

Time-series analysis of a native and a non-native amphipod shrimp in two English rivers

Tim Johns^{1,*}, David C. Smith², Stuart Homann¹ and Judy A. England¹

¹Environment Agency, Red Kite House, Howbery Park, Wallingford, Oxfordshire, OX10 8BD, UK

²Environment Agency, Waveney Works, Haddiscoe, Great Yarmouth, Norfolk, NR31 9JA, UK

Author e-mails: tim.johns@environment-agency.gov.uk (TJ), david.c.smith@environment-agency.gov.uk (DS), stuart.homann@environment-agency.gov.uk (SH), judy.england@environment-agency.gov.uk (JE)

*Corresponding author

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Abstract

The Ponto-Caspian amphipod *Dikerogammarus haemobaphes*, known as the demon shrimp, arrived in the UK in 2012 and has since spread rapidly, invading waterways particularly in central England. In this paper we use data from routine Environment Agency surveys to explore how *D. haemobaphes* has spread and assess whether it fits the 2013 predictions of Gallardo and Aldridge, which identified southern, eastern and central England as most vulnerable to Ponto-Caspian invaders. We then focus on two rivers, the Thames and the Trent, utilising a mixture of recent and long term datasets to track the presence of *D. haemobaphes* along the course of each river and compare it to that of the native amphipod *Gammarus pulex*. We observed that *D. haemobaphes* is now the dominant amphipod in the navigable stretches of both rivers and that the spread of the species nationally appears closely linked to the canal network. We suggest that focussing biosecurity controls on the movement of boats and equipment between affected and unaffected catchments will be key to limiting the further spread of this and similar invasive species.

Key words: River Thames, River Trent, *Dikerogammarus haemobaphes*, demon shrimp, *Gammarus pulex*, non-native invasive species

Introduction

The Ponto-Caspian crustacean amphipod *Dikerogammarus haemobaphes* (Eichwald, 1841), known as the “demon” shrimp, was first reported in Britain in 2012 from the River Severn, Gloucestershire and later the same year from the River Thames and River Trent (Aldridge 2013). Like the “killer” shrimp, *Dikerogammarus villosus* (Sowinsky, 1894), which appeared in Britain in 2010 (MacNeil et al. 2010), the presence of *D. haemobaphes* in British waterways was predicted (Gallardo and Aldridge 2013) with the Netherlands being the most likely origin (Gallardo and Aldridge 2014). Range expansion of aquatic Ponto-Caspian species probably began in the 17th century through the interconnection of multiple

waterways in continental Europe (bij de Vaate et al. 2002; Jazdzewski et al. 2002). Genetic studies confirm that *D. villosus* arrived in the UK via a western invasion corridor (Rewicz et al. 2015), from the Black and Caspian Seas through the Rhine-Main-Danube canal to the Atlantic Ocean (Panov et al. 2009) and *D. haemobaphes* likely arrived via the same pathway. Probable transportation vectors include ship ballast and bilge waters and international transport of aquatic organisms and materials (Bacela-Spychalska et al. 2013; Nunes et al. 2015).

The impact of Ponto-Caspian invasive amphipods on freshwater communities in continental Europe has been widely studied and it is generally agreed that the introduction of *Dikerogammarus* species has changed species structures across Europe (Dick and Platvoet 2000; Kinzler et al. 2009; MacNeil et al.

2010; Truhlar et al. 2014). The likely reasons for its success in invading new waterways include very high fecundity, early maturity and high reproduction rates (Kley and Maier 2003; Grabowski et al. 2007; Bacela et al. 2009) in comparison to native species such as *Gammarus pulex* (Linnaeus, 1758). *Dikergammarus* are strongly predatory (Kinzler et al. 2009) and tolerant of large ranges in environmental conditions, including temperature, dissolved oxygen and salinity (Aldridge 2013). These traits have enabled it to dominate invaded waterways and in many cases replace native amphipod species (Dick and Platvoet 2000; MacNeil and Platvoet 2005).

The Environment Agency (EA) conduct routine macroinvertebrate monitoring across all rivers in England to meet UK and European statutory monitoring obligations for water quality and quantity objectives. It currently monitors macroinvertebrate communities from around 2500 river locations annually (EA, unpublished data), and uses these data to determine the ecological status of water bodies (high to bad) defined under the Water Framework Directive (European Parliament and of the Council 2000). The presence of non-native invasive species prevents a water body from achieving high status (UKTAG 2013) and has the potential to alter biological communities, whereby macroinvertebrate metrics used to measure ecological status may fail to function correctly (MacNeil et al. 2012; Mathers et al. 2016; Turley et al. 2017).

In this study our focus is on data from 2010 to 2016, covering the main invasion period just prior to and after the appearance of *D. haemobaphes*, but also considering records back to 2007 to ensure understanding of pre-invasion conditions. Our aim is to describe the expansion in the distribution and abundance of *D. haemobaphes* in England and identify changes in amphipod assemblages at selected sites where *D. haemobaphes* now occurs and where the native amphipod *G. pulex* is known. Our approach is to explore *D. haemobaphes* presence data from the EA monitoring database and examine time-series abundance data on two similar rivers; the Thames and the Trent, where records for both the native and invasive amphipods exist. *Crangonyx pseudogracilis* (Bousfield, 1958) an invasive amphipod from North America, is also known to occur in both rivers. However, in comparison to *Dikergammarus*, this species has been present in Britain much longer (first recorded in 1935) and can co-exist with *Gammarus pulex* (MacNeil et al. 1999). It was rarely reported in large numbers in either the Thames or Trent within the study period and so was not considered further in this study.

Methods

Site and data selection

All data for this study were obtained from the EA's macroinvertebrate monitoring database (BIOSYS) which holds data collected from a network of routine and ad-hoc freshwater invertebrate monitoring sites from across England. An initial data extraction of all records of *D. haemobaphes* held in the database was performed and an annual presence dataset generated (Supplementary material Table S1), from which the spread of *D. haemobaphes* in England since 2012 was mapped using ArcGIS software (ESRI ArcMap 9.3.1.).

Data were then sorted to select only routine monitoring sites (normally sampled spring and autumn) where samples had been collected using the EA's standardised 3-minute kick sample method (Murray-Bligh et al. 1997). From this dataset, sites which contained records with abundance data for *D. haemobaphes* and also *G. pulex* were selected for study. A start date of 2007 was chosen to provide a 10 year dataset of sites where *G. pulex* has been regularly recorded (prior to the appearance of *D. haemobaphes* in 2012) and where *D. haemobaphes* is now known. Two geographically separate river catchments (but connected via river and canal networks) were selected for further examination: the Thames in South East England and the Trent in the Midlands (Figure 1). Both rivers are of similar length and characterised by large navigable stretches. For this study, the navigable stretches were identified on the Thames between the most upstream lock at Lechlade, Gloucestershire and the first lock at Teddington downstream in London; and on the Trent between Alrewas, Staffordshire (the most upstream point on the Trent where boats can enter the river) and Dunham downstream in Nottinghamshire (Figure 1). Stretches further downstream were excluded due to likely fluctuations in salinity.

Within these navigable stretches abundance data from all 3-min. kick sample sites (2007–16) were collated and the number of samples containing *G. pulex* and *D. haemobaphes* in each year summarised in abundance categories (Supplementary material Tables S2A and S2B). Since the number of samples recovered annually within these stretches was fairly low, varying spatially and temporally, the majority of these data were not considered for time-series analysis. For both rivers only a single site on each navigable stretch had a long continuous monitoring record suitable for time series analysis: Penton Hook in west London on the Thames; and Ratcliffe, south of Nottingham on the Trent. For comparison, two further sites with similar length records but located upstream

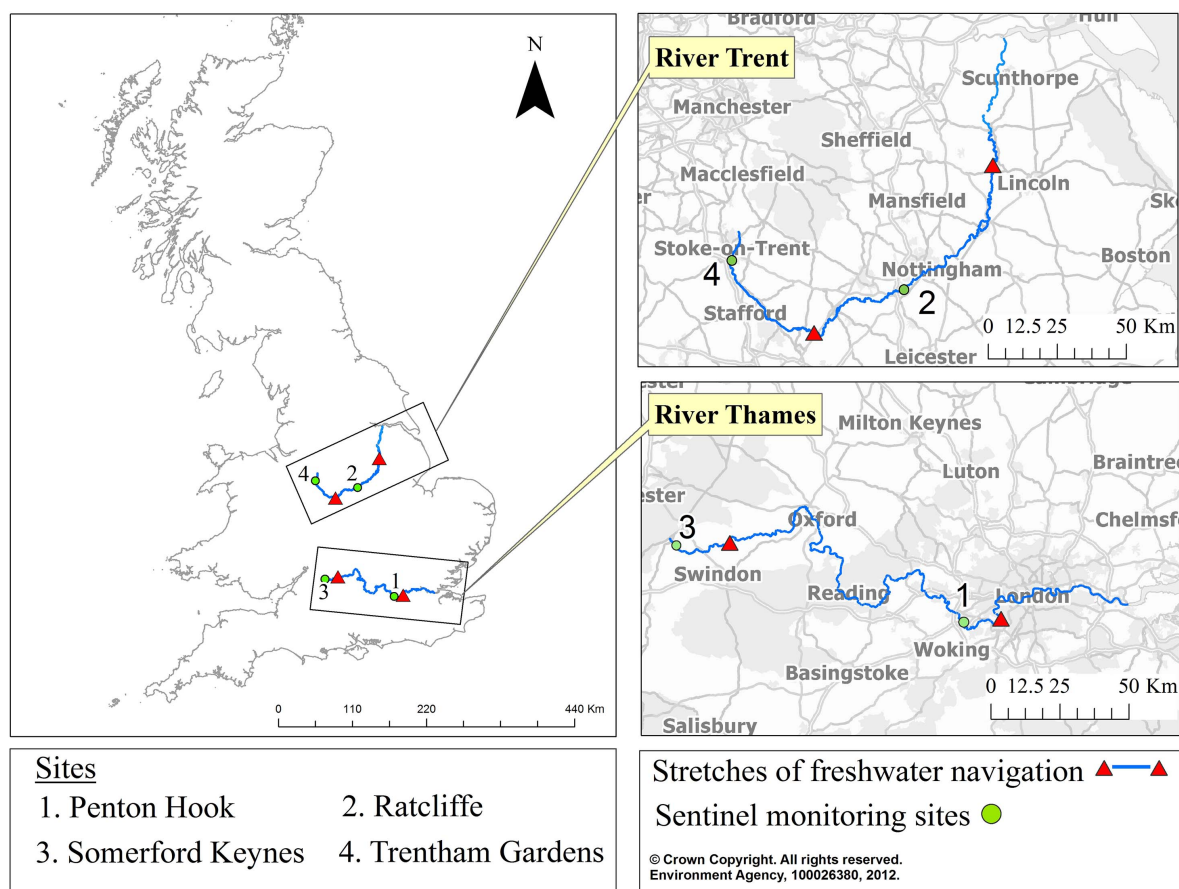


Figure 1. Location map of study area and sites on the River Thames and River Trent. Green dots indicate sentinel study sites at Penton Hook and Somerford Keynes (Thames) and Ratcliffe and Trentham Gardens (Trent). Stretches between red triangles illustrate freshwater navigation.

beyond the navigable sections (where *D. haemobaphes* had not been recorded) were identified: Somerford Keynes (Thames) and Trentham Gardens (Trent) (Figure 1; Supplementary material Table S3). With the exception of Trentham Gardens, all sites had continuous monitoring records from 2009/10 to 2016. Trentham Gardens had a similar record but data were missing for 2013, 2014 and spring 2016. In the absence of a suitable alternative site, missing data were interpolated using a spline function (see data analysis).

Data analysis

From the routine 3-min. kick sample dataset (data from other sample methods were ignored to avoid potential bias) an annual proportion of “affected” sites (i.e. where *D. haemobaphes* was present) was calculated as a percentage of the annual number of all

routine 3-min. kick sample sites monitored nationally. These data were plotted and a regression line fitted.

Abundance data for *G. pulex* and *D. haemobaphes*, recorded from 3-min. kick samples collected within the navigable stretches of each river from 2007 to 2016, were used to derive an annual total and mean abundance for each species. A geometric mean was used to aid comparison between years because of the range in the abundance data. An annual detection rate for each species was also derived, based on the number of samples that each species was recorded in, relative to the total number of samples collected annually.

The following analysis was performed using R Version 3.1.1. (R Development Core Team 2017). Time series plots were produced for *D. haemobaphes* and *G. pulex* using biannual abundance data, recorded between 2009/10–2016, at the four sentinel sites (Penton Hook, Somerford Keynes, Ratcliffe and Trentham Gardens). Raw abundance data were seasonally

Table 1. *Dikerogammarus haemobaphes* (Dh) records recorded in Environment Agency routine sample sites as a proportion of all macroinvertebrate sampling sites (monitored using the EA standardised 3-min. kick sampling method).

	2012	2013	2014	2015	2016
Total annual number of sites where EA standard 3 min kick samples taken ¹	2140	5482	3029	2628	2358
Total annual number of sites where Dh recorded (in 3 min. kick samples)	10	47	54	78	78
Proportion of sites where Dh recorded (in 3 min kick samples)	0.47%	0.86%	1.78%	2.97%	3.31%
Percentage increase from previous year	–	0.39%	0.93%	1.19%	0.34%

¹Majority of routine kick sample sites, sampled biannually (spring & autumn), total number of samples therefore approx. double this figure.

adjusted and plotted along a time series axis. Missing data points for the Trentham Gardens site were interpolated using a cubic spline function in the time series (tseries) package (Trapletti and Hornik 2017), based on uninterrupted antecedent data from 2003–2012 and postcedent for 2015. For each plot, step changes in the *Gammarus pulex* abundance data were identified and plotted as a red line, using the “changepoint” package (Killick and Eckley 2013). This detects changes in the mean and the variance in the observed time series data using the At Most One Change (AMOC) method. This was not applied to the *D. haemobaphes* data since it has a shorter time-series and clearly displays an upward trend.

To assess changes in the abundance of *D. haemobaphes* and *G. pulex* over time, cumulative data from 2010 onwards, recorded at the Penton Hook and Ratcliffe sites, were used to produce comparative time-series plots, using a similar approach to that used by Almeida et al. (2014) for comparison of native and non-native crayfish populations. In line with this method and to aid comparison, due to the range in abundances between the two sites, the data were log-transformed. As *D. haemobaphes* was absent/not detected prior to 2012, an initial starting abundance of 0.1 was assumed for *Dikerogammarus* prior to transforming the cumulative data. A ratio between the cumulative abundance of *D. haemobaphes* (Dh) and *G. pulex* (Gp) was also calculated and plotted as a comparative line on a secondary axis. A dotted line was added on this axis at a value of 1.0 to indicate the point at which the cumulative abundance for the two species were equal (Dh/Gp = 1/1). No ecological significance is inferred by this but extension beyond the vertical dotted line indicates dominance of the invasive species.

Results

National scale

Environment Agency monitoring data reports a steady rise in the number of sites where *D. haemobaphes* has been recorded in English waterways since its discovery in 2012 (Table 1). Noting the species may

have been misidentified previous to 2012, *D. haemobaphes* appears to have spread out from a roughly geographically central location, identified by early records from the Severn, Thames and Trent (Figure 2). Although records concentrate around navigable river sections and canals in the Midlands, new records such as those from the Leeds and Liverpool canal in the northwest (2015) and the Ripon canal in Yorkshire to the north (2016) illustrate the species' gradual range expansion. However, the number of sites with *D. haemobaphes*, as a proportion of all sites monitored using the 3-min. kick sample method, remains relatively small (approx. 3.3% in 2016) but has increased. Our records show that between 2012 and 2016 the number of sites with records of *D. haemobaphes* increased by 2.8%, at an average of 0.7% per year (Table 1; Figure 3).

Local scale

The presence and abundance of *D. haemobaphes* has risen since first recorded in 2012, in both the Thames and the Trent (although total abundance has fluctuated). Concurrently, the abundance of *G. pulex* appears to have declined, and it is now rarely recorded in large numbers in stretches on either river where boat navigation exists (Tables S2A and S2B). For example, in the four years preceding 2012 (2008–2011) the average annual abundance of *Gammarus pulex* was 415 in the Thames and 627 in the Trent. Comparing this to the four years post 2012 (2013–2016), recorded annual abundance was 94 and 90 respectively, whilst noting the number of samples in each year vary and are not matched pre and post 2012.

Site scale

Long term time series monitoring at Penton Hook (Thames) and Ratcliffe (Trent) (Table S3) show a declining trend in *G. pulex* numbers, with a downwards step-change in abundance detected (using the At Most One Method) between 2011–2013 (Figures 4A and 4B). At the comparative sentinel site at Somerford Keynes (Thames) (Figure 5A) a step change is also detected in 2012, but corresponds to an upward

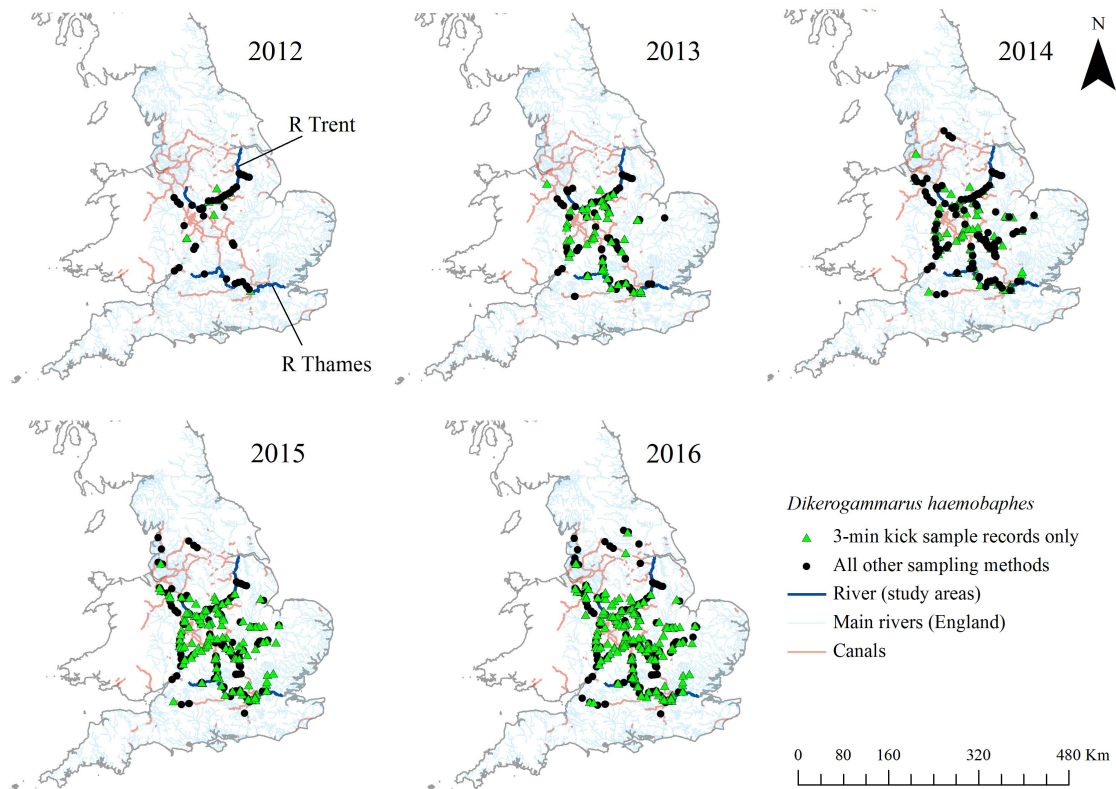


Figure 2. Presence data for *Dikerogammarus haemobaphes* recorded at Environment Agency invertebrate monitoring sites between 2012–2016. (Note: records displayed are cumulative). Records are from all monitoring events using a variety of sampling methods, green dots indicate where the samples have been recovered using the EA standard 3-min kick sample method, black dots show samples collected by all other methods.

trend in *G. pulex* abundance, albeit a fluctuating one. The site at Trentham Gardens (Trent) (Figure 5B) shows no step change, although *G. pulex* abundance increases post 2012 (noting 2013–14 data were interpolated).

Cumulative abundance for *D. haemobaphes*, where it occurs at Penton Hook and Ratcliffe, has risen sharply (Figures 6A and 6B), indicating a rise in annual populations. Conversely *G. pulex* abundance in both rivers post 2012 did not increase noticeably, as would be expected if the annual population were not declining. The ratio between the number of *D. haemobaphes* to the number of *G. pulex* mirrors the rise in *D. haemobaphes* abundance, with the invasive species being recorded slightly earlier on the Trent (spring 2012) compared to the Thames (autumn 2012). The point at which the ratio of *D. haemobaphes* to *G. pulex* exceeded 1/1 (i.e. when the cumulative abundance of the invasive species surpassed that of the native) was reached about 18 months earlier on the Thames (spring 2015) than on the Trent (autumn 2016).

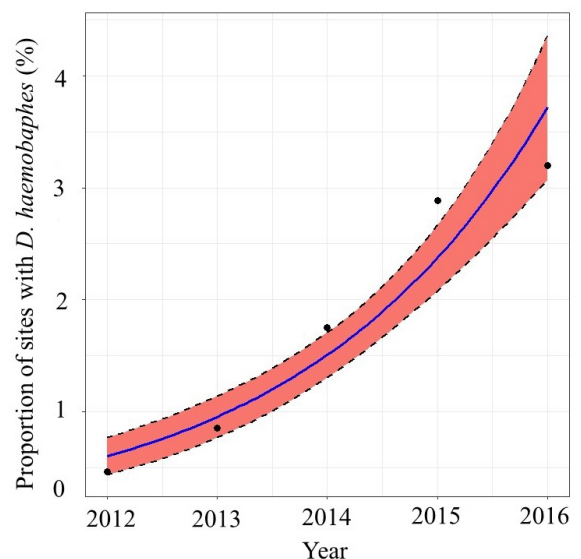


Figure 3. Proportion of sites where *Dikerogammarus haemobaphes* has been recorded annually, expressed as a percentage of all routine sites monitored annually using the 3-min. kick sampling method. Binomial regression line fitted using glm() function in R.

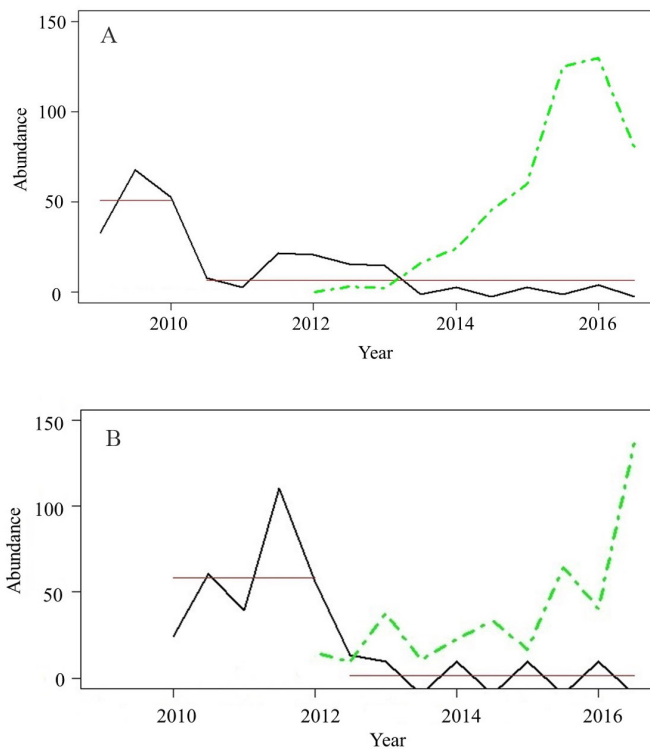


Figure 4. Seasonally adjusted time series plots from biannual monitoring of *Gammarus pulex* (black line) and *Dikerogammarus haemobaphes* (green line) abundance recorded at the downstream navigable study sites; (A) Penton Hook (River Thames) and (B) Ratcliffe (River Trent). Data available from 2009 (Penton Hook) and 2010 (Ratcliffe) to 2016. Change points in abundance (red line) identified using the At Most Once Change (AMOC) method (Killick and Eckley 2013).

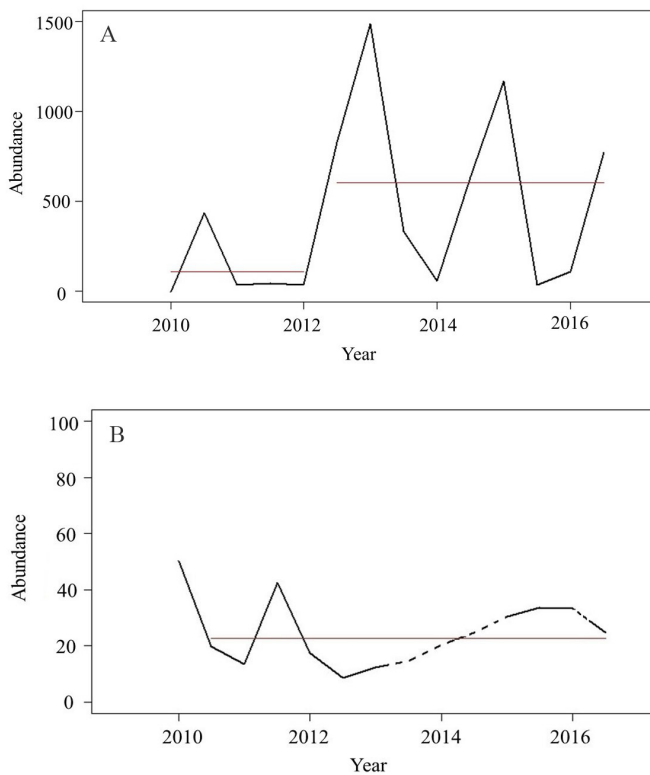


Figure 5. Seasonally adjusted time series plots from biannual monitoring of *Gammarus pulex* (black line) abundance recorded at the upstream non-navigable study sites; (A) Somerford Keynes (River Thames) and (B) Trentham Gardens (River Trent). Data available from 2010 to 2016. (Note missing data points at Trentham Gardens (2013, 2014 & spring 2016) interpolated, indicated by dotted line). Change points in abundance (red line) identified using the At Most Once Change (AMOC) method (Killick and Eckley 2013).

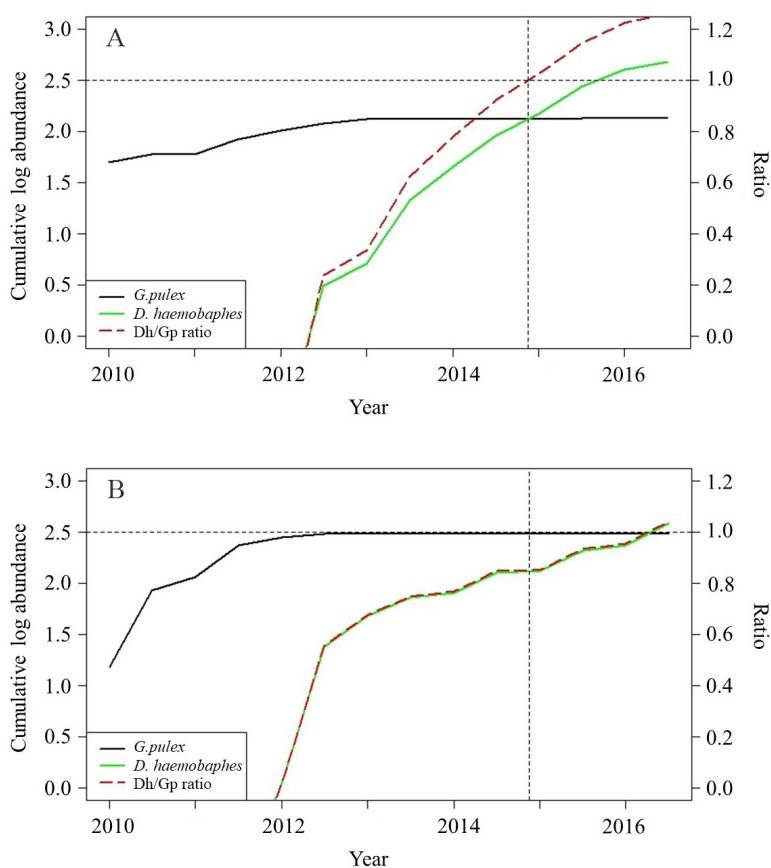


Figure 6. Cumulative log abundance plots of native *Gammarus pulex* (black) and non-native *Dikerogammarus haemobaphes* (green) from biannual monitoring data (2010–2016) recorded at the study sites; (A) Penton Hook (River Thames) and (B) Ratcliffe (River Trent). The ratio of non-native to native (Dh/Gp) cumulative abundance is presented as red long dotted line, the black short dotted lines indicate when a 1:1 ratio is achieved (i.e. the cumulative abundance of both species is matched, above which the invasive species is dominant).

Discussion

Environment Agency data indicates the presence of *D. haemobaphes* has increased annually since its appearance in 2012 (Table 1, Figure 3). It has expanded its range whereby it now occurs in half of all the river basin districts monitored, although this does not mean it is present in all watercourses within these districts or catchments. In comparison to *D. villosus*, which appeared in England in 2010, *D. haemobaphes* has spread far more rapidly and more widely (Etxabe et al. 2015), although experience from southern Germany suggests *D. villosus* may in time displace it in some rivers (Kinzler et al. 2009).

In Gallardo and Aldridge (2013) review of the invasion potential of Ponto-Caspian species into Great Britain, south-east England was identified as being at highest risk of invasion. Their study used bioclimatic modelling (using parameters such as alkalinity, altitude and climate) to construct species specific heat maps to identify areas of greatest invasion risk. The heat map produced for *D. haemobaphes* aligns reasonably well to the current distribution reported in our study,

with the exception of the eastern and southern seaboard regions, areas highly suitable for invasion but where the species has not yet been recorded. This is probably related to the lack of canals, and therefore less artificial connections between water bodies, in these areas compared to central England.

The role of canals in facilitating the range expansion of Ponto-Caspian species in continental Europe is well documented (Jazdzewski 1980; Mastitsky and Makarevich 2007; Labat et al. 2011; Chen et al. 2012). Unsurprisingly, this also appears to be the case in England, with the majority of *D. haemobaphes* records located in the Midlands where there are the most canals (Figure 1). Here the canal and river networks interconnect allowing boats to move freely between the two systems. The River Trent for example, links with the Trent and Mersey canal via direct connections and overflows from the canal into the river and its tributaries. This system also links circuitously to the River Thames, with boats able to enter or leave the system at Oxford and several other points further downstream in London.

Our examination of routine macroinvertebrate monitoring data from the Thames and Trent shows that native amphipod (*G. pulex*) populations in navigable stretches of both rivers have declined in recent years, based on falling detection rates in the number of samples in which *G. pulex* has been recorded and its total abundance (Tables S2A and S2B). Conversely, data for *D. haemobaphes* from the same samples shows an increase in the presence and abundance of this species over the same time period. At the site level, similar changes in the abundance of both species are apparent at Penton Hook and at Ratcliffe (Table S3). The decline in the abundance of the native species occurs at similar times at both sites, roughly coinciding with the first recorded appearance of *D. haemobaphes* in the country in 2012 (Figures 4A and 4B). Other studies report similar declines in the abundance of native amphipods, including some local extinctions following the appearance of *Dikerogammarus* species, where it has exerted a competitive advantage (Dick and Platvoet 2000; Dick et al. 2002; Bollache et al. 2008). However, natural variation in benthic communities and fluctuations in the densities of taxa, such as *G. pulex* (Graça et al. 1994), make it difficult to detect community change through the appearance of a single invasive species, particularly where a river basin is subject to other multiple pressures (van Riel et al. 2006). Significant flooding in England in 2012/13 (Met Office 2012) for example, could have contributed to the decline in *G. pulex* abundance recorded at Penton Hook and Ratcliffe, although no decline was observed upstream at Somerford Keynes or Trentham Gardens, where abundance actually rose (Figures 5A and 5B).

The cumulative abundance of native and invasive amphipod populations in the Thames at Penton Hook and the Trent at Ratcliffe suggest that *D. haemobaphes* appeared in the Trent in 2012, slightly before it was found in the Thames. This may be because it was overlooked in earlier samples from the Thames or it could point to the origin of the invading population being in the Midlands. Whether the invasion of *D. haemobaphes* in England occurred as a result of a single introduction or multiple ones is unknown, but given its first recorded appearance was in the River Severn in the Midlands (Aldridge 2013), it may well have spread out from here, so a later appearance in the Thames seems plausible. What is perhaps more interesting is the rate at which the cumulative abundance of *D. haemobaphes* has risen and the rapidity at which it has overtaken that of *G. pulex*. Such dominance is in line with studies of *Dikerogammarus* from continental Europe, where it quickly became super abundant (Rewicz et al. 2014). MacNeil and Platvoet (2005), examining the predatory impact

of *D. villosus* on *G. pulex*, identify the importance of habitat complexity in helping determine whether the species' co-exist or if *G. pulex* is driven to extinction by *D. villosus*. Although habitat was not examined in our study it could be a contributing factor in the more rapid replacement of *G. pulex* by *D. haemobaphes* observed at Penton Hook. Further national study of rivers impacted by non-native invasive species, examining variables such as habitat and propagule pressure, would help develop our understanding of the control and management of *D. haemobaphes*.

Conclusions

Within the navigable stretches of the Thames and Trent *D. haemobaphes* is now the dominant freshwater amphipod species, having virtually replaced the native *G. pulex*. The observation that *D. haemobaphes* is largely limited to such navigable waterways is a further illustration of the species association with boat traffic. Interestingly, beyond these investigated navigable stretches *D. haemobaphes* appears largely absent. While this may be a function of propagule pressure rather than the suitability of the receiving waters, it illustrates the importance of biosecurity measures in maintaining a low invasion pressure. Successfully controlling the spread of *D. haemobaphes*, and potentially *D. villosus* in future, will therefore depend on efficient biosecurity and surveillance monitoring, focusing on unaffected rivers which are not intricately connected to navigable waterways.

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References

- Aldridge D (2013) GB non-native organism rapid risk assessment for *Dikerogammarus haemobaphes* (Eichwald, 1841). <http://www.nonnative-species.org/downloadDocument.cfm?id=870> (accessed 12 May 2017)
- Almeida D, Ellis A, England J, Copp GH (2014) Time-series analysis of native and non-native crayfish dynamics in the Thames River Basin (south-eastern England). *Aquatic Conservation: Marine and Freshwater Ecosystems* 24: 192–202, <https://doi.org/10.1002/aqc.2366>
- Bacela-Spychalska K, Grabowski M, Rewicz T, Konopacka A, Wattier R (2013) The “Killer Shrimp” *Dikerogammarus villosus* (Crustacea, Amphipoda) invading alpine lakes: Overland transport by recreational boats and scuba-diving gear as potential entry vectors? *Aquatic Conservation: Marine and Freshwater Ecosystems* 23: 606–618, <https://doi.org/10.1002/aqc.2329>
- Bacela K, Konopacka A, Grabowski M (2009) Reproductive biology of *Dikerogammarus haemobaphes*: An invasive gammarid (Crustacea: Amphipoda) colonizing running waters in Central Europe. *Biological Invasions* 11: 2055–2066, <https://doi.org/10.1007/s10530-009-9496-2>

- bij de Vaate A, Jazdzewski K, Ketelaars HAM, Gollasch S, Velde G van der (2002) Geographical patterns in range extension of Ponto-Caspian macroinvertebrate species in Europe. *Canadian Journal of Fisheries and Aquatic Sciences* 59: 1159–1174, <https://doi.org/10.1139/r02-098>
- Bollache L, Dick JTA, Farnsworth KD, Montgomery WI (2008) Comparison of the functional responses of invasive and native amphipods. *Biology Letters* 4: 166–169, <https://doi.org/10.1098/rsbl.2007.0554>
- Chen W, Lipkowski K, Jourdan J, Plath M, Streit B, Klaus S (2012) *Dikerogammarus haemobaphes* in the River Lahn, Germany, with notes on the dynamics of Amphipoda assemblages. *Lauterbornia* 1976(1994): 87–93
- Dick JT, Platvoet D (2000) Invading predatory crustacean *Dikerogammarus villosus* eliminates both native and exotic species. *Proceedings of the Royal Society of London* 267: 977–983, <https://doi.org/10.1098/rspb.2000.1099>
- Dick JTA, Platvoet D, Kelly DW (2002) Predatory impact of the freshwater invader *Dikerogammarus villosus* (Crustacea: Amphipoda). *Canadian Journal of Fisheries and Aquatic Sciences* 59: 1078–1084, <https://doi.org/10.1139/r02-074>
- Etxabe AG, Short S, Flood T, Johns T, Ford AT (2015) Pronounced and prevalent intersexuality does not impede the “Demon Shrimp” invasion. *PeerJ* 3: e757, <https://doi.org/10.7717/peerj.757>
- European Parliament and of the Council (2000) Directive 2000/60/EC of the European Parliament and of the Council of 23 October 2000 establishing a framework for Community action in the field of water policy. *Official Journal of the European Union* L327: 0001–0073
- Gallardo B, Aldridge DC (2013) Priority setting for invasive species management: risk assessment of Ponto-Caspian invasive species into Great Britain. *Ecological applications: a publication of the Ecological Society of America* 23: 352–364, <https://doi.org/10.1890/12-1018.1>
- Gallardo B, Aldridge DC (2014) Is Great Britain heading for a Ponto-Caspian invasional meltdown? *Journal of Applied Ecology* 52: 41–49, <https://doi.org/10.1111/1365-2664.12348>
- Grabowski M, Bacela K, Konopacka A (2007) How to be an invasive gammarid (Amphipoda: Gammaroidea) - Comparison of life history traits. *Hydrobiologia* 590: 75–84, <https://doi.org/10.1007/s10750-007-0759-6>
- Graża MAS, Maltby L, Calow P (1994) Comparative ecology of *Gammarus pulex* (L.) and *Asellus aquaticus* (L.): I: population dynamics and microdistribution. *Hydrobiologia* 281: 155–162, <https://doi.org/10.1007/BF00028678>
- Jazdzewski K (1980) Range extension by some Gammaridean species in European inland waters caused by human activity. *Crustaceana Suppl* 6: 84–107
- Jazdzewski K, Konopacka A, Grabowski M (2002) Four Ponto-Caspian and one American gammarid species (Crustacea, Amphipoda) recently invading Polish waters. *Contributions to Zoology* 71: 115–122
- Killick R, Eckley I (2013) changepoint: An R Package for changepoint analysis. *Lancaster University* 58: 1–15, <https://doi.org/10.1359/JBMR.0301229>
- Kinzler W, Kley A, Mayer G, Waloszek D, Maier G (2009) Mutual predation between and cannibalism within several freshwater gammarids: *Dikerogammarus villosus* versus one native and three invasives. *Aquatic Ecology* 43: 457–464, <https://doi.org/10.1007/s10452-008-9206-7>
- Kley A, Maier G (2003) Life history characteristics of the invasive freshwater gammarids *Dikerogammarus villosus* and *Echinogammarus ischnus* in the river Main and the Main-Donau canal. *Archiv Für Hydrobiologie* 156: 457–469, <https://doi.org/10.1127/0003-9136/2003/0156-0457>
- Labat F, Piscart C, Fontan B (2011) First records, pathways and distributions of four new Ponto-Caspian amphipods in France. *Limnologia* 41: 290–295, <https://doi.org/10.1016/j.limno.2010.12.004>
- MacNeil C, Boets P, Platvoet D (2012) “Killer shrimps”, dangerous experiments and misguided introductions: how freshwater shrimp (Crustacea: Amphipoda) invasions threaten biological water quality monitoring in the British Isles. *Freshwater Reviews* 5: 21–35, <https://doi.org/10.1608/FRJ-5.1.457>
- MacNeil C, Elwood RW, Dick JTA (1999) Differential microdistributions and interspecific interactions in coexisting *Gammarus* and *Crangonyx* amphipods. *Ecography* 22: 415–423, <https://doi.org/10.1111/j.1600-0587.1999.tb00578.x>
- MacNeil C, Platvoet D (2005) The predatory impact of the freshwater invader *Dikerogammarus villosus* on native *Gammarus pulex* (Crustacea: Amphipoda); influences of differential microdistribution and food resources. *Journal of Zoology* 267: 31, <https://doi.org/10.1017/S0952836905007351>
- MacNeil C, Platvoet D, Dick JTA, Fielding N, Constable A, Hall N, Aldridge D, Renals T, Diamond M (2010) The Ponto-Caspian “killer shrimp”, *Dikerogammarus villosus* (Sowinsky, 1894), invades the British Isles. *Aquatic Invasions* 5: 441–445, <https://doi.org/10.3391/ai.2010.5.4.15>
- Mastitsky SE, Makarevich OA (2007) Distribution and abundance of Ponto-Caspian amphipods in the Belarusian section of the Dnieper River. *Aquatic Invasions* 2: 39–44, <https://doi.org/10.3391/ai.2007.2.1.4>
- Mathers KL, Chadd RP, Extence CA, Rice SP, Wood PJ (2016) The implications of an invasive species on the reliability of macroinvertebrate biomonitoring tools used in freshwater ecological assessments. *Ecological Indicators* 63: 23–28, <https://doi.org/10.1016/j.ecolind.2015.11.051>
- Met Office (2012) November 2012 Flooding. <http://www.metoffice.gov.uk/learning/learn-about-the-weather/weather-phenomena/case-studies/november-2012-flooding> (accessed 9 July 2017)
- Murray-Bligh J, Furse M, Jones F, Gunn R, Dines R, Wright J (1997) Procedure for collecting and analysing macroinvertebrate samples for RIVPACS. 1997, 155
- Nunes AL, Tricarico E, Panov VE, Cardoso AC, Katsanevakis S (2015) Pathways and gateways of freshwater invasions in Europe. *Aquatic Invasions* 10: 359–370, <https://doi.org/10.3391/ai.2015.10.4.01>
- Panov VE, Alexandrov B, Arbaciauskas K, Binimelis R, Copp GH, Grabowski M, Lucy F, Leuven RSEW, Nehring S, Paunovic 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, https://doi.org/10.1897/IEAM_2008-034.1
- R Development Core Team (2017) A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria, <https://www.r-project.org>
- Rewicz T, Grabowski M, MacNeil C, Bacela-Spychalska K (2014) The profile of a “perfect” invader - the case of killer shrimp, *Dikerogammarus villosus*. *Aquatic Invasions* 9: 267–288, <https://doi.org/10.3391/ai.2014.9.3.04>
- Rewicz T, Wattier R, Grabowski M, Rigaud T, Bacela-Spychalska K (2015) Out of the Black sea: Phylogeography of the invasive killer shrimp *Dikerogammarus villosus* across Europe. *PLoS ONE* 10: 1–20, <https://doi.org/10.1371/journal.pone.0118121>
- Riel MC van, Velde G van der, Dehaers F, bij de Vaate A, Rajagopal S, Marguillier S (2006) Trophic Relationships in the Rhine Food Web during Invasion and after Establishment of the Ponto-Caspian Invader *Dikerogammarus villosus*. *Hydrobiologia* 565: 39–58, <https://doi.org/10.1007/s10750-005-1904-8>
- Trapletti A, Hornik K (2017) tseries: Time Series Analysis and Computational Finance. R package version 0.10-43. <https://cran.r-project.org/package=tseries>
- Truhlar AM, Dodd JA, Aldridge DC (2014) Differential leaf-litter processing by native (*Gammarus pulex*) and invasive (*Dikerogammarus villosus*) freshwater crustaceans under environmental extremes. *Aquatic Conservation: Marine and Freshwater Ecosystems* 24: 56–65, <https://doi.org/10.1002/aqc.2375>

Turley MD, Bilotta GS, Gasparrini A, Sera F, Mathers KL, Humphreyes I, England J (2017) The effects of non-native signal crayfish (*Pacifastacus leniusculus*) on fine sediment and sediment-biomonitoring. *Science of the Total Environment* 601–602: 186–193, <https://doi.org/10.1016/j.scitotenv.2017.05.106>

UKTAG (2013) Guidance on the Assessment of Alien Species Pressures. UK Technical Advisory Group on the Water Framework Directive, <https://www.wfduk.org/resources%20guidance-assessment-alien-species-pressures> (accessed 1 March 2017)

Supplementary material

The following supplementary material is available for this article:

Table S1. Environment Agency geo-referenced records of *Dikerogammarus haemobaphes* presence in England, 2012–2016.

Table S2A. Summary of number of samples where *Gammarus pulex* (Gp) and *Dikerogammarus haemobaphes* (Dh) have been recorded, together with total abundance for each species in all samples recovered from the River Thames (Lechlade-Teddington) between 2007–2016.

Table S2B. Summary of number of samples where *Gammarus pulex* (Gp) and *Dikerogammarus haemobaphes* (Dh) have been recorded, together with total abundance for each species in all samples recovered from the River Trent (Alrewas –Dunham) between 2007–2016.

Table S3. Summary of total annual abundance of *Gammarus pulex* (Gp) and *Dikerogammarus haemobaphes* (Dh) recorded from 3-min kick samples at the four sentential monitoring sites upstream at Somerford Keynes (Thames) and Trentham Gardens (Trent), and downstream at Penton Hook (Thames) and Ratcliffe (Trent), between 2010–2016.

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