

## The profile of a ‘perfect’ invader – the case of killer shrimp, *Dikerogammarus villosus*

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### 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 focussed 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.

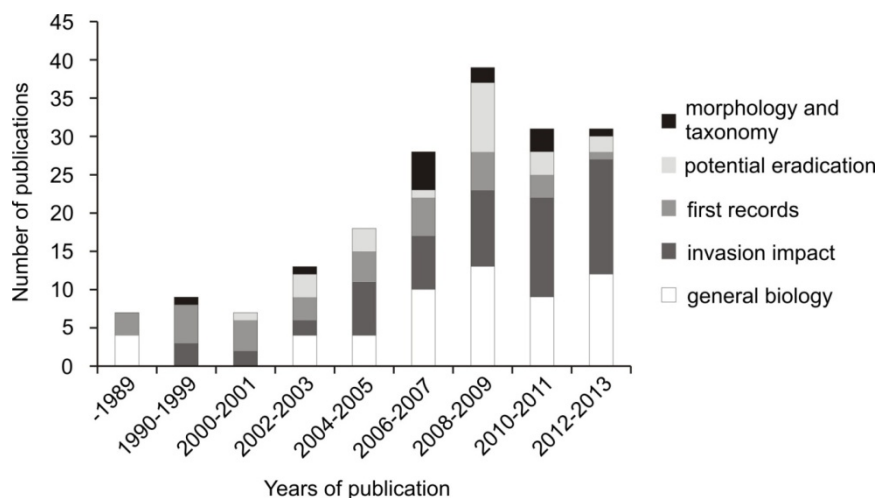
**Key words:** biological invasions, non-indigenous species, Amphipoda, Ponto-Caspian, risk assessments, aquatic invasive species (AIS)

### Introduction

Alien species represent a major threat to conservation management on both a continental and global scale (Leppäkoski et al. 2002; Chandra and Gerhardt 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; Bączela 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 *Obesogammarus*, are grouped in the family Pontogammaridae 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 haemobaphes* (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. Caraușu 1943; Caraușu 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 Belaye, 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 de 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 (Žganec et al. 2009) and in the River Vah in Slovakia in 2011 (Hupało et al.



**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 <i>D. villosus</i> | 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                                       | Bączela-Spychalska et al. 2013a |

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, Bączela-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 *Dikerogammarus* 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). Laboratory 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 significantly 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 naïve 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 acanthocephalan and several microsporidians (Table 3).

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; Bączela-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 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 (Bączela -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



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

**Table 3.** Known parasites infecting *Dikerogammarus villosus*.

| Parasite  | Observed max prevalence | Geographic region  | Source   |
|---|-------------------------|--|--|
| Acanthocephala  |                         |  |  |
| <i>Pomphorhynchus tereticollis</i> (Rudolphi, 1809)                               | 0.04%                   | The River Rhine  | Emde et al. 2012   |
| Apicomplexa, Gregarina  |                         |  |  |
| <i>Cephaloidophora similis</i> Codreanu-Balcescu, 1995                            | na                      | invaded waterbodies: i.e. Vistula, Oder                            | Ovcharenko et al. 2009   |
| <i>Cephaloidophora mucronata</i> Codreanu-Balcescu, 1995                          | na                      | invaded waterbodies: i.e. Vistula, Oder                            | Ovcharenko et al. 2009   |
| <i>Uradiophora longissima</i> (von Siebold in von Kölliker, 1848)                 | na                      | invaded waterbodies: i.e. Vistula, Oder                            | Ovcharenko et al. 2009   |
| <i>Uradiophora ramosa</i> Balcescu-Codreanu, 1974                                 | na                      | invaded waterbodies: i.e. Vistula, Oder                            | Ovcharenko et al. 2009   |
| Microsporidia   |                         |  |  |
| <i>Cucumispora</i> = <i>Nosema dikerogammari</i> (Ovcharenko and Kurandina, 1987) | 74%                     | whole range  | Ovcharenko and Kurandina, 1987; Wattier et al. 2007; Ovcharenko et al. 2009; Bacela-Spychalska et al. 2012 |
| <i>Nosema granulosis</i> Terry et al. 1999  | 4%                      | invaded waterbodies i.e. the upper Danube, the Rhine, Seine, Loire | Wattier et al. 2007  |
| <i>Dictyocoela muelleri</i>   | 3.4%                    | Rhine drainage   | Wattier et al. 2007  |
| <i>D. berillonum</i>  | 2%                      | Meuse River  | Wattier et al. 2007  |
| <i>D. roeselium</i>   | 2%                      | the upper Danube, the Rhine  | Wattier et al. 2007  |

increased mortality; with infected but asymptomatic ones exhibiting the same survivorship as uninfected individuals (see Bacela-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 (Bacela-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 (Brujjs 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 (Baćela-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, Baćela-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 (Bączela-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 macroinvertebrate 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 *Echinogammarus 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 development 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 *Echinogammarus 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.

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## 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.

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