, it would require only one or two *D. villosus* females to establish a viable population in a newly colonized water-body (Pöckl 2007).

The killer shrimp hitchhikers

Several "hitchhikers" in the form of parasites, probably accompanied *Dikerogammarus villosus* during the invasion process and so were spread with their hosts into new and perhaps naive systems. A survey investigating parasite diversity in the central corridor showed that Ponto-Caspian amphipod hosts have a significant role as vectors for gregarines which belong to protozoa and for microsporidia (Fungi) (Ovcharenko et al. 2008; Ovcharenko et al. 2009). It appeared that *D. villosus* is a host for these parasite taxa, with four gregarine species identified infecting *D. villosus*, including one acanthocepahalan and several microsporidians (Table 3). On the other hand a thorough survey by Bojko et al. (2013) focusing on populations of the killer shrimp that colonised UK and two continental populations from the invaded range confirmed "the parasite release hypothesis" in case of the UK populations. They showed significantly lower diversity and prevalence of parasites (especially microsporidians were not noticed at all) compared to the continental populations.

Microsporidia have been well studied as obligatory intracellular parasites, infecting many animal taxa and are very common amphipod parasites. They are transmitted both horizontally and vertically (MacNeil et al. 2003; Haine et al. 2004; Haine et al. 2007) and depending on the transmission mode they can be either lethal or relatively harmless to their hosts (Terry et al. 2004). While most microsporidian species are relatively rare in *D. villosus* host populations, with prevalence typically below 4 % (Wattier et al. 2007), *Cucumispora dikerogammari* which infects *D. villosus* within and outside its native range, can attain a prevalence of up to 74% (Wattier et al. 2007; Ovcharenko et al. 2010; Bącela-Spychalska et al. 2012). This microsporidian parasite was seldom detected in amphipod hosts other than *D. villosus* and when it was, its host range was restricted to other Ponto-Caspian amphipods

Table 2. Data matrix of life history traits and ecological tolerance of *Dikerogammarus villosus* and other gammarid species (after Grabowski et al. 2007a, modified). x – the number of generation per year cannot be estimated as the reproduction is continuous throughout the year.

Species	mean breeding female size (mm)	mean brood size	partial fecundity	breeding period in months	maturity index	number of genera-tions per year	salinity tole-rance	human impacts	Sources (combined with own data)
G .fossarum	10.14	16.88	1.66	10.00	0.79	2	1	1	Jazdzewski 1975; Brzezinska-Blaszczyk and Jazdzewski 1980
G. lacustris	11.28	18.75	1.66	4.00	0.71	1	2	2	Hynes 1955; Hynes and Harper 1992
G.varsoviensis	13.50	25.17	1.86	5.00	0.74	1	1	2	Jazdzewski 1975; Konopacka 1988
G. pulex	8.90	14.79	1.66	10.67	0.88	1	2	2	Hynes 1955; Jazdzewski 1975
G.leopoliensis	9.40	16.70	1.78	7.00	0.79	1	1	1	Zielinski 1998
G. balcanicus	9.10	7.88	0.87	7.00	0.84	1	2	2	Jazdzewski 1975; Zielinski 1995
G. roeselii	12.55	25.60	2.04	6.00	0.68	2	1	2	Jazdzewski 1975; own data
P. robustoides	12.65	64.45	5.10	7.00	0.63	3	3	3	Bacela and Konopacka 2005; Dedju 1966, 1967, 1980; Kasymov 1960;
D. haemobaphes	10.99	42.84	3.90	5.50	0.57	3	2	3	Musko 1993; Kiticyna 1980; Kurandina 1975
D. villosus	11.39	50.66	4.45	11.00	0.57	3	2	3	Devin et al. 2004; Kley and Maier 2003; Mordukhai-Boltovskoi, 1949
O. crassus	8.81	25.33	2.87	7.00	0.68	3	3	2	Kurandina 1975
C. ischnus	7.83	17.33	2.21	8.00	0.64	2	2	2	Kley and Maier 2003; Konopacka and Jesionowska 1995; Kurandina 1975; Mordukhai-Boltovskoi,1949
G. tigrinus	7.94	20.31	2.56	9.00	0.50	3	3	3	Bousfield 1958; Chambers 1977; Pinkster et al. 1977 ; Steele and Steele 1975
L. scutariensis	7.90	15.53	0.51	12.00	0.76	x	1	1	Grabowski et al. 2014
E. cari	5.60	8.6	1.59	10.00	-	x	1	1	Zganec et al. 2011

Table 3. Known parasites infecting *Dikerogammarus villosus*.

Parasite		Observed max prevalence	Geographic region	Source
Trematoda	*Plagioporus skrjabini*	nd	the Volga River,	Chernogorenko et al. 1978
	Not identified	<2%	UK fresh waters	Bojko et al. 2013
Acanthocephala	*Pomphorhynchus tereticollis* (Rudolphi, 1809)	0.04%	the River Rhine, Vistula River	Emde et al. 2012; Bojko et al. 2013
Apicomplexa, Gregarinia	*Cephaloidophora* sp.	65%	UK fresh waters	Bojko et al. 2013
	Cephaloidophora similis Codreanu-Balcescu, 1995	na	invaded waterbodies: i.e. Vistula, Oder	Ovcharenko et al. 2009
	Cephaloidophora mucronata Codreanu-Balcescu, 1995	na	invaded waterbodies: i.e. Vistula, Oder	Ovcharenko et al. 2009
	Uradiophora sp.	65%	UK fresh waters	Bojko et al. 2013
	Uradiophora longissima (von Siebold in von Kölliker, 1848)	na	invaded waterbodies: i.e. Vistula, Oder	Ovcharenko et al. 2009
	Uradiophora ramosa Balcescu-Codreanu, 1974	na	invaded waterbodies: i.e. Vistula, Oder	Ovcharenko et al. 2009
Microsporidia	*Cucumispora* = *Nosema dikerogammari* (Ovcharenko and Kurandina, 1987)	74%	whole range, despite UK	Ovcharenko and Kurandina, 1987; Wattier et al. 2007; Ovcharenko et al. 2009; Bącela-Spychalska et al. 2012; Bojko et al. 2013
	Nosema granulosis Terry et al. 1999	4%	invaded waterbodies i.e. the upper Danube, the Rhine, Seine, Loire	Wattier et al. 2007
	Dictyocoela muelleri	3.4%	Rhine drainage	Wattier et al. 2007
	D. berillonum	2%	Meuse River	Wattier et al. 2007
	D. roeselum	2%	the upper Danube, the Rhine	Wattier et al. 2007
Bacteria	*not identified*	< 1%	the Vistula River	Bojko et al. 2013
Viruses	*Dikerogammarus villosus bacilliform virus*	< 1%	the Vistula River	Bojko et al. 2013

such as *D. haemobaphes*, *Echinogammarus ischnus* and *Chelicorophium curvispinum* and always at a low prevalence (less than 4%). Such findings indicate that *C. dikerogammari* is virtually specific for the *D. villosus* host (Bącela -Spychalska et al. 2012). This parasite is virulent only in the later stages of infection, with only symptomatic individuals with a high parasite load exhibiting increased mortality; with infected but asymptomatic ones exhibiting the same survivorship as uninfected individuals (see Bącela-Spychalska et al. (2012). Transmission to other non-*D. villosus* hosts is also limited by a lack of macroinvertebrate predation on *D. villosus*. In summary, this particular microsporidian cannot, as yet, be considered as a new threat to resident amphipods in systems invaded by *D. villosus*. However, the parasite may modify the impact of *D. villosus* on the macroinvertebrate assemblages within invaded systems, as it significantly diminishes predation rate by the *D. villosus* host, thus potentially reducing predation pressure (Bącela-Spychalska et al. 2013b).

The killer shrimp as a model species for Amphipod morphology – AMPIS

The Amphipoda Pilot Species Project (AMPIS), based on complex images in the macro- and micro-scanning electron microscope (SEM) scale, was initiated in 2005 (Platvoet et al. 2006b) to address the lack of a comprehensive database of amphipod morphology. The plan was to create a standardized database containing complete descriptions of several species of Amphipoda, which could be used as templates for taxonomic and morphological studies. *Dikerogammarus villosus* was chosen as a pilot species for the program, due to its prominence as an important European invader, its large body size, predatory behaviour and its potential impact on invaded communities (Platvoet et al. 2007).

Extensive study of the body surface ultrastructure of *D. villosus* revealed the presence of some unexpected structures. For instance females have two pores on the first pereionite, which are larger than any other pores in the amphipod cuticle. Although the function of such structures remains unidentified, it has been hypothesized that they are associated with reproductive behavior and the release of chemical attractants (Platvoet et al. 2006b). Other structures described may be part of the 'locking-on' system used in amplexus stage, as males and females pair up. For instance,

females possess swollen edges of the first and fifth pereionite, which fit or 'lock' to the male's first gnathopod's palm and palmar angle. This would enable correct size-selection during mate choice and it could have other functions such as stimulating hormonal processes in males and females, stabilization of amplexus and promote energy conservation during paired swimming (Platvoet et al. 2006c). SEM pictures of the *D. villosus* cephalon reveal depressions on each side, probably signifying the presence of statocysts or balance sensory receptors. These are associated with geosense and spatial orientation and in *D. villosus* may act as movement detectors and/or monitors of hydrostatic pressure (Platvoet et al. 2006d). In common with many other amphipods, *D. villosus* possesses a lateral line organ comprised of two rows of specialized receptors units on each side of the body. Similar to other animals (particularly fish and amphibians) such receptors may be linked to chemo-, mechano-, and electro-sensory functions (Platvoet et al. 2007).

How to kill the killer shrimp – the 'perfect' invader has weaknesses

No invader is perfect, not even *Dikerogammarus villosus* and any perceived weaknesses need to be exploited if this invader's spread and impact are to be minimised. In its native range, *D. villosus* occurs in many different types of water bodies including limans, lakes, reservoirs and the mouths and main channels of large rivers and many of these exhibit very changeable physico-chemical conditions, particularly in respect of salinity and temperature regimes. *D. villosus* has been found surviving in brackish water up to 10 psu, and can even acclimatize to 20 psu under laboratory conditions (Bruijs et al. 2001; Brooks et al. 2008). In addition, although degradation of eggs has been observed at 20 psu, at salinities as high as 15 psu development of embryos is still possible and hatching of juveniles has been recorded (Bącela-Spychalska pers. obs). This ability significantly increases its potential for long distance transport within ship ballast water and will consequently enhance range expansion (Brooks et al. 2008; Santagata et al. 2009; Piscart et al. 2011). However, this tolerance does have its limits, so a simple but effective tool against introduction of *D. villosus* via overseas shipping, would be to replace brackish ballast water obtained from ports/harbours with high salinity open ocean water (Santagata et al. 2008; Santagata et al. 2009).

We have previously noted the ability of *D. villosus* to survive at least 6 days outside a waterbody and within damp zebra mussel shell clusters covering the sides of boats (Martens and Grabow 2008). In addition, Bącela-Spychalska et al. (2013a) has reported survival for 3–5 days within the folds of a moist neoprene diving suit. *D. villosus* has also been observed to survive up to 6 days in a pile of macrophytes and roots left out of water (Rewicz et al. pers. obs.). Poznańska et al. (2013) also reported that individual *D. villosus* exposed to air without shelter exhibited grouping behaviour, enhancing their survival to desiccation as compared to more exposed single individuals who would be more liable to drying out. This high tolerance to air exposure obviously greatly increases the potential for overland transport and rapid range expansion. Despite this, temperature tolerance of *D. villosus* is similar to the majority of native European freshwater amphipods, with a critical threshold level of 31°C, a temperature lower than some other invaders, such as *Gammarus tigrinus* (37°C) or *Echinogammarus ischnus* (35°C) (Wijnhoven et al. 2003; van der Velde et al. 2009). However, Maazouzi et al. (2011) reported that under laboratory conditions the limiting temperature for *D. villosus* was as low as 26°C compared to 30°C for the native *Gammarus pulex* and the authors accounted for this difference to the earlier studies by the relatively long duration of their experiment (15 days). Our own data (unpublished) obtained from the native range of *D. villosus*, shows that water temperatures ranged from 25°C to almost 29°C in July. Wijnhoven et al. (2003) showed that *D. villosus* has a reduced tolerance to temperature in waters with low conductivity and this could account for its preference for larger rivers with higher temperatures and conductivities, compared to smaller tributaries/ streams with lower temperatures/conductivities (Grabowski et al. 2009).

Amphipods are sensitive to a wide range of toxicants (Felten et al. 2008a) and are increasingly recognised as important bioindicators in ecotoxicological tests (Kunz et al. 2010). *D. villosus*, being an increasingly common species in European watercourses, has also started to be recognized as a robust pollution indicator (Sebesvari et al. 2005). It has been used to measure metal bioaccumulation and provide information about contamination levels in aquatic ecosystems (Barkács et al. 2002). For instance, Sebesvari et al. (2005) showed that *D. villosus* is a useful bioindicator of tin, as its concentration in the amphipod's tissues has a strong correlation with its background environmental concentration. Similarly, *D. villosus* has a physiological ability to respond to higher copper concentrations by decreasing its total fatty acids content (Maazouzi et al. 2008; Sroda and Cossu-Leguille 2011). Interestingly, other amphipods such as *Gammarus roeselii* are more sensitive to copper levels, so copper pollution could further enhance *D. villosus* invasion by weakening/eliminating potentially competitive native species. In contrast, *D. villosus* is very sensitive to fluoride (Gonzalo et al. 2010) and cadmium (Boets et al. 2012), and accumulates these quicker than many resident amphipods. Thus, high fluoride/cadmium levels may make some water bodies relatively resistant to *D. villosus* invasion and successful establishment. In addition, cadmium exposure has been shown to interfere with antipredatory behavior (i.e. aggregation with conspecifics, refuge use, exploration and mobility) in *D. villosus* and may cause disrupt function of chemosensors (Sornom et al. 2012). Such high sensitivity for various chemical stressors displayed by *D. villosus* populations could be related to the rapid expansions into the new areas, reflecting low genetic diversity in founder populations and a bottle-neck effect (Piscart et al. 2011; Boets et al. 2012).

Establishing methods to both eradicate *Dikerogammarus villosus* and prevent further spreading are current priorities of government environmental protection agencies such as the Environment Agency in England and Wales. High attachment abilities of *D. villosus* to objects submerged in the water like ropes, wet suits, boat hulls, nets etc. has already been recognized (Bącela-Spychalska et al. 2013a) and there is an increasing focus on ways to 'stop the spread' by concentrating on ways to sterilize such equipment of any potential *D. villosus* 'hitchhikers'. Such research has been conducted by the Centre for Environment, Fisheries and Aquaculture Science (CEFAS) and the Science and Technical Advisory Group (STAG) in Great Britain. Thirteen chemical and physio-chemical treatments were assessed as potential *D. villosus* eradicators i.e.: pH, salinity, iodine/iodophor, chlorine/sodium hypochlorite, virkon S, temperature, acetic acid, methanol, citric acid, urea, hydrogen peroxide, carbonated water and sucrose (Stebbing et al. 2011). After considering all these options, the most effective eradication method was found to be simple application of heated water (50°C), which resulted in 100% mortality level instantly. In contrast, carbonated water only induced narcosis, but is

cheap and easier to implement in the field. It is hoped public education campaigns like the "check, clean, dry" (GB non native species secretariat) approach in the U.K., coupled with establishing decontamination places and protocols in marinas, reservoirs and other popular tourist areas, will stop or at least slow down the spread of *D. villosus*.

The recent arrival of *D. villosus* in British freshwaters

Since the initial detection of *Dikerogammarus villosus* in British freshwaters in 2010, its subsequent range expansion and that of another recent Ponto-Caspian amphipod invader to Great Britain, *Dikerogammarus haemobaphes* is currently the focus of much study (Gallardo et al. 2012; MacNeil et al. 2012; Gallardo and Aldridge 2013a; Gallardo and Aldridge 2013c; MacNeil et al. 2013). Spread of both invaders has been relatively rapid (MacNeil et al. 2013), leading to the instigation of killer shrimp monitoring programmes and evaluation of risk factors that could facilitate/ accelerate range expansion (MacNeil et al. 2012; 2013). Based on climatic (e.g. temperature), physico-chemical (level of oxygen, conductivity) and socio-economic factors (human activities) SDM (species distribution) and HSM (habitat suitability) models were developed (Gallardo et al. 2012; Boets et al. 2013b*;* Gallardo and Aldridge 2013a; 2013b; 2013c). These multifactor models assess the invasive adaptations and 'potential' of *D. villosus* and predict those areas most vulnerable to *D. villosus* invasion. Geographically, about 60% of Great Britain was found to be potentially suitable for *D. villosus*, including the vast majority of central and southern England, with areas containing harbours, ports and lakes with high angler/tourism pressure being particularly vulnerable to invasion (Gallardo et al. 2012; Gallardo and Aldridge 2013c). In addition, MacNeil and Platvoet (2013) highlighted the fact that artificial in-stream structures such as fish passes and bank reinforcements may represent optimal habitat types for *D. villosus* and *D. haemobaphes*. Indeed, the presence of such structures may allow these invader species to penetrate small rivers and facilitate invasion of in watercourses which were previously considered unsuitable for these species in terms of 'natural' habitat with muddy, soft substrates. In the long term, climate change may promote the establishment of new invaders and facilitate

further spread of existing invaders such as *D. villosus* and *D. haemobaphes*, as invaders may be better adapted to cope with changing conditions than native species (Gallardo and Aldridge 2013b; 2013c).

Lessons for the future

Dikerogammarus villosus has earned its moniker of the 'killer shrimp'. It is a voracious predator and a very successful invader, capable of rapid range expansion, is highly adaptable to new environmental regimes and physiologically tolerant enough to survive transport in both ship ballast water and overland transport. Undoubtedly, it can have profound impacts on resident macroinvertebrate communities and its arrival has negative connotations for biodiversity. The impacts of this species can be so significant to the structure of invaded communities and consequent functioning of ecosystems, that we can propose that in many invaded systems, it effectively acts as an 'ecosystem engineer' (van Riel et al. 2006).

When considering the potential negative impacts of *D. villosus* invasion and range expansion in Europe and whether it is worthwhile to expend large amounts of resources in an attempt to stop or even slow the spread of this invader, we must first acknowledge that in common with many other invasion scenarios, anthropogenic pressures fuelled this particular invasion (Pyšek et al. 2010). Construction of canals, alteration of river flow regimes, in-stream engineering altering substrate types and bankside structures, increasing industrial pollution and last but not least, the enormous traffic flow of boats and barges throughout Europe's watercourse have all contributed to the rapid spread and successful establishment of this species. Although it is an unpalatable truth, in all likelihood the ecosystem changes wrought by *D. villosus* invasion are profound and probably irreversible. Recently implemented restoration programmes for European rivers, may make them less suitable for *D. villosus*, but this is mere speculation at present. Realistically it will be impossible to eliminate *D. villosus* from invaded European rivers or prevent its further spread to interconnected river networks. Although this seems desperate, we can take some positive steps. We need to implement *D. villosus* monitoring systems, to provide crucial information on spread, vectors, biology, impact on local biota and subsequent economic impacts. Measures should be implemented to stop

overland transport of this species to isolated river systems or lakes. Thus, acknowledging the biosecurity risk posed by people using different waterbodies for recreational purposes, specific procedures exist to stop the accidental spread of invasive species. For example, in Great Britain, cleaning boat sides and propellers as well as sport gear has been recommended as a standard procedure, before leaving an invaded or invasion risk site or moving onto a new site (Madgwick and Aldridge 2011; Anderson et al. 2014). Such boat cleaning procedures have already been instigated as standard practice at Grafham Water Reservoir (MacNeil, pers. obs.). The adoption of such rigorous biosecurity measures may be crucial in the protection of the unique freshwater ecosystems of southern Europe with their great biodiversity and relatively pristine macroinverte-brate and fish communities. Indeed, catastrophic impacts have already been witnessed in Lake Garda, where the killer shrimp has decimated the population of the resident amphipod *Echino-gammarus stammeri* (S. Karaman, 1931), as well as preying on the eggs and fry of native fish (Casellato et al. 2006; Ciutti et al. 2011). The ancient Lake Ohrid in the Balkan Peninsula is an example of a water body where *D. villosus* could have similar devastating impacts. We regard this as particularly vulnerable as at least 34% of the resident animal assemblage is endemic, giving it the highest endemic diversity among all the ancient lakes in the world taking into account the lake surface area (Albrecht and Wilke 2009). In some animal groups, such as amphipods, more than 90% are endemic to this lake (Wysocka et al. 2013). The arrival of a highly competitive and predatory invader such as *D. villosus* has the potential to severely reduce this rich native diversity and this threat is unfortunately growing as tourist develop-ment rapidly increases, as this picturesque and rather isolated lake becomes an increasingly attractive destination for boating and diving – activities already proven to facilitate spread of the invader. Similar risk factors apply to other Balkan ancient lakes such as the Shkoder, Prespa, Trichonis and Doiran. The biodiversity of these lakes has not been well studied so the arrival of *D. villosus* could irreversibly change these lake assemblages, even before they have been documented pre-invader impact.

It should be acknowledged, that in practical terms, we consider it impossible to eradicate this invader or effectively stop its expansion within invaded European freshwaters. Thus it worthwhile to consider an alternative strategy of focusing efforts/resources on preventing the spread of the killer shrimp to isolated basins, such as Alpine lakes or areas of the defined or putative high freshwater endemic diversity. Taking into account the isolation of the lakes from the river systems already invaded, the previously discussed preventative measures to stop spread by boats and diving equipment, if applied vigorously, should greatly reduce the risk of *D. villosus* invasion.

Another potential destination for *D. villosus* is the system of the North American Laurentian Great Lakes (U.S. EPA 2008). This has already been invaded by several Ponto-Caspian species conveyed in ship ballast water (i.e. zebra mussel (*Dreissena polymorpha*) and quagga mussel (*D. bugensis*), fishhook waterflea (*Cercopagis pengoi*), gammarid *Echinogammaraus ischnus* and gobies round boby (*Neogobius melanostomus*) and tubenose goby (*Proterorhinus semilunaris*) (Ricciardi and MacIsaac 2000). Again, simple measures, if commonly applied, may prevent such introductions. However, there is still much to be done to improve the tools against introduction of invasive species in the Great Lakes. In case of ballast water management, only ballast water exchange and saltwater flushing are mandatory till the year 2016 (Government of Canada 2006; SLSDC 2008). After that time the management should be improved by implementing new, and hopefully, more efficient systems to avoid exchange of biota (Wang et al. 2012; Briski et al. 2013). It is also stressed that preventing non-native species spread in the Northern America should be also implemented for the inland ship transport as the intensive water exchange via ballast tanks is present between Saint Lawrence River to the Great Lakes (Adebayo et al. 2014). However, till now there is "easy entrance" for the killer shrimp to invade the North American Lakes as the preventing method used now are not efficient for Ponto-Caspian invaders as is *D. villosus* (U.S. EPA 2008).

The killer shrimp is a prime example of an invader, whose spread has focussed the attention of the international scientific community and in particular government agencies tasked with nature conservation and the protection of aquatic ecosystems (GB NNSS 2011). This interest has been generated by the relatively early alerts on the potentially highly deleterious impacts the invader posed for vulnerable benthic communities.

Given this level of interest in both the scientific and general media, it remains surprising, that although over the past two decades, many aspects of *D. villosus* ecology have been relatively well studied, studies on the factors either facilitating or mitigating against its spread remain scarce (GB NNSS 2011; Stebbing et al. 2011). This knowledge 'gap' undoubtedly has contributed to the lack of preventive measures that could be practically undertaken to stop or at least slow down its spread that can be estimated using risk assessments. Only recently have such measures been tentatively proposed in places such as Great Britain, and only after a multitude of rivers, lakes and reservoirs have already been invaded (GB NNSS 2010; Madgwick and Aldridge 2011). In hindsight, the case of the killer shrimp may provide a general lesson for invasion ecologists, that studies on the underlying mechanisms of invader spread should be undertaken at earliest stage of the invasion process. Only then can one hope to slow its progress within invaded systems and more importantly prevent it reaching new systems, before it causes irreversible ecosystem changes. A new EC proposal on the prevention and management of the introduction and spread of invasive alien species was agreed in March 2014 [COD(2013)0307].This new regulation applies a list of invasive species of "Union concern" that should not be introduced, transported, placed on the market, offered, kept, grown or released into the environment. In the case of invasive species already introduced, the Member States will be responsible for establishing the method of elimination of the species from the environment. It is not known, at this time, whether the killer shrimp, will be listed as a species of "Union concern". In a very thought provoking review, Richardson and Ricciardi (2013) pointed out that despite its critics, invasion ecology remains a thriving and increasingly relevant science, especially to anyone concerned with preventing the loss of biodiversity and ecosystem services. To conclude on a relatively positive note, the invasion and spread of the 'killer shrimp' has undoubtedly led to significantly increased financial support and political/public interest for research into alien species, the mechanisms of invasion and potential methods to prevent the spread of damaging invaders and their associated negative impacts on taxonomically, culturally and economically valuable ecosystems. In the end, the least damaging invasion is the one which is prevented from happening.

Conclusions

A. *Dikerogammarus villosus* has earned its moniker of the 'killer shrimp' and although not 'perfect', it is a very, very successful invader. It is a voracious predator capable of having a profound impact on freshwater macroinvertebrate community structure and function. It is highly adaptable, physiologically tolerant and its continued rapid range expansion has negative connotations for native biodiversity on both a European and potentially global scale.

B. This Ponto-Caspian amphipod has spread within a few decades throughout Europe's inland waters. Its range extension has been associated mainly with commercial shipping in large waterways (i.e. the Danube, Rhine, Mittelland Canal – a circuitous route comprising almost 4500 km) but it has also been transported overland to many isolated Alpine lakes and has recently moved out of mainland Europe to reach the British Isles. Further potential destinations for *D. villosus* include the North American Laurentian Great Lakes system.

C. Inherent life history traits make *D. villosus* an excellent colonizer, with one female capable of producing more offspring per brood than females of most native European Amphipod species. Potentially, it would require only one or two *D. villosus* females to establish a viable population in a newly colonized water-body.

D. The capability to function as both a highly efficient predator and also as an extreme opportunist omnivore as the need arises confers a huge competitive advantage over many other European macroinvertebrate taxa, including previously successful invaders.

E. The invasion of isolated Alpine Lakes by *D. villosus* has been linked with overland transport associated with recreational activities. Similar transport risk factors also apply to several Balkan ancient lakes. The biodiversity of these latter lakes has not been well studied so the arrival of *D. villosus* could irreversibly change these lake assemblages, even before they have been documented. To stop or more realistically slow the invader's spread, very simple 'preventative' measures such as mechanical cleaning and washing of water sports gear would greatly reduce the risk factors. For example in the UK, a recent public education initiative 'Check, Clean and Dry', provides simple guidance for the public. It recommends simply checking equipment

and clothing for live organisms. Cleaning and drying of equipment is then a simple way to remove/kill invaders and so stop their spread.

F. Efforts to improve river/lake water quality and wastewater treatment need to be accelerated as improving water quality would allow native species to better compete with the invader. This approach would require considerable economic resource and political will. One positive aspect of the *D. villosus* invasion has been significantly increased financial support and political/public interest for research into alien species generally.

G. The killer shrimp is a prime example of an invader, whose spread has focussed the attention of the international scientific community and in particular government agencies tasked with biodiversity conservation and the protection of aquatic ecosystems. This interest has been generated by the relatively early alerts on this invader's highly deleterious impacts. Hopefully forewarned is forearmed.

Acknowledgements

References

Abrams PA (1990) The effects of adaptive behavior on the Type-2 functional response. *Ecology* 71: 877–885, http://dx.doi.org/10.2307/1937359

Adebayo AA, Zhan S, Bailey SA, MacIsaac HJ (2014) Domestic ships as a potential pathway of nonindigenous species from the Saint Lawrence River to the Great Lakes. *Biological Invasions* 16: 793–801, http://dx.doi.org/10.1007/s10530-013-0537-5

Albrecht C, Wilke T (2009) Ancient Lake Ohrid: biodiversity and evolution. In Wilke T, Väinölä R, Riedel F (eds), Patterns and Processes of Speciation in Ancient Lakes: Developments in Hydrobiology. Springer Netherlands, pp 103–140

Anderson LG, White PCL, Stebbing PD, Stentiford GD, Dunn AM (2014) Biosecurity and Vector Behaviour: Evaluating the Potential Threat Posed byAnglers and Canoeists as Pathways for the Spread of Invasive Non-Native Species and Pathogens. *PLoS ONE* 9(4): e92788, http://dx.doi.org/10.1371/journal.pone.0092788

Arim M, Marquet PA (2004) Intraguild predation: a widespread interaction related to species biology. *Ecology Letters* 7: 557–564, http://dx.doi.org/10.1111/j.1461-0248.2004.00613.x

Barkács K, Ovari M, Oertel N, Szabo E, Szurdoki E, Zaray G (2002) Elemental analysis of *Dikerogammarus villosus* samples for river water monitoring. *Microchemical Journal* 73: 99–111, http://dx.doi.org/10.1016/S0026-265X(02)00056-5

Barnard JL, Barnard CM (1983) Freshwater Amphipoda of the world. Hayfield Association, Mt. Vernon, Virginia, 830 pp

Bącela K, Konopacka A (2005) The life history of *Pontogammarus robustoides*, an alien amphipod species in Polish waters. *Journal of Crustacean Biology* 25: 190–195, http://dx.doi.org/10.1651/C-2519

Bącela K, Grabowski M, Konopacka A (2008) *Dikerogammarus villosus* (Sowinsky, 1894) (Crustacea Amphipoda) enters Vistula–the biggest river in the Baltic basin. *Aquatic Invasions* 3: 95–98, http://dx.doi.org/10.3391/ai.2008.3.1.16

Bącela-Spychalska K, Wattier RA, Genton C, Rigaud T (2012) Microsporidian disease of the invasive amphipod *Dikerogammarus villosus* and the potential for its transfer to local invertebrate fauna. *Biological Invasions* 14: 1831–1842, http://dx.doi.org/10.1007/s10530-012-0193-1

Bącela-Spychalska K, Grabowski M, Rewicz T, Konopacka A, Wattier R (2013a) The 'killer shrimp' *Dikerogammarus villosus* (Crustacea, Amphipoda) invading Alpine lakes: overland transport by recreational boats and scuba-diving gear as potential entry vectors? *Aquatic Conservation-Marine and Freshwater Ecosystems* 23: 606–618, http://dx.doi.org/10.1002/aqc.2329

Bącela-Spychalska K, Riguad T, Wattier RA (2013b) A co-invasive microsporidian parasite that reduces the predatory behaviour of its host *Dikerogammarus villosus* (Crustacea, Amphipoda). *Parasitology* 141: 254–258, http://dx.doi.org/10.1017/S0031182013001510

Berezina NA, Duris Z (2008) First record of the invasive species *Dikerogammarus villosus* (Crustacea: Amphipoda) in the Vlatava River (Czech Republic). *Aquatic Invasions* 3: 455–460, http://dx.doi.org/10.3391/ai.2008.3.4.16

Bij de Vaate A, Jazdzewski K, Ketelaars HAM, Gollasch S, Van der Velde G (2002) Geographical patterns in range extension of Ponto-Caspian macroinvertebrate species in Europe. *Canadian Journal of Fisheries and Aquatic Sciences* 59: 1159–1174, http://dx.doi.org/10.1139/f02-098

Bij de Vaate A, Klink AG (1995) *Dikerogammarus villosus* Sowinsky (Crustacea: Gammaridae) a new immigrant in the Dutch part of the Lower Rhine. *Lauterbornia* 20: 51–54

Birstein YA, Romanova NN (1968) Amphipoda. In: Birstein YA, Vinogradova LG, Kondakova NN (eds), Atlas bespozvonochnykh Kaspiiskogo morya, Pishchevaya Promyshlennost, Moscow, USSR, pp 241–289

Blackburn TM, Pyšek P, Bacher S, Carlton JT, Duncan RP, Jarošík V, Wilson JRU, Richardson DM (2011) A proposed unified framework for biological invasions. *Trends in Ecology & Evolution* 26: 333–339, http://dx.doi.org/10.1016/j.tree.2011.03.023

Boets P, Lock K, Messiaen M, Goethals PLM (2010) Combining data-driven methods and lab studies to analyse the ecology of *Dikerogammarus villosus*. *Ecological Informatics* 5: 133–139, http://dx.doi.org/10.1016/j.ecoinf.2009.12.005

Boets P, Lock K, Goethals PLM, Janssen CR, De Schamphelaere KAC (2012) A comparison of the short-term toxicity of cadmium to indigenous and alien gammarid species. *Ecotoxicology* 21: 1135–1144, http://dx.doi.org/10.1007/s10646-012-0868-5

Boets P, Holguin GJE, Lock K, Goethals PLM (2013a) Data-driven habitat analysis of the Ponto-Caspian amphipod *Dikerogammarus villosus* in two invaded regions in Europe. *Ecological Informatics* 17: 36–45, http://dx.doi.org/10.1016/j.ecoinf.2012.07.001

Boets P, Pauwels IS, Lock K, Goethals PLM (2013b) Using an integrated modelling approach for risk assessment of the 'killer shrimp' *Dikerogammarus villosus*. *River Research and Applications* 30: 403–412, http://dx.doi.org/10.1002/rra.2658

Bojko J, Stebbing PD, Bateman KS, Meatyard JE, Bacela-Spychalska K, Dunn AM, Stentiford GD (2013) Baseline histopathological survey of a recently invading island population of "killer shrimp", *Dikerogammarus villosus*. *Diseases of Aquatic Organisms* 106: 241–253, http://dx.doi.org/10.3354/dao02658

Bollache L (2004) *Dikerogammarus villosus* (Crustacea: Amphipoda): another invasive species in Lake Geneva. *Revue Suisse De Zoologie* 111: 309–313

Bollache L, Devin S, Wattier R, Chovet M, Beisel JN, Moreteau JC, Rigaud T (2004) Rapid range extension of the Ponto-Caspian amphipod *Dikerogammarus villosus* in France: potential consequences. *Archiv Für Hydrobiologie* 160: 57–66, http://dx.doi.org/10.1127/0003-9136/2004/0160-0057

Bollache L, Dick JTA, Farnsworth KD, Montgomery WI (2008) Comparison of the functional responses of invasive and native amphipods. *Biology Letters* 4: 166–169, http://dx.doi.org/10.1098/rsbl.2007.0554

Bousfield E (1958) Freshwater crustaceans of glaciated North America. *Canadian Field Naturalist* 72: 55–113

Bousfield EL (1977) A new look at the systematics of Gammaridean amphipods of the world. *Crustaceana Supplement* 4: 282–316

Briski E, Bailey SA, Casas-Monroy O, DiBacco C, Kaczmarska I, Lawrence JE, Leichsenring J, Levings C, MacGillivary ML, McKindsey CW, Nasmith LE, Parentau M, Piercey GE, Rivkin RB, Rochon A, Roy S, Simard N, Sun B, Way C, Weise AM, MacIsaac HJ (2013) Taxon- and vector-specific variation in species richness and abundance during the transport stage of biological invasions. *Limnology and Oceanography* 58: 1361–1372

Brooks SJ, Platvoet D, Mills CL (2008) Cation regulation and alteration of water permeability in the amphipod *Dikerogammarus villosus*: an indicator of invasion potential. *Fundamental and Applied Limnology* 172: 183–189, http://dx.doi.org/10.1127/1863-9135/2008/0172-0183

Brtek J (2001) Príspevok k poznaniu amphipod Slovenska (I. Gammaroidea, Crangonyctoidea, Corophioidea). *Acta Rerum Naturalium Musei Nationalis Slovenici* 47: 65–89

Bruijs MCM, Kelleher B, van der Velde G, Bij de Vaate A (2001) Oxygen consumption, temperature and salinity tolerance of the invasive amphipod *Dikerogammarus villosus*: indicators of further dispersal via ballast water transport. *Archiv Für Hydrobiologie* 152: 633–646

Brzezinska-Blaszczyk E, Jazdzewski K (1980) Reproductive cycle of *Gammarus fossarum* Koch (Crustacea, Amphipoda) in different thermic conditions. *Acta Universitatis Lodziensis, Nauki Matematyczno - Przyrodnicze* S. II 33: 129–153

Buřič M, Koči L, Petrusek A, Kouba A, Kozák P (2009) Invaders eating invaders: potential trophic interactions between the amphipod *Dikerogammarus villosus* and juvenile crayfish *Orconectes limosus*. *Knowledge and Management of Aquatic Ecosystems* 394–395: 05, http://dx.doi.org/10.1051/kmae/2009015

Carauşu S (1943) Amphipodes de Roumanie. I. Gammarides de type Caspien. Institutul De Cercetari Piscicolae Al Romanei. Bucuresti, Romania, 293 pp

Carauşu S, Dobreanu E, Manolache C (1955) Amphipoda forme salmastre si de apa dulce. Fauna Republicii Populare Romine. Bucuresti, Romania, 409 pp

Casellato S, La Piana G, Latella L, Ruffo S (2006) *Dikerogammarus villosus* (Sowinsky, 1894) (Crustacea, Amphipoda, Gammaridae) for the first time in Italy. *Italian Journal of Zoology* 73: 97–104, http://dx.doi.org/10.1080/11250000500502293

Casellato S, Visentin A, La Piana G (2007) The predatory impact of *Dikerogammarus villosus*, a danger for fish. In: Gherardi F (ed), Biological invaders in inland waters: profiles, distribution, and threats. Invading Nature: Springer Series in Invasion Ecology. Springer, Dordrecht, The Netherlands, pp 495–506, http://dx.doi.org/10.1007/978-1-4020-6029-8_27

Chambers MR (1977) The population ecology of *Gammarus tigrinus* (Sexton) in the Reed Beds of the Tjeukemeer. *Hydrobiologia* 53: 155–164

Chandra S, Gerhadt A (2008) Invasive species in aquatic ecosystems: issue of global concern. *Aquatic Invasions* 3: 1–2, http://dx.doi.org/10.3391/ai.2008.3.1.1

Chernogorenko MI, Komarovova TI, Kurandina DP (1978) Life cycle of the trematode, *Plagioporus skrjabini* Kowal, 1951 (Allocreadiata Opecoelidae). *Parazitologiia* 12: 479−486

Chepalyga AL (2007) The late glacial Great Flood in the Ponto-Caspian basin. In: Yanko-Hombach V, Gilbert AS, Panin N, Dolukhanov PM (eds), The Black Sea Flood question: changes in coastline, climate and human settlement Springer, pp 119–148

Ciolpan O (1987) Zur fortpflanzung von *Dikerogammarus villosus* Sow. Mart. Crustacea-Amphipoda im Eisernes Tor–Stausee Bahna-Golf, 1983–1984. *Revue Roumaine de biologie* 32: 71–74

Ciutti F, Beltrami ME, Confortini I, Cianfanelli S, Cappelletti C (2011) Non-indigenous invertebrates, fish and macrophytes in Lake Garda (Italy). *Journal of Limnology* 70: 315–320, http://dx.doi.org/10.4081/jlimnol.2011.315

Constable D, Fielding NJ (2011) *Dikerogammarus villosus*: An Anglian Perspective. *Practice: Bulletin of the Institute of Ecology and Environmental Management* 72: 9–11

DAISIE (2009) Handbook of Alien Species in Europe. Springer, Dordrecht, The Netherlands

Dedju II (1966) Morfologicheskaya izmienchivost', rasprostranenie i ekologicheskaya kharakteristika bokoplava *Niphargoides* (*Pontogammarus*) *robustoides* (Grimm). *Biologicheskie resursy vodoemov Moldavii* 4: 47–49

Dedju II (1967) Amfipody i mizidy bassejnov rek Dniestra i Pruta. Izdatelstvo „Nauka", Moskva, 172 pp

Dedju II (1980) Amfipody presnykh i solonovatykh vod yugozapada SSSR. Izdatelstvo „Shtiinca'', Kishinev, 223 pp

Devin S, Beisel JN, Bachmann V, Moreteau JC (2001) *Dikerogammarus villosus* (Amphipoda: Gammaridae): another invasive species newly established in the Moselle river and French hydrosystems. *Annales De Limnologie-International Journal of Limnology* 37: 21–27, http://dx.doi.org/10.1051/limn/2001001

Devin S, Piscart C, Beisel JN, Moreteau JC (2003) Ecological traits of the amphipod invader *Dikerogammarus villosus* on a mesohabitat scale. *Archiv Für Hydrobiologie* 158: 43–56, http://dx.doi.org/10.1127/0003-9136/2003/0158-0043

Devin S, Piscart C, Beisel JN, Moreteau JC (2004) Life history traits of the invader *Dikerogammarus villosus* (Crustacea: Amphipoda) in the Moselle River, France. *International Review of Hydrobiology* 89: 21–34, http://dx.doi.org/10.1002/iroh.200310667

Dick JTA, Platvoet D (2000) Invading predatory crustacean *Dikerogammarus villosus* eliminates both native and exotic species. *Proceedings of the Royal Society B-Biological Sciences* 267: 977–983, http://dx.doi.org/10.1098/rspb.2000.1099

Dick JTA, Platvoet D, Kelly DW (2002) Predatory impact of the freshwater invader *Dikerogammarus villosus* (Crustacea : Amphipoda). *Canadian Journal of Fisheries and Aquatic Sciences* 59: 1078–1084, http://dx.doi.org/10.1139/f02-074

Dick JTA, Alexander ME, MacNeil C (2013) Natural born killers: an invasive amphipod is predatory throughout its life-history. *Biological Invasions* 15: 309–313, http://dx.doi.org/10.1007/s10530-012-0287-9

Dodd JA, Dick JTA, Alexander ME, MacNeil C, Dunn AM,. Aldridge DC (2013) Predicting the ecological impacts of a new freshwater invader: functional responses and prey selectivity of the invasive 'killer shrimp', *Dikerogammarus villosus*, compared with the native, *Gammarus pulex*. *Freshwater Biology* 59: 337–352, http://dx.doi.org/10.1111/fwb.12268

Dumont HJ (2000) Endemism in the Ponto-Caspian fauna, with special emphasis on the Onychopoda (Crustacea). *Advances in Ecological Research* 31: 181–196, http://dx.doi.org/10.1016/S0065-2504(00)31012-1

Eggers TO, Martens A (2001) A key to the freshwater Amphipoda (Crustacea) of Germany. *Lauterbornia* 42: 1–70

Emde S, Rueckert S, Palm HW, Klimpel S (2012) Invasive Ponto-Caspian Amphipods and Fish Increase the Distribution Range of the Acanthocephalan *Pomphorhynchus tereticollis* in the River Rhine. *Plos One* 7(12): e53218, http://dx.doi.org/10.1371/journal.pone.0053218

Environmental Agency (2012) Invasive Shrimp, *Dikerogammarus villosus*. Briefing Note 5, pp 1–7

European Commission (2013) Proposal for a regulation of the European parliament and of the council on the prevention and management of the introduction and management of the introduction and spread of invasive alien species COD(2013)0307, Brussels

Felten V, Charmantier G, Mons R, Geffard A, Rousselle P, Coquery M, Garric J, Geffard O (2008a) Physiological and behavioural responses of *Gammarus pulex* (Crustacea: Amphipoda) exposed to cadmium. *Aquatic Toxicology* 86: 413–425, http://dx.doi.org/10.1016/j.aquatox.2007.12.002

Felten V, Dolédec S, Statzner B (2008b) Coexistence of an invasive and a native gammarid across an experimental flow gradient: flow-refuge use, -mortality, and leaf-litter decay. *Fundamental and Applied Limnology* 172: 37–48, http://dx.doi.org/10.1127/1863-9135/2008/0172-0037

Gallardo B, Errea MP, Aldridge DC (2012) Application of bioclimatic models coupled with network analysis for risk assessment of the killer shrimp, *Dikerogammarus villosus*, in Great Britain. *Biological Invasions* 14: 1265–1278, http://dx.doi.org/10.1007/s10530-011-0154-0

Gallardo B, Aldridge DC (2013a) Evaluating the combined threat of climate change and biological invasions on endangered species. *Biological Conservation* 160: 225–233, http://dx.doi.org/10.1016/j.biocon.2013.02.001

Gallardo B, Aldridge DC (2013b) The 'dirty dozen': socio-economic factors amplify the invasion potential of 12 high-risk aquatic invasive species in Great Britain and Ireland. *Journal of Applied Ecology* 50: 757–766, http://dx.doi.org/10.1111/1365-2664.12079

Gallardo B, Aldridge DC (2013c) Priority setting for invasive species management: risk assessment of Ponto-Caspian invasive species into Great Britain. *Ecological Applications* 23: 352–364, http://dx.doi.org/10.1890/12-1018.1

GB NNSS (2011) Great Britain Non-native Species Secretariat (GB NNSS), http://www.nonnativespecies.org (Accessed 05 July 2014)

Gergs R, Rothhaupt KO (2008a) Effects of zebra mussels on a native amphipod and the invasive *Dikerogammarus villosus*: the influence of biodeposition and structural complexity. *Journal of the North American Benthological Society* 27: 541–548, http://dx.doi.org/10.1899/07-151.1

Gergs R, Rothhaupt KO (2008b) Feeding rates, assimilation efficiencies and growth of two amphipod species on biodeposited material from zebra mussels. *Freshwater Biology* 53: 2494–2503, http://dx.doi.org/10.1111/j.1365-2427.2008.02077.x

Gonzalo C, Camargo JA, Masiero L, Casellato S (2010) Fluoride toxicity and bioaccumulation in the invasive Amphipod *Dikerogammarus villosus* (Sowinsky, 1894): a laboratory study. *Bulletin of Environmental Contamination and Toxicology* 85: 472–475, http://dx.doi.org/10.1007/s00128-010-0132-8

Government of Canada (2006) Ballast water control and management regulations. Canada Gazette 140(l3), http://gazette.gc.ca/archives/p2/2006/2006-06-28/html/sor-dors129-eng.html (Accessed 10 December 2012)

Grabow K, Eggers TO, Martens A (1998) *Dikerogammarus villosus* Sowinsky (Crustacea: Amphipoda) in norddeutschen kanälen und flüssen. *Lauterbornia* 33: 103–107

Grabowski M, Bącela K, Konopacka A (2007a) How to be an invasive gammarid (Amphipoda: Gammaroidea)-comparison of life history traits. *Hydrobiologia* 590: 75–84, http://dx.doi.org/10.1007/s10750-007-0759-6

Grabowski M, Bącela K, Wattier R (2007b) *Dikerogammarus villosus* (Sovinsky, 1894) (Crustacea, Amphipoda) colonizes next alpine lake – Lac du Bourget, France. *Aquatic Invasions* 2: 268–271, http://dx.doi.org/10.3391/ai.2007.2.3.13

Grabowski M, Jażdżewski K, Konopacka A (2007c) Alien Crustacea in Polish waters – Amphipoda. *Aquatic Invasions* 2: 25–38, http://dx.doi.org/10.3391/ai.2007.2.1.3

Grabowski M, Bącela K, Konopacka A, Jażdżewski K (2009) Salinity-related distribution of alien amphipods in rivers provides refugia for native species. *Biological Invasions* 11: 2107–2117, http://dx.doi.org/10.1007/s10530-009-9502-8

Grabowski M, Bącela-Spychalska K, Pešić V (2014) Reproductive traits and conservation needs of the endemic gammarid *Laurogammarus scutarensis* (Schäferna, 1922) from the Skadar Lake system, Balkan Peninsula. *Limnologica* 47: 44–51, http://dx.doi.org/10.1016/j.limno.2014.04.001

Grabowski M, Jażdżewska A, Bacela-Spychalska K, Rewicz T, Özbek M (2011) How many *Dikerogammarus* species we have? A DNA-barcoding approach. In: Lo Brutto S, Ketmaier V, Marrone F, Pavesi L (eds), New frontiers in monitoring European biodiversity. The role and importance of amphipod crustaceans, Palermo, Italy 27-29 September 2011, 72 pp

Haine ER, Brondani E, Hume KD, Perrot-Minnot MJ, Gaillard M, Rigaud T (2004) Coexistence of three microsporidia parasites in populations of the freshwater amphipod *Gammarus roeseli*: evidence for vertical transmission and positive effect on reproduction. *International Journal for Parasitology* 34: 1137–1146, http://dx.doi.org/10.1016/j.ijpara.2004.06.006

Haine ER, Motreuil S, Rigaud T (2007) Infection by a vertically-transmitted microsporidian parasite is associated with a female-biased sex ratio and survival advantage in the amphipod *Gammarus roeseli*. *Parasitology* 134: 1363–1367, http://dx.doi.org/10.1017/S0031182007002715

Hesselschwerdt J, Necker J, Wantzen KM (2008) Gammarids in Lake Constance: habitat segregation between the invasive *Dikerogammarus villosus* and the indigenous *Gammarus roeselii*. *Fundamental and Applied Limnology* 173: 177–186, http://dx.doi.org/10.1127/1863-9135/2008/0173-0177

Holdich DM, Pöckl M (2007) Invasive crustaceans in European inland waters. In: Gherardi F (ed), Biological invaders in inland waters: profiles, distribution and threats. Springer, Berlin, pp 29–75

Holling CS (1966) The functional response of invertebrate predators to prey density. *Memoirs of the Entomological Society of Canada* 48: 1–86, http://dx.doi.org/10.4039/entm9848fv

Holt RD, Polis GA (1997) A theoretical framework for intraguild predation. *The American Naturalist* 149: 745–764, http://dx.doi.org/10.1086/286018

Hupało K, Rewicz T, Bącela-Spychalska K, Konopacka A, Grabowski M (2014) First record of the killer shrimp, *Dikerogammarus villosus* (Sovinsky, 1894), in the Váh River, Slovakia. *Lauterbornia* 77: 9–13

Hynes HBN (1955) The reproductive cycle of some British freshwater Gammaridae. *Journal of Animal Ecology* 24: 352–387

Hynes HBN, Harper F (1992) The life histories of *Gammarus lacustris* and *G. pseudolimnaeus* in southern Ontario. *Crustaceana Supplement* 3: 329–341

Ioffe TI, Maximova LP (1968) Biology of some crustaceans, perspective for acclimatization in reservoirs. *Proceedings of GosNIORKH* 67, pp 87–104

Jażdżewski K (1975) Morfologia, taksonomia i występowanie w Polsce kiełży z rodzajów *Gammarus* Fabr. i *Chaetogammarus* Mart. (Crustacea, Amphipoda). Acta Universitatis Lodziensis, 185 pp

Jażdżewski K (1980) Range extensions of some gammaridean species in European inland waters caused by human activity. *Crustaceana Supplement* 6: 84–107

Jażdżewski K, Konopacka A (2002) Invasive Ponto-Caspian species in waters of the Vistula and Oder basins and of the southern Baltic Sea. In: Leppäkowski E, Olenin S, Gollasch S (eds), Invasive Aquatic Species of Europe. Distribution, Impact and Management. Kluwer Academic Publishers, Dordrecht, The Netherlands, pp 383–398, http://dx.doi.org/10.1007/978-94-015-9956-6_39

Jażdżewski K, Konopacka A, Grabowski M (2005) Native and alien malacostracan Crustacea along the Polish Baltic Sea coast in the twentieth century. *Oceanological andand Hydrobiological Studies* 24: 195–208

Josens G, Bij de Vaate A, Usseglio-Polatera P, Cammaerts R, Cherot F, Grisez F, Verboonen P, Vander Bossche JP (2005) Native and exotic Amphipoda and other Peracarida in the River Meuse: new assemblages emerge from a fast changing fauna. *Hydrobiologia* 542: 203–220, http://dx.doi.org/10.1007/s10750-004-8930-9

Kasymov AG (1960) Biologiya bokoplava *Pontogammarus robustoides* (Grimm). *Zoologicheskii Zhurnal* 39: 1151–1155

Kinzler W, Maier G (2003) Asymmetry in mutual predation: possible reason for the replacement of native gammarids by invasives. *Archiv Für Hydrobiologie* 157: 473–481, http://dx.doi.org/10.1127/0003-9136/2003/0157-0473

Kinzler W, Maier G (2006) Selective predation by fish: A further reason for the decline of native gammarids in the presence of invasives? *Journal of Limnology* 65: 27–34, http://dx.doi.org/10.4081/jlimnol.2006.27

Kinzler W, Kley A, Mayer G, Waloszek D, Maier G (2009) Mutual predation between and cannibalism within several freshwater gammarids: *Dikerogammarus villosus* versus one native and three invasives. *Aquatic Ecology* 43: 457–464, http://dx.doi.org/10.1007/s10452-008-9206-7

Kiticyna LA (1980) Ekologo-fiziologicheskie osobennosti bokoplava *Dikerogammarus haemobaphes* (Eich.) v raione sbrosa podogretykh vod Tripolskoj GRES. *Gidrobiologicheskij Zhurnal* 16: 77–85

Kley A, Maier G (2003) Life history characteristics of the invasive freshwater gammarids *Dikerogammarus villosus* and *Echinogammarus ischnus* in the river Main and the Main-Donau canal. *Archiv Für Hydrobiologie* 156: 457–469, http://dx.doi.org/10.1127/0003-9136/2003/0156-0457

Kley A, Maier G (2005) An example of niche partitioning between *Dikerogammarus villosus* and other invasive and native gammarids: A field study. *Journal of Limnology* 64: 85–88, http://dx.doi.org/10.4081/jlimnol.2005.85

Kley A, Maier G (2006) Reproductive characteristics of invasive gammarids in the Rhine-Maine-Danube catchment, South Germany. *Limnologica* 36: 79–90, http://dx.doi.org/10.1016/j.limno.2006.01.002

Kley A, Kinzler W, Schank Y, Mayer G, Waloszek D, Maier G (2009) Influence of substrate preference and complexity on co-existence of two non-native gammarideans (Crustacea: Amphipoda). *Aquatic Ecology* 43: 1047–1059, http://dx.doi.org/10.1007/s10452-009-9242-y

Klingenberg CP, Leigh RHB, Keddie BA, Spence JR (1997) Influence of gut parasites on growth performance in the water strider *Gerris buenoi* (Hemiptera: Gerridae). *Ecography* 20: 29–36, http://dx.doi.org/10.1111/j.1600-0587.1997.tb00344.x

Konopacka A (1988) Life history of *Gammarus varsoviensis* Jażdżewski, 1975 from Kampinoski National Park (Central Poland). *Zoologica Poloniae* 35: 165–177

Konopacka A (2004) Inwazyjne skorupiaki obunogie (Crustacea, Amphipoda) w wodach Polski. *Przeglad Zoologiczny* 48: 141–162

Konopacka A, Jażdżewski K (2002) *Obesogammarus crassus* (G.O. Sars, 1894) – one more Ponto-caspian gammarid species in Polish waters. *Fragmenta Faunistica* 45: 19–26, http://dx.doi.org/10.3161/00159301FF2002.45.1.019

Konopacka A, Jesionowska K (1995) Life history of *Echinogammarus ischnus* (Stebbing, 1898) (Amphipoda) from artificially heated Licheńskie Lake (Poland). *Crustaceana* 68: 341–349

Krisp H, Maier G (2005) Consumption of macroinvertebrates by invasive and native gammarids: A comparison. *Journal of Limnology* 64: 55–59, http://dx.doi.org/10.4081/jlimnol.2005.55

Kunz PY, Kienle C, Gerhardt A (2010) *Gammarus* spp. in aquatic ecotoxicology and water quality assessment: aoward integrated multilevel tests. *Reviews of Environmental Contamination and Toxicology* 205: 1–76, http://dx.doi.org/10.1007/978-1-4419-5623-1_1

Kurandina DP (1975) Nekotorye dannye o razmnozhenii i plodovitosti kaspijskikh gammarid v Kremenchugskom Vodokhranilishche. *Gidrobiologicheskij Zhurnal* 11: 35–41

Lambertini M, Leape J, Marton-Lefevre J, Mitter-Meier RA, Rose M, Robinson JG, Stuart SN, Waldman B, Genovesi P (2011) Invasives: A Major Conservation Threat. *Science* 333: 404–405, http://dx.doi.org/10.1126/science.333.6041.404-b

Leppäkoski E, Gollasch S, Olenin S (eds) (2002) Invasive aquatic species of Europe: distribution, impacts and management. Kluwer Academic Publishers, Dordrecht, The Netherlands, 583 pp, http://dx.doi.org/10.1007/978-94-015-9956-6

Lipták B (2013) Non-indigenous invasive freshwater crustaceans (Crustacea: Malacostraca) in Slovakia. *Water Research and Management* 3(3): 21–31

Lods-Crozet B, Reymonnd O (2006) Bathymetric expansion of an invasive gammarid (*Dikerogammarus villosus*, Crustacea, Amphipoda) in Lake Léman. *Journal of Limnology* 65: 141–144, http://dx.doi.org/10.4081/jlimnol.2006.141

Lubini V, Stucki P, Schiess H, Vincentini H, Wagner A (2006) Révision des listes rouges nationales. Organismes aquatiques – MEPT (Mollusca, Ephemeroptera, Plecoptera et Trichoptera). Rapport activité 2006, CSCF, Neuchâtel, Tome 129, 129 pp

Maazouzi C, Masson G, Izquierdo MS, Pihan JC (2007) Fatty acid composition of the amphipod *Dikerogammarus villosus*: Feeding strategies and trophic links. *Comparative Biochemistry and Physiology a-Molecular andand Integrative Physiology* 147: 868–875

Maazouzi C, Masson G, Izquierdo MS, Pihan JC (2008) Chronic copper exposure and fatty acid composition of the amphipod *Dikerogammarus villosus*: results from a field study. *Environmental Pollution* 156: 221–226, http://dx.doi.org/10.1016/j.envpol.2007.12.010

Maazouzi C, Piscart C, Legier F, Hervant F (2011) Ecophysiological responses to temperature of the "killer shrimp" *Dikerogammarus villosus*: Is the invader really stronger than the native *Gammarus pulex? Comparative Biochemistry and Physiology a-Molecular andand Integrative Physiology* 159: 268–274

MacNeil C, Platvoet D (2005) The predatory impact of the freshwater invader *Dikerogammarus villosus* on native *Gammarus pulex* (Crustacea: Amphipoda); influences of differential microdistribution and food resources. *Journal of Zoology* 267: 31–38, http://dx.doi.org/10.1017/S0952836905007351

MacNeil C, Platvoet D (2013) Could artificial structures such as fish passes facilitate the establishment and spread of the 'killer shrimp' *Dikerogammarus villosus* (Crustacea: Amphipoda) in river systems? *Aquatic Conservation-Marine and Freshwater Ecosystems* 23: 667–677

MacNeil C, Dick JTA, Elwood RW (1997) The trophic ecology of freshwater *Gammarus* (Crustacea: Amphipoda); problems and perspectives concerning the functional feeding group concept. *Biological Reviews* 72: 349–364

MacNeil C, Dick JTA, Hatcher MJ, Fielding NJ, Hume KD, Dunn AM (2003) Parasite transmission and cannibalism in an

amphipod (Crustacea). *International Journal for Parasitology* 33: 795–798, http://dx.doi.org/10.1016/S0020-7519(03)00110-3

MacNeil C, Platvoet D, Dick JTA (2008) Potential roles for differential body size and microhabitat complexity in mediating biotic interactions within invasive freshwater amphipod assemblages. *Fundamental and Applied Limnology* 172:175–182, http://dx.doi.org/10.1127/1863-9135/2008/0172-0175

MacNeil C, Platvoet D, Dick JTA, Fielding N, Constable A, Hall N, Aldridge D, Renals T, Diamond M (2010) The Ponto-Caspian 'killer shrimp', *Dikerogammarus villosus* (Sowinsky, 1894), invades the British Isles. *Aquatic Invasions* 5: 441–445, http://dx.doi.org/10.3391/ai.2010.5.4.15

MacNeil C, Dick JTA, Platvoet D, Briffa M (2011) Direct and indirect effects of species displacements: an invading freshwater amphipod can disrupt leaf-litter processing and shredder efficiency. *Journal of the North American Benthological Society* 30: 38–48, http://dx.doi.org/10.1899/10-056.1

MacNeil C, Boets P, Platvoet D (2012) 'Killer shrimps', dangerous experiments and misguided introductions: how freshwater shrimp (Crustacea: Amphipoda) invasions threaten biological water quality monitoring in the British Isles. *Freshwater Reviews* 5: 21–35, http://dx.doi.org/10.1608/FRJ-5.1.457

MacNeil C, Boets P, Lock K, Goethals PLM (2013) Potential effects of the invasive 'killer shrimp' (*Dikerogammarus villosus*) on macroinvertebrate assemblages and biomonitoring indices. *Freshwater Biology* 58: 171–182, http://dx.doi.org/10.1111/fwb.12048

Madgwick G, Aldridge DC (2011) Killer Shrimps in Britain: hype or horror? The facts about our latest invasive animal. *British Wildlife* 22: 408–412

Maier G, Kley A, Schank Y, Maier M, Mayer G, Waloszek D (2011) Density and temperature dependent feeding rates in an established and an alien freshwater gammarid fed on chironomid larvae. *Journal of Limnology* 70: 123–128, http://dx.doi.org/10.4081/jlimnol.2011.123

Martens A, Grabow K (2008) Das risiko der verschleppung neozoischer Amphipoda beim überlandtransport von yachten. *Lauterbornia* 62: 41–44, http://dx.doi.org/10.3391/ai.2007.2.1.4

Mastitsky SE, Makarevich OA (2007) Distribution and abundance of Ponto-Caspian amphipods in the Belarusian section of the Dnieper River. *Aquatic Invasions* 2: 39–44, http://dx.doi.org/10.3391/ai.2007.2.1.4

Mayer G, Maier G, Maas A, Waloszek D (2008) Mouthparts of the Ponto-Caspian invader *Dikerogammarus villosus* (Amphipoda: Pontogammaridae). *Journal of Crustacean Biology* 28: 1–15, http://dx.doi.org/10.1651/07-2867R.1

Mayer G, Maier G, Maas A, Waloszek D (2009) Mouthpart morphology of *Gammarus roeselii* compared to a successful invader, *Dikerogammarus villosus* (Amphipoda). *Journal of Crustacean Biology* 29: 161–174, http://dx.doi.org/10.1651/08-3056R.1

Mayer G, Maas A, Waloszek D (2012) Coexisting native and non-indigenous gammarideans in Lake Constance – Comparative morphology of mouthparts (Crustacea, Amphipoda, Gammaridea). *Spixiana* 35: 269–285

Mordukhai-Boltovskoi FD (1949) Zhiznennyj cykl nekotorykh kaspijskikh gammarid. *Doklady Akademii Nauk SSSR* 65: 997–999

Mordukhai-Boltovskoi FD (1960) Caspian Fauna in Azov and Black Seas Basin. Izdatelstvo Akademii nauk USSR, Moskva, Leningrad, 288 pp

Mordukhai-Boltovskoi FD (1964) Caspian fauna beyond the Caspian Sea. *International Review of Hydrobiology and Hydrography* 49: 139–176, http://dx.doi.org/10.1002/iroh.19640490105

Mordukhai-Boltovskoi FD (1969) Besonderheiten der kaspischen Fauna im Bassin der Donau. Limnologische Donauforschungen, Kiev, pp 98–105

Mordukhai-Boltovskoi FD, Greeze II, Vasilenko SV (1969) Otryad amphipody ili raznonogie – Amphipoda Latreille, 1816-17. In: Kiseleva MI, Mordukhai-Boltovskoi FD, Murina VV (eds), Opredelitel fauny Chernogo i Azovskogo morei. Izdatelstvo Naukova Dumka, Kiev, USSR, pp 440–524

Müller JC, Schramm S, Seitz A (2002) Genetic and morphological differentiation of *Dikerogammarus* invaders and their invasion history in Central Europe. *Freshwater Biology* 47: 2039–2048, http://dx.doi.org/10.1046/j.1365-2427.2002.00944.x

Müller O, Zettler ML, Gruszka P (2001) Verbreitung und Status von unteren Strom-Oder und den angrenzenden Wasserstrassen. *Lauterbornia* 41: 105–112

Mürle U, Becker A, Seitz A (2003) Ein neuer Flohkrebs im Bodensee: *Dikerogammarus villosus* (Grosser Höckerflohkrebs). http://bodensee-ufer.de (Accessed 15 November 2012)

Muskó IB (1989) Amphipoda (Crustacea) in the littoral-zone of Lake Balaton (Hungary) - qualitative and quantitative studies. *Internationale Revue Der Gesamten Hydrobiologie* 74: 195–205, http://dx.doi.org/10.1002/iroh.19890740206

Muskó IB (1990) Qualitative and quantitative relationships of amphipoda (Crustacea) living on macrophytes in Lake Balaton (Hungary). *Hydrobiologia* 191: 269–274, http://dx.doi.org/10.1007/BF00026062

Muskó IB (1993) The life history of *Dikerogammarus haemobaphes* (Eichw) (Crustacea, Amphipoda) living on macrophytes in Lake Balaton (Hungary). *Archiv Für Hydrobiologie* 127: 227–238

Nehering S (2002) Biological invasions into German waters: an evaluation of the importance of different human-mediated vectors for nonindigenous macrozoobenthic species. In: Leppäkowski E, Gollasch S, Olenin S (eds), Invasive aquatic species of Europe - Distribution, impacts and management. Kluwer Academic Publishers, Dordrecht, The Netherlands, pp 373–383, http://dx.doi.org/10.1007/978-94-015-9956-6_38

Nesemann H, Pöckl M, Wittmann KJ (1995) Distribution of epigean Malacostraca in the middle and upper Danube (Hungary, Austria, Germany). *Miscellanea Zoologica Hungarica* 10: 49–68

Olden JD, McCarthy JM, Maxted JT, Fetzer WW, Vander Zanden JM (2006) The rapid spread of rusty crayfish (*Orconectes rusticus*) with observations on native crayfish declines in Wisconsin (U.S.A.) over the past 130 years. *Biological Invasions* 8: 1621–1628, http://dx.doi.org/10.1007/s10530-005-7854-2

Ovcharenko NA, Kurandina DP (1987) New species of microsporidia from amphipods of the Dnieper basin. *Parazitologiya* 21: 710–715

Ovcharenko M, Codreanu-Balcescu D, Wita I, Grabowski M, Konopacka A (2008) Microparasites of invasive and native gammarid species (Amphipoda, Gammaroidea) occurring in Poland. Preliminary records. *Limnological Papers* 3: 53–58, http://dx.doi.org/10.2478/v10232-011-0017-9

Ovcharenko M, Codreanu-Balcescu D, Grabowski M, Konopacka A, Wita I, Czaplinska U (2009) Gregarines (Apicomplexa) and microsporidians (Microsporidia) of native and invasive gammarids (Amphipoda, Gammaroidea), occurring in Poland. *Wiadomosci Parazytologiczne* 55: 237–247

Ovcharenko MO, Bącela K, Wilkinson T, Ironside JE, Rigaud T, Wattier RA (2010) *Cucumispora dikerogammari* n. gen. (Fungi: Microsporidia) infecting the invasive amphipod *Dikerogammarus villosus*: a potential emerging disease in European rivers. *Parasitology* 137: 191–204, http://dx.doi.org/10.1017/S0031182009991119

Özbek M, Özkan N (2011) *Dikerogammarus istanbulensis* sp. n., a new amphipod species (Amphipoda: Gammaridae) from Turkey with a key for the genus. *Zootaxa* 2813: 55–64

Panov VE, Alexandrov B, Arbačiauskas K, Binimelis R, Copp GH, Grabowski M, Lucy F, Leuven RS, Nehring S, Pauović M, Semenchenko V, Son MO (2009) Assessing the risks of aquatic species invasions via European inland waterways: from concepts to environmental indicators. *Integrated Environmental Assessment and Management* 5: 110–126, http://dx.doi.org/10.1897/IEAM_2008-034.1

Pinkster S, Smit H, Brandse-De Jong N (1977) The introduction of the alien amphipod *Gammarus tigrinus* Sexton, 1939, in The Netherlands and its competition with indigenous species. *Crustaceana Supplement* 4: 91–105

Piscart C, Bergerot B, Laffaille P, Marmonier P (2010) Are amphipod invaders a threat to regional biodiversity? *Biological Invasions* 12: 853–863, http://dx.doi.org/10.1007/s10530-009-9506-4

Piscart C, Devin S, Beisel JN, Moreteau JC (2003) Growth-related life-history traits of an invasive gammarid species: evaluation with a Laird-Gompertz model. *Canadian Journal of Zoology* 81: 2006–2014, http://dx.doi.org/10.1139/z03-188

Piscart C, Kefford BJ, Beisel JN (2011) Are salinity tolerances of non-native macroinvertebrates in France an indicator of potential for their translocation in a new area? *Limnologica* 41: 107–112, http://dx.doi.org/10.1016/j.limno.2010.09.002

Pjatakova GM, Tarasov AG (1996) Caspian Sea amphipods: biodiversity, systematic position and ecological peculiarities of some species. *Journal of Salt Lake Research* 5: 63–79, http://dx.doi.org/10.1007/BF01996036

Platvoet D, Dick JTA, Konijnendijk N, van der Velde G (2006a) Feeding on micro-algae in the invasive Ponto-Caspian amphipod *Dikerogammarus villosus* (Sowinsky, 1894). *Aquatic Ecology* 40: 237–245, http://dx.doi.org/10.1007/s10452-005-9028-9

Platvoet D, Hou ZE, Li SQ, van der Velde G (2006b) Enigmatic pores in females of *Dikerogammarus villosus* (Sowinsky, 1894) (Amphipoda). Amphipod pilot species project (AMPIS) Report 1. *Crustaceana* 78: 1399–1404, http://dx.doi.org/10.1163/156854005776759852

Platvoet D, Song YJ, Li SQ, van der Velde G (2006c) A lock-on system in precopulae of *Dikerogammarus villosus* (Sowinsky, 1894), also present in *Gammarus pulex pulex* (Linnaeus, 1758) (Amphipoda). Amphipod pilot species project (Ampis) report 2. *Crustaceana* 79: 993–1003, http://dx.doi.org/10.1163/156854006778815964

Platvoet D, Hou ZE, Li SQ, van der Velde G (2006d) Presumed statocysts in the cephalon of *Dikerogammarus villosus* (Sowinsky, 1894) (Peracarida, Amphipoda). Amphipod Pilot Species Project (AMPIS) Report 3. *Crustaceana* 79: 1123–1127, http://dx.doi.org/10.1163/156854006778859722

Platvoet D, Song YJ, Li SQ, van der Velde G (2007) Description of the lateral line organ of *Dikerogammarus villosus* (Sowinsky, 1894), with discussion on its function (Peracarida, Amphiopda). *Crustaceana* 80: 1373–1392, http://dx.doi.org/10.1163/156854007782605619

Platvoet D, Dick JTA, MacNeil C, van Riel MC, van der Velde G (2009a) Invader-invader interactions in relation to environmental heterogeneity leads to zonation of two invasive amphipods, *Dikerogammarus villosus* (Sowinsky) and *Gammarus tigrinus* Sexton: amphipod pilot species project (AMPIS) report 6. *Biological Invasions* 11: 2085–2093, http://dx.doi.org/10.1007/s10530-009-9488-2

Platvoet D, van der Velde G, Dick JTA, Li SQ (2009b) Flexible omnivory in *Dikerogammarus villosus* (Sowinsky, 1894) (Amphipoda) - Amphipod Pilot Species Project (Ampis) Report 5. Crustaceana 82: 703–720, http://dx.doi.org/10.1163/156854009X423201

Pöckl M (1992) Effects of temperature, age and body size on molting and growth in the freshwater Amphipods *Gammarus fossarum* and *Gammarus roeseli*. *Freshwater Biology* 27: 211–225, http://dx.doi.org/10.1111/j.1365-2427.1992.tb00534.x

Pöckl M (2007) Strategies of a successful new invader in European fresh waters: fecundity and reproductive potential of the Ponto-Caspian amphipod *Dikerogammarus villosus* in the Austrian Danube, compared with the indigenous *Gammarus fossarum* and *G. roeseli*. *Freshwater Biology* 52: 50–63, http://dx.doi.org/10.1111/j.1365-2427.2006.01671.x

Pöckl M (2009) Success of the invasive Ponto-Caspian amphipod *Dikerogammarus villosus* by life history traits and reproductive capacity. *Biological Invasions* 11: 2021–2041, http://dx.doi.org/10.1007/s10530-009-9485-5

Polis GA, Myers CA, Holt RD (1989) The ecology and evolution of intraguild predation - potential competitors that eat each other. *Annual Review of Ecology and Systematics* 20: 297–330, http://dx.doi.org/10.1146/annurev.es.20.110189.001501

Poznańska M, Kakareko T, Krzyżynski M, Kobak J (2013) Effect of substratum drying on the survival and migrations of Ponto-Caspian and native gammarids (Crustacea: Amphipoda). *Hydrobiologia* 700: 47–59, http://dx.doi.org/10.1007/s10750-012-1218-6

Pyšek P, Jarošík V, Hulme PE, Kühn I, Wild J, Arianoutsou M, Bacher S, Chiron F, Didžiulis V, Essl F, Genovesi P, Gherardi F, Hejda M, Kark S, Lambdon, PW, Desprez-Loustau ML, Nentwig W, Pergl J, Poboljšaj K, Rabitsch W, Roques A, Roy D, Shirley S, Solarz W, Vilà M, Winter M (2010) Disentangling the role of environmental and human pressures on biological invasions across Europe. *Proceedings of the National Academy of Sciences of the United States of America* 107: 12157–12162, http://dx.doi.org/10.1073/pnas.1002314107

Ricciardi A, MacIsaac HJ (2000) Recent mass invasion of the North American Great Lakes by Ponto-Caspian species. *Trends in Ecology andand Evolution* 15: 62–65

Richardson DM, Ricciardi A (2013) Misleading criticisms of invasion science: a field guide. *Diversity and Distributions* 19: 1461–1467, http://dx.doi.org/10.1111/ddi.12150

Rudolph K (2000) Gebietsfremde malakostrake Krebse in mittleren Teil Brandenburgs. Aktueller Stand der Verbreitung. *Neozoen* 3: 10–11

Sala OE, Chapin FS, Armesto JJ, Berlow E, Bloomfield J, Dirzo R, Huber-Sanwald E, Huenneke LF, Jackson RB, Kinzig A, Leemans R, Lodge DM, Mooney HA, Oesterheld M, Poff NL, Sykes MT, Walker BH, Walker M, Wall DH (2000) Biodiversity - Global biodiversity scenarios for the year 2100. *Science* 287: 1770–1774, http://dx.doi.org/10.1126/science.287.5459.1770

Santagata S, Bącela K, Reid DF, Mclean KA, Cohen JS, Cordell JR, Brown CW, Johengen TH, Ruiz GM (2009) Concentrated sodium chloride brine solutions as an additional treatment for preventing the introduction of nonindigenous species in the ballast tanks of ships declaring no ballast on board. *Environmental Toxicology and Chemistry* 28: 346–353, http://dx.doi.org/10.1897/08-140.1

Santagata S, Gasiunaite ZR, Verling E, Cordell JR, Eason K, Cohen J, Bącela K, Quilez-Badia G, Johengen TH, Reid DF, Ruiz GM (2008) Effect of osmotic shock as a management strategy to reduce transfers of nonindigenous species among low-salinity ports by ships. *Aquatic Invasions* 2: 60–76, http://dx.doi.org/10.3391/ai.2008.3.1.10

SCBD (Secretariat of the Convention on Biological Diversity) (2010) Global Biodiversity Outlook 3, Montreal, 94 pp

Sebesvari Z, Ettwig KF, Emons H (2005) Biomonitoring of tin and arsenic in different compartments of a limnic ecosystem with emphasis on *Corbicula fluminea* and *Dikerogammarus villosus*. *Journal of Environmental Monitoring* 7: 203–207, http://dx.doi.org/10.1039/b410717a

SLSDC (Saint Lawrence Seaway Development Corporation) (2008) Seaway Regulations and Rules: Periodic Update, Various Categories. Code of Federal Regulations 33-CFR Part 401

Snyder WE, Clevenger GM, Eigenbrode SD (2004) Intraguild predation and successful invasion by introduced ladybird beetles. *Oecologia* 140: 559–565, http://dx.doi.org/10.1007/s00442-004-1612-5

Sornom P, Gismondi E, Vellinger C, Devin S, Ferard JF, Beisel JN (2012) Effects of sublethal cadmium exposure on antipredator behavioural and antitoxic responses in the invasive amphipod *Dikerogammarus villosus*. *Plos One* 7: e42435, http://dx.doi.org/10.1371/journal.pone.0042435

Šporka F (1999) First record of *Dikerogammarus villosus* (Amphipoda, Gammaridae) and *Jaera istri* (Isopoda, Asselota) from the Slovak-Hungarian part of the Danube river. *Biologia - Section Zoology* 54: 538

Sroda S, Cossu-Leguille C (2011) Effects of sublethal copper exposure on two gammarid species: which is the best competitor? *Ecotoxicology* 20: 264–273, http://dx.doi.org/10.1007/s10646-010-0578-9

Stebbing P, Sebire M, Lyons B (2011) Evaluation of a number of treatments to be used as biosecurity measures in controlling the spread of the invasive killer shrimp (*Dikerogammarus villosus*) - Final report (September 2011). Cefas contract report C5256, 40 pp

Steele DH, Steele VJ (1975) The biology of Gammarus (Crustacea, Amphipoda) in the northwestern Atlantic. XI. Comparison and discission. *Canadian Journal of Zoology* 53: 1116–1126

Steinmann P (2008) Makrozoobenthos und aquatische Neozoen im Greifensee und Pfäffikersee. Untersuchung im Auftrag der Baudirektion des Kantons Zürich AWEL Amt für Abfall, Wasser, Energie und Luft, Germany, 28 pp

Steinmann P (2010) Neuester Fund: *Dikerogammarus villosus* im Zugersee, Juni 2010. Aquatische Neozoen: http://www.psteinmann.net/neo_karten.html. (Accessed 10 September 2012)

Steinmann P, Mürle U, Ortlepp J (2006) *Dikerogammarus villosus* in der Aare und ihren Zuflüssen. Report, Hydra Büro für Gewasserökologie, Öschelbronn, 8 pp

Stock JH (1974) The systematics of certain Ponto-Caspian Gammaridae (Crustacea, Amphipoda). *Mitteilungen aus dem Hamburgischen Zoologischen Museum und Institut* 70: 75–95

Terry RS, Smith JE, Sharpe RG, Rigaud T, Littlewood DTJ, Ironside JE, Rollinson D, Bouchon D, MacNeil C, Dick JTA, Dunn AM (2004) Widespread vertical transmission and associated host sex-ratio distortion within the eukaryotic phylum Microspora. *Proceedings of the Royal Society B-Biological Sciences* 271: 1783–1789, http://dx.doi.org/10.1098/rspb.2004.2793

Tricarico E, Mazza G, Orioli G, Rossano C, Scapini F, Gherardi F (2010) The killer shrimp, *Dikerogammarus villosus* (Sowinsky, 1894), is spreading in Italy. *Aquatic Invasions* 5: 211–214, http://dx.doi.org/10.3391/ai.2010.5.2.14

U.S. EPA (Environmental Protection Agency) (2008) Predicting future introductions of nonindigenous species to the Great Lakes. *National Center for Environmental Assessment, Washington,* DC; EPA/600/R-08/066F. Available from the National Technical Information Service, Springfield, VA, and http://www.epa.gov/ncea

Van der Velde G, Rajagopal S, Kelleher B, Muskó IB, Bij De Vaate A (2000) Ecological impact of crustacean invaders: General considerations and examples from the Rhine River. *Biodiversity Crisis and Crustacea* 12: 3–33

Van der Velde G, Leuven RSEW, Platvoet D, Bącela K, Huijbregts MAJ, Hendriks HWM, Kruijt D (2009) Environmental and morphological factors influencing predatory behaviour by invasive non-indigenous gammaridean species. *Biological Invasions* 11: 2043–2054, http://dx.doi.org/10.1007/s10530-009-9500-x

Van Riel MC, van der Velde G, Rajagopal S, Marguillier S, Dehairs F, Bij de Vaate A (2006) Trophic relationships in the Rhine food web during invasion and after establishment of the Ponto-Caspian invader *Dikerogammarus villosus*. *Hydrobiologia* 565: 39–58, http://dx.doi.org/10.1007/s10750-005-1904-8

Van Riel MC, Healy EP, van der Velde G, Bij de Vaate A (2007) Interference competition among native and invader amphipods. *Acta Oecologica-International Journal of Ecology* 31: 282–289, http://dx.doi.org/10.1016/j.actao.2006.12.006

Van Riel MC, van der Velde G, Bij de Vaate A (2009) Interference competition between alien invasive gammaridean species. *Biological Invasions* 11: 2119–2132, http://dx.doi.org/10.1007/s10530-009-9486-4

Van Riel MC, van der Velde G, Bij De Vaate A (2011) Dispersal of invasive species by drifting. *Current Zoology* 57: 818–827

Wang X, Qiu Z, Söffker D (eds) (2013) Uncertainty based design optimization in engineering: model, algorithm, and application. Journal of Applied Mathematics, 91 pp

Wang TN, Bailey SA, Reid DF, Johengen TH, Jenkins PT, Wiley CJ, MacIsaac HJ (2012) Efficacy of NaCl brine for treatment of ballast water against freshwater invasions. *Journal of Great Lakes Research* 38: 72–77, http://dx.doi.org/10.1016/j.jglr.2011.10.001

Wattier RA, Beguet J, Gaillard M, Müller JC, Bollache L, Perrot-Minnot MJ (2006) Molecular markers for systematic identification and population genetics of the invasive Ponto-Caspian freshwater gammarid *Dikerogammarus villosus* (Crustacea, Amphipoda). *Molecular Ecology Notes* 6: 487–489, http://dx.doi.org/10.1111/j.1471-8286.2006.01283.x

Wattier RA, Haine ER, Beguet J, Martin G, Bollache L, Muskó IB, Platvoet D, Rigaud T (2007) No genetic bottleneck or associated microparasite loss in invasive populations of a freshwater amphipod. *Oikos* 116: 1941–1953, http://dx.doi.org/10.1111/j.0030-1299.2007.15921.x

Welton JS, Clarke RT (1980) Laboratory studies on the reproduction and growth of the Amphipod, *Gammarus pulex* (L). *Journal of Animal Ecology* 49: 581–592, http://dx.doi.org/10.2307/4265

Wijnhoven S, van Riel MC, van der Velde G (2003) Exotic and indigenous freshwater gammarid species: physiological tolerance to water temperature in relation to ionic content of the water. *Aquatic Ecology* 37: 151–158

Wysocka A, Grabowski M, Sworobowicz L, Burzyński A, Kilikowska A, Kostoski G, Sell J (2013) A tale of time and depth: intralacustrine radiation in endemic *Gammarus* species flock from the ancient Lake Ohrid. *Zoological Journal of the Linnean Society* 167: 345–359

Yakovleva AV, Yakovlev VA (2010) Modern fauna and quantitative parameters of invasive invertebrates in zoobenthos of upper reaches of the Kuybyshev Reservoir, Russia. *Russian Journal of Biological Invasions* 1: 232–241

Zettler ML (1999) Erstnachweis von *Dikerogammarus villosus* (Sovinski, 1894) und Wiederfund von *Gammarus varsoviensis* Jażdżewski, 1975 in Mecklenburg-Vorpommern (Crustacea: Amphipoda). *Archiv des Vereins der Freunde der Naturgeschichte in Mecklenburg* 38: 231–233

Žganec K, Đurić P, Gottstein S (2011) Life history traits of the endangered endemic Amphipod *Echinogammarus cari* (Crustacea, Gammaridae) from the Dinaric Karst. *International Review of Hydrobiology* 96: 686–708, http://dx.doi.org/10.1002/iroh.201111370

Žganec K, Gottstein S, Hudina S (2009) Ponto-Caspian amphipods in Croatian large rivers. *Aquatic Invasions* 4: 327–335, http://dx.doi.org/10.3391/ai.2009.4.2.4

Zieliński D (1995) Life history of *Gammarus balcanicus* Schaferna, 1922 from the Bieszczady Mountains (Eastern Carpathians, Poland). *Crustaceana* 68: 61–72, http://dx.doi.org/10.1163/156854095X00386

Zieliński D (1998) Life cycle and altitude range of *Gammarus leopoliensis* Jazdzewski and Konopacka, 1989 (Amphipoda) in south-eastern Poland. *Crustaceana* 71: 129–143, http://dx.doi.org/10.1163/156854098X00112

Zuravel PA (1963) Zasolenie Nikolaevskogo i Juznovo vodochranilisc Ukrainy faunoj limannogo kompleksa cerez kanaly. *Zoologicheskii Žurnal* 42: 28–31

Zuravel PA (1965) Ob akklimatizacii fauny limanno-kaspijskoj fauny v novych vodoemach S.S.S.R. *Gidrobiologičeskij Žurnal* 1: 59–63

Supplementary material

The following supplementary material is available for this article:

Table S1. Records of *Dikerogammarus villosus* in native range.
Table S2. Major steps of invasion of *Dikerogammarus villosus* in Europe.

This material is available as part of online article from:
http://www.aquaticinvasions.net/2014/Supplements/AI_2014_Rewicz_etal_Supplement.xls