

**Management in Practice****Options for the control of *Dikergammarus villosus* (killer shrimp) and other invasive amphipods**Louisa E. Wood<sup>1,\*,#</sup>, Emily R.C. Smith<sup>2,#</sup>, Jamie Bojko<sup>3,4</sup> and Paul Stebbing<sup>1,5</sup><sup>1</sup>Centre for Environment Fisheries and Aquaculture Science, Weymouth, Dorset, DT4 8UB, UK<sup>2</sup>Angling Trust, The Old Police Station, Wharncliffe Rd, Ilkeston, DE7 5GF, UK<sup>3</sup>National Horizons Centre, Teesside University, Darlington, DL1 1HG, UK<sup>4</sup>School of Health and Life Sciences, Teesside University, Middlesbrough, TS1 3BA, UK<sup>5</sup>APEM Ltd, A17 Embankment, Business Park, Heaton Mersey, Manchester, SK4 3GN, UK<sup>#</sup>These authors contributed equally to the writing of this manuscript

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**Received:** 17 December 2020**Accepted:** 25 March 2021**Published:** 27 April 2021**Thematic editor:** Calum MacNeil**Copyright:** © Wood et al.This is an open access article distributed under terms of the Creative Commons Attribution License ([Attribution 4.0 International - CC BY 4.0](https://creativecommons.org/licenses/by/4.0/)).**OPEN ACCESS****Abstract**

Aquatic invasions are a major ecological and socio-economic concern. Management of invasive aquatic populations requires a robust understanding of the effectiveness and suitability of control methods. In this review, we consider multiple control options for the management of invasive aquatic amphipods, exploring their efficacy and application constraints. Technological opportunities (pheromone, RNAi, biotechnologies) and gaps in our understanding around control mechanisms are identified, with the aim to improve management success of this order. Within this review, the UK invasion of the killer shrimp, *Dikergammarus villosus* (Sowinsky, 1894) is used as a case study of the best explored example of invasive amphipod control. This species has had a range of ecological, physiological, pathological, and experimental research conducted upon it, which is highlighted from a management perspective. This same data, where available, has been synthesised for 46 other invasive amphipods, to probe for weaknesses that future management methods can exploit and be developed around. Successful management examples for invasive amphipod species remain rare. A lack of currently available tested options severely limits the possibility for amphipod management, post establishment. For future management to be successful, further work is needed to develop targeted and specific control methods, which ideally, are cost effective, have no/little associated ecological impacts, and can be broadly applied in closed and open water systems. Our synthesis presents opportunities for the further, informed development of control systems for invasive amphipods.

**Key words:** Amphipoda, eradication, invasive aquatic species, management, conservation**Introduction**

Global biological invasions in aquatic environments present a major concern to resource managers, conservationists, and policy makers (Leung et al. 2002; Lodge et al. 2016; Gallardo and Aldridge 2020). Aquatic invasive non-indigenous species (NIS) can negatively impact native biodiversity and ecosystem integrity (Pyšek and Richardson 2010), adversely affect

human livelihoods and well-being (Shackleton et al. 2019), result in economic losses at local, national and international scales (Pimentel et al. 2005; Diagne et al. 2020) and can introduce disease (Roy et al. 2017; Bojko et al. 2020). The Convention on Biological Diversity (CBD) prioritises preventing the introduction of invasive NIS and thereby avoiding these impacts, which is widely accepted as the most cost-effective approach to management (Leung et al. 2002; Hussner et al. 2017). Invasions cannot always be prevented making management measures to control establishment and spread post-introduction essential (Hänfling et al. 2011).

Management of established invasive NIS aims for species eradication, complete reproductive removal, containment, and/or population suppression (Robertson et al. 2020). Eradication may be possible after early detection and, if successful, can reduce long-term impact and minimise overall management costs (Edwards and Leung 2009; Simberloff 2020). Where eradication is not possible, or fails, managers often focus on identifying management strategies (complete reproductive removal, containment, and population suppression), that minimises the spread and impact of an invasion (Robertson et al. 2020). Control options for management of aquatic invasive NIS can be categorised as either physical, biological, chemical, or integrated approaches. Consideration of the appropriate management response, such as where in the invasion process management options should be targeted, requires a multidisciplinary approach with input from a range of disciplines including ecology, social sciences, resource management and economics, in addition to invasion science (Simberloff et al. 2013). Economic costs associated with management attempts for invasive NIS can often lead to scepticism, especially in the light of failed attempts (Parkes and Panetta 2009). To avoid unsuccessful management attempts it is essential that the feasibility of management programmes is carefully considered (Stebbing et al. 2014a). Risk analysis provides a method of assessing the feasibility of management options, accounting for the suitability of control methods given the ecological and socio-economic context of the invasion (Booy et al. 2017).

Amphipods (Crustacea: Malacostraca) are common invaders and are represented in almost all aquatic environments, currently totalling 46 known invaders across multiple databases (Bojko et al. 2020; Supplementary material Table S1). Most invasive amphipods are present in the Gammaroidea (~ 27 species). These non-indigenous amphipod species have been reported globally and are disproportionately represented by salt-tolerant (e.g., brackish) species (Cuthbert et al. 2020). Some 20% of non-indigenous amphipods originate from the Ponto-Caspian region, with high proportions invading Eurasian freshwaters, North American freshwaters, and Baltic Sea waters. As the Ponto-Caspian region is subject to highly changeable abiotic conditions, native species exhibit life history traits that predispose high environmental tolerance, and therefore greater invasion success (Casties et al. 2016). These

traits combined with human-mediated movement, such as increased shipping intensity and canal development, result in a greatly facilitated invasion risk (Ricciardi and Maclsaac 2000; Rewicz et al. 2014). Impacts of invasive Ponto-Caspian amphipods on invaded systems can be severe (Krisp and Majer 2005; van der Velde et al. 2009; Piscart et al. 2011; Bacela-Spychalska and van der Velde 2013). They can compete successfully with native species, eventually dominating or even replacing other species in native locations (Dick and Platvoet 1996, 2000; Jazdzewski et al. 2004). Certain species can have a significant predatory impact on other macroinvertebrate species (Taylor and Dunn 2017). Others incur impact through the introduction of disease (Bojko and Ovcharenko 2019; Bojko et al. 2019; Allain et al. 2020; Subramaniam et al. 2020), which can cause health issues in native species (Roy et al. 2017; Hatcher et al. 2019).

The aptly named killer shrimp, *Dikerogammarus villosus* (Sowinsky, 1894), is a Ponto-Caspian invasive NIS and one of the most prominent amphipod invaders in Europe (Platvoet 2010). This species is the only amphipod listed on the “100 worst alien species” watchlist in Europe and has been called a “perfect invader” (DAISIE 2009; Rewicz et al. 2014). Consequently, this species has been the focus of extensive control research, predominantly in relation to containment, and has become a useful invasion model. Over the past ~ 30 years, *D. villosus* has spread over much of mainland Europe (Rewicz et al. 2014), with reports of considerable impact on native ecosystems and biodiversity, wherever it is introduced (Dick and Platvoet 2000; van der Velde et al. 2002, 2009; Van Riel et al. 2006; Leuven et al. 2009). *Dikerogammarus villosus* has driven localised extinctions of native macroinvertebrates and has dramatically reduced native population sizes through competition and predation (Dodd et al. 2014). Additionally, it has a high relative functional response, high environmental tolerance, and broad diet preference, including a tendency to be preferentially predatory (Rewicz et al. 2014; Taylor and Dunn 2017).

In the UK, the species was first detected at Grafham Water, Cambridgeshire, in 2010 (Platvoet 2010) and is currently restricted to six, geographically isolated, socio-economically distinct sites (Table 1). *Dikerogammarus villosus* is recognised as a priority species for the UK water industry due to its negative impacts on threatened species, native biodiversity and UK anglers (Gallardo et al. 2012, Gallardo and Aldridge 2020). Management costs associated with aquatic invasive NIS management in the UK are extensive at around £26 million a year in 2010, with £4.6 million spent by water companies alone (Oreska and Aldridge 2011). Given its restricted extent, eradication of *D. villosus*, defined as “the complete and permanent removal of all wild populations from a defined area by a time-limited campaign” (Bomford and O’Brien 1995) could be considered a possibility. However, eradication feasibility is dependent on several factors, including the effectiveness of available control methods and their suitability for application in light of the invader’s distribution (Booy et al. 2017).

**Table 1.** UK sites where killer shrimp *Dikerogammarus villosus* has been reported.

Site Name	Type of site	Closed/ open system	Area (ha)	Ecological Importance	Economic Importance	Social Importance	Owned/managed by
Grafham Water	Freshwater reservoir	Closed	811.9	Site of Special Scientific Interest (SSSI)	Drinking water reservoir	Bird watchers, anglers, walkers, and boaters/sailers water sportsmen.	Anglian Water Services Ltd
Pitsford Water	Freshwater reservoir	Closed	409	Site of Special Scientific Interest (SSSI)	Drinking water reservoir	Bird watchers, anglers, walkers, and boaters/ water sportsmen.	Anglian Water Services Ltd
Eglwys Nunydd, Port Talbot	Freshwater reservoir	Closed	105	Site of Special Scientific Interest (SSSI)	Supplies water to Margam Steelworks	Bird watchers, anglers, walkers, and boaters/ water sportsmen.	Margam Steelworks
Norfolk Broads	Network of rivers and lakes	Open	30300	Special Area Conservation (SAC), Special Protection Area (SPA), Ramsar Site	Tourism value	Bird watchers, anglers, walkers, and boaters/ water sportsmen.	Broad's Authority
Cardiff Bay	Freshwater bay	Semi-closed	200	Cardiff Bay Wetland Reserve (Site of Special Scientific Interest (SSSI)	Tourism value	Bird watchers, sailing and fishing	Cardiff Harbour Authority (operated by)
Trinity Broads	Freshwater lakes	Open	165	Special Area Conservation (SAC), Special Protection Area (SPA), Site of Special Scientific Interest (SSSI)	Drinking water, tourism value	Bird watchers, anglers, walkers, boaters/ sailers, water sportsmen.	Essex and Suffolk Water

In this study, the physical, biological, and chemical control methods available for invasive amphipod control are reviewed. Field application of these methods to the management of invasive amphipods are considered alongside their likely effectiveness in the context of the UK invasion of *D. villosus* in freshwater systems. Attention is also given to the ecological and socio-economic factors that influence the choice of management actions and control options at invaded sites. Where potential control strategies to manage invasive amphipods are identified, but its application against amphipods is relatively unexplored, examples are provided from the control of other aquatic invasive NIS. In this review, the application of methods in “aquatic” systems is primarily considered in the context of freshwater environments, given the focus on assessing management feasibility in relation to *D. villosus*. Further, new avenues for research in control methods are discussed, highlighting the species specific ecological, physical, and pathological information required for targeted control, and what is known currently in this area.

### Physical control

Commonly used physical control methods for the management of aquatic invasive NIS include trapping, drainage interventions, and habitat alterations. These methods are frequently labour intensive, time consuming, and/or

can induce long-term changes to the environment, but also can be the most accessible to managers and easily applied. As with most population control methods, physical control typically has limited success in open systems for abundant, ubiquitous, and highly fecund species (Rudnick et al. 2003; Reynolds and Souty-Grosset 2012) and are more suited to closed water systems, although some success has been found in head waters (Chadwick et al. 2020). Below, the physical control efforts currently in place for invasive amphipods are explored.

### *Trapping*

Trapping and removal of the target invader has not yet been used in the management of invasive amphipods. Trapping has had some success in the eradication of invasive fish populations (Rytwinski et al. 2019), and population suppression of invasive aquatic invertebrate populations (Hansen et al. 2013; Kats et al. 2013; Stebbing 2016; Milligan et al. 2017), with most of these attempts requiring intensive, continuous trapping over a long period (Rytwinski et al. 2019). For example, trapping was successful in maintaining low population numbers of the red swamp crayfish *Procambarus clarkii* (Girard, 1852) in Trancas Creek in the Santa Monica Mountains, USA, allowing native California newt populations to recover (Kats et al. 2013; Milligan et al. 2017). Trapping often has fewer detrimental non-target impacts compared to other control methods whilst still reducing the impact of the invasive NIS in the invaded system (Kerby et al. 2005; Kats et al. 2013; Milligan et al. 2017). To date, the application of trapping methods to management of invasive amphipod species has instead focussed on integration with early detection monitoring programmes (Stadig 2016). Traps were initially applied to monitor the colonisation of Grafham Water, and the connected compensation discharge channels, in the early stages of the UK invasion of *D. villosus* (Constable and Fielding 2011). First deployed in December 2010, high yields were reported, with > 400 individuals caught per trap (Constable *pers. comm*). Redeployment of the traps a year later found ~ 100% increase in the number of individuals caught, with ~ 1100 *D. villosus* caught in one trap in 2012 (Constable *pers. comm*).

To improve trapping efficacy to facilitate both management and detection of invasive amphipods, a detailed understanding of the biology and behaviour of the target species to tailor trap design, placement, colour, and bait type is required (De Palma-Dow et al. 2020). For example, for species such as *Chaetogammarus warpachowskyi* (Sars, 1897), *Chelicorophium robustum* (Sars, 1895), *Dikerogammarus bispinosus* (Martynov, 1925) and *Obesogammarus obesus* (Sars, 1894) which show preferences for stones and gravel (Table S1), trapping could focus on such habitat and even incorporate coarse substrate to improve colonisation by these species, such as with Artificial Refuge Traps (Green et al. 2018). Similarly, addition of sand/fine

sediment and macrophytes to traps could increase the efficacy of catching *Echinogammarus berilloni* (Catta, 1878) and *Gammarus varsoviensis* (Jazdzewski, 1975) based on their habitat preferences (Table S1). *Dikerogammarus villosus* shows a preference for stony substrates (Van Riel et al. 2006; MacNeil et al. 2010; Kobak et al. 2015), warranting adaption of the traps at Grafham Water to use custom artificial refuges, consisting of a 5.5 mm mesh basket containing coarse cobble and pebble substrate.

Visual attractants also show promise in improving trapping efficiency; Stadig (2016) reported a significantly higher catch per unit effort using light attractants to capture multiple amphipod species, including *Echinogammarus ischnus* (Stebbing, 1899), in Maumee Bay, western Lake Erie, USA. However, no differences were observed between trap types (Stadig 2016). Species-specific patterns also show promise in this regard. Associations between *D. villosus* and zebra mussel *Dreissena polymorpha* (Pallas, 1771) shells have been identified on multiple occasions, for various reasons (Devin et al. 2003; Gergs and Rothhaupt 2008; Martens and Grabow 2008; Kobak et al. 2014). Incorporation of a striped pattern to mimic *D. polymorpha* shells into trap design could be used to increase trapping efficacy (Roqueplo et al. 1995) and merits further exploration.

Sex pheromones have been used in terrestrial pest management as effective bait but require significant research to develop and have not been extensively examined for use in aquatic systems (Stebbing et al. 2003). Although relatively unexplored for amphipods, the use of pheromones has been found to be effective to attract and trap the crayfish *P. clarkii* (Aquiloni and Gheradi 2010) and invasive fish (Bajer et al. 2011).

At present, trapping is unlikely to result in eradication of invasive amphipods from closed or open systems, but could be used as a long-term management strategy to suppress and contain the population within the invaded system (Table 2); making this technique suitable for application but likely of limited effectiveness across all six UK invaded sites (Table 1). One of the potential issues with trapping is the potential attraction of non-target organisms, such as fish, which required traps to be checked on a regular basis to remove bycatch. As amphipods are small, entrance size can be reduced enough to omit the ingress of fish species, which would eliminate most of the costs associated with trapping as a management approach caused by the requirement for regular, labour-intensive trap checks. The development of traps types that could be effectively left in the environment, while remaining effective at removing target species, without the need for the re-provisioning of attractants i.e. bait, such as habitat traps, would reduce cost while providing a continuous control measure.

#### *Barriers, drainage, and habitat interventions*

Barriers, such as weirs, can also be utilised to contain populations of invasive amphipods, limiting further dispersal (Constable and Fielding 2011).



**Table 2.** Synthesis of the different methods used to manage invasive amphipods, with a class-level evaluation of their efficacy and application according to the following criteria: Species specificity (capacity of the method to specifically target the invasive amphipod species), closed vs open (method can be applied to closed/open water bodies), field application (method is already applied in the field), ecological impact (potential ecosystem damages), time (duration of the application to be effective), cost (expenses of the method), acceptance (public acceptance of use of the method), efficacy (capacity to manage the target invasive amphipod species).

Method	Species-specificity	Closed vs open	Field Application	Ecological Impact	Time	Cost	Acceptance	Efficacy
<b>Physical control</b>								
Trap	+	Both	+++	+	+++	+++	+++	+
Barriers and dams	+	Closed	+++	++	+	++	++	++
Habitat modification	++	Both	++	++	++	++	++	++
<b>Biological control</b>								
Natural predators	++	Both	+	++	++	++	++	++
Pathogens	+++	Both	–	?	+	+	+	+++
<b>Chemical control</b>								
Rotenone	+	Closed	++	+++	+	+	+	++
Synthetic pyrethroids	++	Both	–	+++	+	+	+	++
RNA interference	+++	Both	–	?	+	++	++	+++

+, low; ++, medium; +++, high; –, irrelevant; ?, unknown. Classes were assigned qualitatively based on this study and expert opinion.

The construction of artificial barriers has been used to successfully contain *D. villosus* populations in the UK. Screens installed into the compensation channel of Grafham Water restricted further spread downstream, preventing introduction to the River Ouse. The compensation flow channel was subsequently redirected back into the reservoir to create a closed system (Constable and Fielding 2011). In addition, detection of *D. villosus* at Eglwys Nunydd, Wales resulted in the installation of three weirs to minimise the risk of natural dispersal into adjacent waters (Environment Agency *pers. comm.*). A similar strategy could be used for containment of *D. villosus* populations in Cardiff Bay, since the presence of the Cardiff Bay Barrage already contains the site to a degree, allowing some restriction to be implemented on water movement (Table 1).

As well as hard-standing constructions, electric barriers have been used as a control method for invasive aquatic invertebrates with some limited success, although this method has not yet been applied to invasive amphipods. For example, along with mass trapping, electric fences were used to manage rusty crayfish *Faxonius rusticus* (Girard, 1852), suppressing the crayfish population to reduce their impact on macrophytes (Peters et al. 2008). Preliminary evidence indicates that electric shock methods may be used to aggregate target amphipod species for removal. Perrot-Minnot et al. (2017) report that low voltage electric shock treatment resulted in the exhibition of sheltering behaviours in *Gammarus fossarum* (Koch, 1836), with enhanced and prolonged sheltering behaviour observed in response to increasing the number of electric shocks. Exposure to high electrical currents (via electrofishing) results in substantial numbers of aquatic invertebrates, including amphipods, being dislodged from the substratum and drifting to the water surface for removal (Elliott and Bagenal 1972; Bisson 1976). Electrofishing could be used to aggregate amphipods to facilitate and improve

the efficiency of physical removal methods; however, efficacy is unlikely to be species dependent and multiple non-target species will be impacted.

Chemical barriers also present a viable option for containment of populations. Carbonated water has been shown to cause narcosis in *D. villosus* and therefore could present a viable option to limit the distribution of the species (Sebire et al. 2018) for example around boat launching/landing areas in populated lakes, although further research is needed before this is field applied.

Drainage of closed water bodies, such as a reservoir, lake, or pond, sometimes followed by quicklime (calcium oxide) treatment, may be an effective approach to manage amphipod invasions in closed water bodies. Drainage has been successfully applied to eradicate populations of the hairy marron crayfish *Cherax tenuimanus* (Smith, 1912), from two small ponds in Auckland, New Zealand (Gould 2005; Duggan and Collier 2018). The efficacy of this method has not yet been field tested for amphipods, but short-term drying events have severely reduced amphipod population densities in some cases (Stubbington et al. 2009; Poznańska et al. 2013; Pařil et al. 2019). Drying interventions such as these alter community structure, resulting in the absence of reproductive females and a severe reduction in juveniles in the first months after water flow resumed, as documented for *G. fossarum* (Pařil et al. 2019). The addition of quicklime also alters the physio-chemical water properties of the site which could be used to reduce the suitability of an invaded system to a particular invasive amphipod (Table S1). However, the logistical challenges and non-target impacts of drainage and quicklime applications to large water bodies include contaminated water deposition; financial costs; and environmental consequences of removing a substantial volume of water and changing water pH, which makes this method unsuitable for many invaded systems as the drain down of large reservoirs in many cases is operationally impossible (Table 2). Drainage and quicklime application would not be suitable in water bodies of high socio-ecological value, such as the closed waterbodies Grafham Water, Pitsford Water, Eglwys Nunydd, and Trinity Broads in the UK (Table 1). However, where it was possible to apply moderate drawdown to expose the preferred habitats of the aquatic NIS (Table S1), this would likely be an effective control method to reduce the population of the target invasive NIS, although non-target species would also be impacted.

Habitat manipulation can reduce the suitability of a habitat to colonisation by the target species. Alternatively, the habitat can be manipulated to encourage aggregation of individuals on a substrate for easier removal or to exclude species from certain areas (Stebbing et al. 2012). Again, given the strong preference for amphipod species for certain habitat types (Table S1), the removal of a suitable habitat type, for example around areas with high in water activity such as boat launching/landing areas could reduce the local population density, limiting the risk of translocation. For example,



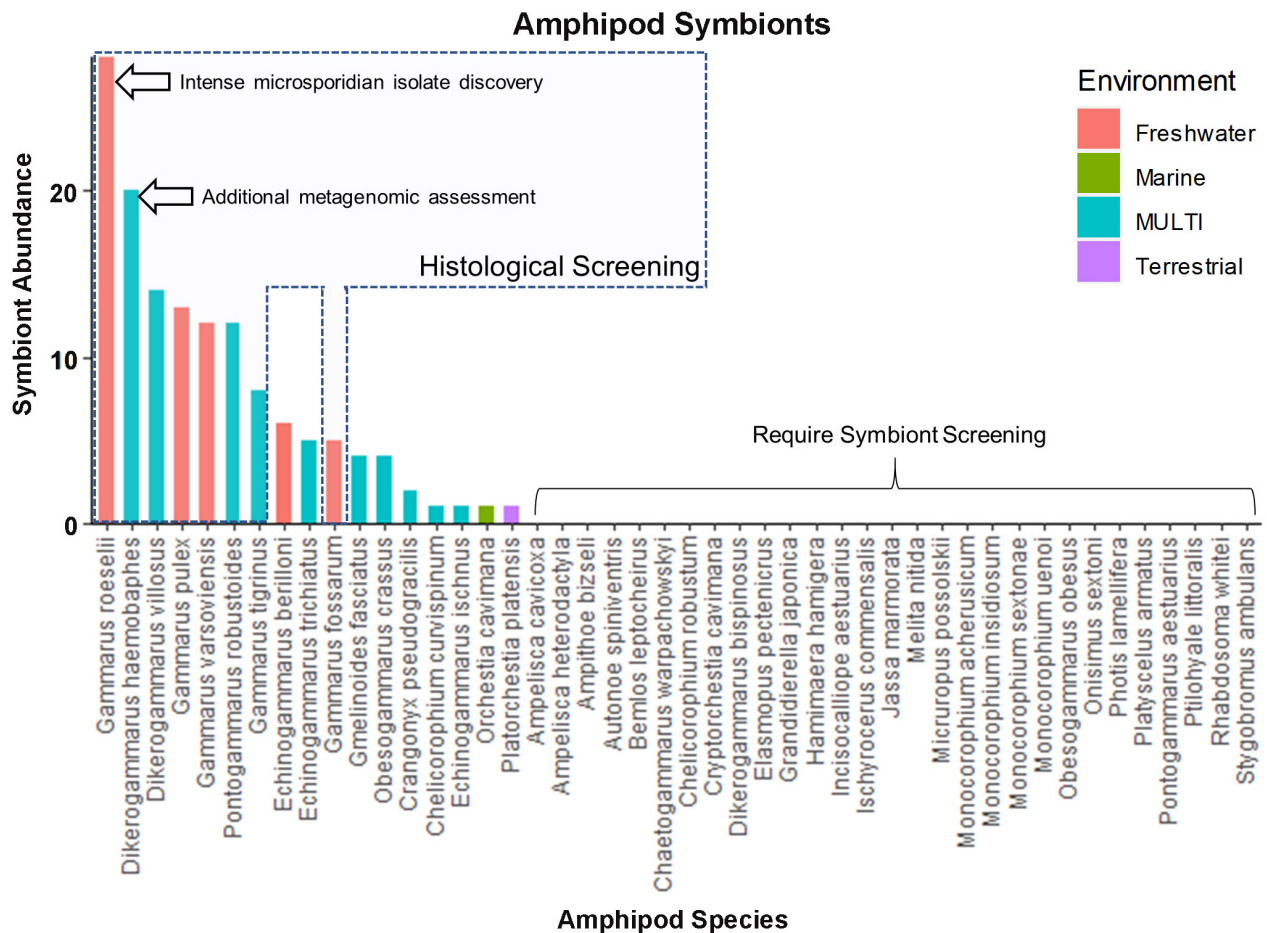
utilising the preference of *D. villosus* for coarse substrates (MacNeil and Platvoet 2013; Table S1), it may be possible to deposit pebbles or boulders to encourage congregation of individuals for later removal. Alternatively, the habitat could be altered to make it less suitable, for example by installing fine particle substrates such as sand, or by planting of shorelines with native macrophytes. There are, however, no known examples of the use of habitat manipulation in eradication or long-term management attempts for invasive aquatic invertebrate species to date.

### **Biological control, autocidal control and biotechnology**

Biocontrol agents have been applied extensively in agriculture to regulate pest and invasive populations of animals and plants (Lacey et al. 2015). Biocontrol is increasingly considered as a management strategy for aquatic invasive NIS, although it has not yet been used to manage invasive amphipods. Multiple studies that explore amphipod predators, competitors and pathogens build on our understanding of pathogen diversity and potential agents for future biocontrol efforts.

Currently, the application of predators to control invasive amphipods is limited by the lack of highly specific co-evolved predators (Bajer et al. 2019). Instead, amphipods may be controlled by broad-spectrum predators found in the invasive range (Balcombe et al. 2005). Amphipods are commonly consumed by predatory species, including fish, aquatic insects (i.e. Odonata), semi-aquatic mammals (rodents) and birds (Balcombe et al. 2005; Aquiloni et al. 2010; Musseau et al. 2015; Bajer et al. 2019). Although the introduction of predators as biocontrol agents presents a potentially effective approach to manage invasive amphipod populations, the introduction of predatory species can have substantial cascading ramifications for non-target species within the invaded ecosystems (Simberloff and Stiling 1996) and advanced exploration of non-target effects are important in all instances. Alternatively, rather than the introduction of new native predators, there is the possibility to conserve and augment native predators, such as fish species, already present in the system to reduce the invasive population and aid in invasive amphipod control.

In the UK, it has been suggested that the introduction and augmentation of native fish species such as brown trout *Salmo trutta* (Linnaeus, 1758) or European perch *Perca fluviatilis* (Linnaeus, 1758) may help to control populations of *D. villosus* through predation (Platvoet 2010). However, these species are generalist predators, consuming non-target aquatic invertebrates. Further, in environments where coarse substrate dominates, native amphipods are consumed in greater quantities than *D. villosus* (Kinzler and Maier 2006). This is attributed to invasive amphipods such as *D. villosus* having a higher substrate affinity and lower activity, making the native amphipods comparatively more vulnerable to predation (Kinzler and



**Figure 1.** Bar graph to outline the amphipod species, the environment in which the species is found, and the number of symbionts identified to date. In addition, known screening techniques that have been applied to find pathological agents are highlighted. The graph was developed in R v3.6.0 (R Core Team 2013) using the data and associated references available in Table S1.

Maier 2006; Kobak et al. 2014). The use of predators as a biocontrol strategy is therefore not recommended at present.

The use of competitor species for biocontrol are less studied but have been shown to have positive effects on populations (Gong et al. 2005; Gashaw et al. 2008; Hill et al. 2020). Several amphipod species have been size-matched and undergone behavioural assessment using various metrics such as Functional Response and Relative Invader Impact Potential (FR/RIP) (Dick et al. 2014, 2017) to indicate relative competitive capability, but no suggestions for competitive based biocontrol have been made or acted upon for amphipods, possibly due to biosecurity considerations.

A biocontrol system more commonly suggested is the use of pathogenic species, of which a growing literature base is available, encompassing viruses through to large metazoan parasites of amphipods (Bojko and Ovcharenko 2019; Table S1; Figure 1). Although the application of pathogens is yet to pass the experimental stage in the aquatic environment, the use of viruses has been instrumental to the long-term management of invasive rabbits in Australia and New Zealand (Gumbrell 1986; McColl et al. 2014). However, although initially effective, often achieving over 90% mortality immediately

after virus release, rabbits often gained resistance in two to three generations. As a result, new viral strains have been released to maintain landscape-scale population suppression (Kerr et al. 2021). Release of pathogenic species therefore should be augmented by other control strategies to increase effectiveness (Saunders et al. 2010). At present potential symbionts have only been identified for 29 of the 46 invasive amphipods (Table S1). For *D. villosus*, ~ 14 symbiotic species have been identified (Figure 1; Table S1) with various levels of predicted control success. Most (gregarines, trematodes, isopods, ciliates) exist as symbiotic species or parasites with complex life cycles that are unlikely to result in host mortality or population suppression (Bojko et al. 2013). Others, such as viruses and Microsporidia, are mortality drivers and may be capable of lowering *D. villosus* population size and disrupting fecundity. The most studied is *Cucumispora dikerogammari*, which acts as a mortality driver (Ovcharenko et al. 2010). This microsporidian has also been shown to have adverse ecological impacts for *D. villosus* populations, and a low capability to infect and become established in non-target hosts (Bacela-Spychalska et al. 2012). However, Iltis et al. (2018), indicate that heavy *C. dikerogammari* infection might increase the predation pressure of *D. villosus* on local prey populations under certain conditions. Another potential pathogen includes the likely nudivirus, *Dikerogammarus villosus nudivirus* (DvNV) (Bojko et al. 2013). Nudiviruses are currently used as biocontrol agents of pest insects (Etebari et al. 2020) and may also be applicable in amphipod invasion systems.

In the UK, research into *D. villosus* populations revealed a lack of microsporidian and viral pathogens, outlining that enemy release (loss of pathogens) is likely to have occurred (Bojko et al. 2013). The loss of these pathogen groups has likely resulted in an increased fitness in the *D. villosus* populations of the UK. For example, the population in the Norfolk Broads invasion site (Table 1) harboured only commensal symbionts and no pathogenic species in over 200 sampled specimens (Bojko et al. 2013). These observations suggest that the introduction, or further invasion of parasites to UK populations of *D. villosus* could insight control.

Shortly after *D. villosus* was detected in the UK, its sister species, *Dikerogammarus haemobaphes* (Eichwald, 1841), was also identified (Aldridge 2013). The stark difference between the two species was that the *D. haemobaphes* invasion carried a high number of parasites and exhibited a lower impact on UK native species and the environment (Bojko et al. 2015, 2019; Bovy et al. 2015; Allain et al. 2020; Subramaniam et al. 2020). The microsporidian (*Cucumispora ornata*) and viral pathogens (*Nudiviridae* and *Mininucleoviridae*) (Table S1) of the *D. haemobaphes* appear to successfully control this invader in UK river systems as natural biocontrol agents (Bojko et al. 2019). It has been suggested that the conservation or augmentation of these pathogens could be applied to increase prevalence

and overall population mortality levels (Bojko et al. 2019). Further, it has been considered whether these pathogens, now present in the UK, may be feasible control agents of *D. villosus*. A comparison of the different pathogen groups carried by both species, and their current range extension was explored by Hatcher et al. (2019). Many appear to be related but are essentially different species of pathogen. For example, *D. villosus* harbours *C. dikerogammari* at high prevalence but this pathogen is rare in *D. haemobaphes*, whereas *C. ornata* is highly prevalent in *D. haemobaphes* but rare in *D. villosus*. This level of host specificity may benefit the biocontrol of the target species and is supported by both environmental PCR data and infection trials (Bacela-Spychalska et al. 2012; Bojko et al. 2019).

The viral pathogens of both species require laboratory trials to determine whether either may be viable as a control agent. *Dikerogammarus haemobaphes* Mininucleovirus (DhMV) was determined to drive mortality in infected individuals, but specificity trials are required (Bojko et al. 2019; Subramaniam et al. 2020). *Dikerogammarus haemobaphes* Nudivirus (DhNV) has been shown to have behavioural effects, but no determination has been made for either mortality driving or host specificity factors (Bojko et al. 2019; Allain et al. 2020).

Since *D. haemobaphes* has already introduced these pathogens to the UK, and the *D. villosus* and *D. haemobaphes* populations are likely to merge across UK waterways, it seems prudent to monitor whether these pathogens are exchanged naturally between the two invaders. To evaluate this, it is important to continue to monitor invasive and native amphipod species for any future pathogen acquisition.

Autocidal methods of control are characterised by the species self-destruction and include the use of sterile animals or carriers of harmful genetic code (Gherardi et al. 2011). The release of sterile males as a control mechanism has been extensively used in the control of terrestrial pest insects (e.g. Knipling 1955). Within this context the large numbers of males of the target species are either captured or bred, sterilised, and then released into the wild to compete with un-sterilised males for mates. Sterilisation has been examined for application with invasive crayfish species (Aquiloni et al. 2009; Stebbing et al. 2014a; Green et al. 2020). Key advantages with the use of sterile males are that its effectiveness is inversely proportional to the density of the un-sterilised population and it is species specific (Stebbing et al. 2012). No attempts to sterilise amphipods is available in the literature to the best of the authors knowledge. There are several methods in which invertebrates have been sterilised which may be relevant to amphipods. Chemical treatments have been used previously, but these present an inherent danger to operators and the environment (Parker and Mehta 2007). Irradiation is also used, leading to the partial or total sterility of the treated subjects (Aquiloni et al. 2009). Physical neutering of crayfish with the removal of modified pleopods (Stebbing et

al. 2014a; Green et al. 2020) has also been used but may prove difficult with smaller animals such as amphipods. One of the major drawbacks with this method is the need to either capture or breed large numbers of males or for them to be released into the wild.

Further research into suitable biocontrols should include the discovery and understanding of host-specific pathogens that can be identified using screening methods, laboratory trials and environmental sampling (Bojko and Ovcharenko 2019), including the exploration of more autocidal control options, for example parasites that reduce fecundity and increase sterility (Bojko 2017). Determining whether a pathogen is suitable for application in a wild environment to control an invasive NIS is difficult and complex; however, the result can be economically viable and provide sustainable population suppression. Invaders may bring with them multiple pathogens that naturally regulate their invasive population, avoiding the need to administer biocontrol measures. In cases where invasive NIS undergo enemy release it is important to know whether a biocontrol mitigation effort could be feasible and safe to apply. In addition, genetic technologies, such as RNAi or CRISPR, which have been successfully applied for pest control in managed systems may have some application to invasive species control (Zhang et al. 2013; McFarlane et al. 2018). Whilst ambitious, and still in the early stages of development, there is much enthusiasm about the potential of this technology for managing established invasive NIS (Simberloff 2020). However, there is also concern about the potential unintended consequences of applying new technologies, such as transfer of a driven gene into an untargeted species (Simberloff 2020). Finally, breaching into chemical control, with a biological twist, Bt toxin (derived from *Bacillus thuringiensis*) is a widely applied crystalline protein in insect control and similar systems show some promise for amphipod control, using instead the pathological effects of *Vibrio parahaemolyticus*, using PirA and PirB toxins. These toxins have host-specific effects in penaeid shrimp (Lee et al. 2015). In all cases where novel technologies are applied, in-depth and rigorous health and safety assessments are required, to be sure that no non-target effects are likely, as well as full consideration of the social risks and barriers.

### Chemical control

At present, chemical control for aquatic invertebrate species is restricted to the use of generic pesticides, many of which have not yet been field tested. Although historically chemicals have been used to manage multiple aquatic invasive NIS (Freeman et al. 2010; Rytwinski et al. 2019), today other control options are often preferred to avoid the associated non-target species effects (Sanchez-Bayo 2012; Milan et al. 2018). For example, rotenone, a naturally occurring ketone ( $C_{23}H_{22}O_6$ ), has commonly, and



often successfully, been applied in non-indigenous fish eradication attempts (Finlayson et al. 2000; Ling 2002; Rytwinski et al. 2019) and for population suppression in invasive fish species (Beamesderfer 2000). This chemical is extremely toxic to many aquatic invertebrates by inhibiting respiratory enzymes, causing death through oxygen deprivation (Eriksen et al. 2009). Rotenone is non-specific and would impact aquatic invertebrates and fish (depending on its concentration), within the treatment area. Degradation rates are dependent on water temperature, light exposure and absorption by suspended solids and benthic deposits (Meadows 1973; Ling 2002; Allen et al. 2006). With a single rotenone treatment, the native macroinvertebrate diversity and taxonomic richness could recover to pre-treatment conditions within 4–12 months of rotenone application, as evidenced following treatment in a New Zealand stream (Pham et al. 2018). However, to achieve successful eradication, multiple treatments would likely be required (Sandodden et al. 2018), which may result in long-term impacts that prevent widespread application of this approach.

Whilst significant advancements have been made in designing efficient, targeted and less environmentally damaging chemicals in terrestrial environments, such progress has not been mirrored in aquatic settings, where only a handful of chemical control methods are presently available (Ling 2002; Solomon and Thompson 2003). To date, no targeted chemical control methods exist for invasive amphipods. Studies investigating the impact of synthetic pyrethroids on freshwater macroinvertebrates have found that exposure can alter locomotory behaviour in *Gammarus pulex* (Linnaeus, 1758), including drifting to the water surface for easy removal (Heckmann et al. 2005; Nørum et al. 2010). Synthetic pyrethroid options can also be highly toxic to a spectrum of aquatic invertebrates, with most  $LC_{50}$  values being below  $1 \mu\text{g l}^{-1}$  (Coats et al. 1989). Preliminary testing indicates synthetic pyrethroids may be highly effective for chemical control of *D. villosus*, resulting in considerable behaviour changes (Stebbing et al. 2014b). Deltamethrin; a sodium channel activator that targets the nervous system of arthropod pest species, was given to *D. villosus* individuals in medicated feed at different doses. In all replicates there was an acute, marked change to the animals swarming behaviour resulting in a loss of coordination and reduction in the normal negative phototactic response. The chemical was found to be effective against *D. villosus* at concentrations  $> 50 \mu\text{g/kg}$  feed resulting in  $> 60\%$  mortality.  $LD_{98}$  was reported to be approximately  $0.7 \text{ ng/animal}$  (average  $20 \text{ mg}$  body weight), although with some uncertainty and assumption of feeding rate. In addition, mechanisms for the delivery of Deltamethrin to *D. villosus* individuals were designed and assessed. Deployment of a cylindrical tube with Deltamethrin suspended in a bespoke bait matrix was used as a delivery mechanism. *Dikerogammarus villosus* rapidly swarmed and settled on, and within, the feeding station even in the presence of other substrate and hardware and were effectively



exposed to Deltamethrin (Stebbing et al. 2014b). Further work is needed to assess the environmental impact of the widespread use of this chemical and refine species-specific dosage levels and delivery mechanisms. However, Deltamethrin has been used with great success in the control of invasive crayfish species (Peay et al. 2019) and is likely to be effective for amphipod control if deployment can be designed to limit availability to target species only.

The future of chemical control for invasive amphipod species is limited by our ability to apply sufficient dosage of the chemical to individuals across large water bodies. Providing a concentration of chemical high enough to cause mortality in a large water body is expensive and poses major logistical challenges. Targeted chemical control will also require a robust understanding of the spatial distribution of the invasive amphipod within the water body. Instead, alternative methods that can aid the delivery of the compound could be considered. These could include delivery methods, such as nanoparticles carrying the compound that may sustain in the environment for long periods of time (Kumar et al. 2014) or using pheromone or “attractive” traps to bring higher numbers of species closer to administer the dose (Witzgall et al. 2010). Commercial systems have already been established for the manufacture of chemical control products for agriculture. There is an opportunity to determine whether these systems could be used to develop highly targeted chemical treatments for invasive amphipods. Whilst there will be significant barriers to registration and market access of chemical products, these are not insurmountable.

### **Integrated management approaches**

Given the diversity of amphipod species and invaded habitats, no single bullet, or standalone approach to invasive amphipod control is likely to be effective (Freeman et al. 2010). However, there is increasing consensus that integrating several different control methods can lead to some success against the target species (Stebbing et al. 2014a). To date, no examples of integrated management currently exist for invasive or pest amphipods; however, successes have been made with other crustacean groups (Hänfling et al. 2011). One system includes the control and removal of *F. rusticus* (Hein et al. 2006). In this example, predatory fish (biological control) and trapping methods (physical control) were used to control the invasive crayfish population. An integrated management approach forms the principle of integrated pest management (IPM) tools that have been widely used in agriculture and are increasingly being applied to invasive NIS management (Di Tomaso et al. 2017; Phelps et al. 2017).

Predatory fish and trapping methods have also been identified as control methods for Amphipoda but have currently been applied separately. Integration of these methods may prove valuable, following the information outlined by Hein et al. (2006). To advance this area further it is important

to consider the consolidation of methods that could be valuable for the control of invasive amphipods. Using *Dikerogammarus* sp. as an example, trapping, parasitic biocontrol, and chemical control agents are all potential applications. Combining different techniques, such as general trapping methods, chemical control options, and the introduction of microsporidian and viral parasites of amphipods like *D. haemobaphes*, may result in a marked decrease of the invasive population based on the separately collected data on *D. villosus* (Van Riel et al. 2006; MacNeil et al. 2010; Kobak et al. 2015) and *D. haemobaphes* (Bojko et al. 2019). Accounting for the affinity of invasive amphipods to certain habitats (Table S1) would help to specify control efforts and increase general efficacy of management (Table S1). Although often neglected in integrated approaches at present, it is important that such an integrated approach also considers whether control methods are effective against co-introduced symbionts, which may be among the main impacts the invasive amphipod species has in the introduced environment.

### **Prospects for future research and management of invasive amphipods**

A current lack of species-specific control options severely limits opportunities to manage established populations of invasive amphipod species, as illustrated in this study by *D. villosus* management in the UK (Table 2). To improve management options available to control invasive amphipods, the development of targeted control methods should be prioritised, with several potentially promising areas recognised among traditional and emerging methods. Firstly, to provide the foundation for improving targeted control methods, basic research on the biology and life-history traits of invasive amphipod species is required, with a synthesis of what is known to date provided in this study (Table S1). Secondly, the efficacy of physical control methods could be improved using advanced monitoring methods, such as telemetry and environmental DNA (eDNA). Telemetry has been used to detect seasonal aggregations of invasive NIS, improving our understanding of their behaviour and increasing capture/removal rate of physical control methods (Bajer et al. 2011; Diggle et al. 2012; Donkers et al. 2012). Molecular monitoring methods, such as eDNA to detect invasive amphipods have resulted in multiple species-specific assays, developed and validated for *D. villosus* (Blackman et al. 2018), *D. haemobaphes* (Mauvisseau et al. 2019), *G. fossarum* (Blackman et al. 2017), *Crangonyx pseudogracilis* (Bousfield, 1958) (Mächler et al. 2014) and *G. pulex* (Mächler et al. 2014), that could be used to better target sites for physical removal efforts. Thirdly, new technologies based on highly specific and well-studied pathogenic biological control agents, advanced genetic methods, or targeted delivery options for chemical control, may also present effective future control options. However,

development of these methods is still in its early stages, and significant research investment is needed to overcome technical barriers, assess associated risks, and understand the implications of public acceptance before such methods can be applied in field. Ultimately, given the lack of a single bullet approach to invasive NIS control, research efforts should focus on developing integrated approaches to management, whereby the effectiveness of several control methods are considered in combination.

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### Supplementary material

The following supplementary material is available for this article:

**Table S1.** Invasive amphipod species, their habitat preference, tolerances and known predators and symbionts.

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