

Short communication

The Ponto-Caspian ‘killer shrimp’, *Dikerogammarus villosus* (Sowinsky, 1894), invades the British Isles

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Abstract

The Ponto-Caspian amphipod *Dikerogammarus villosus* was found both in the margins and open water areas of Grafham Water, a large reservoir in Cambridgeshire, U.K., in September 2010. Both adults and juveniles were present in large numbers and were most frequent in the boulder/cobble areas dominating the margins of the reservoir. Precopula pairs were also evident, as were egg bearing females.

Key words: amphipod, crustacean, *Dikerogammarus villosus*, Grafham Water, U.K., alien, first record

Due to its highly predatory behaviour towards a wide variety of macroinvertebrate taxa (Dick et al. 2002) and fish (Casellato et al. 2007; Platvoet et al. 2009), the amphipod crustacean *Dikerogammarus villosus* (Sowinsky, 1894) has been called the ‘killer shrimp’. After the opening of the Danube-Main-Rhine canal in 1992, this Ponto-Caspian native has invaded many central and western European waters (Dick and Platvoet 2000; Müller et al. 2002; Mayer et al. 2008) and, during the last decade, it has also invaded the Baltic Sea drainage system (Grabowski et al. 2007; Bacela et al. 2008). It has wide environmental tolerances (Devin et al. 2003), being capable of surviving in ship ballast water (Bruijs et al. 2001) and can survive for at least 6 days out of water, affording it the potential to be spread by overland transport of boats (Martens and Grabow 2008). Tricarico et al. (2010) highlighted how *D. villosus* exhibits many life history characteristics typical of an invasive species, such as rapid growth, early sexual

maturity and a large reproductive capacity (Pöckl 2009), with a greater reproductive output than many other native and invasive amphipods, with up to almost 200 eggs per clutch (Pöckl 2007). It can also be super-abundant within invaded sites, dominating the benthic assemblage (van Riel et al. 2006). Given the rate that *D. villosus* is dispersing throughout Europe and beyond (Mayer et al. 2008), an ever increasing number of water bodies and their resident macroinvertebrate assemblages can be predicted to suffer the severe predation pressure associated with *D. villosus* establishment, leading to a simplification of assemblage structure and trophic links (see also Dick et al. 2002), as has been witnessed in the River Rhine (van der Velde et al. 2000). In addition, Kinzler and Maier (2006) found the smaller amphipod *Gammarus pulex* was more frequently predated by fish than the larger *D. villosus*. Therefore, decreasing densities of co-occurring *Gammarus* spp., in conjunction with increasing densities of



Figure 1. *Dikerogammarus villosus* in various life stages from Grafham Water reservoir, U.K., September, 2010 (Photograph copyright of Phase4 Environmental Limited).

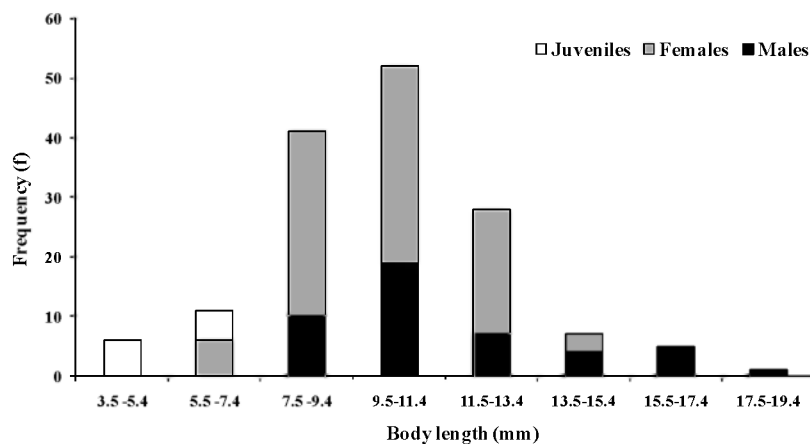
the less predation prone and larger *D. villosus*, could have long term implications for native fish populations. In a conceptual risk-assessment model for invasive species in European waterways, *D. villosus* was cited as a species constituting a high risk in terms of dispersal, establishment and ecological damage (Panov et al. 2009).

On 3/9/2010, an angler fishing in the margins of Grafham Water, a reservoir of 6.07 km² area and 50 000 000 m³ volume, in Cambridgeshire, U.K. (52°17.51'N, 00°19.44'W), found specimens of an amphipod subsequently identified as *D. villosus* (confirmed by D. Platvoet, 9/9/2010). Subsequent site visits to Grafham Water by U.K. Environment Agency staff confirmed the amphipod was present in high numbers throughout the reservoir, with densities reaching approximately 390m⁻² on the reservoir margins. A wide range of size-classes was present (see Figure 1), with precopula pairs, adult females with eggs and juveniles all evident. Of the

specimens recovered on 12/9/2010, adult males ranged from 10-20mm body length and females 7-13mm (n=30, both cases). Of the specimens recovered on 26/10/2010 by kick sampling, adult males ranged from 9-18mm (n=46) and adult females 6-13.5mm (n=94) with the adult male: female ratio approximately 1:2. In the latter sample, there was also a small number (n=11) of unsexed sub-adults/juveniles and these ranged from 3.5-6mm body length. On both sampling dates, only a small percentage (less than 3%) of adult females were bearing eggs. Figure 2 shows the relative abundance of size cohorts in the population sampled on 26/10/2010.

Although *D. villosus* was found around all edges of the reservoir, it most frequently occurred where there were marginal bankside boulders and/or a substrate matrix of cobble/pebbles. In these areas there was blue-green algae present but little macrophyte cover (only a few sparse patches of *Elodea nuttallii* (Planch.) pondweed). It was also found under

Figure 2. Frequency distribution of body length of male, female and juvenile *Dikerogammarus villosus* from Grafham Water reservoir, October 2010.



buoys in open water areas. Scraping of concrete structures in the reservoir such as a ‘draw-off’ tower also revealed the presence of *D. villosus*. The only part of Grafham Water where *D. villosus* was not found was on the North-West margin, at Savages Creek, where a silt substrate dominated, with some *Phragmites australis* (Cav.) growth. Anglers fishing in many marginal areas of the reservoir reported seeing *D. villosus* swimming in the water column and have noted them clinging onto boots and waders. Concurrent mean water chemistry values for the reservoir on 12/9/2010 were pH = 8.58, temperature (°C) = 12.15, conductivity (μScm^{-1}) = 808.57, BOD (mg l^{-1}) = 1.24, ammonia (mg l^{-1}) = 0.04 and orthophosphate (mg l^{-1}) = 0.15.

Both *Crangonyx pseudogracilis* (Bousfield) and *Gammarus tigrinus* Sexton were also present in Grafham Water, but it was noted that *D. villosus* appeared more active, swimming and crawling faster than either of these two amphipod species (N. Fielding pers. obs.). The Ponto-Caspian zebra mussel *Dreissena polymorpha* (Pallas, 1771) was also present in Grafham Water. Other studies have indicated that *D. polymorpha* may facilitate the establishment and spread of *D. villosus* by providing suitable substrate and shelter (MacNeil et al. 2008), thus the mussel may be playing a similar role in Grafham Water. The genus *Dikerogammarus* is easily distinguished from *Gammarus* spp. and *C. pseudogracilis* by high elevations on urosome segments one and two (the first two of the last three body segments). The second gnathopods of males are also much larger than the first. *D. villosus* distinguishes itself from other *Dikerogammarus* species by a combination of

characters; the elevations on the urosomes are very high and conical and in larger males (>16mm) there are usually more than two apical spines (3-5) and the second antennae have sparsely haired peduncle and flagella with very dense ‘brush-like’ tufts of setae (*D. Platvoet pers. obs.*).

The success of *D. villosus* in newly invaded habitats is undoubtedly partially due to its ability to exploit a diverse food base (Dick et al. 2002; Kley and Maier 2003; Casellato et al. 2007; Platvoet et al. 2009). However, it is particularly noted for its highly predatory behaviour, with stable-isotope analysis indicating it to be on the same trophic level as predatory fish (Marguiller 1998). A diverse array of non-amphipod native taxa belonging to a range of trophic groups including mayflies (scrapers), damselflies (predators), chironomids (collector-gatherers), water fleas (filterers) and isopods (detritivore-shredder) are all heavily preyed by *D. villosus* (Dick et al. 2002; MacNeil and Platvoet 2005; Bollache et al. 2008). Moreover, *D. villosus* exhibits a significantly greater type II functional response to prey than do native and other introduced amphipods in Europe, indicating it will be a far more voracious predator and may have greater negative effects on prey populations than native and other introduced amphipods (Bollache et al. 2008). This amphipod is a ‘keystone’ species capable of impacting on other trophic levels (MacNeil and Platvoet 2005; van Riel et al. 2006; MacNeil et al. in press). For instance, ongoing species displacements by *D. villosus* within invaded systems may lead to changes in organic matter cycling in the form of leaf-litter processing efficiency, since *D. villosus*

may eliminate many amphipod and non-amphipod leaf shredders from an invaded system (MacNeil et al. in press).

In The Netherlands, *D. villosus* has invaded many of the preferred habitats of the native European amphipod *Gammarus duebeni* Lilljeborg, 1851 and a previously highly successful North American invader *Gammarus tigrinus* Sexton, 1939 (Dick and Platvoet 2000; MacNeil et al. 2008). Declines of *G. duebeni* and *G. tigrinus* in Dutch water bodies shortly after the arrival of *D. villosus* have been attributed to severe predation by *D. villosus*, as witnessed in laboratory mesocosms (Dick and Platvoet 2000). Furthermore, predation of native *Gammarus pulex* (Linnaeus, 1758) by *D. villosus* has also been observed (MacNeil and Platvoet 2005), and this species is under imminent threat of displacement within invaded systems because the spatial niches of these species overlap significantly (Devin et al. 2003; MacNeil and Platvoet 2005) and laboratory populations of *D. villosus* thrived in water obtained from an uninvaded *G. pulex* site in the Netherlands (MacNeil and Platvoet 2005).

In addition, the arrival of *D. villosus* may have implications for river water quality monitoring as the macroinvertebrate taxa which contribute to biotic indices of water quality may be impacted by the invader. The EU Water Framework Directive (WFD; European Commission 2000) requires the maintenance of good and high ecological status in freshwaters (i.e. near pristine macroinvertebrate assemblages) where it already exists and achievement of a minimum of good ecological status in all freshwaters by 2015. Unfortunately, invasives such as *D. villosus* may represent a major biological pressure and threat to these fundamental WFD objectives, with many European macroinvertebrate assemblages severely biocontaminated (Arbačiauskas et al. 2008). Biotic indices such as the Biological Monitoring Working Party (BMWP) score in the U.K. are routinely used to ascertain river biological water quality and rely on the presence/absence of macroinvertebrate families based on their perceived relative sensitivities to organic enrichment. However, invasives such as *D. villosus* may have a major impact on biodiversity and overall assemblage structure through competition and predation and consequently may undermine the accuracy of biotic indices generated from these assemblages to reflect water quality (MacNeil 2010).

Žganec et al. (2009) noted that knowledge on alien amphipod distribution is essential for preservation of native biodiversity and biocontamination assessment. Boets et al. (2010) combined laboratory results, field data and modelling techniques in an attempt to construct habitat suitability models for *D. villosus*, concluding that *D. villosus* is mainly found in freshwater habitats with artificial banks, high oxygen saturation and low conductivity. Such an approach could prove useful should the Grafham Water introduction not be contained, or if there are currently as yet undetected populations of *D. villosus* in U.K. freshwaters. Currently, the pathway of introduction of *D. villosus* to Grafham Water is unknown and investigation of the invasion pathways and potential vectors is ongoing.

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References

- Arbačiauskas K, Semchenko V, Grabowski M, Leuven RSEW, Paunovic M., Son MO, Csanyi B, Gumuliauskaite S, Konopacka A, Nehring S, van der Velde G, Vezhnovetz V, Panov VE (2008) Assessment of biocontamination of benthic macroinvertebrate communities in European inland waterways. *Aquatic Invasions* 3: 211–230, doi:10.3391/ai.2008.3.2.12
- Bacela 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, doi:10.3391/ai.2008.3.1.16
- 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, doi:10.1016/j.ecoinf.2009.12.005
- Bollache L, Dick JTA, Farnsworth KD, Montgomery WI (2008) Comparison of the functional responses of invasive and native amphipods. *Biology Letters* 4: 166–169, doi:10.1098/rsbl.2007.0554
- Brujns 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 transport. *Archiv für Hydrobiologie* 152: 633–646
- 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, Berlin, pp 495–507, doi:10.1007/978-1-4020-6029-8_27

- 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: 43–46, doi:10.1127/0003-9136/2003/0158-0043
- Dick JTA, Platvoet D (2000) Invading predatory crustacean *Dikerogammarus villosus* eliminates both native and exotic species. *Proceedings of the Royal Society of London B*, 267: 977–983, doi: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, doi:10.1139/f02-074
- European Commission (2000) EC Water Framework Directive (2000/60/EC). Official Journal of the European Communities. European Commission, Brussels, 154 pp
- Grabowski M, Jazdzewski K, Konopacka A (2007) Alien Crustacea in Polish waters – Amphipoda. *Aquatic Invasions* 2: 25–38, doi:10.3391/ai.2007.2.1.3
- 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
- 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* 157: 473–481, doi:10.1127/0003-9136/2003/0157-0473
- MacNeil C (2010) Threats to European freshwater biodiversity from invasive amphipods. In: Riley AT (ed) *Advances in Environmental Research* (3). Nova Publishers, pp 72–82
- MacNeil C, Dick JTA, Platvoet D, Briffa M (in press) Direct and indirect effects of species displacements; the invading amphipod crustacean *Dikerogammarus villosus* can disrupt aquatic ecosystem energy flow and function. *Journal of the North American Benthological Society*.
- 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: 1–8
- 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. *Archiv für Hydrobiologie* 172/3: 175–182
- Martens A, Grabow K (2008) Das Risiko der Verschleppung neozoischer Amphipods beim Überlandtransport von Yachten. Risk of spreading of non-indigenous Amphipoda due to overland transport of recreation boats. *Lauterbornia* 62: 41–44
- Marguiller S (1998) Stable isotope ratios and food web structure of aquatic ecosystems. Thesis, University of Brussels, 209 pp
- 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, doi:10.1651/07-2867R.1
- Müller JC, Schramm S, Seitz A (2002) Genetic and morphological differentiation of *Dikerogammarus villosus* invaders and their invasion history in Central Europe. *Freshwater Biology* 47: 2039–2046, doi:10.1046/j.1365-2427.2002.00944.x
- 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, doi:10.1897/TEAM.2008-034.1
- Platvoet D, Dick JTA, MacNeil C, van Reil M, van der Velde G (2009) 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, doi:10.1007/s10530-009-9488-2
- 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. roseli*. *Freshwater Biology* 52: 50–63, doi: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, doi:10.1007/s10530-009-9485-5
- 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, doi:10.3391/ai.2010.5.2.14
- 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. *Crustacean Issues* 12: 3–33
- Van Riel MC, van der Velde G, Rajagopal S, Marguiller 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, doi:10.1007/s10750-005-1904-8
- Žganec K, Gottstein S, Hudina S (2009) Ponto-Caspian amphipods in Croatian large rivers. *Aquatic Invasions* 4: 327–335, doi:10.3391/ai.2009.4.2.4