Review of the ecological impact and invasion potential of Ponto Caspian invaders in Great Britain

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CAMBRIDGE
ENVIRONMENTAL CONSULTING

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by

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EXECUTIVE SUMMARY

Concerned with the impact of invasive species on ecosystems and native communities, Great Britain has promoted action to avoid the intentional and accidental introduction and spread of non-native species. However, specific strategies are needed for key ecosystems and donor areas that take into account their habitat-specific vulnerability, pathways of introduction and potential impacts.

This project focuses on a high-risk group of freshwater invaders originating from the Ponto-Caspian region (SE Europe). The project seeks to assess the full scope of the threat posed by Ponto-Caspian species as basis for creation of an informed strategy of prevention across Britain. Furthermore, this project aims to provide the foundation for future risk assessments, prevention plans, early detection schemes and monitoring programmes of Ponto-Caspian species.

The project is divided into three interlinked sections, comprising a comprehensive review of 23 alert Ponto-Caspian invaders, analysis of likely spatio-temporal patterns of introduction, and modelling of their potential distribution and spread in England and Wales. The project is based on data extracted from the literature and maps obtained from global, European and national data bases. All the information collected was summarized and analysed using state-of-the-art techniques to develop predictive models that allows the inference of likely future scenarios of invasion.

A number of key messages and biosecurity recommendations can be drawn from this project:

Message 1: There are evident gaps in the literature regarding the basic biology and ecology of alert Ponto-Caspian species and their environmental and economic impacts.

Information on the basic biology and ecology of invasive species, such as their reproductive ability, feeding behaviour and interaction with other species, is fundamental to understand their potential impacts. Currently, there is a great imbalance between the number of studies addressing widely known invaders (e.g. *Dreissena r. bugensis, Dikerogammarus villosus*) and those essentially neglected (e.g. *Corophium sowinskyi, Chaetogammarus warpachowski, Dikerogammarus bispinosus*).

Recommendation 1: It is fundamental to develop basic laboratory and field studies to gain full knowledge on the basic biology and ecology of Ponto-Caspian invasive species. Otherwise we might underestimate their potential impacts. Cross-country collaboration and information sharing is fundamental to avoid duplicating efforts in risk assessment.

Message 2: There are a number of alert Ponto-Caspian species thriving in the Rhine estuary and ports of The Netherlands with serious risk of being transported into Great Britain in the short term.

At least 15 out of the 23 alert Ponto-Caspian organisms investigated are well established in the Rhine estuary and Dutch ports. Four of these species have recently crossed the channel and established in Great Britain. The time lag between a given species' first record in The Netherlands and Great Britain has been reduced in the last century from an average 30 to merely 5 years.

Regression models suggest that alert Ponto-Caspian species present in The Netherlands are under a critical risk of being transported (and could even have arrived already) to Great Britain. Special attention should be paid to the quagga mussel (*D. r. bugensis*), since time lags for molluscs seem to be substantially shorter than for other types of organisms.

Recommendation 2: Great Britain is on the brink of multiple Ponto-Caspian invasions and there is little leeway to set up a strategy for prevention and early detection. Areas with an especially high frequency of invasive species reports, such as the Thames estuary (where ca. 40% of Britain's freshwater invaders were first recorded) and the Anglian region (20%) should be prioritized for the early prevention and control of aquatic invasions.

Message 3: The south and east of England show the highest suitability for the establishment of multiple alert Ponto-Caspian species.

According to species distribution models (SDM) performed with data on the current spatial distribution of alert Ponto-Caspian invaders, the cumulative risk of invasion of multiple alert Ponto-Caspian species is highest in the SE of England and decreases north and westwards.

Annual and coldest temperature were relevant predictors in SDM, which relate to the basic physiological constrains and habitat availability for Ponto-Caspian species. The significant contribution of the Human Influence Index to classic climate-based SDM revealed the important role of human activities in the transport and establishment of invaders.

Recommendation 3: Maps developed in this study can be used to guide monitoring schemes for the early detection of Ponto-Caspian species. Special attention should be paid to areas under risk of multiple invasions, such as the lower reaches of the Great Ouse, Broadlands, Thames and Severn rivers, projected to be affected by up to 20 alert Ponto-Caspian species.

Message 4: River and lake typologies characterized by small-sized catchments, low altitude and calcareous geology are most vulnerable to invasion.

Ponto-Caspian species are not likely to affect all types of British rivers and lakes in the same way. River types 2, 5 and 8, and lake HA- types meet all characteristics that favour the establishment of Ponto-Caspian invaders. These water body types are widespread in England and Wales, representing 40% the typed river length. River types 5 and 8 showed highest cumulative risk scores in SDM (>15 species predicted present on average) and the highest number of native species potentially affected by Ponto-Caspian invaders (e.g. Gammaridae, Asellidae, Unionidae, Caenidae, Hydropsychidae, Chironomidae and Oligochaeta).

Important alterations in the structure of habitats and aquatic communities can be expected, although the direction of such change is difficult to anticipate, depending to a great extent on the number and density of invaders.

Recommendation 4: Current sampling protocols do not consider the native/invasive status of species thereby leading to misguiding ecological status evaluations. A simple biocontamination index based on the richness and abundance of invaders applicable to data collected during routine monitoring is therefore recommended.

Message 5: Once introduced, alert Ponto-Caspian species can quickly disperse through the interconnected network of water bodies and artificial canals.

Alert Ponto-Caspian species can disperse at very high velocities (on average 87 km/year upstream and 80 km/year downstream) aided by human activities such as boating or fishing, through hull fouling, attachment to boat material, trailers or fishing gear.

According to Network Analysis, the potential for secondary spread of alert Ponto-Caspian species is particularly high within the Great Ouse, Nene catchments and the Broadland Rivers because of the high interconnectivity of their hydrological networks.

Recommendation 5: Spread velocities used in this report are rough estimates subject to multiple limitations, thus real information based on laboratory and field trials is still needed to evaluate the potential for secondary spread of alert Ponto-Caspian species. The Network Analysis provides an innovative tool to improve the early control of invasive species, but requires further advancement.

Recommendation 6: River Basin Management Plans offer a pivotal tool to coordinate efforts towards preventing and managing invasion species at the regional scale. A continuing process of evaluation of existing and potential invaders should be implemented since problems and vectors change over time.

1. INTRODUCTION

Biological invasions constitute a growing concern to environmental managers and stakeholders because of their diverse impacts on biodiversity, ecosystem services and associated eradication costs, necessitating effective management policies (Gallardo and Aldridge 2013a). According to the European RINSE project (www.rinse-europe.eu) approximately 20% of all non-native species described in Europe (ca. 12,000, www.europe-aliens.com) have been already reported in Great Britain (Gallardo et al. 2013), with total annual costs for the British economy of approximately £1.7 billion (Williams et al. 2010).

Concerned with the impact of invasive species on ecosystems and native communities, Great Britain is among the first in Europe that has promoted action to avoid the intentional introduction and spread of non-native species, to prevent accidental introductions and to build an information system on invasive species (www.nonnativespecies.org). Consequently, there are several well-established systems in place to address invasive species issues in Great Britain. However, they are strongly biased towards areas of traditional economic importance such as plant and animal health (GB-NNSS 2008). Furthermore, specific strategies are needed for key ecosystems that take into account their habitat-specific vulnerability, pathways of introduction and potential impacts.

Freshwater ecosystems are particularly vulnerable because of the high intrinsic dispersal ability of freshwater species when compared with terrestrial organisms, and the high level of human disturbance in aquatic ecosystems that attract biological invasions more than pristine systems (Gherardi 2007). According to a recent risk assessment, approximately 6% of all invasive species in Great Britain are freshwater (Gallardo et al. 2013), with estimated control costs of £26.5 million per year (Oreska and Aldridge 2011). Moreover, there is a high potential for future invasion of multiple species belonging to different taxonomic groups and regions of origin (Gallardo and Aldridge 2013a).

An exceptional ‘donor hot spot’ of freshwater invaders towards Western Europe and Great Britain is the Ponto-Caspian region, located between the Black, Azov and Caspian Seas (Bollache et al. 2008). Over a hundred species are currently known to have spread from this region (Ojaveer et al. 2002; Dumont et al. 2004; Copp et al. 2005; Alexandrov et al. 2007). The colonization success of Ponto-Caspian invaders can be attributed to several biological features. The most important are their tolerance to wide temperature and salinity ranges, omnivorous opportunistic feeding, and rapid reproduction (e.g. high fecundity, fast growth, early maturity) (bij de Vaate et al. 2002). In addition, the availability and human enhancement of invasion corridors between ecosystems with suitable environmental conditions for the invading species (Reid and Orlova 2002) and facilitation of invasions through positive interaction between species (i.e. invasional meltdown) altogether explain their collective success colonizing new environments (Berezina 2007).

Clear geographic patterns in the spread of 16 Ponto-Caspian species towards Western Europe and Great Britain depending on their main dispersal corridor (i.e. central Black Sea-Baltic Sea through Dnieper and Nemunas rivers, or southern Black Sea-North Sea through the Danube-Main-Rhine waterways), were observed by Gallardo and Aldridge (2012). In addition, Gallardo and Aldridge (2012) suggested that high alkalinity > 120 mg/L favours the establishment of Ponto-Caspian invaders, and pointed to SE England as the most vulnerable region to their establishment because of its similar climatic conditions with the invaded continental Europe. Another report highlighted 14 Ponto-Caspian species as posing the greatest threat of introduction and spread in Great Britain, and identified shipping (ballast water and hull fouling) as the most important pathway of Ponto-Caspian species introduction into Great Britain, and recreational activities (boating, fishing) as the most common pathways of secondary spread (Godard et al. 2012).

Ponto-Caspian species have multi-level abiotic and biotic impacts. They change the energy flow of ecosystems, become dominant members of various trophic levels (e.g. herbivores, detritivores, predators), displace native species through competition or predation, and may severely affect fisheries (Ojaveer et al. 2002). Ponto-

Caspian invasive species have also far reaching abiotic impacts, changing habitat conditions and the energy flow between biotic and abiotic compartments (Ojaveer et al. 2002). Ponto-Caspian species therefore constitutes a group of high concern for environmental managers and stakeholders that requires scientifically informed tools for their prevention and control.

To cover needs underlined in previous investigations, this project aims to assess the full scope of the threat posed by invasive Ponto-Caspian species as basis for a Great Britain informed strategy of prevention. Following key actions proposed by the Great Britain Non-Native Species Secretariat (GB-NNSS 2008), the assessment reviews all available scientific information on the invasive species group of concern, their ecological and economic impacts, and the ecosystems invaded (Wittenberg and Cock 2001). The assessment also identifies the highest impact species that are most likely to enter and establish themselves in Great Britain by producing ranked lists (as recommended by GB-NNSS, 2008). Finally, recommendations provided as part of the assessment enables a more efficient allocation of resources for the early detection of Ponto-Caspian invasive species.

1.1 STUDY APPROACH AND OBJECTIVES

Building upon previous research, the main objective of this project is to underpin all risk assessments, prevention, detection, surveillance and monitoring of Ponto-Caspian species with the highest quality science available. The project is divided into three interlinked sections, comprising a comprehensive review of alert Ponto-Caspian invaders, analysing the likely spatio-temporal patterns of introduction, and modelling the potential distribution of Ponto-Caspian invaders into England and Wales (Figure 1):

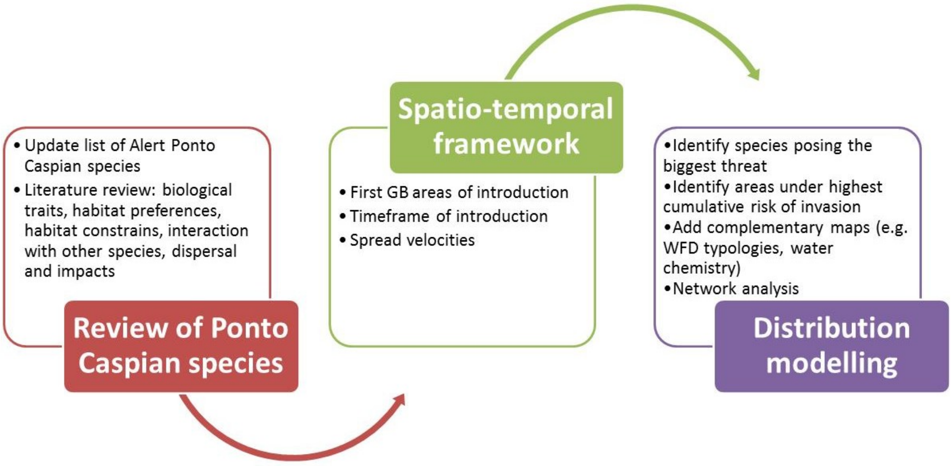

Figure 1 Objectives and approach to a Great Britain strategy for Ponto-Caspian freshwater invaders.

Specific questions that this project aims to answer include:

- Which Ponto-Caspian species pose the biggest threat?
- Why are they successful colonizing new environments?
- Where are Ponto-Caspian species most likely to appear for the first time?
- When are they likely to invade? How much time do we have to set up a strategy of prevention and management?
- Which areas match the current range of the species and are thus most vulnerable?
- How far potentially could alert Ponto-Caspian species spread?
- How are alert Ponto-Caspian species likely to affect the ecological status of water bodies assessed under the Water Framework Directive? Is the vulnerability different across WFD typologies?

Answering these fundamental questions will provide a scientific baseline to evaluate the risk associated to alert Ponto-Caspian species and elaborate an efficient strategy to prevent their introduction and uncontrolled spread.

2. METHODS

2.1. CONSOLIDATE A LIST OF ALERT PONTO-CASPIAN SPECIES

To define a strategy for Ponto-Caspian invasive species, we first need to identify which organisms pose the most realistic threat to British freshwaters. In 2013 a workshop gathered in Wallingford experts on biological invasions to horizon-scan future high-risk invasive species into Great Britain (Roy et al., in prep). The list of freshwater invaders included 16 Ponto-Caspian organisms. To this list we added seven species that were identified as potential threats to British freshwaters in previous reports (Gallardo and Aldridge 2012; Godard et al. 2012). Additional species included four crustaceans already recorded in Great Britain whose distribution is still limited but that have potential for further spread such as the Caspian mud shrimp (*C. curvispinum*), the bloody red mysid (*H. anomala*), the killer shrimp (*D. villosus*) and demon shrimp (*D. haemobaphes*). These organisms were included in our list because they are considered to have the potential for considerable increase in distribution and abundance across Great Britain. In addition, these species can serve as important controls to check the reliability of predictive tools developed upon this project. The final list of alert Ponto-Caspian invaders included 23 organisms (Table 1). The complete list of Ponto Caspian invasive species known to be spreading out of their native range, with mention of species currently present in Great Britain and the 23 species evaluated in this report can be consulted in Appendix A.

Table 1 Alert Ponto-Caspian species reviewed in this project.

Scientific came	English name	Order
Cercopagis pengoi	Fish hook waterflea	Cladocera
Chaetogammarus warpachowski		Amphipoda
Chelicorophium curvispinum*	Caspian mud shrimp	Amphipoda
Chelicorophium robustum		Amphipoda
Chelicorophium sowinskyi		Amphipoda
Dikerogammarus bispinosus		Amphipoda
Dikerogammarus haemobaphes*	Demon shrimp	Amphipoda
Dikerogammarus villosus*	Killer shrimp	Amphipoda
Dreissena r. bugensis	Quagga mussel	Veneroida
Echinogammarus ischnus		Amphipoda
Echinogammarus trichiatus		Amphipoda
Hemimysis anomala*	Bloody-red shrimp	Mysida
Hypania invalida **		Canalipalpata

Jaera istri		Isopoda
Limnomysis benedeni	Mysid shrimp	Mysida
Lithoglyphus naticoides	Gravel snail	Neotaenioglossa
Neogobius gymnotrachelus	Racer goby	Perciformes
Neogobius melanostomus	Round goby	Perciformes
Obesogammarus crassus		Amphipoda
Obesogammarus obesus		Amphipoda
Pontogammarus robustoides		Amphipoda
Proterorhinus marmoratus	Tubenose goby	Perciformes
Proterorhinus semilunaris	Freshwater tubenose goby	Perciformes

* species already recorded in Great Britain but showing a limited distribution.

2.1.1 EXPERT RANKING OF SPECIES

During the aforementioned workshop, experts scored in a 1-5 scale the probability of arrival, establishment and negative environmental impact of invasive species (Roy et al., in prep). Scores were multiplied to generate a total risk value ranging from 1 (very low invasion risk) to 125 (maximum invasion risk). Following similar guidelines, we calculated scores for the seven extra species not assessed during the workshop. Risk scores provide a preliminary rank of species according to the risk of invasion perceived by invasion biologists. Importantly, selection and ranking of the species was based on biodiversity impacts and not economic risk.

2.2 LITERATURE REVIEW

After defining the list of alert Ponto-Caspian species, we reviewed their biological characteristics, environmental preferences and impacts. To that end, a literature search was undertaken utilizing each species scientific name at the ISI Web of Knowledge. Additionally, Google Scholar was employed to locate additional scientific papers, articles from non-indexed journals (such as Aquatic Invasions) and grey literature (e.g. national reports, PhD dissertations).

Aspects of alert Ponto-Caspian species that were extracted from the literature included:

- Biological traits (e.g. life history, feeding habitats, phenotypic plasticity) that may explain the success of Ponto-Caspian invaders
- Habitat preference and environmental limits (if any are documented)
- Mechanisms and velocity of dispersal
- Interaction with other Ponto-Caspian species
- Ecological and economic impacts
- Year of first report in The Netherlands

Information compiled during this review is fundamental to support subsequent parts of the project such as defining the rate of spread of Ponto-Caspian species to develop network analyses, interpreting the output of distribution models and discussing the potential impact of species on the ecological status of British freshwaters.

2.3. SPATIO-TEMPORAL PATTERNS OF INTRODUCTION

Ponto-Caspian species are likely to arrive in Great Britain through the central and southern European corridors described by bij de Vaate et al. (2002). These corridors lead species from their native Ponto-Caspian range towards the Rhine River and coastal areas of The Netherlands, from where they are eventually transported to Great Britain accidentally in ballast water or as contaminants of ornamental plants, animals and aquatic equipment (e.g. attached to boats, fishing gear) (see the review of introduction pathways by Godard et al. 2012).

In this study we therefore assume The Netherlands is the most likely origin of Ponto-Caspian invasive species towards Great Britain, although they can also originate from other North Sea ports and coastal regions such as France and Belgium. The Netherlands is currently the European country that exchanges the greatest volume of trade with the UK, with the largely freshwater port of Rotterdam accounting for 7.6% of total tonnage loaded and unloaded at UK ports in 2008 (Talbot et al. 2009). Although the introduction of freshwater invaders into Great Britain depends largely on stochastic events, we also assume that the longer an invasive species is present in donor areas (The Netherlands in this case), the higher the probability that such random event occurs.

We analysed spatial and temporal patterns of freshwater invasion to calculate the probability of introduction of new invaders. Because the number of Ponto-Caspian invaders present in Great Britain is very limited (only 5 organisms), we extended the spatio-temporal analysis to all freshwater invasive species regardless of their native origin. Thus, location and dates of first observation of freshwater invasive species in Great Britain and The Netherlands were obtained from the literature (Agence de l'Eau Rhin Meuse 2005; Hill et al. 2005; Keller et al. 2009) and internet accessible databases (e.g. Great Britain-Non Native Species Secretariat). Because spatio-temporal patterns of introduction might change over time, we limited our analyses to those invasive species recorded after 1900.

2.3.1 FIRST AREAS OF ESTABLISHMENT

Locations of first invasion of 48 species (including species from all origins) were mapped in order to identify major hot-spots of introduction. The identification of the first invaded location was limited by the available information, often too vague to clearly identify the first water body infested. For instance, several species were reported from the Grand Union canal, with little information on the specific stretch of the ca. 140 miles canal where the species was first found. For this reason, we assigned species to the closest management catchment (see definition of management catchment under section 2.4.5). The year and location of first report for each freshwater invader considered can be consulted in Appendix B.

Certain spatial bias towards areas submitted to a high frequency of sampling can be assumed. For instance, a new invasive species in a water-body not routinely monitored by the Environment Agency might not be detected until it spreads towards other more intensively sampled areas.

2.3.2 TIMEFRAME OF INTRODUCTION

We further investigated the relationship between the date a species was first reported in The Netherlands and Great Britain, under the general assumption that the longer a species is present in The Netherlands, the greater the probability is that propagules are unintentionally introduced into Great Britain. We used information from 28 species (including freshwater species of any origin and excluding cases where the species was first spotted in Great Britain and only afterwards in The Netherlands) to calculate time lags (i.e. difference between years of first report) between both countries. Species finally included in the calculation and their time lags can be consulted in Appendix C.

Data collected in this study correspond to the first report in the wild of invasive species, which does not necessarily correspond to the place and time the species first established. Some species –and especially freshwater organisms that require expert identification—are reported long after they've been introduced, usually once they present large established populations. For instance, the abundance and coverage of the killer shrimp (*D. villosus*) in Grafham reservoir–presenting a wide range of body sizes including juveniles and adult females with eggs—suggest a well-established population (MacNeil et al. 2010a). Thus the introduction of the killer shrimp can be probably dated a few years before it was first detected in this reservoir. Something similar can be presumed about *D. haemobaphes*, although no studies on the population structure of this amphipod in Great Britain have been yet published. In this study we use the term 'time lag' to describe the difference between years of first report in Great Britain and The Netherlands, and not between the arrival and first detection of a species in any of the two countries.

Linear regression models were used to investigate the relationship between time lag (response variable) and the year the species was reported from The Netherlands (explanatory variable). The model was used to predict the likely timeframe of introduction of alert Ponto-Caspian species already present in The Netherlands, and tested against data from four species that are already located in Great Britain (*D. villosus*, *D. haemobaphes, H. invalida* and *H. anomala*). The Caspian mud shrimp (*C. curvispinum*) could not be used in this case as control because it was detected in Great Britain in 1935, earlier than in The Netherlands (1987). In this study we are interested in The Netherlands towards Great Britain direction only.

2.4 SPECIES DISTRIBUTION MODELLING

The establishment and spread of invasive species is likely to be affected by geographic patterns such as the match between the bioclimatic conditions of the native and invaded ranges, vectors and pathways of introduction (Gallardo and Aldridge 2013b). Species Distribution Models (SDM) are a statistical technique often used to locate areas at continental or regional scale which are environmentally most similar to the current range of an invasive species, and thus are most susceptible to successful colonisation in the event of an introduction (Guisan and Thuiller 2005). In this study we used SDM to locate areas in England and Wales that might be most vulnerable to the establishment of alert Ponto-Caspian species.

2.4.1 SPECIES OCCURRENCE GATHERING

Information on the current spatial distribution of invasive species was obtained from the Global Biodiversity Information Facility (GBIF, data.gbif.org), The Netherlands Biodiversity Information Facility (NLBIF, www.nlbif.nl) and the National Biodiversity Network (NBN, Gateway data.nbn.org.uk) Additionally, we used occurrence points gathered for the modelling of Ponto-Caspian invaders in previous studies (Gallardo and Aldridge 2012, 2013a, b; Gallardo et al. 2013). Other literature references used to complement the geographic distribution of Ponto-Caspian species not assessed in previous publications are listed in Table 2.

Table 2 References used to complete the known native and invasive distribution of 23 Ponto-Caspian species.

Reference
Arbačiauskas (2008) Amphipods of the Nemunas River and the Curonian Lagoon, the Baltic Sea Basin: Where and which Native Freshwater Amphipods Persist? *Acta Zoologica Lituanica*, **18**, 10-16.
Arbačiauskas, K. & Gumuliauskaitė, S. (2007) Invasion of the Baltic Sea basin by the Ponto-Caspian amphipod *Pontogammarus robustoides* and its ecological impact. *Biological invaders in inland waters: Profiles, distribution, and threats* (ed. by F. Gherardi), pp. 463-477. Springer Netherlands.
Arbaciauskas, K., Rakauskas, V. & Virbickas, T. (2010) Initial and long-term consequences of attempts to

improve fish-food resources in Lithuanian waters by introducing alien peracaridan species: a retrospective overview. *Journal of Applied Ichthyology*, **26**, 28-37.

Berezina, N.A. & Gubelit, Y.I. (2012) Changes in coastal ecosystem of the eastern Baltic Sea under eutrophication and climate variability. 2012 IEEE/OES Baltic International Symposium (BALTIC), 4 pp.

Boets, P., Holguin, G.J.E., Lock, K. & Goethals, P.L.M. (2012) Data-driven habitat analysis of the Ponto-Caspian amphipod Dikerogammarus villosus in two invaded regions in Europe. Ecological Informatics, in press

Bollache, L., Devin, S., Wattier, R., Chovet, M., Beisel, J.N., Moreteau, J.C. & Rigaud, T. (2004) Rapid range extension of the Ponto-Caspian amphipod Dikerogammarus villosus in France: potential consequences. Archiv Fur Hydrobiologie - Supplementbände, 160, 57-66

Borza, P., Czirok, A., Deak, C., Ficsor, M., Horvai, V., Horvath, Z., Juhasz, P., Kovacs, K., Szabo, T. & Vad, C.F. (2011) Invasive mysids (Crustacea: Malacostraca: Mysida) in Hungary: distributions and dispersal mechanisms. North-Western Journal of Zoology, 7, 222-228

Heiler, K., Brandt, S., Albrecht, C., Hauffe, T. & Wilke, T. (2012) A new approach for dating introduction events of the quagga mussel (Dreissena rostriformis bugensis). Biological Invasions, 14, 1311-1316

Zoric, K., Jakovcev-Todorovic, D., Djikanovic, V., Vasiljevic, B., Tomovic, J., Atanackovic, A., Simic, V. & Paunovic, M. (2011) Map distribution of the Ponto-Caspian polychaeta Hypania invalida (Grube, 1860) in inland waters of Serbia. *Aquatic Invasions,* **6,** 33-38.

Nesemann, H., Pockl, M. & Wittmann, K.J. (1995) Distribution of epigean malacostraca in the middle and upper Danube (Hungary, Austria, Germany). *Miscellanea Zoologica Hungarica,* **10,** 49-68.

Paunovic, M., Jakovcev-Todorovic, D., Simic, V., Stojanovic, B. & Cakic, P. (2007) Macroinvertebrates along the Serbian section of the Danube River (stream km 1429–925). *Biologia,* **62,** 214-221.

Wittmann, K.J. (2007) Continued massive invasion of Mysidae in the Rhine and Danube river systems, with first records of the order Mysidacea (Crustacea: Malacostraca: Peracarida) for Switzerland. *Revue Suisse De Zoologie,* **114,** 65-86.

Wozniczka, A., Gromisz, S. & Wolnomiejski, N. (2011) Hypania invalida (Grube, 1960), a polychaete species new for the southern Baltic estuarine area: the Szczecin Lagoon and the River Odra mouth. *Aquatic Invasions,* **6,** 39-46.

Wittmann, K.J. (2007) Continued massive invasion of Mysidae in the Rhine and Danube river systems, with first records of the order Mysidacea (Crustacea: Malacostraca: Peracarida) for Switzerland. *Revue Suisse De Zoologie,* **114,** 65-86.

Wozniczka, A., Gromisz, S. & Wolnomiejski, N. (2011) Hypania invalida (Grube, 1960), a polychaete species new for the southern Baltic estuarine area: the Szczecin Lagoon and the River Odra mouth. *Aquatic Invasions,* **6,** 39-46.

Once we obtained the most accurate distribution map for a species, the software ENMTools v1.3 (enmtools.blogspot.co.uk, Warren et al. 2010) was used to remove duplicate records. This procedure leaves only one occurrence point per pixel of 5 arcminutes, thereby avoiding redundancies that may bias output predictions.

2.4.2 SPATIAL PREDICTORS

Several environmental layers were used to calibrate the environmental preferences of alert Ponto-Caspian invaders. First, 19 bioclimatic variables were obtained from WorldClim-World Climate Database (www.worldclim.org) with a 5 arcminutes resolution. Afterwards, we checked the correlation of bioclimatic variables with ENMTools v1.3, and only 7 variables with a Pearson correlation r< 0.8 were selected for modelling to avoided Type I error (obtaining false significant relationships) (Figure 2):

- Annual Mean Temperature (˚C)
- Temperature Seasonality (standard deviation) (˚C)
- Maximum Temperature of the warmest month (˚C)
- Minimum Temperature of the coldest month (˚C)
- Annual Precipitation (mm)
- Precipitation of the driest month (mm)
- Precipitation seasonality (coefficient of variation) (mm)

In addition, we obtained altitude from WorldClim. Slope and roughness were calculated from altitude using ArcView. However, because the three variables were highly correlated (Pearson r> 0.8) we only used altitude for modelling. Altitude may be especially relevant for freshwater species generally associated to lowland areas.

Data on onshore geological units was obtained from the Commission for the Geological Map of the world (CCGM-CGMW, Paris 2010, http://ccgm.free.fr/) and included seven bedrock geologies: endogenous plutonic or metamorphic rocks, extrusive volcanic rocks, island, lake, ophiolitic complex, sedimentary rocks and undifferentiated facies. The geological map – initially in the form of a shapefile -was converted into a raster with the same resolution (5 arcminutes) and projection (WGS1984) as bioclimate layers. A project attempting to establish a European geochemical baseline (weppi.gtk.fi/publ/foregsatlas/index.php) found a direct relationship between bedrock geology and relevant water, sediment and soil characteristics for the study of invasive species (Salminen et al. 2005). For instance, low calcium concentration and alkalinity in European waters, relevant for molluscs and crustaceans, were significantly related to acid igneous and metamorphic rocks (e.g. granite and sandstone), while sedimentary rocks (e.g. limestone and dolomite) supply most of the calcium in stream waters (Salminen et al. 2005).

In addition to environmental factors, in this project we introduced a number of socio-economic factors as potential large-scale predictors of the distribution of species. This is based on the assumption that drivers controlling the global scale distribution of invasive species differ from native species, because their transport and introduction are more dependent on human activities. Furthermore, socio-economic factors can be related not only to propagule pressure, but also to the vulnerability of ecosystems to invasion, since invasive species often benefit from weakened, disturbed native ecosystems (Gallardo and Aldridge 2013a). We therefore expect socio-economic factors to promote the suitability of large geographic areas to the establishment of alert Ponto-Caspian invaders. A total of five socio-economic factors were considered for modelling (Figure 2):

- Global Human Influence Index (HII, Socio-Economic Data and Applications Centre, sedac.ciesin.columbia.edu). This map is produced through the overlay of a number of global data layers that represent various factors presumed to exert an influence on ecosystems: human population distribution, urban areas, roads, navigable rivers, and various agricultural land uses. The combined influence of these factors yields HII, which ranges from 0 (conditions close to pristine) to 64 (most heavily influenced systems).

- Land use was obtained from IGBP- International Geosphere-Biosphere Programme (MODIS Global Land Cover Classification v2, www.modis.bu.edu/landcover) and included nine categories: forest, shrubland, savannah, grassland, wetland, cropland/natural vegetation, urban, snow/ ice and barren/sparsely vegetated.

- Density of human population (Oak Ridge National Laboratory, www.ornl.gov/sci/landscan).

- Distance (in km) from the closest commercial port. A list of ports with > 30 megatons total cargo volume in 2009 was obtained from the American Association of Port Authorities (www.aapa-ports.org, last accessed 10th March 2012). The euclidean distance to the closest port was then calculated using ArcGIS 10.0 ©ESRI.

- Distance (in km) from the closest road. A global map of transportation was obtained from ESRI (www.esri.com/). The Euclidean distance to the closest primary road was calculated using ArcGIS 10.0 ©ESRI.

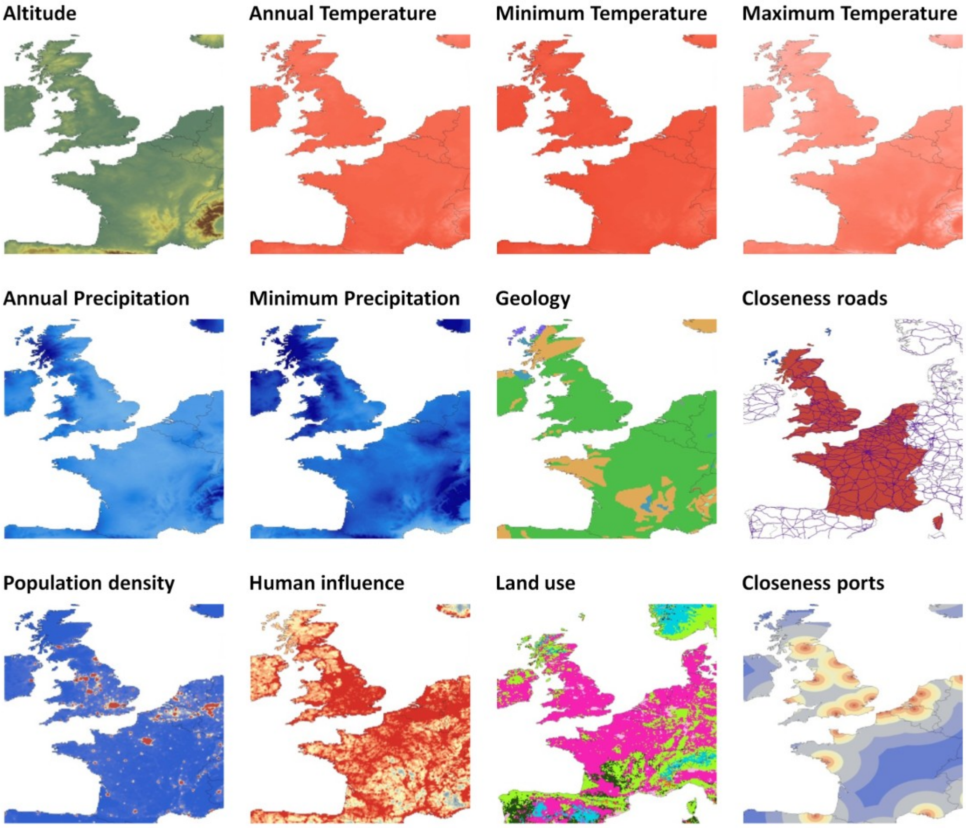

Figure 2 Environmental and socio-economic maps used to model the potential distribution of alert Ponto-Caspian species in England and Wales. Please note that global maps were employed for modelling, whereas only Great Britain and neighbouring countries are shown here for clarity.

2.4.4 SPECIES DISTRIBUTION MODELLING APPROACH

MaxEnt version v3.3k (www.cs.princeton.edu/~schapire/maxent) was used to measure the spatial suitability for Ponto-Caspian species, by projecting a model of the known species distribution into the region of interest (Guisan and Thuiller 2005). For input, MaxEnt models use the dataset of species occurrences and the set of environmental and socio-economic predictors that might affect the likelihood of species establishment. To test the accuracy of predictions, occurrence data were split into two sets: 70% of the data was used for modelling and the remaining 30% for testing the model. Because no absence data was available, a total of 10,000 random background points were generated from the study area. To assess model performance, the Area Under the Receiving Operating Characteristic (ROC) Curve (AUC) (Hanley and McNeil 1982) was used, which represents the probability that a random occurrence locality is classified as more suitable than a random pseudo-absence. A model that performs no better than random has an AUC of 0.5, whereas a model with perfect discrimination scores 1.

Regularisation reduces the likelihood of overfitting models, thus increasing the ability of models beyond the training region (Elith et al. 2010). For this reason, it is often recommended increasing the regularisation when evaluating the potential distribution of invasive species (MaxEnt tutorial available at www.cs.princeton.edu). Yet, no clear guidelines on the appropriate degree of regularisation exist. In this study, we tested a regularisation modifier of 1, 2, 3 and 4 and selected the best model minimising the size-corrected Akaike Information Criterium (AIC_c) calculated using ENMTools v1.3.

After calibration, models were projected onto England and Wales to obtain suitability maps, ranging from 0= conditions completely different to those of the current range of the species, to 100%= complete match with the current range of the species. While calibration layers were used at a 5 arcminutes resolution, we used a set of higher resolution layers (30 arcseconds) covering England and Wales for projection.

The threshold maximising the sensitivity (i.e. number of presences correctly predicted) and specificity (i.e. number of background points correctly predicted) of the model was used to transform suitability maps into a presence/absence maps (Liu et al. 2005). This threshold tends to favour sensitivity (true presences) over specificity (true absences), which is preferable in the case on invasive species, and has been consistently found to produce the most accurate predictions (Barbet-Massin et al. 2012). Thresholded maps provided a simple absence/presence prediction for each species allowing identification of broad geographic regions whose environmental conditions may facilitate the successful establishment of an invasive species.

Finally, all maps were combined together into a single 'heat map' reflecting the cumulative risk of invasion in England and Wales for all evaluated species together. Spatial statistics by country (i.e. England and Wales) and management catchments (as defined by the Environment Agency, see section 2.4.5) were calculated to identify major hot-spots of vulnerability in the study area.

A previous project identified an alkalinity threshold of 120 mg/L as likely favouring the establishment of Ponto-Caspian invaders. For this reason, we overlaid an alkalinity map onto our cumulative heat map to investigate whether water chemistry could be a barrier for Ponto-Caspian invaders. The map was extracted from Gallardo and Aldridge (2013b) and consisted on a interpolation of alkalinity values across Great Britain.

2.4.5 RISK OF INVASION BY WATER FRAMEWORK DIRECTIVE TYPOLOGIES

The Water Framework Directive (WFD, Directive 2000/60/EC of the European Parliament) commits European Union member states to achieve good qualitative and quantitative status of all water bodies by 2015. The WFD became part of UK law in December 2003.

One important aspect of the WFD is the introduction of River Basin Districts (RBD). These areas have been designated, not according to administrative or political boundaries, but rather according to the river basin (the spatial catchment area of the river) as a natural geographical and hydrological unit. In this report, RBD are used to describe major areas under risk of invasion in England and Wales. Within RBD, management catchments are a geographic division delineated by the Environment Agency by using river water body catchments as 'building blocks' that were aggregated together to form larger catchments of similar size, practical for management purposes. Management catchments provide a local scale spatial unit useful to provide a more detailed identification of areas under risk of invasion.

As part of the characterisation process for typing waters in each RBD, the WFD required undertaking an analysis of its characteristics according to common technical specifications. This resulted in the classification of British rivers and lakes into homogeneous categories sharing morphological and chemical characteristics (Table 3).

Table 3 River typologies established for the implementation of the Water Framework Directive and their main characteristics in Great Britain. Data extracted from UKTAG document "*Type Specific Reference Condition Descriptions for Rivers in Great Britain*" (http://www.wfduk.org).

Type	Description	Type	Description
Type 1	Small catchment area (10-100km^2), low mean catchment altitude (<200m), with a predominantly siliceous geology	**Type 10**	Small catchment area (10-100km^2), medium mean catchment altitude (200-800m), predominantly siliceous geology
Type 2	Small catchment area (10-100km^2), low mean catchment altitude (<200m), with a predominantly calcareous geology	**Type 11**	Small catchment area, (10-100 km^2), medium mean catchment altitude (200-800m), predominantly calcareous geology
Type 3	Small catchment area (10-100km^2), low mean catchment altitude (<200m), with predominantly organic surface deposits	**Type 12**	Small catchment area (10-100km^2), medium mean catchment altitude (200-800m) predominantly organic surface geology
Type 4	Medium sized catchment area (100-1000 km^2), low mean catchment altitude (<200m), with a predominantly siliceous geology	**Type 13**	Medium sized catchment area (100-1000km^2), medium mean catchment altitude (200-800m), predominantly siliceous geology
Type 5	Medium size catchment area (100-1000 km^2), low mean catchment altitude (<200m), with a predominantly calcareous geology	**Type 14**	Medium sized catchment area (100-1000 km^2), medium mean catchment altitude (200-800m), predominantly calcareous geology
Type 6	Medium size catchment area (100-1000 km^2), low mean catchment altitude (<200m), with a predominantly organic surface geology	**Type 15**	Medium sized catchment area (100-1000km^2), medium mean catchment altitude (200-800m), predominantly organic surface geology
Type 7	Large catchment area (>1000 km^2), low mean catchment altitude (<200m), with a predominantly siliceous geology	**Type 16**	Large catchment area (>1000km^2), medium mean catchment altitude (200-800m), predominantly siliceous geology
Type 8	Large catchment area (>1000 km^2), low mean catchment altitude (<200m), predominantly calcareous geology	**Type 17**	Large catchment area (>1000 km^2), medium mean catchment altitude (200-800m), predominantly calcareous geology
Type 9	Large catchment area (>1000 km^2), low mean catchment altitude (<200m), predominantly organic surface geology	**Type 18**	Medium sized catchment area (100-1000km^2), high mean catchment altitude (>800m), predominantly siliceous geology

The dominant typology in England and Wales is Type 2 (i.e. small catchment size, low altitude, calcareous), which represents 34% of river waters (Figure 3).

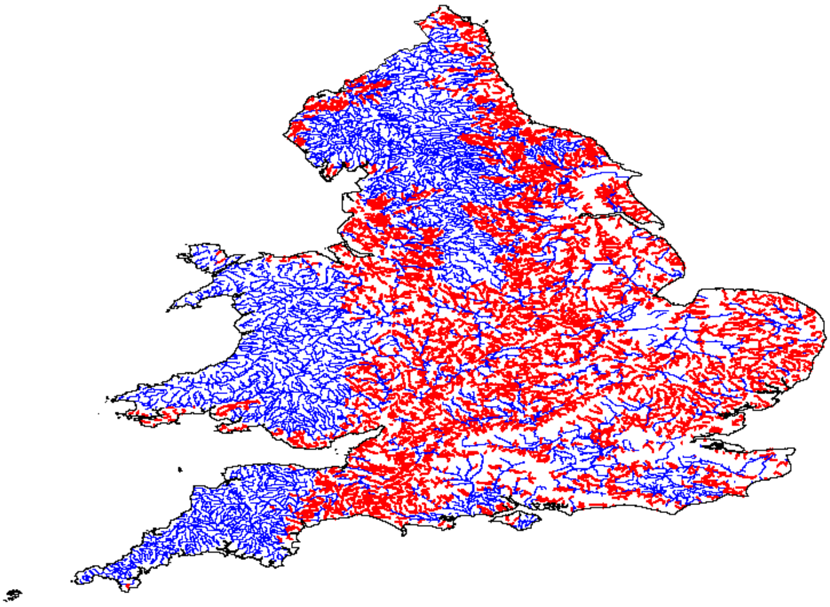

Figure 3 Type 2 rivers (in red) are the most frequent in England representing more than 30% of the typed river length.

Lake typology was based on altitude, latitude, longitude, depth, geology and size. Of these divisions catchment geology and lake depth are believed to be the most important in explaining the natural variation of ecological conditions in lakes. Catchment geology influences background fertility and a simple division between very shallow and deeper lakes divides them into those where underwater plants (macrophytes) and those where algae (phytoplankton) dominate the lake.

Ultimately, the WFD aims for 'good status' for all ground and surface waters (rivers, lakes, transitional waters, and coastal waters) in the European Union. The structure and diversity of aquatic community assemblages (fish, macroinvertebrates, and aquatic flora) is used to evaluate the ecological status of lakes and rivers. More specifically, the ecological status of a given water body is determined according to its closeness with the reference conditions corresponding to its specific typology.

To identify WFD typologies under highest risk of invasion, we summarized information regarding the size, altitude and dominant geology of catchments colonized by the species in mainland Europe. In addition, we calculated risk statistics (i.e. SDM-based cumulative risk scores) for water body types identified as suitable for invasion.

2.4.5 NETWORK ANALYSIS

After identifying water bodies under the highest risk of invasion, the potential area of influence of invasive species within each high-risk catchment was calculated. To that end we applied the Network Analyst, a GIS application normally used in traffic design to calculate the service area of facilities such as gas stations, pharmacies or fire houses. An example of a service area analysis is provided in Figure 4, where areas at a 10/20/30 minute driving distance from major stores have been delineated.

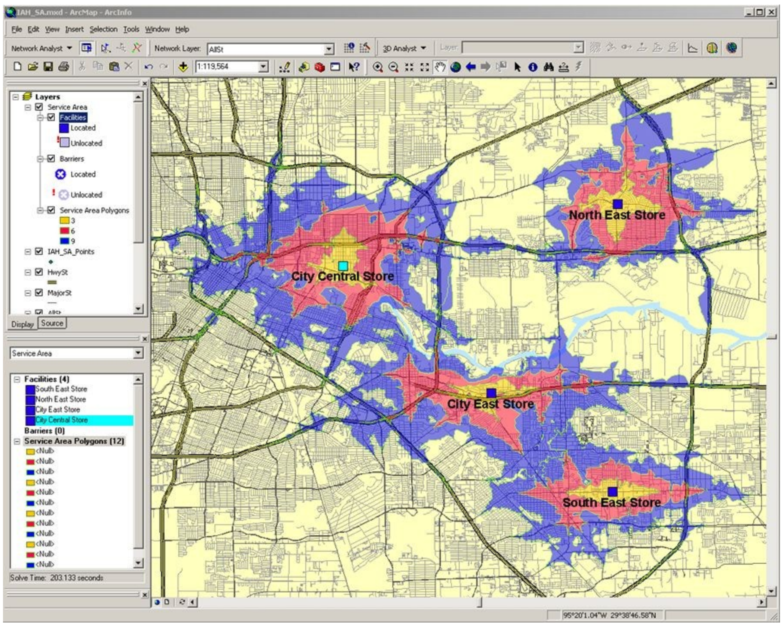

Figure 4 Example of service area calculated using ArcGIS. Colour areas around stores delineate the area that can be reached driving from the store in 10, 20 and 30 minutes respectively.

Following a similar methodology, we used the hydrological network as the main transport route and water bodies with highest cumulative risk (identified through SDM) as locations of interest. The "service area" in this case would identify major influence zones in the catchment that would be under a high risk of invasion through natural secondary spread. The area under risk would actually depend on multiple natural (e.g. river flow, barriers to dispersal, availability of habitat, presence of predators, population density and reproductive stage) and artificial (e.g. recreational activities such as boating and fishing, direct connecting routes between places) factors. However, this service area concept may help identify hot-spots on introduction with wider zones of influence. The Network Analyst has been successfully used before to investigate the potential spread of the killer shrimp (*D. villosus*) in Great Britain (Gallardo et al. 2012) and Belgium (Boets et al. 2013)

Catchment boundaries and the hydrological network were downloaded from the Environment Agency's Geostore (http://www.geostore.com/environment-agency/, last accessed 23 May 2013). We afterwards created a network dataset using the Network Analyst extension of ArcView v10.1 (©ESRI, Redwoods California). This is therefore a simplification of the natural conditions of the hydrological network, considering that the flow is homogeneous and no influence of roughness, barriers to flow or water quality. Rivers and lakes identified as being most vulnerable for Ponto-Caspian invasion in our SDM were selected as potential first areas of introduction. A number of points at regular distances of 5-10 km were located within high risk river stretches, while a single point was located in the centre of high risk lakes. Network analyst was used to create a series of polygons that represent the distance that can be reached from any given introduction point, particularly 10, 20, 30, 40 and 50 km. These are known as "service area polygons".

Spread velocities were obtained from the literature for different alert Ponto-Caspian invaders and used together with service area maps to investigate their potential for secondary spread. Spread rates are often calculated by simply looking in a map at the locations where the species has been identified in consecutive years (e.g. Leuven et al. 2009). Such velocities can be misleading for several reasons. First, unless exhaustive samplings are performed each year along a water course, it is often difficult to know the year of appearance of a species. Also, human-assisted transport often results in very high spread velocities that do not really correspond to the species natural ability to disperse. This explains the extraordinary spread velocities found in the literature for Ponto-Caspian species such as the quagga mussel (*D. r. bugensis*), for which Matthews et al. (2013) reported upstream velocities of 120 km/year, even though bivalves are believed to naturally spread at velocities no higher than 0.1 km/year (Kappes and Haase 2011). A 1000-fold increased velocity can only be explained by the use of anthropogenic vectors, with specimens most probably attached to the hull of boats navigating the Rhine. In this study, we compiled information on spread rates from mainland Europe to discuss the potential for secondary spread of alert Ponto-Caspian species in Great Britain.

3. RESULTS

3.1 REVIEW OF PONTO-CASPIAN SPECIES

Ponto-Caspian species are receiving increasing attention by the scientific community, and this is reflected in a growing number of publications on the topic (Figure 5). Such proliferation of references on Ponto-Caspian species mirrors the intensification in their spread and impact in the last decades both in Europe and North America.

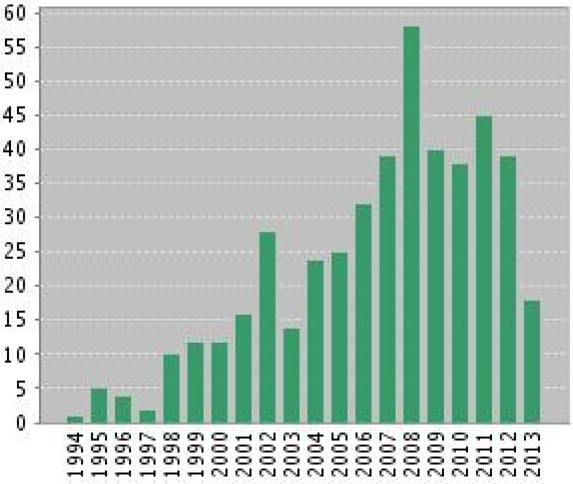

Figure 5 Evolution in the number of scientific publications about Ponto-Caspian invaders. Data obtained from the simple search "Ponto-Caspian species" at the Isi Web of Knowledge, which yielded 499 scientific papers. Note the smaller bar for 2013 reflects data that were published during an incomplete year. Date of search: May 2013.

Information regarding the life history, dispersal, interaction and impacts of alert Ponto-Caspian species was retrieved from c. 260 publications and summarized in Appendix D. This Appendix is intended to offer a compilation of information regarding Ponto Caspian invaders but it does not purport to be a comprehensive review. Much of the information regarding Ponto Caspian invaders is included in grey literature and publications in foreign (e.g. Russian) languages, therefore difficult to access.

Notable gaps in the information available for Ponto-Caspian species were detected, overall regarding the basic biology and ecology of the species (e.g. reproduction, feeding), which are directly related with their impact. As way of example, over 40 studies have approached the feeding behaviour of the killer shrimp (*D. villosus*), while no information exists at all on other amphipods such as *C. sowinskyi* or *D. bispinosus*.

3.1.1 EXPERT RANKING OF SPECIES

During a workshop in 2013 British experts scored the risk of arrival, establishment and impact of 16 Ponto-Caspian invaders. Using information gathered during the literature assessment (Appendix D), we scored the extra seven species evaluated in this project (Table 4).

Species were ranked and categorized into High, Moderate and Low risk (Table 4). Organisms in the first 25% of data (i.e. total score > 90, highest risk) included Ponto-Caspian species already present in Great Britain such as

D. villosus and *C. curvispinum*, and additionally highlighted the risk associated to the quagga mussel (*D. r. bugensis*), round goby (*N. melanostomus*), and freshwater tubenose goby (*P. semilunaris*) (Table 4). The bottommost 25% of the ranked list (total score <45, lowest risk) included gammarids such as *O. obesus* and *C. warpachowski*, the gravel snail (*L. naticoides*), the cladoceran *C. pengoi* and the isopod *J. istri*.

Table 4 Risk scores for Ponto-Caspian species posing a threat to British freshwaters. Scores range from 1-very unlikely to 5-very likely. Shaded in red, species in the first quartile of risk (with scores > 90). In green, species situated in the lower risk quartile (<45) with orange assigned to species with intermediate risk scores.

Scientific came	Arrival	Establishment	Impact	AxBxC
Dreissena r. bugensis	5	5	5	125
Chelicorophium curvispinum	5	5	4	100
Dikerogammarus villosus	5	5	4	100
Neogobius melanostomus	4	5	5	100
Proterorhinus semilunaris	4	5	5	100
Proterorhinus marmoratus	4	4	5	80
Neogobius gymnotrachelus	4	5	4	80
Dikerogammarus haemobaphes	5	5	3	75
Echinogammarus ischnus	5	5	3	75
Echinogammarus trichiatus	5	5	3	75
Hemimysis anomala	5	5	3	75
Dikerogammarus bispinosus	4	5	3	60
Limnomysis benedeni	4	5	3	60
Obesogammarus crassus	4	5	3	60
Pontogammarus robustoides	4	5	3	60
Hypania invalida	4	4	3	48
Chelicorophium robustum	3	5	3	45

Chelicorophium sowinskyi	3	5	3	45
Jaera istri	4	5	2	40
Chaetogammarus warpachowski	3	4	3	36
Obesogammarus obesus	3	4	3	36
Lithoglyphus naticoides	4	4	2	32
Cercopagis pengoi	3	4	2	24

3.2 SPATIO-TEMPORAL PATTERNS OF INTRODUCTION

3.2.1 FIRST AREAS OF ESTABLISHMENT

We obtained the location of first report in the wild of 48 freshwater invasive species, resulting in the density map presented in Figure 6. Information on the species identity, origin, year and location of first report can be consulted in Appendix B.

38.5% of invasive freshwater species were reported for the first time from the Thames RBD, mostly in the London, Wey, Loddon and Medway management catchments. The second RBD in number of first records is the Anglian (21.1%) including the Nene and Ouse catchments, and the Broadland Rivers. The Humber RBD also recorded a high number of first introductions (17.3%), concentrated along the River Trent.

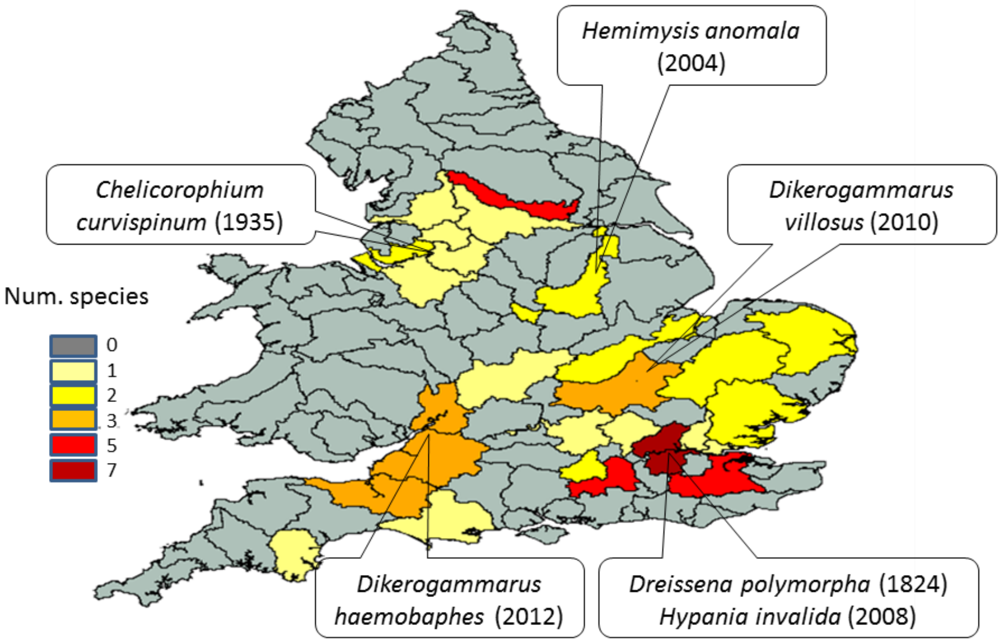

Figure 6 Number of freshwater invasive species reported by management catchment. Data correspond to species introduced into Great Britain after 1900s. The date and location of Ponto-Caspian invaders is highlighted with call bubbles.

3.2.2 TIMEFRAME OF INTRODUCTION

Upon analysis of introduction dates, a change in spatio-temporal invasion patterns between The Netherlands and Great Britain emerged. The time lag between a given species report in The Netherlands and Great Britain has notably decreased over the last century (Figure 7A). Before 1950s invasive freshwater species took on average 13 years to cross the channel, whereas after 1950s this time was reduced to only 9 years. More information on the species considered in the analysis and their reported dates in Great Britain and The Netherlands can be obtained in Appendix C.

By taxonomic groups, the time lag of first discovery between The Netherlands and Great Britain is less than 10 years for crustaceans and molluscs. Time lags for fish are slightly more prolonged, and even longer for aquatic plants (Figure 7B).

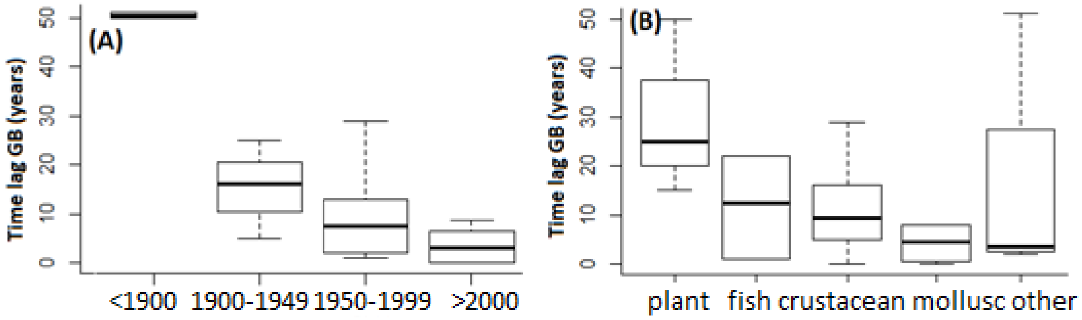

Figure 7 Time lags between a species report in the Netherlands and Great Britain by (A) main time period, and (B) main group of organisms (including data from all years). N=28. More information can be obtained from Appendix C.

A linear regression model was fitted to model the relationship between reporting dates in both countries. Ponto-Caspian species recently introduced to Great Britain such as *H. anomala, H. invalida, D. villosus* and *D. haemobaphes* were not included in this model, but used as controls to test its accuracy. The model was highly significant and able to explain 70% of the variance in the response variable (time lag between report dates) (Figure 8). The model showed a negative linear relationship, illustrating the tendency towards shorter time lags already detected in Figure 7A.

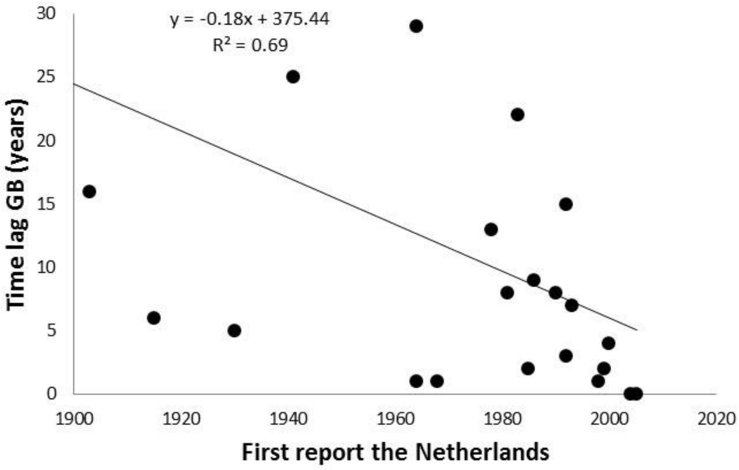

Figure 8 Modelled relationship between the year of report in The Netherlands and Great Britain. The model equation and R^2 are showed within the figure. $F_{1,\,22}$=51.7, *P*<0.001.

The model equation was used to predict the likely year of introduction in Great Britain of freshwater invasive species already reported in The Netherlands. Predicted timeframes of introduction shown in Table 5 include their 95% confidence interval, which means that there are 95% probabilities that the species will be reported in Great Britain within any particular range of dates.

Table 5. Predicted dates of introduction ± standard error of alert Ponto-Caspian invasive species already reported in The Netherlands. 95% confidence intervals around the mean value are also provided. “Year reported GB” corresponds to the real year in which four of the species were reported in Great Britain.

	Year Netherlands	Predicted year GB	95% Confidence Interval	Year reported GB
E. ischnus	1991	1998.7±3.0	1993-2006	
D. villosus	1994	2001.1±3.1	1995-2008	2010
H. invalida	1995	2002±3.1	1996-2009	2008
J. istri	1997	2003.5±3.1	1998-2011	
H. anomala	1997	2003.5±3.1	1998-2011	2004
L. benedeni	1998	2004.4±3.1	1998-2011	
D. bispinosus	1998	2004.4±3.1	1998-2011	
D. haemobaphes	2000	2006±3.2	2000-2013	2012
E. trichiatus	2001	2007±3.2	2001-2014	
P. marmoratus	2002	2007.6±3.2	2002-2015	
C. robustum	2003	2008.4±3.2	2008-2016	
N. melanostomus	2004	2009.3±3.2	2004-2016	
D. bugensis	2006	2011±3.2	2006-2018	

P. semilunaris	2008	2013±3.3	2008-2020

Dates of first report of species already located in Great Britain were used to test the robustness of the model. While the introduction of *H. anomala, H. invalida* and *D. haemobaphes* agreed with our model, predictions regarding *D. villosus* failed by two years. Furthermore, our model suggests that there is 95% possibility that another four Ponto-Caspian species (*E. ischnus, J. istri, L. benedeni* and *D. bispinosus*) are already located in Great Britain, despite not having been reported yet. Special attention should be paid to the quagga mussel, since time lags for mussels seem to be substantially shorter than for other types of species (Figure 7B) and our regression model predicts its likelihood of introduction to be very high since 2011 (Table 5).

3.3 SPECIES DISTRIBUTION MODELLING

The accuracy of models ranged from 0.97 to 0.99 AUC, which can be considered a very high quality. A summary of modelling outputs, including accuracy, the contribution of each predictor to the model and variable permutation importance can be consulted in Appendix E.

Environmental variables were able to explain on average 60% of Ponto-Caspian species' current geographic distribution. The contribution of socio-economic factors, nearly 40%, was remarkable (Appendix E).

Among environmental variables, minimum precipitation of the driest month was an important driver for the distribution of all species investigated, which might be related to the availability of habitats during the dry season. Graphics shown in Figure 9 correspond to *P. robustoides* and are representative of the response of all Ponto-Caspian species. The suitability for Ponto-Caspian species peaked at a minimum precipitation of the driest month of 0-50 mm (Figure 9a). Besides precipitation, minimum temperature of the coldest month was relevant to explain the species' European distribution, showing in this case a peak between -5 and 0 minimum temperatures (Figure 9b). Apart from climatic conditions, altitude was also an important driver, since all investigated species are characteristic of lowland areas (Figure 9c).

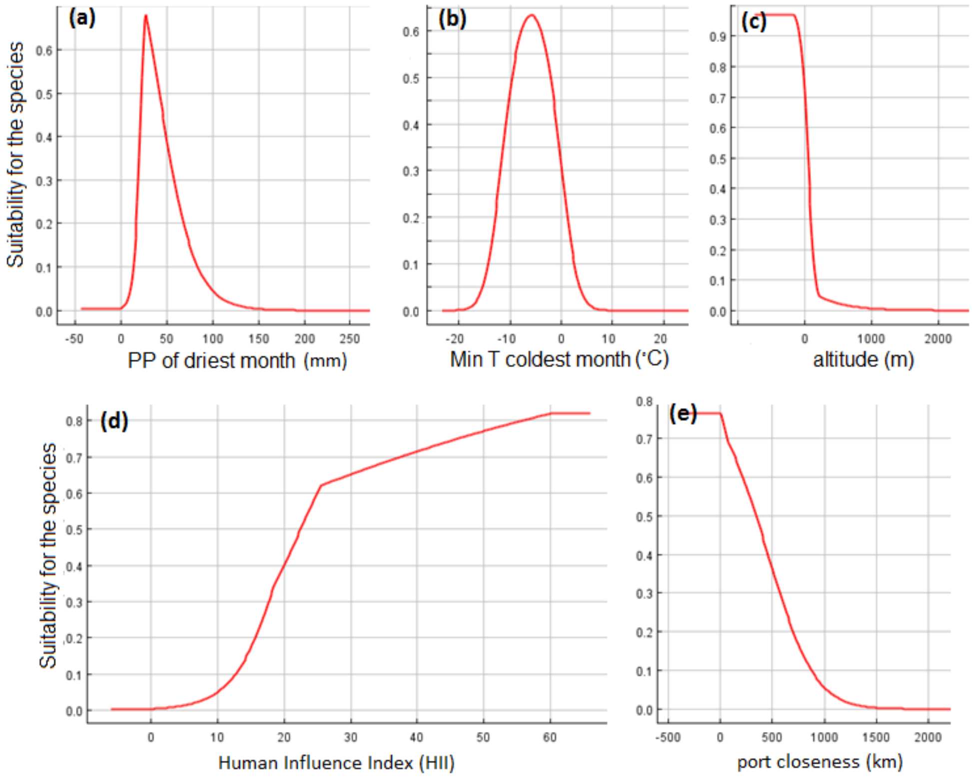

Figure 9 Response of alert Ponto-Caspian species to the most important drivers of their current distribution according to Species Distribution Models (SDM). Suitability higher than 50% indicates a high probability of successful introduction of the species. Graphs correspond to *P. robustoides* taken as a representative example. PP= precipitation; Min T= minimum temperature.

Interestingly, models revealed the human influence index (HII) as one of the most important drivers of alert Ponto-Caspian species distribution. HII combines the influence of several human activities directly and indirectly related to the transport and spread of invasive species such as closeness to transport routes, population density or land-use change. HII alone explained more than 25% of the distribution of *C. curvispinum, C. sowinskyi, D. haemobaphes, D. villosus* and *O. obesus* (Appendix E). Moreover, all species showed a strikingly similar response to HII (Figure 9d): suitability was extremely low at low HII levels (<10 HII), which are supposed to represent pristine areas with low population density and far from transport routes. A level of 10 HII triggered an exponential increase in invasion risk that reached 50% around 25 HII for all species. Suitability plateaus between 30 and 50 HII, with no notable increase in species suitability and even slight decreases at HII> 50. This may indicate certain saturation for species suitability, or even the fact that ecosystems that are too transformed by human activities are not able to host any species at all. A map of HII levels can aid the identification of major areas in England and Wales prone to invasion (Figure 10). We can assume this map represents propagule pressure, since the probability of species introduction is directly related to activities accounted for by HII.

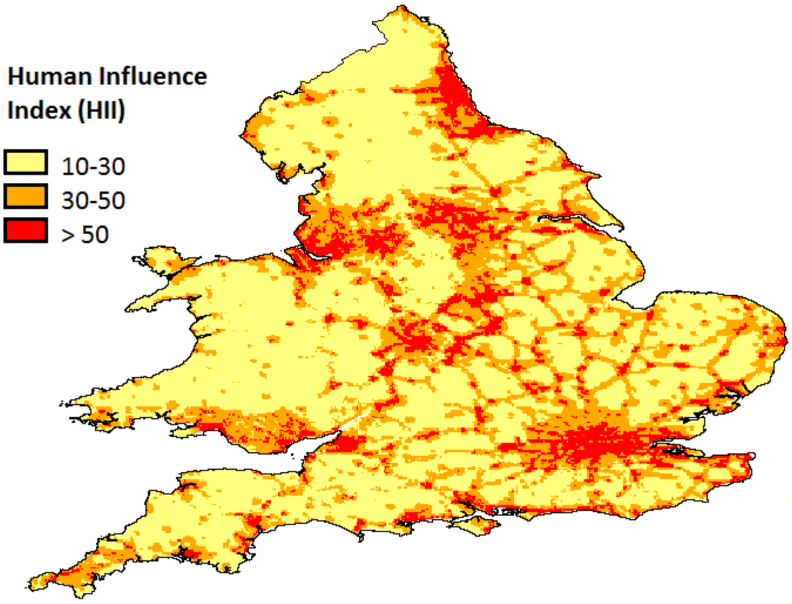

Figure 10 Human Influence Index (HII) across England and Wales. According to Species Distribution Models (SDM), the suitability for Ponto-Caspian invasive species is lowest under HII<30, and highest at HII between 30 and 50. HII is unit-less and ranges from 0-pristine conditions, to 64-most influenced by human activities. HII was obtained from the Socio-Economic Data and Applications Centre (sedac.ciesin.columbia.edu)

The influence of other *a priori* relevant indicators, such as port closeness or population density was lower than expected, quite likely because the HII already accounts for these factors. In the case of port closeness, we can see that species suitability is highest closest to ports and sharply declines as we move farther apart (Ffigure 9e).

Suitability scores for alert Ponto-Caspian invaders were generally highest towards the SE of England. The only species showing relatively low suitability scores across Great Britain were *C. pengoi, E. ischnus, C. warpachowski, C. sowinskyi* and *O. crassus*. More information on the predicted distribution of each Ponto-Caspian species can be found in Appendix F.

3.3.1 ALERT PONTO-CASPIAN SPECIES HEAT MAP

The 23 individual species maps were converted into simpler presence/absence maps using species-specific suitability thresholds (see Section 2.4.4 for more information). Maps were subsequently combined to generate a ‘heat map’ that reflects spatially the cumulative total number of species predicted present (Figure 11). The heat map highlighted the lower reaches of the Great Ouse, Broadland, Thames and Severn rivers as the most prone to invasion, with up to 20 alert Ponto-Caspian species predicted to be or become present (Figs. 11 and 12). Most of England was under threat of multiple invasions while the risk in Wales was considerably lower and limited to a strip along the south coast.

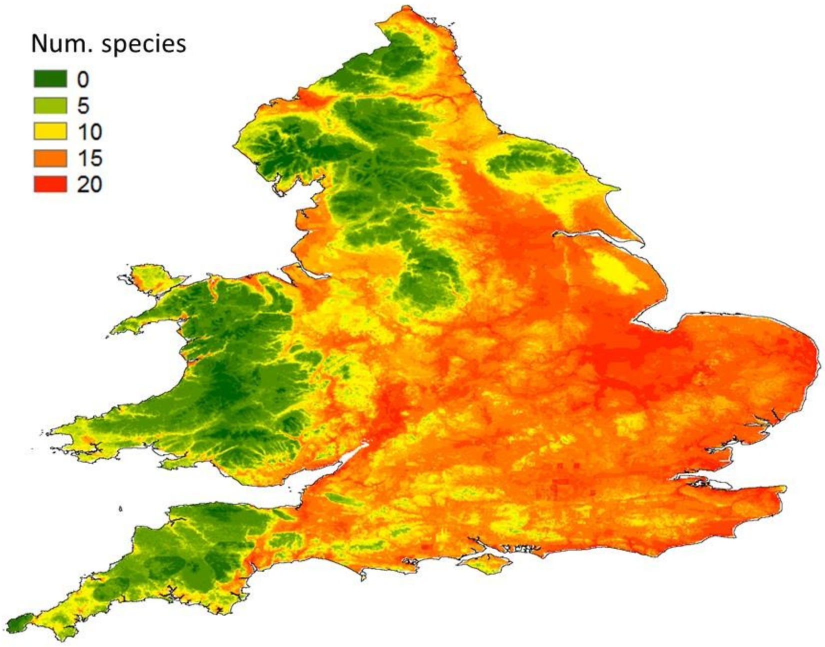

Figure 11 Heat map showing the cumulative probability of presence of 23 alert Ponto-Caspian species. The estuaries and lower reaches of the Thames, Great Ouse, Broadland and Severn rivers are prone to the invasion of up to 20 different invasive Ponto-Caspian species and for this reason are considered potential hot-spots of invasion.

Figure 12 identifies management catchments with highest cumulative risk of Ponto-Caspian species. This representation coincides to a great extent to management catchments illustrating the highest number of freshwater invasive species' first records (Figure 6), thereby emphasizing the ability of SDM to locate areas at national scale most vulnerable to invasion.

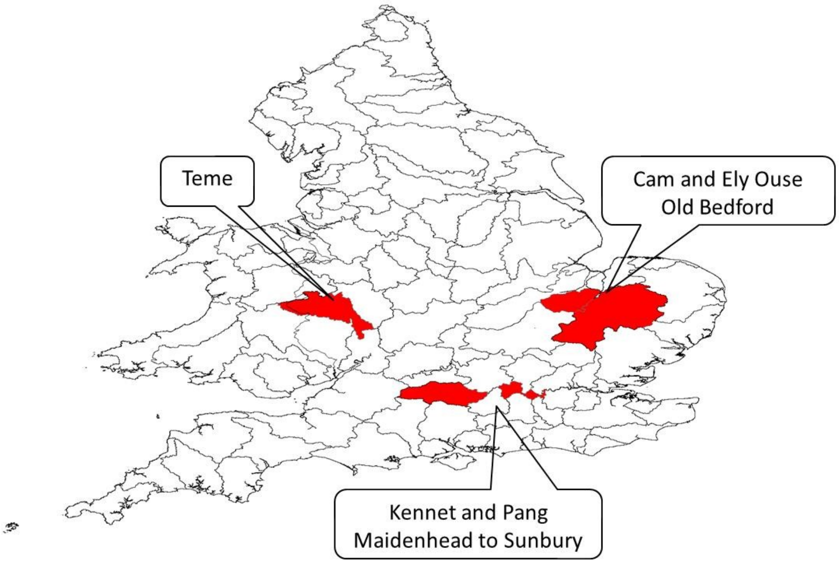

Figure 12 Management catchments showing the highest number of Ponto-Caspian species predicted present.

Surface water alkalinity of the risk area is > 120 mg/L (Figure 13) and therefore poses no physic-chemical barrier to the establishment of Ponto-Caspian freshwater invasive species.

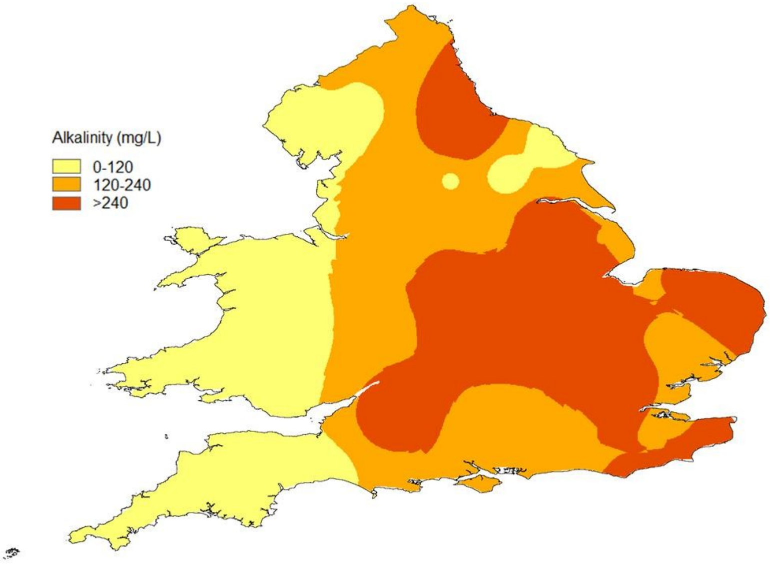

Figure 13 Alkalinity of surface water in England and Wales. Values > 120 mg/L are favorable for the establishment of Ponto-Caspian invaders. Extracted from Gallardo and Aldridge (2012)

3.3.2 POTENTIAL IMPACT OF PONTO-CASPIAN SPECIES ON THE WATER FRAMEWORK DIRECTIVE

According to the WFD, river water bodies are divided into a number of typologies depending on catchment size, mean altitude of the catchment and dominant geology (Table 3). To identify British river types most susceptible to the colonization of Ponto-Caspian invaders, we summarized information from sites colonized in mainland Europe (Table 6).

Table 6 Characteristics of catchments invaded by alert Ponto-Caspian species in Europe.

	Catchment Size (km^2)	Catchment Altitude (m)	Dominant geology
C. curvispinum	153.8±222.7	57.6±92.9	Calcareous
C. pengoi	77.2±117.6	59.3±48.9	Calcareous
C. robustum	107.4±168.5	82.4±109.6	Calcareous
C. sowinskyi	79.1±165.0	135.9±103.7	Calcareous
C. warpachowski	102.4±193.4	45.8±62.7	Calcareous
D. bispinosus	112.4±159.5	98.2±92.0	Calcareous
D. haemobaphes	60.6±134.5	128.6±123.2	Calcareous
D. r. bugensis	79.5±142.8	88.0±107.9	Calcareous
D. villosus	122.9±213.1	103.8±119.9	Calcareous
E. ischnus	35.8±68.1	140.3±119.9	Calcareous

E. trichiatus	103.0±163.4	121.2±181.3	Calcareous
H. anomala	98.3±158.1	88.5±109.5	Calcareous
H. invalida	218.3±256.1	35.4±73.7	Calcareous
J. istri	48.8±119.3	146.0±115.1	Calcareous
L. benedeni	172.5±220.8	38.4±89.4	Calcareous
L. naticoides	134.6±214.1	94.0±130.6	Calcareous
N. gymnotrachelus	31.3±57.1	122.7±71.9	Calcareous
N. melanostomus	111.4±165.2	125.1±192.3	Calcareous
O. crassus	74.4±135.0	66.6±78.3	Calcareous
O. obesus	88.0±142.8	98.3±112.5	Calcareous
P. marmoratus	84.6±185.7	146.9±131.8	Calcareous
P. robustoides	66.3±142.7	56.2±85.4	Calcareous
P. semilunaris	166.2±286.8	99.1±123.0	Calcareous
MEAN TOTAL	**124.4±202.3**	**79±112.1**	**Calcareous**

Table 6 suggests small and medium sized catchments located in lowlands and with a predominant calcareous geology are suitable for invasion by the 23 evaluated Ponto-Caspian invaders. These characteristics correspond to river types 2 and 5, which together represent 38% of the typed river length in Great Britain (Figure 14). River type 8 (large sized catchments, low altitude, calcareous geology) might also be susceptible to colonization since no evidence suggest large catchments cannot be colonized by these species. According to SDM, the average cumulative risk of invasion of alert Ponto-Caspian invaders in river types 2, 5 and 8 ranges between 15 and 17 species. Furthermore, these river types are widespread across the south-east of England (Figure 14), where SDM suitability is highest (Figure 11).

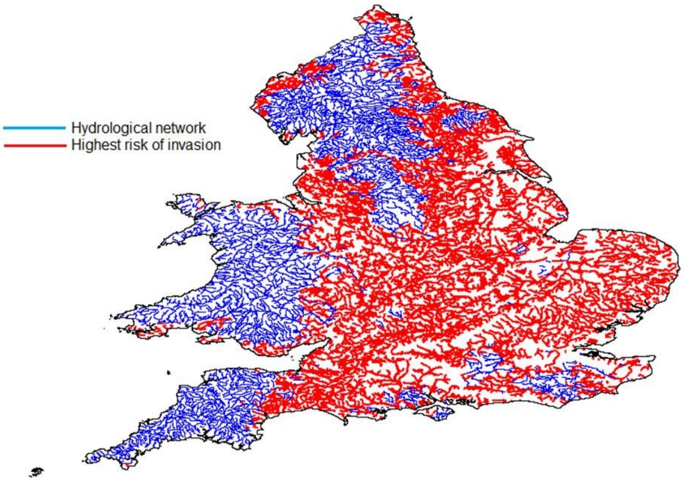

Figure 14 River types 2, 5 and 8, highlighted in red, show the highest cumulative risk scores (SDM score >15) and suitable characteristics for the establishment of Ponto-Caspian invaders (i.e. low altitude, gravel substrata, high alkalinity).

Regarding lakes, HAVS, HAD and HAS showed the highest cumulative scores in SDM (between 14 and 17). All of them are lakes located on calcareous geologies, with high alkalinity (>50 mg/L) and conductivity (>250 µS/cm); characteristics that are known to favour the establishment of Ponto-Caspian species. HAVS identify lakes that are very small (1 to 9 ha) and therefore not routinely monitored. HAS on the contrary are slightly bigger lakes of 10 to 49 ha that require monitoring according to the WFD. HAD are deeper lakes (> 3 m) that might be especially suitable to deep water species such as the quagga mussel. Some of the lakes showing the highest cumulative risk scores are highlighted in Figure 15.

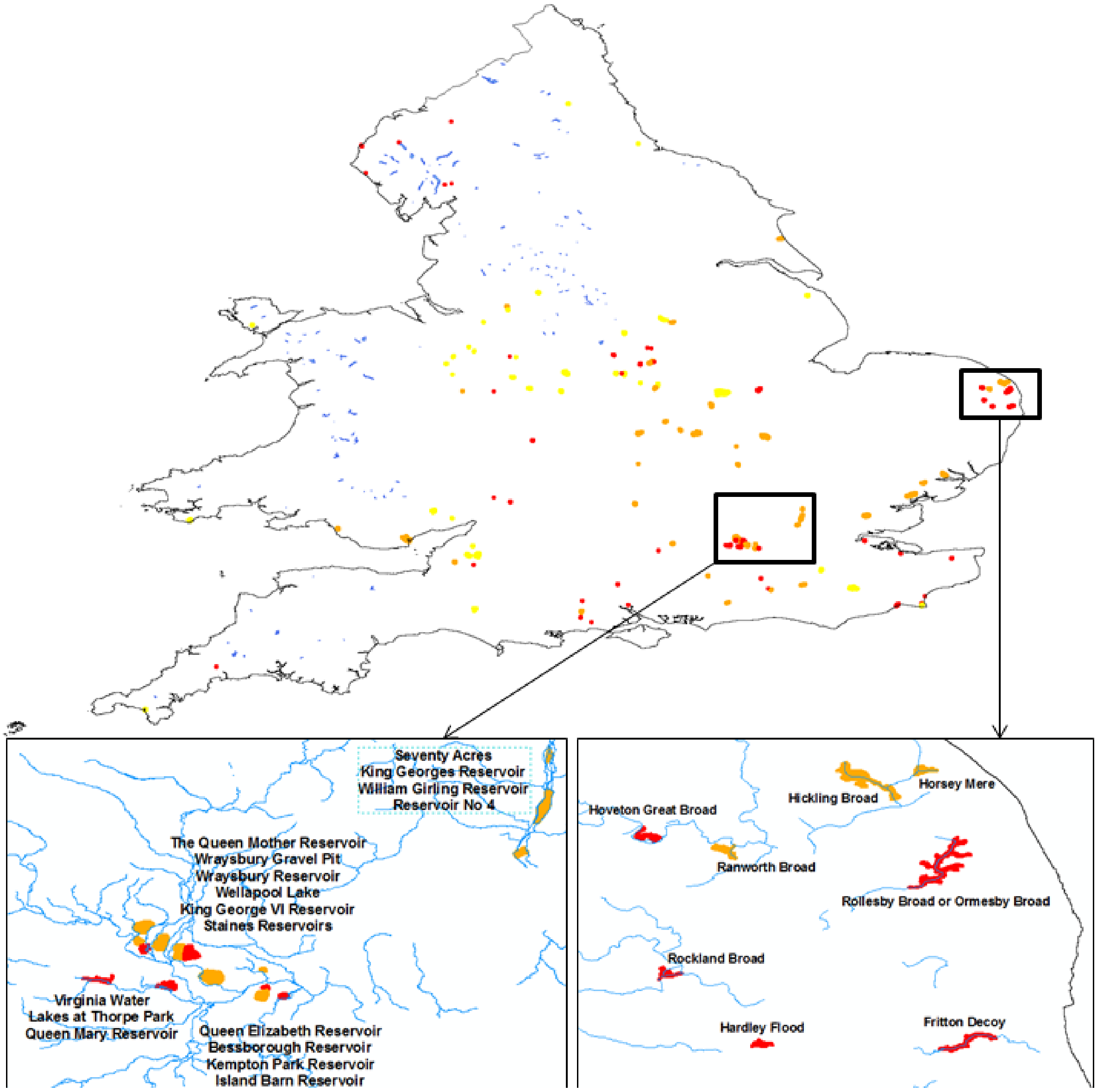

Figure 15 Lake types showing highest cumulative invasion risk scores (score > 15: orange colour; > 18: red colour).

Ponto-Caspian species may affect multiple native species typical of British rivers and lakes (Table 7). River types 3, 5, 6, 8, 11 and 17 accumulate more than five reference taxa vulnerable to invasion. Of them, our risk analyses suggest Ponto-Caspian invaders represent a serious threat only to river types 5 and 8, since alkalinity and altitude of the river types 3, 6, 11 and 17 are not suitable for Ponto-Caspian invasion.

Table 7 Reported impacts of Ponto-Caspian species on aquatic assemblages of British water bodies. A description of river types is provided in Table 3. River types potentially affected include all those rivers in which the species affected form part of their reference aquatic communities. More information on each species diet is provided in Appendix D.

Species affected	**Ponto-Caspian species involved**	**Water bodies potentially affected**	**Reference**
Phytoplankton	*C. curvispinum* *D. r. bugensis* *H. anomala* *H. invalida* *L. benedeni* *L. naticoides* *N. melanostomus*	Rivers & lakes in general	Kelly *et al.* 2010 Ketelaars *et al.* 1999 Borcherding *et al.* 2006 Surugiu 2005 Hanselmann *et al.* 2013 Biserova 1990 Kuhns & Berg 1999
Zooplankton: Cladocera, Ostracoda, Rotifera, Copepoda	*C. pengoi* *H. anomala* *L. benedeni* *N. melanostomus*	Rivers & lakes in general	Leppäkoski *et al.* 2002 Ketelaars *et al.* 1999 Borcherding *et al.* 2006 Hanselmann *et al.* 2013 Rakauskas *et al.* 2008
Macroinvertebrate richness & abundance	*C. curvispinum* *D. villosus* *D. r. bugensis* *O. crassus* *P. robustoides*	Rivers & lakes in general	Van der Velde *et al.* 2000 Burlakova *et al.* 2005 Karatayev *et al.* 1997 Arbaciauskas *et al.* 2010 Gumuliauskaite & Arbaciauskas 2008
Fish: perch, pike, pikeperch, bullhead, cyprinids, eel	*C. pengoi* *D. r. bugensis* *H. anomala* *J. istri* *L. benedeni* *L. naticoides* *N. gymnotrachelus* *N. melanostomus* *P. robustoides* *P. semilunaris*	Rivers & lakes in general	Leppäkoski *et al.* 2002 Karatayev 1992 Laruelle *et al.* 2002 Kipp & Ricciardi 2007 Sures *et al.* 1999 Hanselmann *et al.* 2011 Biserova 1990 Plachocki *et al.* 2012 Almqvist *et al.* 2010 Ovcharenko *et al.* 2006 Jurajda *et al.* 2005

Gammaridae	*D. villosus* *E. ischnus* *N. melanostomus* *P. robustoides*	River types 1-8, 11, 14, 17	bij de Vaate *et al.* 2002 Dick & Platvoet 2000 Kinzler *et al.* 2009 Jazdzewski *et al.* 2004 Rakauskas *et al.* 2008 Gumuliauskaite & Arbaciauskas 2008
Asellidae	*C. curvispinum* *D. villosus* *P. robustoides*	River types 3, 5-6, 8	Kinzelbach 1997 Ricciardi & Rasmussen 1998 Dick *et al.* 2002 Gumuliauskaite & Arbaciauskas 2008
Unionidae	*D. r. bugensis*	River type 5	Kelly *et al.* 2010
Margaritiferidae	*N. melanostomus*	River types 11, 16	Zmudziński & Osowiecki 1991
Caenidae	*D. villosus*	River types 3, 5, 8, 10, 12-13, 15-17	Dick *et al.* 2002
Coenagrionidae	*D. villosus*	River types 3, 5	Dick *et al.* 2002
Corixidae	*D. villosus*	RIver types 3, 6	Dick *et al.* 2002
Hydropsychidae	*C. curvispinum*	River types 1-7, 10-17	Kinzelbach 1997 Ricciardi & Rasmussen 1998
Chironomidae	*D. villosus* *N. melanostomus* *P. robustoides*	River types 1-3, 5-8, 11, 14, 17-18	Rakauskas *et al.* 2008 Berezina *et al.* 2007 Dick *et al.* 2002
Oligochaeta	*D. villosus*	River type 2-8, 11, 14, 17-18	Krisp & Mailer 2005

3.4 NETWORK ANALYSIS

Dispersal rates of Ponto-Caspian species observed in mainland Europe are summarized in Table 8. Ponto-Caspian species disperse on average at 87 km/year upstream and slightly slower, 80 km/year downstream.

Table 8 Dispersal rates of alert Ponto-Caspian freshwater invaders reported in the literature.

Species name	**Upstream**	**Downstream**	**River (Reference)**
N. fluvialitis		120 km/year	Vistula (Grabowska

			et al. 2010)
D. villosus	30-40 km/year	30-60 km/year	Meuse (Josens et al. 2005)
		112 km/year	Rhine (Leuven et al. 2009)
O. obesus	35 km/year	130 km/year	Rhine (Leuven et al. 2009)
D. r. bugensis	120 km/year		Europe (Matthews et al. 2013)
	23 km/year		Waal (Matthews et al. 2012)
	87 km/year		Meuse (bij de Vaate et al. 2013)
	105 km/year		Hollands Diep (Bij de Vaate 2009)
	383 km/year		Danube (bij de Vaate et al. 2013)
C. curvispinum	15-17km/year		Meuse (Josens et al. 2005)
		44 km/year	Rhine (Leuven *et al.* 2009)
J. istri		109 km/year	Rhine (Leuven *et al.* 2009)
	44 km/year	30.5 km/year	Meuse (Josens et al. 2005)
D. haemobaphes	22.5 km/year	129.5 km/year	Meuse (Josens *et al.* 2005)
H. anomala	157 km/year		Meuse (Josens *et al.* 2005)
N. melanostomus	14.2 km/year	5.2 km/year	Trent-Severn waterway (Bronnenhuber et al. 2011)

After identifying major regions in Great Britain vulnerable to invasion with SDM (Figure 11), we selected water bodies showing highest risk scores (> 18 cumulative score for rivers and > 17 for lakes) and selected them as first areas of potential establishment. A number of points at regular distances of 5-10 km were located within high risk river stretches, while a single point was located in the centre of high risk lakes (black dots in Figure 16). Most of these water bodies are certainly located in management catchments where freshwater invasive species are most frequently discovered for the first time, such as the Nene and Great Ouse catchments, the Broadland Rivers or the River Trent (Figure 6). Other high risk lakes and reservoirs were located along the south and east of England (see high risk lakes at Figure 15).

Output of the Network Analyst identifies major areas of potential spread of invasive species from the first places of introduction (Figure 16).

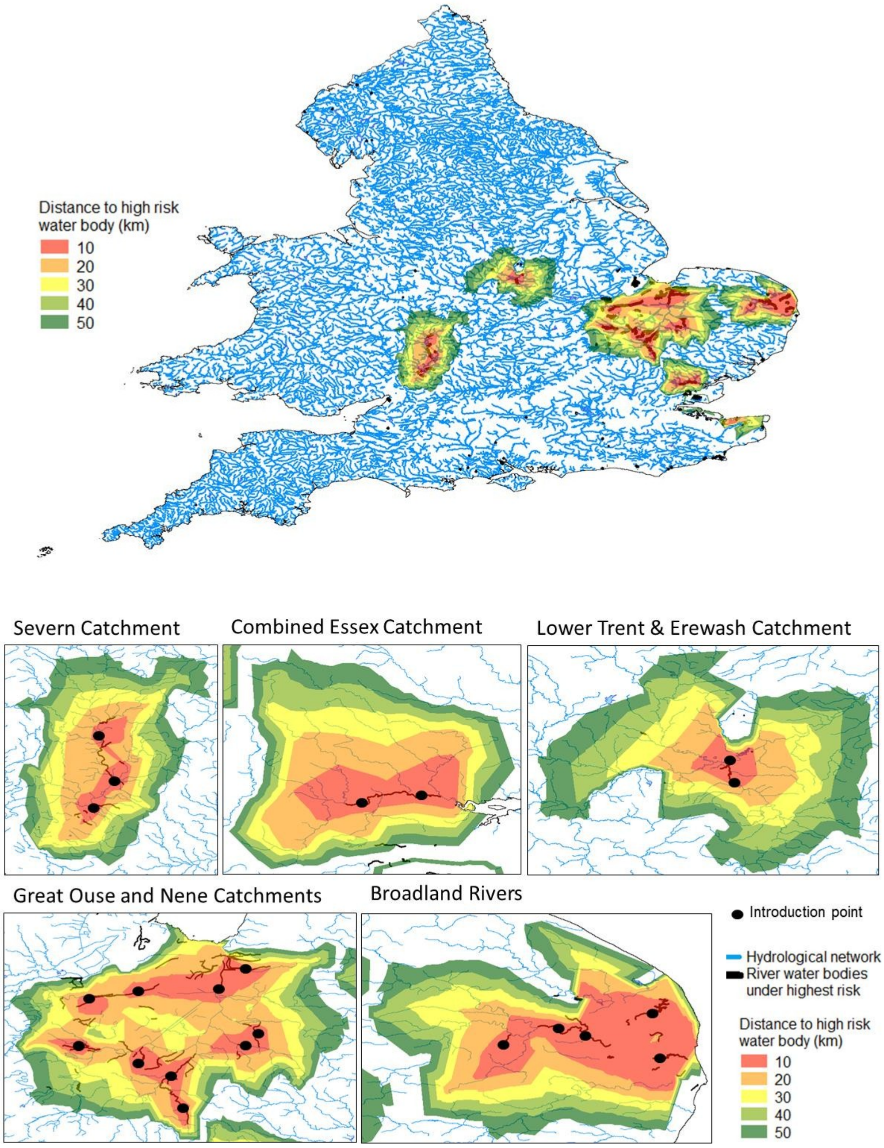

Figure 16 Results of Network analysis performed with rivers and lakes showing the highest cumulative risk scores as potential points of introduction, and the river network as main transport route. Points of introduction were selected on the basis of risk scores calculated with species distribution models (see Section 3.3). Resulting polygons define the areas that could be potentially reached through secondary spread at different velocities.

Results from Network Analysis allow identifying the potential area of influence of Ponto-Caspian species should they invade water bodies under the highest risk. Areas in a 10-20 km area from introduction spots are particularly vulnerable to invasion through active and passive dispersal. From the different catchments evaluated, the Great Ouse, Nene and Broadland Rivers seem to have the widest areas of influence, overall due to multiple reaches considered as potential introduction points and the high interconnectivity of their hydrological networks. Lakes were hydrologically disconnected and for that reason their area of influence was much smaller, although this is not necessarily true in the case of reservoirs.

3.5 INTEGRATION OF RESULTS

In order to rank the alert Ponto-Caspian species according to their overall risk, we summarized all the information compiled and analysed throughout this study. Category A-Introduction was based on the predicted timeframe of introduction into Great Britain based on the species' first appearance in The Netherlands (Table 5). For species not present anywhere near the Netherlands, we considered the distance to their closest location in Europe (i.e. the farther the species is located, the lower the score in this category). The fraction of the area of England and Wales predicted suitable for each species was used to score the probability and potential extent of B-Establishment (5-where most of England and Wales is predicted suitable for the species; 1-where the species presents a very limited and patchy predicted distribution, based on Appendix F maps). Information on dispersal velocity (Table 8) and vectors (Appendix D) were used to assign C-Spread scores. Species able to exploit multiple vectors and pathways of invasion scored high, whereas species with a more limited capacity to use multiple natural or human vectors obtained low scores. For instance, fishes scored high (3-4) because of their swimming activity, but lower than crustaceans (up to 5) because fishes are bigger and more difficult to be transported unnoticed. D-Impact was based on published evidence reviewed in Appendix D. When no impacts were reported in the literature (for instance *D. bispinosus, E. trichiatus*) a score of 1 was assigned, although it should be noticed that this is not necessarily true and may simply reflect a gap in our knowledge.

Table 9 Summary of information gathered in this study for 23 Ponto-Caspian species. Scores range from 1-very unlikely to 5-very likely. Species are ranked according to the risk associated to their introduction, establishment and spread. The top five species are highlighted in red and the lowest five scoring species in green.

Scientific name	A-Introduction (timing)	B-Establishment (suitability)	C-Spread (velocity)	D-Impact	AxBxCxD
Dreissena r. bugensis	5	5	5	5	625
Dikerogammarus villosus	5	5	5	5	625
Neogobius melanostomus	4	4	4	5	320
Chelicorophium curvispinum	5	4	3	4	240
Proterorhinus semilunaris	3	5	3	4	240
Hemimysis anomala	5	5	3	3	225
Dikerogammarus haemobaphes	5	4	5	2	200
Jaera istri	5	5	4	2	200
Hypania invalida	5	4	4	2	160
Limnomysis benedeni	5	4	3	2	120
Neogobius gymnotrachelus	1	4	4	4	64

Proterorhinus marmoratus	4	5	3	1	60
Pontogammarus robustoides	1	5	3	4	60
Echinogammarus ischnus	5	1	3	3	45
Lithoglyphus naticoides	1	4	2	4	32
Dikerogammarus bispinosus	5	5	1	1	25
Cercopagis pengoi	1	1	5	5	25
Echinogammarus trichiatus	4	3	2	1	24
Chelicorophium robustum	4	5	1	1	20
Obesogammarus obesus	1	4	5	1	20
Obesogammarus crassus	1	2	2	2	8
Chelicorophium sowinskyi	1	2	1	1	2
Chaetogammarus warpachowski	1	2	1	1	2

The resulting ranked list of Ponto-Caspian alert species is very similar to that developed by invasion biology experts based on their experienced opinion and reported in Table 4. Only slight changes in the lower tier of the table are observed. The top 5 species with highest risk scores remains the same including two species already located in Great Britain (*D. villosus* and *C. curvispinum*) and three that are expected to invade in the short term (*D. r. bugensis, N. melanostomus* and *P. semilunaris*).

4. DISCUSSION

4.1 WHICH PONTO-CASPIAN SPECIES POSE THE BIGGEST THREAT?

According to invasion biology experts and previous research, at least 23 freshwater invasive species originating from the Ponto-Caspian region currently threat the future ecological integrity of British freshwaters. The list is dominated by gammarids, represented by 12 organisms, and also includes four fishes, two mysids, a mollusc, isopod, cladoceran and polychaete. Five of these identified threats are already present in UK (i.e. *C. curvispinum, H. anomala, D. villosus* and *D. haemobaphes, H. invalida*) but have yet to spread to their fully anticipated extent. Nine species occur in high risk donor areas such as the estuary of the Rhine River and Dutch ports. Additional species could be incorporated to this list in the future, since over a hundred Ponto-Caspian species (including those investigated in this study) are known to be spreading towards Western Europe (see the complete list in Appendix A).

The first step towards a rigorous risk assessment is to gather all scientific evidence regarding the basic biology and ecology of the species, its current distribution, vectors and pathways of introduction and potential impacts, which is available in Appendix D. The information available for some of the most well-known species, such as the quagga mussel (*D. r. bugensis*) or the killer shrimp (*D. villosus*) allowed a formal risk assessment. It was nevertheless surprising the scarcity of information available for other Ponto-Caspian species; such is the case of *C. warpachowski, C. robustum, O. obesus, D. bispinosus* and *C. sowinskyi*. If we use the number of publications as indicator of the impact of species, a low risk would be assumed for these organisms. The precautionary principle calls nevertheless for prevention of all invasive species when not much information is available. Further investigation and analysis are needed to reveal the real risk associated with Ponto-Caspian invaders individually and in combination.

4.2 WHY ARE PONTO-CASPIAN SPECIES SUCCESSFUL?

The success of Ponto-Caspian species and therefore their threat to British waters is grounded in a number of characteristics common to most of the species investigated and summarized in Appendix D. In the first place we highlight the exceptional capacity for reproduction and rapid growth of Ponto-Caspian invasive species that generally exhibit short life-span, short generation time, protection of juveniles and body size substantially bigger or smaller than competing species (Morton 1997; bij de Vaate et al. 2002).

D. villosus exemplifies the reproductive effectiveness of Ponto-Caspian invaders with its high fecundity, early sexual maturity, short generation time, life span not exceeding 1 year (with up to three generations and 14 cohorts being present at the same time), high growth rates (resulting in large body size), short duration of embryonic development, large numbers of small eggs in the brood pouch (>100 eggs), and optimal timing (i.e. to release the maximum number of neonates per female in May/June thereby maximizing rapid growth at high summer temperatures and at times of plentiful food) (Kley and Maier 2006; Grabowski et al. 2007). Additional examples include *C. pengoi* that can reproduce parthenogenetically and gametogenetically depending on environmental cues (Grigorovich et al. 2000). The quagga mussel, *D. r. bugensis,* is able to produce up to 1.000.000 eggs per season (Astanei et al. 2005). The amphipod *E. ischnus* produces few but large eggs (10-35 eggs as opposed to >100 in *Dikerogammarus* spp.), which could be beneficial at sites where food is scarce (Kley and Maier 2006). Such attributes explain the high capacity of Ponto-Caspian species for colonization, expansion and rapid dominance of local food webs.

A second characteristic to highlight is their capacity to disperse widely. Ponto-Caspian species are able to spread naturally through passive dispersal (e.g. with water currents, transported by animals) and active swimming through waterways and open canals. The capacity to spread naturally along rivers and lakes is particularly high in the case of species with a planktonic stage such as *C. pengoi* (Panov et al. 2004) and *D. r. bugensis* (Karatayev et al. 2003); active swimmers such as *E. ischnus* (Nalepa et al. 2001) and several gobies (Ahnelt et al. 1998); and passive drifters like *E. trichiatus*, *J. istri* (Van Riel et al. 2011) and *L. benedeni* (Wittmann and Ariani 2009). However human dispersal explains their rapid expansion outside the geographic limits of their native range. After reviewing the multiple vectors and pathways of invasion of Ponto-Caspian species, Godard et al. (2012) highlighted shipping (e.g. hull fouling, ballast water) as the most important vector of introduction in Great Britain, followed by inland boating, unintentional stocking, angling gear and intentional release.

Millions of years of evolution with widely varying climates, salinities, water levels and connectivity have resulted in Ponto-Caspian species with extraordinary broad environmental tolerances and phenotypic plasticity (Reid and Orlova 2002). The broad climatic and environmental tolerance displayed by Ponto-Caspian species such as the zebra and quagga mussel (*D. polymorpha* and *D. r. bugensis*), the bloody red mysid (*H. anomala*) and the killer shrimp (*D. villosus*) has potentially contributed to their being able to colonize wide areas of Europe and/or North America, and probably to adapt rapidly to global changes (Hellmann et al. 2008). As much as 60% of Great Britain shows climatic conditions suitable for the establishment of Ponto Caspian species such as *D. villosus* (Gallardo et al. 2012) and other Ponto-Caspian invaders (Gallardo and Aldridge 2013b).

Ponto-Caspian species are able to withstand a wide range of water temperature (up to 25-30 ˚C in the case of *C. pengoi*) (Kane et al. 2003), oxygen (*D. villosus* and *E. ischnus* can survive concentrations as low as 0.1-0.3 mg/L dissolved oxygen by becoming motionless) (Mordukhai-Boltovskoi 1960) and salinity (up to 15-19‰ which corresponds to brackish water; Kane et al. 2003) conditions that explain their capacity to survive transport in ballast water and overland. Actually, extreme conditions usually related to pollution may provide certain competitive advantage to Ponto-Caspian species, because they can enter and establish in a disturbed habitat more easily than into a system that is stable and so has resistance to the establishment of new species (Gallardo and Aldridge 2013b). This is why we find a preponderance of invasive species in newly changed habitats (Emerton and Howard 2008).

Ponto-Caspian species displace both native and invasive species through predation and competition thanks to their opportunistic feeding and aggressive behaviour that further supports a rapid dominance of the food web. In terms of protection, a high phenotypic plasticity, with forms that range from melanic to dark striped, is an important anti-predator strategy displayed by some Ponto-Caspian species such as the quagga mussel and the killer shrimp (Devin et al. 2004). Gregariousness, or the accumulation of thousands of organisms, also helps preventing predation in the case of *C. pengoi* (Grigorovich et al. 2000) and *H. anomala* (bij de Vaate et al. 2002). Both strategies may increase their competitive advantage over native species.

Niche complementarity between species in terms of habitat use and feeding behaviour is also important to explain the success of Ponto-Caspian species as a collective. While gammarids are able to exploit a great variety of resources depending on their availability –from algae, to deposited organic matter and preying other small planktonic organisms—filter-feeders take advantage of nutrients dissolved in the water-column, and fishes benefit from the increased abundance of prey. Although certain competition for space and resources exists, positive interactions between Ponto-Caspian species are more frequent, resulting in facilitation between the invaders (consult specific examples of synergistic interaction in Appendix D).

From this review it is clear that Ponto-Caspian species share many attributes that justify developing a group-specific strategy of management. However, certain differences exist between species that are fundamental to understand, as they can mark the difference between a devastating invader and one that remains mostly unnoticed.

4.3 WHERE ARE PONTO-CASPIAN SPECIES MOST LIKELY TO APPEAR IN GREAT BRITAIN?

After mapping locations of first report of freshwater invaders (Figure 6), we identified a higher concentration of invasive species towards the south east of England and in close relation to the location of major ports in the London area (e.g. London and Medway), the East of England (e.g. Ipswich, Lowestoft, Felixstowe), the south of Wales (e.g. Bristol, Cardiff, Port Talbot) and North West England (Liverpool, Manchester). The south east of England has been recently highlighted as suitable for 25 aquatic invaders regardless of their native origin, with invasion risk progressively increasing north and westwards under future scenarios 2015, 2021, 2027 and 2050 (Environment Agency 2013). According to research carried out by Newcastle University, these ports receive between 2.9 and 5.1 MMT ballast water annually, predominantly from North Europe, thus exacerbating the risk of Ponto-Caspian species being inadvertently transported in the ballast tank of ships (Enshaei and Mesbahi 2009). The importance of ports as gateways of invasive species is well known, with at least 10,000 species estimated to be transported around the world in ships (Bax *et al.*, 2003). Invasive species are transported as commodities and deliberately released or escape from captivity, or can be involuntarily transported as contaminants or stowaways (Hulme, 2009; Keller *et al.*, 2009). As well as providing an entrance point, ports are highly disturbed areas, providing an artificial environment where invasive species can establish and increase in abundance (Bax et al. 2003).

Prevention strategies based on pathways rather than on individual species provide the most efficient way to concentrate efforts at sites where pests are most likely to enter national boundaries and to intercept several potential invaders linked to a single pathway (Wittenberg and Cock 2001). In the case of Great Britain, ports are important gateways of introduction of invasive nuisances that are transported in the ballast water of ships, attached to their hulls or as contaminants of transported commodities. Areas surrounding ports should be therefore routinely inspected for the early detection of invasive species.

4.4 WHEN ARE PONTO-CASPIAN SPECIES LIKELY TO INVADE?

Time lags between invasive species arrival into The Netherlands and UK are different among taxonomic groups. According to our analyses, plants show considerably longer time lags than animals, with molluscs representing the quickest group to cross the channel. This observation can be attributed to differences in their main vectors of introduction. While plants and fish are mainly introduced intentionally through the ornamental and aquarium/fishing trade respectively, crustaceans and molluscs are mostly accidentally introduced (Gallardo et al. 2013). Unintentional introductions are obviously more difficult to control than intentional ones, which may explain the rapid spread of molluscs across countries.

Dates of introduction in The Netherlands and UK were used to predict the likely timeframe of introduction of Ponto-Caspian invaders. Species already located in UK were used to assess the reliability of predictions. In accordance to our predictions, the bloody red mysid, *H. anomala*, was reported in 2004 in the Humber district; *H. invalida* has been recently located in 2008 samples from the River Thames, and the demon shrimp (*D. haemobaphes*) was first seen in the Severn Vale in 2012. However, the killer shrimp (*D. villosus*) was reported in the Great Ouse River two years later than predicted (Table 5). Nevertheless, experts suggested the killer shrimp may have established in the wild years before being noticed, based on its abundance, size spectra and reproductive stage of individuals (MacNeil et al. 2010b).

Four Ponto-Caspian species were predicted to have arrived into Great Britain from 2006 to 2011 with a 95% confidence (Table 5); such is the case of amphipods *E. ischnus, J. istri* and *D. bispinosus,* and the mysid *L. benedeni.* Two alternative explanations can be suggested to explain this result. First, species might have been certainly introduced into Great Britain but not yet reported as we already suggested for *D. villosus*. Considering the difficulty of identifying taxonomically Ponto-Caspian species and the lack of appropriate monitoring plans for their early detection, this option cannot be disregarded. Alternatively, the species abundance and geographic spread in The Netherlands might be too limited to trigger the species expansion, which highlights the role of propagule pressure. Information about the likely timeframe of introduction should be thus analysed jointly with information on the species abundance and spread in donor areas in order to provide more realistic predictions. Nonetheless, we can assume that the longer a species is present in The Netherlands the higher the probabilities are of unwanted introduction in Great Britain and for this reason, species in Table 5 are of especial concern.

The rate of colonization of invasive species into UK coming from The Netherlands seems to be accelerating in recent decades, which can be probably attributed to increasing globalization, and thus travel and freight transport. This is worrying, as the number of invasive species in The Netherlands not yet present in UK is high, and pose a serious threat to the conservation of British aquatic ecosystems. Besides Ponto-Caspian species, another 30 freshwater and 64 marine invasive species are currently present in The Netherlands and have not yet been detected in UK (Gallardo et al. 2013), which further stress the biosecurity threat posed by shipments from Dutch ports mentioned before. Cross-country sharing and updating of information on the status of invasive species is fundamental so that the presence of known invasive species is detected early, and the risks they pose are rapidly assessed. The sooner action is taken to address any threat, the greater the chance of success and the less costly it will be both in terms of biodiversity and other resources (GB-NNSS 2008).

4.5 WHICH LARGE SCALE AREAS ARE UNDER HIGHEST RISK?

Species distribution models (SDM) displayed high performance for all Ponto-Caspian species modelled. Models allowed investigating the partial influence of environmental and socio-economic drivers on their current distribution, and identifying the large scale areas most vulnerable to multiple invasions.

The permutation importance of environmental variables in SDM ranged between 63 and 100% (Appendix F). Amongst climate factors, minimum temperature was the most important driver of the investigated species distribution, in accordance with previous studies in the area (Gallardo et al. 2012; Gallardo and Aldridge 2013b, a). Temperature affects the body size, reproduction, growth, ecological role and survival of species (Gillooly *et al.*, 2001), and is a key factor determining success in the colonization and establishment stages of invasion (Theoharides & Dukes, 2007). The role of cold temperature in shaping the distribution of species has been recently highlighted by Araujo et al. (2013), who after reviewing a large set of endotherms, ectotherms and plants concluded that the upper tolerance of species to temperature is relatively similar, with differences in the global distribution of species largely driven by their cold tolerance level.

Notwithstanding the important effect of temperature, and in spite of their relative low permutation importance, socio-economic factors seemed to significantly affect the spatial distribution of alert Ponto-Caspian species. Conspicuously higher suitability scores could be observed in densely populated areas, close to the coast and in clear relationship with transport routes (see individual species maps in Appendix F and a cumulative heat map in Figure 11). Likewise, in a recent study the addition of socio-economic factors to SDM resulted in 20% amplification of risk scores in highly developed areas of Great Britain and Ireland (Gallardo & Aldridge, 2013a).

Closeness to ports was identified as the most important socio-economic predictor for at least ten Ponto-Caspian species, and was able to explain more than 10% of the predicted distribution of *P. marmoratus, E. trichiatus, D. bispinosus* and *C. ischnus* (Appendix E). The importance of ports as gateways of invasive species has been pointed out before in this study, but port closeness also reflects coastline proximity. Coastal landscapes are being transformed as a consequence of the increasing demand for infrastructures to sustain residential, commercial and tourist activities. Thus, intertidal and shallow marine habitats are largely being replaced by a variety of artificial substrata (e.g. breakwaters, seawalls, jetties) that are very susceptible to invasion (Airoldi & Bulleri, 2011), specially by Ponto-Caspian species which tolerate brackish waters and show preference for hard artificial substrates and high salinity.

The Human Influence Index (HII) was the most important predictor for species such as *C. curvispinum, C. sowinskyi, D. haemobaphes, L. benedeni* and *D. r. bugensis* (Appendix E). Modelled species showed a consistent logistic response to the HII (Figure 9) that suggests the higher the level of human influence, the greater are the probabilities of invasion (Gallardo and Aldridge 2013a). This is because human activities responsible for the introduction of invasive species such as the pet trade, fishing, boating and other leisure use of water bodies are more frequent in densely populated areas. Land-use pressure can decrease the capacity of natural environments to buffer biological invasions, and transport routes provide pathways along which species can disperse. All these factors are captured within HII.

While individual prediction maps can be useful to address the risk posed by individual species, the heat map featured in Figure 11 synthesizes information regarding the risk associated with Ponto-Caspian species collectively. The heat map suggests there is room for expansion of current invaders while at the same time the arrival of newcomers poses a tremendous challenge in terms of prevention and management. This is because species can modify their habitat facilitating subsequent invasions (sensu 'invasional meltdown', Simberloff and Von Holle 1999). Such invasional meltdown implies an accelerated accumulation of invasive species, whose combined impacts are even greater than their independent effects (Simberloff and Von Holle 1999). According to the literature review, the relationship among Ponto-Caspian species is complex although positive interactions are more frequent than negative or neutral ones (Appendix D).

4.6 HOW FAR CAN PONTO-CASPIAN SPECIES SPREAD IN GREAT BRITAIN?

Alert Ponto-Caspian species can disperse at very high velocities, on average 87 km/year upstream and 80 km/year downstream (Table 7) aided by human activities such as boating or fishing, through hull fouling or attachment to trailers and fishing gear. According to the network analysis, the Great Ouse, the Nene and the Broadland Rivers seem to be most vulnerable in terms of influence area, primarily due to multiple reaches that could act as potential introduction points and the high interconnectivity of their hydrological networks. These three catchments have been repeatedly pointed out in this report as posing the greatest threat of first introduction, establishment and also secondary spread. The vulnerability of the Great Ouse to secondary invasion of invasive Ponto-Caspian species such as the killer shrimp (*D. villosus*) has been recently highlighted (Gallardo et al. 2012), in line with results from this study. However, after three years since it was first recorded, no further spread of the killer shrimp has been detected in the Great Ouse catchment. The early detection of the species while it was still confined to Grafham reservoir and the Environment Agency's efforts to prevent further contamination of the catchment have surely contributed to this observation, which highlights the cost-effectiveness of prevention measures. In contrast, isolated lakes represent less of a threat unless they are intensively use for leisure, sport or fishing activities, as might be the case of reservoirs in the Thames catchment, highlighted in Figure 15.

The actual area of influence of Ponto-Caspian invaders ultimately depends on their mobility and ability to disperse using alternative vectors. Organisms that can freely move in the water column—such as cladocerans, mysids, fishes and some crustaceans—can actively migrate both upstream and downstream along a watercourse. These species have significantly benefited from the extensive canal construction in central Europe that has connected previously isolated catchments (bij de Vaate et al. 2002). Mobile species represent a great threat to Great Britain because of the network of canals in the Midlands that can assist their spread. Special attention should be paid to gobies, because of their extraordinary upstream rates of dispersal, with values as high as 120 km/year (Ahnelt et al. 1998). Another group with a very high potential for secondary spread includes *C. pengoi*, *D. r. bugensis* and *D. villosus* that can efficiently attach to surfaces in contact with water such as boats, fishing gear or water equipment (e.g. boots, waders), thereby facilitating their transport overland (e.g. MacIsaac et al. 1999; Johnson et al. 2001). Resistance to desiccation is in this case important, allowing species to survive outside water for up to 3-5 days, which enable them to disperse long distances (e.g. Ricciardi et al. 1995; Bacela-Spychalska et al. 2013). Other means of dispersal are reviewed in Appendix D and discussed in section 4.2.

Spread rates extracted from the literature and summarized in Table 8 are subject to several limitations that have been discussed in section 2.4.5. Consequently, real information based on laboratory and field trials is still needed to evaluate the potential for secondary spread of Ponto-Caspian species.

The Network Analysis provides an innovative tool to improve the early control of invasive species that requires further advancement. In this study we have used it to identify the area of influence of likely introduction points for Ponto-Caspian invaders. Other applications of the Network Analyst include modelling potential routes of invasion, adding the road network to investigate overland transport of propagules, including data on the overland movements between water bodies of pleasure craft and anglers, and the location of strategic dispersal barriers capable of preventing further secondary spread.

4.7 HOW MUCH IMPACT CAN WE EXPECT?

Ponto-Caspian species have multiple reported abiotic and biotic impacts that could dramatically affect the integrity of British water bodies. And yet Ponto-Caspian species are not likely to affect all types of British rivers and lakes in the same way. Water bodies with a calcareous geology, hard substrate (e.g. gravel, boulders), high alkalinity and conductivity offer the most suitable conditions for the successful invasion of Ponto-Caspian alert species. Such conditions correspond to river types 2, 5, 6, 8, 11, 14 and 17, and lake types HAVS, HAD and HAS.

Of these, types 5 and 8 showed highest cumulative risk scores and the highest number of native species potentially affected by Ponto-Caspian invaders (Table 7). Their location, concentrated in the Anglian and Severn RBD with additional patchy coverage of the Humber and Thames RBD (Figure 14), further confirms the risk associated to these two river types.

River types characterized by siliceous or organic geology, sandy/silt substrata and low alkalinity have a much lower probability of being invaded, and they are often located in the north-west where the climatic suitability for Ponto-Caspian species is rather low anyway.

4.7.1 HOW WILL PONTO-CASPIAN INVASIONS AFFECT WFD EVALUATION OF WATER BODIES?

Currently, the WFD ecological status of UK surface waters is determined by measuring three general elements: biological, physiochemical and hydromorphological. Within these general elements, specific components of the system (e.g. fish abundance, dissolved oxygen, flow conditions) are measured, assessed against a reference, and scored to provide an overall measurement of the ecological status of a water body. The three WFD elements can be affected by the introduction of Ponto-Caspian species with unknown consequences on the ecological classification of water bodies.

Changes in benthic assemblages have been reported after the introduction of Ponto-Caspian species, often leading to the displacement of native competitors and a reduction in overall aquatic biodiversity (see Table 7 for a summary of impacts). Invasive gammarids such as *D. villosus, C. curvispinum* and *P. robustoides* displace both native (e.g. *Gammarus spp., Asellus spp., Echinogammarus sp., Orconectes sp.*) and invasive (e.g. *G. tigrinus and Crangonix pseudogracillis*) species (bij de Vaate et al. 2002; MacNeil and Platvoet 2005; Gumuliauskaite and Arbaciauskas 2008; Kinzler et al. 2009) leading to a notable decline in native species richness and abundance. Caddis flies, mayflies, gammarids and other freshwater crustaceans are reference taxa for calcareous river types, which make them especially vulnerable to Ponto-Caspian gammarids. Several sensitive invertebrates (e.g. unionid molluscs), reference taxa in type 2 rivers, are adversely affected by dreissenids like *D. r. bugensis* (Karatayev and Burlakova 1995). Because molluscs, caddis flies, mayflies and gammarids generally indicate waters with a good ecological status (BMWP score of Caenidae=10, Unionidae= 6, Gammaridae= 10), their displacement through competition and predation by Ponto-Caspian species could lead to a deflation of WFD ecological status scores.

On the other hand, some Ponto-Caspian species predate on invertebrate families indicative of low water quality such as Oligochaeta and Chironomidae (Berezina and Panov 2003; Berezina 2007). Although this may reduce certain richness indicators, it could also result in inflated WFD scores (BMWP score of Oligochaeta= 1, Chironomidae= 2). Ponto-Caspian species score themselves high in WFD charts (BMWP of Gammaridae= 6), and since current WFD evaluations do not consider the native/invasive status of species, a water body completely overrun by invasive Ponto-Caspian species could score as presenting a good ecological status according to current methods (Cardoso and Free 2008).

Changes in the aquatic environment caused by Ponto-Caspian invaders are not restricted to the benthic community but extend to the entire food web. Zooplankton consumers such as mysids (*H. anomala, L. benedeni*), gammarids (*D. villosus, C. warpachowski*) and the cladoceran *C. pengoi* can drastically reduce the population of ostracods, cladocerans, rotifers and copepods (e.g. Ketelaars et al. 1999; Leppakoski et al. 2002; Fink et al. 2012) with knock-on effects on phytoplankton productivity. Other organisms directly consume phytoplankton such as molluscs (*D. r. bugensis, L. naticoides*), mysids (*L. benedeni*) and even some gammarids (*D. villosus*). By eliminating algae and suspended solids, and increasing water transparency, these organisms encourage the growth of submerged vegetation thereby changing the nutrient state of the system with unknown effects on WFD characterization.

While some species have been intentionally introduced as fish food, and invasive species can greatly contribute to the diet of fish (up to 100% in some cases), no significant growth in fish production has been noted in the literature in comparison with lakes were invasive species were not intentionally introduced (Borcherding et al. 2006; Kotta et al. 2006). Ponto-Caspian species may also reduce fish stocks through predation of their eggs and juveniles, and direct competition for food and space (Casellato et al. 2007; Leuven et al. 2009). Some species can also clog and damage fish nets, such as the fishhook waterflea, causing economic damage (Panov et al. 2003).

Many Ponto-Caspian species are able to change the abiotic conditions of the habitat they invade, facilitating not only their own survival but also the successful colonization of additional Ponto-Caspian invaders that would otherwise lack suitable habitat for establishment. Perhaps not surprisingly, several Ponto Caspian species are normally found together in benthic samples that are sometimes composed of Ponto-Caspian organisms only (bij de Vaate et al. 2002). Suspension feeders such as *D. r. bugensis,* and to a lesser extent *L. naticoides* can affect the water chemistry of water bodies and increase the complexity of the substrate (e.g. Biserova 1990; MacIsaac 1996). On the other hand, *C. curvispinum* and *C. sowinskyi* change the bottom structure of rivers from gravels to mud (e.g. Ricciardi and Rasmussen 1998; Van der Velde et al. 2002). Other Ponto-Caspian invaders can have a huge influence on biogeochemical cycles when present in very high densities through their feeding behaviour and accumulation of faecal pellets (e.g. Surugiu 2005; Hanselmann et al. 2011). The abiotic impacts of these habitat engineers can extend over a distance of 200-500 km along a water body (e.g. van den Brink et al. 1993), with great potential to affect the physicochemical and hydrogeomorphological elements of WFD monitoring.

In conclusion, while important changes in the structure of habitats and aquatic communities can be expected, the direction of such change is difficult for us to anticipate with the available knowledge, depending to a great extent on the number of invaders and their density in any particular water body. Several authors have cautioned that current approaches to ecological status invariably ignore the presence of invasive species, and can result in a site with a macroinvertebrate assemblage containing a high proportion of invasive taxa still being classed as having good ecological condition (Arbaciauskas et al. 2008; Cardoso and Free 2008; MacNeil et al. 2010a). In this sense, the UKTAG Alien Species Group has compiled a list of High/ Moderate/ Low risk invasive species (http://www.wfduk.org/resources%20/classification-alien-species). It advices that where invasive species (specially from the High risk group) are detected, and evidence suggest the species is causing more than a slight adverse impact on any biological element, the water body should be classified as 'moderate' ecological status or worse (UKTAG Alien Species Group 2013). However, only three Ponto Caspian species (*D. polymorpha, H. anomala* and *D. villosus*) appear on the High impact list of invaders, whereas *C. curvispinum* is on the Low impact list. This is surprising, as C. curvispinum was considered as one of the species with greatest potential of spread and impact both by invasion ecology experts (Table 4) and our own evidence-based evaluation (Table 9). It is important to update this table with the latest information available, and include high risk invades such as the quagga mussel (*D. r. bugensis*), the round goby (*N. melanostomus*) and the tubenose goby (*P. semilunaris*).

To integrate the effect of invasive species into WFD ecological assessments, a modified sampling protocol that allows extending the area of sampling when dominance of invasive species is visible (to improve the probability of finding the remaining native species) is recommended. An additional metric to quantify the taxonomical completeness of the native community in relation to the dominance of invasive species should be also implemented. Arbaciauskas et al. (2008) suggested a simple biocontamination index based on the richness and abundance of invaders that is applicable to data collected during routine monitoring:

$$ACI = N_i / N_t \qquad RCI = R_i / R_t$$

In the Abundance Contamination Index (ACI), N_i and N_t are the abundance of invasive taxa and the total number of specimens found in a sample. Likewise, in the Richness Contamination Index (RCI), R_i and R_t

correspond to the richness of invasive taxa relative to the total richness of the sample. These seemingly simple indexes were tested against data from the three major corridors of aquatic invasive species in mainland Europe (Arbaciauskas et al. 2008), and also in the Isle of Man (MacNeil et al. 2010a). Results from both studies suggested family level data is enough to discriminate between different levels of biocontamination, thereby reducing the time needed to process and identify all of the organisms in a sample. However, considering the presence of other native gammarids in British waters, it may be necessary to apply the index with data at a higher resolution level, e.g. genera. Although the method was initially developed for aquatic invertebrates, it could be easily extrapolated to other groups of organisms such as fish or macrophytes for a more comprehensive assessment of biocontamination.

4.7.2 The quagga mussel: chronicle of an invasion foretold?

The quagga mussel (*D. r. bugensis*) is the species with the highest overall risk level according to invasion biology experts and our own evaluation. The quagga mussel has been present in The Netherlands since 2006, although evidence suggests an earlier invasion, probably around 2004 (Molloy et al. 2007). The quagga mussel has been found to replace zebra mussels (*D. polymorpha*) at a rate of 36% annually, eventually outcompeting zebra mussels both in Europe (e.g. Dnieper River) and North America (e.g. Great Lakes) (Mills et al. 1996). The competitive advantage of quagga mussels is related to their earlier juvenile settlement than zebra mussels and their ability to live in cold as well as warm water (Dermott and Munawar 1993), allowing them to inhabit deeper waters than zebra mussels (Imo et al. 2010).

The introduction of molluscs into Great Britain is mostly accidental, associated with ship transport and the introduction of contaminated commodities (Gallardo et al. 2013). We may therefore assume that the longer and more abundant the species is in donor areas such as Dutch ports, the higher the probabilities are of the species crossing the channel. Ports in the south and east of England are likely to be the first gateways of introduction of the quagga mussel, because of the high cargo volume managed and the predominant north European origin of ballast water (Enshaei and Mesbahi 2009). Propagules arriving to any of these ports may be afterwards transported inland attached to the hull of boats and other material. Despite the limited upstream dispersal ability of the species through natural means (Orlova and Shcherbina 2002), their tolerance to aerial exposure, surviving for up to 3-5 days out of water (Ricciardi et al. 1995) suggests overland transport may be especially important. The establishment of the quagga mussel in the south east of England would be further favoured by a high match with climatic conditions in the continent (see suitability map in Appendix F). Secondary spread across England would be facilitated by the quagga mussel's extraordinary capacity to utilise multiple vectors ranging from passive downstream drift (Stoeckel et al. 1997) to human related activities such as shipping, fishing and boating (Orlova and Shcherbina 2002).

Potential impacts of the quagga mussel in Great Britain are very similar to those of the zebra mussel but reaching lower depths (up to 130 m) (Mills et al. 1996). Dreissenids can drive changes in water chemistry including a reduction in calcium, alkalinity and turbidity, and an increase in transparency (MacIsaac 1996). Enhanced water clarity increases in turn light transmittance and the growth of benthic plants. Food web changes are related to dreissenid algae filtration that can reduce the stock of zooplankton (copepods, rotifers), which in turn can affect fish survival and growth (Bartsch et al. 2003). Such abiotic and biotic changes lead to dramatic changes in the benthic invertebrate's biomass, species composition, and relative abundance of functional groups (Karatayev et al. 1997; Burlakova et al. 2005). Among benthic invertebrates, unionid molluscs are particularly adversely affected by dreissenids (Aldridge 2010). On the other hand, dreissenids can affect positively certain amphipod crustaceans and predatory fish that exploit the structure associated with or wastes generated by dreissenids (Karatayev and Burlakova 1995).

The quagga mussel is also likely to exert expensive economic impacts on water intake pipes and related systems (Hosler 2011), especially those that take water from deeper layers of the water column (Godard et al.

2012). Fouling of water intake pipes and associated installations can severely impair water delivery to hydroelectric, municipal and industrial users, necessitating proactive or reactive control measures and entailing high economic costs (Connelly et al. 2007). Control costs of the zebra mussel have been estimated annually at £4 million (Oreska and Aldridge 2011). The anticipated arrival of the quagga mussel, able to foul to deeper areas and withstand a wider range of temperatures, may multiply these costs in the future if no preventive actions are set in place.

4.8 IS GREAT BRITAIN ON THE BRINK OF INVASIONAL MELTDOWN OF PONTO-CASPIAN SPECIES?

In this project we have gathered enough information to make the case that Great Britain might be on the brink of invasional meltdown and, as a consequence, confronting the problem of alert Ponto-Caspian invasive species is a vital element for national biosecurity. We furthermore summarized all available information in the form of published literature, databases, predictive models and maps that can provide a basic baseline for future research as well as a national strategy. Results of this risk assessment can be used in decision-making to set priorities for the best use of time and funds and help determine if and what kind of strategy should be adopted. Such a strategy should be integrated with other national initiatives and action plans, and should support a cross-sectorial approach. River Basin Management Plans (RBMP) represent a pivotal tool to coordinate efforts towards controlling and managing invasive species at the regional scale. Finally, a continuing process for evaluating alert species and also new introductions should be established, since invasive species problems are increasing dramatically and the vectors for introduction of potential invasives change over time.

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7. APPENDICES

APPENDIX A. Ponto Caspian species currently known to be spreading outside of their native region.

	Species name	Year reported in Great Britain	Assessed in this report	Reference
Acarina	*Caspihalacarus hyrcanus*			Dumont et al. 2004
Amphipoda	*Amathillina cristata*			Dumont et al. 2004
	Chaetogammarus warpachowskyi		X	Dumont et al. 2004
	Chelicorophium chelicorne			Dumont et al. 2004
	Chelicorophium curvispinum	1935	X	Dumont et al. 2004
	Chelicorophium maeoticum			Dumont et al. 2004
	Chelicorophium mucronatum			Dumont et al. 2004
	Chelicorophium nobile			Dumont et al. 2004
	Chelicorophium robustum		X	Dumont et al. 2004
	Chelicorophium sowinskyi		X	Dumont et al. 2004
	Dikerogammarus bispinosus		X	Dumont et al. 2004
	Dikerogammarus haemobaphes	2012	X	Dumont et al. 2004
	Dikerogammarus villosus	2010	X	Dumont et al. 2004
	Echinogammarus ischnus		X	Dumont et al. 2004
	Echinogammarus trichiatus		X	Dumont et al. 2004
	Gmelina costata			Dumont et al. 2004
	Gmelina kuznetzowi			Dumont et al. 2004
	Gmelina pusilla			Dumont et al. 2004
	Iphigenella			Dumont et al. 2004

	andrussowi			
	Iphigenella shablensis			Dumont et al. 2004
	Niphargus hrabei			Dumont et al. 2004
	Obesogammarus crassus		X	Dumont et al. 2004
	Obesogammarus obesus		X	Dumont et al. 2004
	Pontogammarus aralensis			Dumont et al. 2004
	Pontogammarus maeoticus			Dumont et al. 2004
	Pontogammarus robustoides		X	Dumont et al. 2004
	Pontogammarus sarsi			Dumont et al. 2004
	Pontogammarus subnudus			Dumont et al. 2004
	Stenogammarus carausui			Dumont et al. 2004
	Stenogammarus macrurus			Dumont et al. 2004
	Stygobromus ambulans			Dumont et al. 2004
Annelida	*Archaeobdella esmonti*			Dumont et al. 2004
	Caspiobdella fadejewi			Dumont et al. 2004
	Cystobranchus fasciatus			Dumont et al. 2004
	Hypania invalida	2008	X	Dumont et al. 2004
	Hypaniola kowalewskyi			Dumont et al. 2004
	Manayunkia caspica			Dumont et al. 2004
	Paranais frici			Dumont et al. 2004
	Potamothrix heuscheri			Dumont et al. 2004

	Potamothrix vejdovskyi		Dumont et al. 2004
	Psammoryctides deserticola		Dumont et al. 2004
	Tubifex deserticola		Alexandrov et al. 2007
	Tubifex/Limnodrillus newaensis		Alexandrov et al. 2007
Bryozoa	*Victorella pavida*		Dumont et al. 2004
Cladocera	*Cornigerius bicornis*		Dumont et al. 2004
	Cornigerius maeoticus		Dumont et al. 2004
	Podonevadne trigona ovum		Dumont et al. 2004
	Cercopagis pengoi	X	Dumont et al. 2004
	Cornigerius bicornis		Alexandrov et al. 2007
	Cornigerius lacustris		Alexandrov et al. 2007
	Evadne cornigera		Alexandrov et al. 2007
	Podonevadme trigona		Alexandrov et al. 2007
Cnidaria	*Blackfordia virginica*		Dumont et al. 2004
	Cordylophora caspia		Dumont et al. 2004
	Maeotias marginata		Dumont et al. 2004
	Moerisia maeotica		Dumont et al. 2004
	Polypodium hydriforme		Dumont et al. 2004
Copepoda	*Calanipedia aquaedulcis*		Dumont et al. 2004
	Heterocope caspia		Dumont et al. 2004
	Limnocletodes behningi		Dumont et al. 2004

	Paraleptastacus spinicaudata triseta			Dumont et al. 2004
	Schizopera borutzkyi			Dumont et al. 2004
	Schizopera neglecta			Dumont et al. 2004
Cumacea	*Caspiocuma campylaspoides*			Dumont et al. 2004
	Pseudocuma cercaroides			Dumont et al. 2004
	Pterocuma pectinata			Dumont et al. 2004
	Pterocuma rostrata			Dumont et al. 2004
	Pterocuma sowinskyi			Dumont et al. 2004
	Schizorhynchus eudorelloides			Dumont et al. 2004
	Stenocuma cercaroides			Alexandrov et al. 2007
	Stenocuma tenuicauda			Dumont et al. 2004
Decapoda	*Astacus astacus colchius*			Dumont et al. 2004
	Astacus leptodactylus			Dumont et al. 2004
Harpacticoida	*Ectinosoma abrau*			Alexandrov et al. 2007
	Nitroca incerta			Alexandrov et al. 2007
	Schizopera bobrutzkyi			Alexandrov et al. 2007
Isopoda	*Jaera istri*		X	Dumont et al. 2004
	Jaera sarsi			Alexandrov et al. 2007
Mollusca	*Dreissena bugensis*		X	Dumont et al. 2004
	Dreissena polymorpha	1824		Dumont et al. 2004
	Hypanis colorata			Dumont et al. 2004
	Hypanis pontica			Alexandrov et al.

				2007
	Lithoglyphus naticoides		X	Dumont et al. 2004
	Theodoxus danubialis			Dumont et al. 2004
	Theodoxus pallasi			Dumont et al. 2004
	Valvata naticina			Dumont et al. 2004
Mysidacea	*Hemimysis anomala*	2004	X	Dumont et al. 2004
	Katamysis warpachowskyi			Dumont et al. 2004
	Limnomysis benedeni		X	Dumont et al. 2004
	Mesomysis kowalevskii			Alexandrov et al. 2007
	Paramysis baeri			Dumont et al. 2004
	Paramysis intermedia			Dumont et al. 2004
	Paramysis kessleri			Dumont et al. 2004
	Paramysis lacustris			Dumont et al. 2004
	Paramysis ullskyi			Dumont et al. 2004
Pisces	*Abramis sapa*			Ojaveer et al. 2002
	Acipenser stellatus			Ojaveer et al. 2002
	Clupeonella cultriventris			Copp et al. 2005
	Hucho hucho			Ojaveer et al. 2002
	Huso huso			Ojaveer et al. 2002
	Neogobius fluvialitis			Copp et al. 2005
	Neogobius gorlap			Copp et al. 2005
	Neogobius gymnotrachelus		X	Copp et al. 2005
	Neogobius kessleri			Copp et al. 2005
	Neogobius melanostomus		X	Copp et al. 2005
	Proterorhinus		X	Copp et al. 2005

	marmoratus		
	Proterorhinus semilunaris	X	Copp et al. 2005
	Rutilus frisii kutum		Alexandrov et al. 2007
	Umbra krameri		Ojaveer et al. 2002
Turbellaria	*Dendrocoelum romanodanubiale*		Dumont et al. 2004
	Oligochoerus limnophilus		Dumont et al. 2004

APPENDIX B. Freshwater invasive species present in Great Britain. Data extracted from the Great Britain Non Native Species Secretariat (www.nonnativespecies.org). Closest management catchment assigned using geographic information on the place of first report and management catchments delineated by the Environment Agency (see http://www.environment-agency.gov.uk/research/planning/131506.aspx).

Order	Species name	English name	Origin	Date and location of first Record	Management Catchment
Alismatales	*Egeria densa*	Large-flowered waterweed	South America	1953, Ashton Canal, Droylesden	Irwell
	Elodea nuttallii	Esthwaite water-weed	North America	1966, Beard Mill, Stanton Harcourt	Thames and South Chilterns
	Lagarosiphon major	Curly waterweed	Africa	1944, Nr. Artlessly	Upper and Bedford Ouse
	Lemna minuta	Least duckweed	North and South America	1977, Cambridge	Upper and Bedford Ouse
	Potamogeton epihydrus	American pondweed	Europe and North America	1907, Salterhebble Bridge	Aire and Calder
	Sagittaria latifolia	Duck-potato	North America	1941, Epsom Common	Wey
Amphipoda	*Corophium curvispinum*	Caspian mud shrimp	Europe	1935, River Avon, Tewkesbury	Severn Vale
	Crangonyx pseudogracilis	Northern river Crangonyctid	North America	1935, London	London
	Dikerogammarus haemobaphes	Demon shrimp	Europe	2012, Severn River	Norfolk broads
	Dikerogammarus villosus	Killer shrimp	Europe	2010, Grafham Water Reservoir,	Upper and Bedford Ouse

				Cambridgeshire	
Apiales	*Hydrocotyle ranunculoides*	Floating pennywort	South America	1990, Essex	Combined Essex
Arguloida	*Argulus japonicus*	Japanese fish louse	Asia	1991, Kent	Medway
Bryozoa	*Lophopus crystallinus*	bellflower	Asia	2003, River Loddon	Loddon
Cestoda	*Atractolytocestus huronensis*	Tapeworm	Asia	1993, Thames Valley	London
	Bothriocephalus acheilognathi	Tapeworm	Asia	1979, Yorkshire, Lincolnshire and Hertfordshire	Warfe and Lower Ouse
	Khawia sinensis	Tapeworm	Asia	1986, Gears Mill Farm, Shaftesbury, Dorset	Dorset
	Monobothrium wageneri	Tapeworm	Europe	1992, Spring Lake, Aldershot, Hampshire	Loddon
Cipriniformes	*Catostomus commersoni*	Common white Sucker	North America	1992, R. Gade (Hemel Hempstead)	Severn Vale
Commelinales	*Eichhornia crassipes*	Water hyacinth	South America	1982, Godstone, Surrey	Wey
Compsopogonales	*Compsopogon coerulens*		Unknown	1908, Reddish canal	Upper Mersey
Cypriniformes	*Ctenopharyngodon idellus*	Chinese grass carp	Eurasia	1960, Cambridgeshire Fens	Cam and Ely Ouse
	Leucaspius delineatus	Sunbleak	Europe	1995, Hampshire	Bristol Avon and North Somerset streams
	Misgurnus mizolepis	Chinese weather fish	Asia	2003, Sussex	Medway

	Pimephales promelas	Fathead Minnow (Rosy Reds)	North America	2003, Epping Forest (Middlesex)	London
	Pseudorasbora parva	Topmouth Gudgeon	Asia	1990, Crampmoor fishery (Hampshire)	Bristol Avon and North Somerset streams
	Rhodeus amarus	Bitterling	Eurasia	1920, Cheshire and Lancashire (Blackbrook Canal near St-Helens)	Mersey estuary
Decapoda	*Astacus astacus*	Noble crayfish	Europe	1980, River Chew	Bristol Avon
	Astacus leptodactylus	Turkish crayfish	Eurasia	1970, Loddon	London
	Orconectes limosus	Spinycheek crayfish	North America	1997, East Sussex	Warwickshire
	Procambarus clarkii	Red swamp crayfish	North America	1990, Tilbury and the Grand Union Canal	Nene
Myrtales	*Ludwigia peploides*	Floating water-primrose	North and South America	1999, Barton-on-Sea, Hampshire	Test and Itchen
Mysida	*Hemimysis anomala*	Bloody-red mysid	Europe	2004, English Midlands	Trent river
Nymphaeales	*Cabomba caroliniana*	Carolina water-shield	North America	1971, Forth and Clyde Canal	Scotland
Perciformes	*Ambloplites rupestris*	Rock Bass	North America	1937, Linkside Lake, Oxford	Thames and South Chilterns
	Tilapia zillii	Redbelly tilapia	Africa	1963, Church Street Canal, St-Helens, Lancashire	Mersey estuary

Poecilostomatoida	*Ergasilus briani*	Parasitic copepod	Europe	1982, Gawthorpe, Yorkshire	Wharfe and Lower Ouse
	Ergasilus gibbus	Parasitic copepod	Europe	1969, Slapton Ley, Devon	South Devon
	Ergasilus sieboldi	Parasitic copepod	Europe	1967, Yorkshire	Wharfe and Lower Ouse
	Neoergasilus japonicus	Parasitic copepod	Europe	1980, Horsham, Sussex	Medway
Saxifragales	*Crassula helmsii*	New Zealand pigmyweed	Australia	1956, Essex	Combined Essex
	Myriophyllum aquaticum	Parrot's feather	South America	1960, Lingfield in Surrey	Wey
Siluriformes	*Clarias batrachus*	Walking catfish	Asia	1963, Church Street Canal, St-Helens, Lancashire	Ribble
	Ictalurus punctatus	Channel catfish	North America	1969, Buckinghamshire and Surrey	Wey
Siphonostomatoida	*Tracheliastes maculatus*	Parasitic copepod	Europe	1990, Twine Valley Farm, Lancashire	Mersey estuary
	Tracheliastes polycolpus	Parasitic copepod	Europe	1961, Ouse, Swale, Derwent, Rye	Wharfe and lower Ouse
Spirurida	*Anguillicola crassus*	Eel swim bladder nematode	Asia	1987, River Trent	Lower Trent and Erewash
Veneroida	*Corbicula fluminea*	Asiatic clam	Asia	1998, the River Chet, Norfolk Broads	Broadland rivers
	Musculium transversum	Oblong orb mussel	North America	1856, Kensal Green	London

APPENDIX C. Dates of first report for freshwater invaders in Great Britain and The Netherlands. Only data from species first reported in The Netherlands and afterwards in Great Britain are included. Only species introduced after 1900 were considered. * Species of Ponto Caspian origin.

Organism type	Species Name	Year reported in The Netherlands	Year reported in Great Britain	Time lag
Crustacean	*Caprella mutica*	1993	2000	7
Crustacean	*Dikerogammarus haemobaphes**	2000	2012	12
Crustacean	*Dikerogammarus villosus**	1994	2010	16
Crustacean	*Eriocheir sinensis*	1930	1935	5
Crustacean	*Gammarus tigrinus*	1964	1993	29
Crustacean	*Hemimysis anomala**	1997	2004	7
Crustacean	*Orchestia cavimana*	1878	1942	64
Crustacean	*Orconectes virilis*	2004	2004	0
Crustacean	*Palaemon macrodactylus*	1999	2001	2
Crustacean	*Procambarus clarkii*	1978	1991	13
Fish	*Aristichthys nobilis*	1983	2005	22
Fish	*Carassius auratus*	1600	1694	94
Fish	*Ctenopharyniodon idella*	1968	1969	1
Fish	*Hypophthalmichthys molitrix*	1998	1999	1
Fish	*Lepomis gibbosus*	1903	1919	16
Fish	*Leucaspius delineatus*	1986	1995	9
Mollusc	*Corbicula iluminea*	1990	1998	8
Mollusc	*Crassostrea gigas*	1964	1965	1
Mollusc	*Ensis directus*	1981	1989	8
Mollusc	*Rapana venosa*	2005	2005	0
Other	*Anguillicola crassus*	1985	1987	2
Other	*Botrylloides violaceus*	2000	2004	4
Other	*Cordylophora caspia*	1884	1935	51
Other	*Mytilicola orientalis*	1992	1995	3
Other	*Hypania invalida**	1995	2008	13

Plant	*Acorus calamus*	1618	1668	50
Plant	*Elodea nuttalli*	1941	1966	25
Plant	*Lemna turionifera*	1992	2007	15

APPENDIX D. Literature review of alert Ponto-Caspian species. Information reviewed for each species includes:

Biological traits: Species biological characteristics such as reproduction and feeding behavior that can explain their success in colonizing new environments.

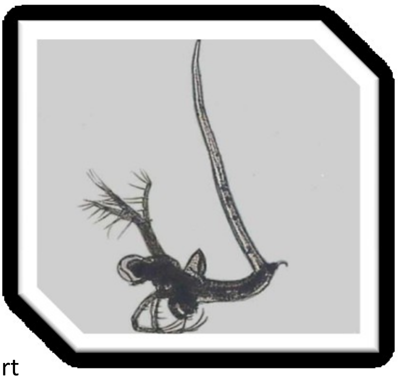
Habitat preference: preferences of the species at the local and regional scales.

Interaction with other PC species: Reported positive and negative interaction between Ponto Caspian invaders.
Dispersal: Vectors, means and velocity of dispersal.

Environmental impacts: Impacts on the abiotic and biotic component of ecosystems.

Economic impacts: Reported economic losses associate to invaders.

Environmental constrains: Conditions limiting the occurrence of the species.
Year reported in Great Britain and The Netherlands



CERCOPAGIS PENGOI, OSTROUMOV, 1891

English name: Fish hook waterflea
Taxonomic classification: Crustacea/ Cladocera/ Cercopagididae
Type of organism: Cladoceran

BIOLOGICAL TRAITS

Key life history characteristics of *Cercopagis* that facilitate dispersal and rapid population growth are: asexual reproduction, short generation times, early sexual maturity, high fecundity, the ability to produce diapausing eggs, and gregariousness, reaching abundances of up to 26000 ind./m^3 (Grigorovich et al. 2000, Makarewicz et al. 2001). It can reproduce parthenogenetically and gametogenetically depending on environmental cues (Grigorovich et al. 2000). *Cercopagis* has a broad diet (opportunistic feeding) on copepods, rotifers and podonis (Uitto et al. 1999).

HABITAT PREFERENCE

Cercopagis is common in the Caspian and Azov seas, in brackish estuaries of the Black Sea, and in the lower reaches of the Danube, Dniester, Bug, Dnieper and Volga Rivers (Mordukhai-Boltovskoi 1968, Mordukhai-Boltovskoi and Rivier 1987, Rivier 1998). It has also been recorded from coastal lakes fringing the Black (Lake Gebedzhinsko, Bulgaria, Valkanov 1951) and Aral Seas (Lake Sudoche, Kazakstan), from man-made reservoirs on the Don and Dnieper Rivers (Mordukhai-Boltovskoi 1968, Glamazda 1971, Mordukhai-Boltovskoi and Galinsky 1974, Gusinskaya and Zhdanova 1978, Volvich 1978) and connecting canals (Bazilevich 1972).

INTERATION WITH OTHER PONTO CASPIAN SPECIES

Not reported

DISPERSAL

Being a planktonic organism with diapausing eggs, *Cercopagis* can easily disperse through lakes and rivers (Kane et al. 2003, Panov et al. 2004). Adult *Cercopagis* are tolerant of high concentrations of salinity and could potentially be transported in ballast tanks flushed with sea water (Panov et al. 2004). Potential methods of secondary dispersal include attachment to fishing gear, bait buckets, and trailer-drawn boats, in plumage or digestive tracts of waterfowl or fish, or on contaminated plankton nets (MacIsaac et al. 1999, Makarewicz et al. 2001). In particular, *Cercopagis* eggs are undamaged by the digestive system of fish that can transport it great distances (Ansulevich and Valipakka 2000). In North America, small private boat traffic operating between Lake Michigan and Muskegon Lake is likely responsible for inland transfer of *Cercopagis* (Therriault et al. 2002).

ENVIRONMENTAL IMPACTS

Cercopagis predates on small zooplankton, and its arrival in the eastern Gulf of Finland –with densities as high as 1800 individuals per m^3—coincided with declines in cladoceran diversity (Leppäkoski et al. 2002). Significant declines and a change in the vertical distribution of the small cladoceran *Bosmina* (a significant component in the diet of planktivorous fish species) was noted following the spread of *Cercopagis* to the Gulf of Riga (Ojaveer et al. 1998, 2004, Pollumae et al. 2004). The effects on fish communities are mixed (Godard et al. 2012). In the Baltic, it is preyed upon by fish such as herring *Clupea harengus* and smelt *Osmerus eperlanus*, but *Cercopagis* is also considered a competitor with the larvae of these species, preying on the same small cladocerans (Ojaveer & Lumberg 1995; Ojaveer et al. 1998; Gorokhova et al. 2005; Kotta et al. 2006).

By adding another link to the food web, *Cercopagis* invasions could increase contaminant concentrations (such as mercury and PCBs) in fish (Van der Ploeg et al. 2002).

ECONOMIC IMPACTS

While *Cercopagis* may at certain times be a significant prey item for commercial fish species, it also has negative economic impacts through the clogging of fishing nets, particularly during its mass occurrences in late summer (Leppäkoski and Olenin 2000, Godard et al. 2012). For instance, losses at a fish farm in the eastern Gulf of Finland from 1996 to 2000 exceeded USD 50,000$ due to a decline in fish catches as a result of net fouling (Panov et al. 2003). In the Baltic, *Cercopagis* is preyed by fish such as herring *Clupea harengus* and smelt *Osmerus eperlanus* (50-100% of their diet), but Cercopagis is also considered a competitor with the larvae of these species, preying on the same small cladocerans (Ojaveer and Lumberg 1995, Ojaveer et al. 1998, 2004, Gorokhova et al. 2005, Kotta et al. 2006). *Cercopagis* may be an important competitor of other planktivorous fish such as juvenile alewife *Alosa pseudoharengus* as well as forming an increasing component of the diet of adult alewifes (Benoit et al. 2002, Bushnoe et al. 2003, Laxson et al. 2003, Warner et al. 2006).

ENVIRONMENTAL CONSTRAINS

Depth: Cercopagis occupies intermediate depths (10-100m) relatively far from the shore (>1km) in the sea. However a contrasting pattern is reported from freshwater reservoirs where the speceis occupied the littoral zone (Gorohkova et al. 2000).

Salinity and ionic elements: *Cercopagis* tolerates a wide range of salinities (from 0.1 to 14% salinity, Kane et al. 2003), with maximum abundance recorded in the Baltic Sea at salinity 5.7-5.8% (Gorohkova et al. 2000). High salinity may prevent the species expansion from the Baltic sea towards the North Sea, although shipping may allow invasion of coastal lakes with access to the sea (Gorohkova et al. 2000).

Temperature and pH: Cercopagis tolerates a wide range of temperatures (7 to 30 ˚C, McIsaak et al. 1999, Kane et al. 2003). Maximum abundance in the Baltic Sea was recorded at temperatures of 12-22 ˚C (Gorohkova et al. 2000). In North America, highest abundance of up to 100.000 idv./m^3 was reported at a temperature of 20-30 ˚C (McIsaac et al. 1999). In the gulf of Finland, population density of *Cercopagis* peaked twice during the vegetation season: at water temperatures 18–19.5 °C (July and August) and at 12.5–14 °C (September) (Telesh et al. 2000).

CHAETOGAMMARUS WARPACHOWSKI, MARTYNOV, 1925

Taxonomic classification: Crustacea/ Amphipoda/ Gammaridea
Type of organism: Gammarid

BIOLOGICAL TRAITS

Relatively short life span and generation time, protection of juveniles, omnivorous feeding, with a broad variety of ecological living conditions including a wide range of salinities (bij de Vaate et al. 2002). No other information on reproductive behaviour was found. Although feeding habits are not reported in the literature, we may assume that, similar to other Ponto Caspian gammarids, *C. warpachowski* is omnivore, feeding from the range of available food sources such as organic deposited material, small cladocerans or algae.

HABITAT PREFERENCE

C. warpachowski inhabits brackish parts of the Caspian Sea and the deltas and estuaries of many large Ponto-Caspian rivers (bij de Vaate et al. 2002).

INTERATION WITH OTHER PONTO CASPIAN SPECIES

Not reported

DISPERSAL

Not reported

ENVIRONMENTAL IMPACTS

No environmental impacts have been reported although similar effects to other Ponto Caspian species (e.g. displacement of native species through competition, food web alterations) might be expected.

ECONOMIC IMPACTS

Not reported

ENVIRONMENTAL CONSTRAINS

Salinity and ionic elements: While the species is tolerant to varying levels of salinity (Holdich and Pockl 2007), experiments showed 100% mortality in sea water within just one hour (Santagata et al. 2008).

Nutrients: The species tends to occur in sites with higher nutrient contamination of the Nemunas River (Lithuania) (Arbačiauskas et al. 2011).

Temperature and pH: Tolerant to varying levels of temperature (Holdich and Pockl 2007).

CHELICOROPHIUM CURVISPINUM, G.O. SARS, 1895

English name: Caspian mud shrimp
Taxonomic classification: Crustacea/ Amphipoda/ Gammaridea
Synonym: *Corophium curvispinum*
Type of organism: Gammarid

BIOLOGICAL TRAITS

C. curvispinum is one of the most successful immigrant shrimp in continental waters thanks to its relatively short life span and generation time, rapid growth, high fecundity, multiple generation sper year, protection of juveniles, gregarious behavior and suspension feeding, with a broad variety of ecological living conditions including a wide range of salinities (bij de Vaate et al. 2002, den Hartog et al. 1992).

HABITAT PREFERENCE

C. curvispinum prefers large, slow flowing stagnant waters in the lower reaches and even brackish waters (Nesseman et al. 1995). It developes dense populations and can become the most numerous macroinvertebrate in the bottom and litoral zone on stones, wooden piles, aquatic macrophytes, algae, silt and sponge debris, on the brickwork of locks and bridges (Nesseman et al. 1995). In the Wloclawek Dam reservoir, it prefers sites distant from shore, overgrown by macrophytes or covered by mussel shells (Zytkowicz et al. 2008).

INTERATION WITH OTHER PONTO CASPIAN SPECIES

C. curvispinum probably reduced the colonization success of *E. ischnus* (a lithophilic dweller) by covering the solid substrates in the river with mud tubes. High densities of *C. curvispinum* observed in the Rhine River strongly impacted the zebra mussel (Van der Velde et al. 1998), although in Lake Balaton (Hungary) and the lower Vistula river they seemed to benefit each other (Sebestyen 1937, Jażdżewski and Konopacka 2002). Although competition and intra-guild predation are often among Ponto Caspian amphipods, MacNeil et al. (2012) found no evidence of competition or predation between *C. curvispinum* and *D. villosus*, thus coexistence may be possible.

DISPERSAL

Dispersal in Russia and Europe has been associated to the construction of canals such as the Pripet-Bug canal between the Vistula and Dnieper (Berezina et al. 2007, Jazdzewski 1980), intentional introduction to improve fish stocks (Alexandrov et al. 2007), ballast water and hull fouling (Leppäkoski and Olenin 2000, bij de Vaate et al. 2002). The British population was likely dispersed by ships sailing from northern Germany ports after their appearance in the Elbe River in 1920 (Harris 1991).

Regarding dispersal rates, in the Meuse river (France) *C. curvispinum* showed an average upstream migration speed between 15 and 17 km/year (Josens et al. 2005, d'Acoz and Stroot 1988). However in the Rhine, velocities reported by Leuven et al. (2008) where much higher: 44km/year on average (minimum 14 and maximum 137 km/year). Moreover, *C. curvispinum* was one of the few species able to move upstream from Kaunas Water reservoir in Lithuania (Arbačiauskas 2008).

Downstream passive dispersal during floods has been also remarked by several studies (Lyakhov, 1961). For instance, in the river Rhine, juveniles of *C. curvispinum* contributed 90% of drifting macroinvertebrates from July to September (van Riel et al. 2011). Water velocity was nevertheless not found to have a significant effect on drifting in this study, which seems to be triggered by the species abundance. Other studies mentioned that floating substratum can aid in its possible transmission (Taylor and Harris 1986, Van den Brink et al. 1993).

ENVIRONMENTAL IMPACTS

Amongst the negative biotic impacts of *C. curvispinum* we can highlight: reduced macroinvertebrate species richness, including benthic animals that are an important source of food for bottom dwelling fish (Van der Velde et al. 1998, Van der Velde et al. 2002), displacement of native species (e.g. *Asellus aquaticus, Hydropsyche* spp., caseless caddisfly larvae and several species of chironomid larvae in the Rhine, Kinzelbach 1997, Ricciardi and Rasmussen 1998), decrease in algae abundance and alteration of the food web (e.g. it is preyed by fish, van Riel at al. 2006).

The abiotic changes produced by this species are related to the collection of suspended particles from the water column for the construction of mud tubes (up to 4 cm thick) on solid substrates in which they live (bij de vaate et al. 2002, Van der Velde et al. 2002). This produces a significant reduction of the total organic carbon and suspended material, and increased water clarity (Van den Brink et al. 1993). Environmental impacts extended over a distance of 200–500 km in the Rhine (Van den Brink et al. 1993).

ECONOMIC IMPACTS

Not economic impacts have been reported although it might affect fisheries and the conservation/ recreational value of waterbodies.

ENVIRONMENTAL CONSTRAINS

Salinity and ionic elements: Experiments showed 100% mortality in sea water within just one hour (Santagata et al. 2008). The success of *C. curvispinum* in the River Rhine was linked with relatively high chloride concentration (Van den Brink et al. 1993). However, Harris and Bayliss (1990) showed its acclimation capacity toward lower ion concentrations that may consequently not prevent its invasion.

YEAR REPORTED IN GREAT BRITAIN AND THE NETHERLANDS

In Great Britain, *C. curvispinum* was first recorded in the River Avon at Tewkesbury in 1935.

Reported from the middle and lower Rhine in 1987 (Van den Brink et al. 1989).

CHELICOROPHIUM ROBUSTUM, G.O. SARS, 1895

Taxonomic classification: Crustacea/ Amphipoda/ Gammaridea
Synonym: *Corophium robustum*
Type of organism: Gammarid

BIOLOGICAL TRAITS

No information on the species reproduction or feeding behaviour was found, although we may assume it similar to *C. curvispinum*.

HABITAT PREFERENCE

C. robustum was noted to occur on hard bottom substrates of the Dniester River as opposed to other coriphiids (Jazdzewski and Konopacka 1985). It has been recorded in rivers, (overall lower stretches such as the the Hungarian section of the Danube) but not in stream or lakes (Borza 2011). It has been also recorded from the River Main (Bernerth and Stein 2003) and the Rhine (Bernaurer and Jansen 2006).

INTERATION WITH OTHER PONTO CASPIAN SPECIES

C. robustum was sampled in combination with *D. villosus, D. haemobaphes* and *C. curvispinum* in France (Labat et al. 2011). In the Rhine it co-occurs with *C. curvispinum* with one or the other dominanting depending on the circumstances (Borza 2011).

DISPERSAL

C. robustum's spread has been related to intentional introduction in Ukraine lakes to improve fish stocks (Alexandrov et al. 2007), and also to the construction of waterways (Leuven et al. 2009) and to ship traffic (e.g. in the Rhine River, Bernauer and Jansen 2006). The species is known to be present in Poland, Germany (Holdich and Pockl 2007), France (Labat et al. 2011), Belarus (Semenchenko et al. 2011) and Hungary (Borza 2011).

ENVIRONMENTAL IMPACTS

Although no impacts have been detailed in the literature, in Hungary *C. robustum* showed a strong dominance over the species present and it was sometimes the only species found. Such mass occurrence affected other amphipods such as *C. curvispinum* and *C. sowinski* only two years after invasion (Borza 2011). *C. robustum* is included in the European Black List of aquatic invaders of Panov et al. (2009) because of its high risk of dispersal, establishment and impact.

ECONOMIC IMPACTS

Not reported

ENVIRONMENTAL CONSTRAINS

Not reported

CHELICOROPHIUM SOWINSKYI, MARTYNOV, 1924

Taxonomic classification: Crustacea/ Amphipoda/ Gammaridea
Synonym: *Corophium sowinskyi*
Type of organism: Gammarid

BIOLOGICAL TRAITS

Relative short life span and generation time, protection of juveniles, suspension feeding, omnivore feeding, with a broad variety of ecological living conditions including a wide range of salinities (bij de Vaate et al. 2002).

HABITAT PREFERENCE

The species was recorded in several off shore lakes of the Black Sea and of the Sea of Marmara (Mordukhai-Boltovskoi 1960, 1964, Jażdżewski 1980). It was also recorded in the Danube upstream of Göd, being the first Corophiidae record in Hungary, in lower reaches of the Titsa River and its major tributaries and in the Dráva (Borza 2011)

INTERATION WITH OTHER PONTO CASPIAN SPECIES

C. sowinskyi is very difficult to distinguish from *C. curvispinum*, thus biogeographical patterns and interaction with other species are difficult to discriminate (Jazdzewski 1980, Jazdzewski and Konopacka 1996). In Hungary, *C. sowinskyi* colonized first and was later replaced by *C. curvispinum* (Borza 2011).

DISPERSAL

Migration patterns of *C. sowinskyi* are unclear because the species is difficult to distinguish from *C. curvispinum* (Gherardi 2007).

ENVIRONMENTAL IMPACTS

Although there are no literature references, impacts of *C. sowinskyi* are expected to be similar to *C. curvispinum* in North America (Ricciardi and Radmussen 1998), including: displacement of cadisflies filter-feeders (*Hydropsyche* sp.) and other benthic invertebrates including zebra mussels (van der Velde et al. 1994), reductions in total organic carbon and suspended material (van den Brink et al. 1993).

ECONOMIC IMPACTS

Not reported

ENVIRONMENTAL CONSTRAINS

Not reported

DIKEROGAMMARUS BISPINOSUS, SOWINSKY, 1894

Taxonomic classification: Crustacea/ Amphipoda/ Gammaridea
Type of organism: Gammarid

BIOLOGICAL TRAITS

D. bispinosus is is often considered and mentioned as a subspecies of *D. villosus* (bij de Vaate et al. 2002). Amongst its succesful biological traits, bij de Vaate et al. (2002) highlights: relatively short life span and generation time, protection of juveniles, non-specific food preference, with a broad variety of ecological living conditions including a wide range of salinities, and larger body size than closely related species, or alternatively much smaller.

HABITAT PREFERENCE

D. bispinosus penetrates farthest upstream in Ponto-Caspian rivers (Jazdzewski and Konopacka 1988). For instance, in the Dniester River, the relative abundance of *D. bispinosus* decreased in the downstream direction (bij de Vaate et al. 2002).

INTERATION WITH OTHER PONTO CASPIAN SPECIES

D. bispinosus co-occurs with *D. villosus* and *E. ischnus* in (Kley and Mayer 2005). Together with *D. haemobaphes*, it outcompetes native *G. roeseli* (bij de Vaate et al. 2002).

DISPERSAL

The most recent observations of *D. bispinosus* have been reported from Austria and Germany (Müller and Schramm 2001).

ENVIRONMENTAL IMPACTS

Not reported

ECONOMIC IMPACTS

Not reported

ENVIRONMENTAL CONSTRAINS

Oxygen: The species was observed at 94-125% DO saturation in the Danube-Rhine (Kley and Maier 2006).

Salinity and ionic elements: Observed at 442-521 µS/cm in the Danube-Rhine system (Kley and Maier 2006).

Nutrients: Observed at 36-69 µg/L phosphate, 0.1-2.6 mg/L nitrate in the Danube-Rhine (Kley and Maier 2006).

Temperature and pH: Observed at 9.2-24.6 ˚C in the Danube-Rhine (Kley and Maier 2006).

YEAR REPORTED IN GREAT BRITAIN AND THE NETHERLANDS

It was detected in 2008 in The Netherlands.

DIKEROGAMMARUS HAEMOBAPHES, EICHWALD, 1841

English name: Demon shrimp
Taxonomic classification: Crustacea/ Amphipoda/ Gammaridea
Type of organism: Gammarid

BIOLOGICAL TRAITS

Very high fecundity thanks to its relatively short life span and generation time, protection of juveniles, nonspecific food preference, euryhalinity and body size larger than closely related species or alternatively much smaller (bij de Vaate et al. 2002, Grabowski et al. 2007a). *D. haemobaphes* has a very high reproductive potential due to its high fecundity, early maturity, and multiple reproduction cycles per year. It reproduces from April to October, but year-round in thermal polluted waters, like cooling water discharges of electric power plants (Kititsyna 1980).

HABITAT PREFERENCE

D. haemobaphes occurs naturally in the lower and middle courses of the Black and Caspian Sea Basin Rivers and brackish lagoons, down to the Sea of Marmara. This species generally occupies deeper areas of southern European rivers but it is adapted to shallower areas with favourable trophic, oxygen and temperature conditions, migrating into deeper water only during storms or when the substratum dries (Berezina et al. 2007, Poznanska et al. 2013).
At the local scale, *D. haemobaphes* prefers solid substrates (Pöckl 1988, 2002), macrophytes, and filamentous algae in large rivers and lakes (Kititsyna 1980, Muskó 1994). In the Wloclawek Dam reservoir, it preferred sites distant from shore (lotic), overgrown by macrophytes or covered by mussel shells (Zytkowicz et al. 2008).

INTERATION WITH OTHER PONTO CASPIAN SPECIES

In the lower sections of rivers, *D. haemobaphes* generally co-occurrs with two other Ponto-Caspian immigrants: *P. robustoides* and *E. ischnus* (bij de Vaate et al. 2002), although *D. haemobaphes* outcompeted them in the Vistula river (Jazdzewski et al. 2004). Its ability to detect and actively select zebra mussel habitats may be beneficial and help it establish stable populations in newly invaded areas (Kobak et al. 2009). According to Muller et al. (2002) *D. haemobaphes* invades first, followed by *D. villosus* which eventually outcompetes *D. haemobaphes*.

DISPERSAL

Dispersal in Ukraine and Russia is associated to the intentional introduction to improve fish stocks (Alexandrov et al. 2007) and the construction of canals such as Volga-Baltic waterway (Berezina and Panov 2003), followed by subsequent natural dispersal (Berezina et al. 2007). The construction of the Main-Danube canal also facilitated the invasion of the Rhine River. Downstream passive dispersal during floods can be relevant (up to 3000 ind/s according to Lyakhov 1961), while upstream dispersal can be also particularly important in large rivers (e.g. the species reached up to 4000 km from their native area in the Volga, Lyakhov 1958). *D. haemobaphes* is able to disperse upstream more than *D. villosus*, which may facilitate certain habitat partition. The construction of reservoirs debilitate native communities and offers new empty niches which may facilitate the introduction of invasive Ponto Caspian species. For instance, after construction of the Dnepropetrovsky Reservoir on the Dnieper River, *D. haemobaphes* colonized the reservoir and became one of the dominant species (Mordukhai-Boltovskoi, 1960).

ENVIRONMENTAL IMPACTS

In comparison to *D. villosus*, there is little information available on its ecological impact (Godard et al 2012). However *D. haemobaphes* is now the dominant amphipod in stretches of the River Vistula (Jazdzewski et al. 2004)

ECONOMIC IMPACTS

Not reported

ENVIRONMENTAL CONSTRAINS

Oxygen: Observed at 102-145% oxygen saturation in the Danube-Rhine (Kley and Maier 2006).

Salinity and ionic elements: Observed at 471-529 µS/cm in the Danube-Rhine (Kley and Maier 2006), although the species tolerates salinities from fresh water up to 8‰ (Ponomareva 1975).

Nutrients: Observed at 22-26 µg/L phosphate, 0.1-2.2 mg/L nitrate in the Danube-Rhine (Kley and Maier 2006).

Temperature and pH: Observed at 9.0-25.4 ˚C in the Danube-Rhine (Kley and Maier 2006), but able to tolerate a wider temperature range (6–30 °C) (Kititsyna 1980).

YEAR REPORTED IN GREAT BRITAIN AND THE NETHERLANDS

Th species reached The Netherlands through the Rhine River in 2000 (bij de Vaate et al. 2002) and was detected in Great Britain in the Severn river in 2012.

DIKEROGAMMARUS VILLOSUS, SOWINSKY, 1894

Engish name: Killer shrimp
Taxonomic classification: Crustacea/ Amphipoda/ Gammaridea
Type of organism: Gammarid

BIOLOGICAL TRAITS

Very high reproductive potential, versatile feeding and high habitat adaptability explain the great invasion success of *D. villosus*. First, its reproductive effectiveness is based on its high fecundity, long reproductive period, early sexual maturity, short generation time, life span not exceeding 1 year (with up to three generations and 14 cohorts being present at the same time), high growth rates (resulting in large body size), short duration of embryonic development, multiple reproduction cycles per year, large numbers of small eggs in the brood pouch (>100 eggs), and optimal timing (i.e. to release the maximum number of neonates per female in May/June thereby maximizing rapid growth at high summer temperatures and at times of plentiful food) (Kley and Maier 2006, Grabowski et al. 2007a, Pockl 2009).

Second, this species appears to be a very versatile feeder, either acting as a filter-feeder exploiting micro-algae (Platvoet et al. 2006) or as a very effective predator preying upon other macroinvertebrates (MacNeil and Platvoet 2005, Krisp and Maier 2005, Kley and Maier 2003, Devin et al. 2003, Dick and Platvoet 2000, Van Riel et al. 2006) and hunting for fish eggs or juveniles (Casellato et al. 2005). Dick and Platvoet (1996) attributed this to the species relatively large body size and un-specified mouth parts. The stout mandibles with well-developed incisors enable the species to kill prey with robust integument. The setae on the maxillae and maxillipeds are used, together with the gnathopods and the antennae, to filter suspended algae and other small particles from the water current and to collect detritus. No specific tool for scraping periphyton from the substratum is observed, however, and the molar surfaces of the mandibles are weakly structured, suggesting a limited efficiency in feeding on macrophytes (Hanfling et al. 2011). The extraordinary feeding capacity of *D. villosus* is further illustrated by isotope analysis (N), that positions it at the benthivorous fish trophic level (Marguillier et al. 1998).

Phenotypic plasticity (from melanic to striped forms) may favour its establishment (Devin et al. 2001, 2004).

HABITAT PREFERENCE

D. villosus is naturally distributed in the lower courses of large rivers in the Black and Caspian Sea basins (Mordukhai-Boltovskoi 1969). Present in rivers with high oxygen saturation, low conductivity, high pH (Boets et al. 2010), *D. villosus* seems to be excluded from the smaller rivers and tributaries in parts of Europe (Bij de Vaate et al. 2002). Notably, the species does not usually invade river tributaries that are more natural, not navigated, flow faster, contain less dissolved salts, are cooler and poorer in phytoplankton than the main river chanel (e.g. the Meuse River, Josens et al. 2005). Nevertheless, its recent recording in the river Doubs and in a second tributary of the river Saône suggests a possible extension of *D. villosus* to whole drainages in the near future (Bollache et al. 2004). Similar to *D. haemobaphes, D. villosus* generally occupies deeper areas of rivers but is adapted to shallower areas with favourable trophic, oxygen and temperature conditions in reservoirs of Russia, migrating into deeper water during storms or substrate drying (Berezina et al. 2007).

At the local scale, *D. villosus* preferred gravel substrate, absent on sand (van Riel et al. 2004). In Flanders, *D. villosus* prefered fresh waters with a non-natural bank structure (e.g. canals) and a fairly good chemical water quality (Boets et al. 2012).

INTERATION WITH OTHER PONTO CASPIAN SPECIES

D. villosus may replace other alien amphipods through competition and intraguild predation (Berezina et al. 2007). For instance, it outcompeted *D. haemobaphes* in the Danube (Nesemann et al. 1995, Weinzierl et al. 1996, Kley and Maier 2003), *G. tigrinus* in the Rhine, and native *G. duebeni* in Lake Ijsselmeer (Kelleher et al. 1999, Dick and Platvoet 2000). *D. villosus* can further prevent the invasion of *D. bispinosus* (Kinzler and Maier 2003) and has been shown to predate on crayfish (*Orconectes virilis*) juveniles in experimental designs (Buric et al. 2009).

Despite its aggressive behaviour, *D. villosus* is also able to coexist and even benefit from the presence of other Ponto Caspian invaders. Most notably, zebra mussel populations may help the colonisation of the killer shrimp by providing habitat complexity through the production of byssus threads, shells and food material through biodeposition (Gergs and Rothhaupt 2008). Furthermore, Devin et al. (2003) described an association between small individuals of *D. villosus* and *C. curvispinum*, which co-evolved over a long period as they originate from the same area. In Dutch lakes coexistence was explained by habitat partitioning observed between *D. villosus*, found on rocks in shallow waters, and *C. curvispinum* in soft sediments in deeper waters (Noordhuis et al. 2009). Another example of habitat partitioning is found in the River Rhine, where *D. villosus* occupy the benthic stony habitats, whereas *E. ischnus* occupies the water column, macrophyte beds and the shoreline (Kley and Maier 2005, van Riel et al. 2009).

DISPERSAL

D. villosus was intentionally introduced in Ukraine lakes to improve fish stocks (Alexandrov et al. 2007). However, it was the opening of canals to connect river basins, such as the Main–Danube–Rhine canal that facilitated the dispersal of *D. villosus* westwards (Dick and Platvoet 2000, Casellato et al. 2006).

According to the review of Godard et al (2012), *D. villosus* is thought to have spread initially either via ship ballast water tanks or as hull foulants (Mayer et al. 2009), followed by natural dispersal. Passive dispersal during floods is one of its natural dispersal methods, juveniles contributing the largest percentage of drifting macroinvertebrates during spring in the Rhine (van Riel et al. 2011). In the Rhine study, water velocity was not found to have a significant effect on drifting, which seemed to be triggered by the species abundance. Upstream dispersal may also be important in this species, able to move up to 4000 km from their native area in the Volga (Lyakhov, 1958). In this sense, Josens et al. (2005) recorded a 30-40 km upstream dispersal in the Meuse, regularly and without 'gaps', which suggest active migration in addition to ship transport.

Secondary invasion into inland lakes is associated to recreational vessels (Casellato et al. 2006), since *D. villosus* can survive up to six days out of water when fouling boats (Martens and Grabow, 2008) and 3.5 days in swimsuits (Bacela et al. 2013).

Bollache et al. (2004) notes the possibility of French harbours helping the species to spread through international shipping. In UK, *D. villosus* is likely to continue its spread facilitated by its broad environmental tolerances, climatic suitability, and the extensive connectivity, both natural and artificial, of the hydrological network (Gallardo et al. 2012).

ENVIRONMENTAL IMPACTS

The numerous impacts associated with the killer shrimp has led to this species being named as one of the 'Top 100' invasive alien species in Europe (www.europe-aliens.org). *D. villosus* displaces both native (e.g. *G. duebeni, G. pulex, G. roeseli, A. asellus, E. berilloni, O. limosus*) and invasive (e.g. *G. tigrinus, G. pseudogracillis, D. haemobaphes*) species (bij de Vaate et al. 2002, Bollache et al. 2004, 2008, Boets et al. 2010, Dick and Platvoet 2000, MacNeil and Platvoet 2005, 2008, Kinzler et al. 2009) leading to a notable decline in native species richness and abundance (Van der Velde et al. 2000). In experimental designs, *D. villosus* actively attacked *Asellus sp., Gammarus duebeni*, larvae of mayflies, chironomids and even aquatic beetles (Dick et al. 2002). Moreover, experimental analyses demonstrated that *D. villosus* can consume up to 25 mg biomass per day (1/3 of its own weight) which illustrates its capacity to

modify aquatic communities (Krisp and Maier 2005). In the Rhine River, *D. villosus* has become one of the key secondary consumers occupying high trophic levels comparable to fish (Van Riel et al. 2006).
Lower efficiency in leave-shredding compared to other native species may change organic matter processing (MacNeil et al. 2011), with a study reporting a decrease in leaf litter decomposition of 66% (Piscart et al. 2011).
D. villosus can be a vector of parasitic microsporidia (e.g. *Nosema dikerogammari, Cucumispora dikerogammari*) and gregarines (e.g. *Uradiophora ramosa, U. longissima, Thelohania* sp. and *Cephaloidophora mucronata*) (Ovcharenko et al. 2006, 2009, 2010), although threre are no reports of transference to other species (Bacela-Spychalska et al. 2012).

ECONOMIC IMPACTS

Not reported

ENVIRONMENTAL CONSTRAINS

Depth: The species prefers depths between 1 and 5 m (Lods-Crozet and Reymond, 2006).

Oxygen: *D. villosus* has been observed at relatively well oxygentaed waters: 33-155% oxygen saturation in Belgium (Boets et al. 2012), 15-126% in Croatia (Boets et al. 2012), 94-125% in the Danube-Rhine (Kley and Maier 2006).

Under low oxygen concentration (0.1-0.3 mg/L) *D. villosus* is able to become motionless (Mordukhai-Boltovskoi 1960).

Salinity and ionic elements: With a wide salinity and temperature tolerance, the species survives up to 10‰ salinity within ten acclimation days. However >25‰ salinity seems lethal (Bruijs et al. 2001). The species has been observed at 97-2710 µS/cm in Belgium, 142-516 µS/cm in Croatia (Boets et al. 2012), 171-444 µS/cm2 in the Alps, and 442-521 µS/cm in the Danube-Rhine (Kley and Maier 2006).

Nutrients: Observed at 1.3-11.9 mg TN/L, 0.49-7.2 mg NO_3/L, 0.09-1.0 mg TP/L, 0.04-2.4 mg NH_4/L in Belgium. Observed at 0.45-7.2 mg TN/L, 0.22-1.81 mg NO_3/L, 0.01-2.75 mg TP/L, 0.02-3.07 mg NH_4/L in Croatia (Boets et al. 2012). Observed at 36-69 µg/L phosphate, 0.1-2.6 mg/L nitrate in the Danube-Rhine (Kley and Maier 2006)

Temperature and pH: Observed at 9.2-24.6 ˚C in the Danube-Rhine (Kley and Maier 2006).

YEAR REPORTED IN GREAT BRITAIN AND THE NETHERLANDS

The species was detected in 1994 in the Rhine estuary (bij de Vaate et al. 2002) and in 2010 in Grafham reservoir (Great Ouse River, UK).

DREISSENA R. BUGENSIS, ANDRUSOV, 1897

English name: Quagga mussel
Taxonomic classification: Mollusca/ Veneroida/ Dreissenidae
Type of organism: Mollusc

BIOLOGICAL TRAITS

The high reproductive potential of *D. r. bugensis*, able to produce up to 1.000.000 eggs per season, explains its invasion success (Astanei et al. 2005). In experimental designs *D. polymorpha* spawned more total eggs in response to serotonin than comparably sized *D. r. bugensis* (Stoeckmann 2003). However, although individual *D. r. bugensis* spawn fewer eggs than *D. polymorpha* over an entire season, their capability of settling, growing, and spawning earlier in the season and in deeper, colder basins that are unsuitable for *D. polymorpha* may give quagga mussels an advantage of building larger total populations in areas that they do colonize (Roe and MacIsaac 1997. Claxton and Mackie 1998, Nalepa et al. 2010).

HABITAT PREFERENCE

D. r. bugensis occurs in several inshore Black Sea lakes (Jazdzewski 1980). *D. r. bugensis* typically colonize the deeper parts of a reservoir before expanding into shallower depths occupied by *D. polymorpha*, which leads to a decline in abundance of the latter species (Mills et al. 1996, Pligin 1984). However, *D. r. bugensis* produce byssal threads slower than *D. polymorpha*, which may explain its lower capacity to survive high water flow (Peyer et al. 2009).

INTERATION WITH OTHER PONTO CASPIAN SPECIES

Dreissenids have been reported to positively affect the establishment of many other Ponto Caspian invaders, such as amphipods and gobiids, through the provision of habitat complexity, shelter and food (e.g. Campbell et al. 2009).

A complex relationship exists between the two most common invasive dreissenids. *D. r. bugensis* has been found to replace *D. polymorpha* at a rate of 36% annually, eventually outcompeting *D. polymorpha* both in Europe (Dnieper Rver) and North America (Great Lakes) (Mills et al. 1996). The competitive advantage of *D. r. bugensis* is related to its ability to live in cold as well as warm water (Dermott and Munawar 1993, Mills et al. 1996), allowing it to inhabit deeper waters than *D. polymorpha* (Imo et al. 2010). In the long run, these larger populations of *D. r. bugensis* may give them the potential to produce more progeny than *D. polymorpha* in the same areas, and hence ultimately to displace *D. polymorpha* (Ram 2012). Other factors that may affect the success of *D. r. bugensis* in displacing *D. polymorpha* include: the production of hybrids and differences in growth and respiration. For instance, higher filtration rates by *D. r. bugensis* (Diggins 2001) produce an approximately 20% higher assimilation rate than *D. polymorpha* when fed natural seston (Baldwin et al. 2002), hence growing to greater lengths and weight (Stoeckmann 2003).

DISPERSAL

D. r. bugensis started spreading in the 1990s when it was first located in the Don and Volga (Orlova et al. 2005) and later on (2006-2007) in the Netherlands (Molloy et al. 2007). However, the size of individuals suggest *D. r. bugensis* started distributing in Western Europe in 2004 (Imo et al. 2010), presumably related to the construction of irrigation canals and river impoundments in its watershed (Orlova et al. 2005). The species is thought to have been discharged in ballast water at the port of Antwerpe resulting in a large number of the species being present (Marescaux 2012).

A planktonic larval stage (veliger) makes *D. r. bugensis* well suited to spread naturally within lakes and reservoirs or downstream within a watershed (Stoeckel et al. 1997, Karatayev et al. 2003). In fact, Dreissenid larvae are able to drift downstream for 3–4 weeks and up to 300 km before they attach and find new populations (Bially and MacIsaac 2000, Bodamer and Bossenbroek 2008). The rapid expansion of *D. r. bugensis* is best illustrated in the river Main, completely invaded in just three years (Imo et al. 2010).

Upstream dispersal is very limited, related to human related activities such as shipping, fishing, boating, conversion or areas from riverine to lacustrine (Orlova and Shcherbina 2002). According to the study of Kappes and Haase (2011), the active upstream dispersal capacity of bivalves is below 0.1 km/year, although this velocity can increase 100x and even 1000x when supported by natural and human vectors respectively. Although the resistance of *D. r. bugensis* to dessication is 15-100% lower than that of *D. polymorpha* (Ricciardi et al. 1995), *D. r. bugensis* may still survive overland transport for 3-5 days.

ENVIRONMENTAL IMPACTS

Impacts of *D. r. bugensis* are very similar to those of *D. polymorpha* but reaching deeper (up to 130 m) (Mills et al. 1996). Changes in water chemistry include a reduction in calcium, alkalinity and turbidity and increase in transparency (Barbiero et al. 2006, MacIsaac 1996). Enhanced water clarity increases in turn light transmittance and growth of benthic plants. *D. r. bugensis*'s algae filtration also leads to important food web changes: it reduces the stock of zooplankton (copepods, rotifers) thereby affecting zooplanktivorous fish survival and growth (Bartsch et al. 2003, McIsaac 1996); benthic invertebrate's total biomass, species composition and relative abundance of functional groups change considerably (Burlakova et al. 2005, Karatayev et al. 1997); sensitive species such as unionid molluscs are particularly impacted by dreissenids; amphipod crustaceans and predatory fish exploit the structure associated with or wastes generated by dreissenids.

D. r. bugensis are affected by at least four types of trematodes (Laruelle et al. 2002) although their effects on the environment are not well known.

ECONOMIC IMPACTS

D. r. bugensis is likely to exert expensive economic impacts on water intake pipes and related systems (Hosler 2011), especially those that take water from deeper layers of the water column (Godard et al 2012). Fouling of water intake pipes and associated installations can severely impair water delivery to hydroelectric, municipal and industrial users, necessitating proactive or reactive control measures and entailing high economic costs (Connelly et al. 2007). However, dreissenids can also produce an increase in water clarity that may positively affect water-related industries (Limburg et al. 2009).

In some cases, dreissenids doubled the size of a lake's fishery by providing a new abundant food source to predatory fish (Karatayev 1992, Karatayev and Burlakova 1995). However, waterfowl predators that consume contaminated *Dreissena* have elevated concentrations of organic pesticides and polychlorinated biphenyl compounds.

ENVIRONMENTAL CONSTRAINS

Depth: Maximum abundance at 4-10 m deep, displaying a much wider range of depths than *D. polymorpha* (Mills et al. 1996). *D. r. bugensis* increased in biomass with increasing substrate size but displayed contrasting patterns with depth in St Lawrence River (Jones and Ricciardi 2005)

Oxygen: Distribution of dreissenids is believed to be limited by temperature (ca. 30˚C) and oxygen levels (ca. 0.1-0.3 mg/L) (Mihuc et al. 1999, Mordukhai-Boltovskoi 1960). *D. r. bugensis* is much more tolerant of low oxygen conditions than *D. polymorpha* (Karatayev et al. 1998).

Salinity and ionic elements: A limit of 5‰ salinity (even lower at warm temperatures) have been reported for this species, with maximum growth at 1-1.5‰ (Spidle 1995, Mills et al. 1996). Other studies suggest *D. r. bugensis* may show a lower salinity level (8‰) than *D. polymorpha* (15‰), which reduces its ability to survive ballast water exchange (Orlova et al. 2005). Most rapid growth in dreisseninds is registered at calcium concentration of 70 mg/L, with a minimum threshold of 12 mg/L (Sprung 1987, Ludyanski et al. 1993). Furthermore, low pH and calcium may preclude its spread (Karatayev et al. 2003). Actually, fouling of native unionids increase with calcium concentration up to an asymptotic threshold at 24 mg/L Ca (Jokela and Ricciardi 2008). *D. r. bugensis* were absent below 12 mg Ca/L in St Lawrence River, suggesting that they have higher calcium requirements (Jones and Ricciardi 2005).

Temperature and pH: *D. r. bugensis* appears to be less tolerant of high temperatures than *D. polymorpha* (Karatayev et al. 1998). Actually, Mills et al. 1996 suggested that depth stratification between *D. polymorpha* and *D. r. bugensis* might be related to temperature tolerance. For instance *D. r. bugensis* show a much higher mortality than D. polymorpha at 30 ˚C (Spidle 1995). Furthermore, the temperature needed to kill 50% of *D. r. bugensis* (LT50) is 2-5 ˚C lower than for *D. polymorpha* (although LT100 was similar, McMahon 1996). Lower thermal tolerance than zebra mussels may explain *D. r. bugensis*'s later spread (Ram 2011). Values < 7.4 pH will sterilize populations of dreissenids and prevent recruitment (Lusyanski et al. 1993).

Year reported in Great Britain and The Netherlands

D. r. bugensis was detected in 2006 in the Holand Diep belonging to the Rhine estuary, suggesting the invasion occurred early, probably in 2004 (Molloy et al. 2007).

ECHINOGAMMARUS ISCHNUS, STEBBING, 1899

Taxonomic classification: Crusctacea/ Amphipoda/ Gammaridea
Synonym: Chaetogammarus ischnus
Type of organism: Gammarid

BIOLOGICAL TRAITS

Relatively short life span and generation time, protection of juveniles, non-specific food preference, with a broad variety of ecological living conditions including a wide range of salinities, are highlighted as some *of E. ischnus*' basic traits (bij de Vaate et al. 2002). *E. ischnus* allocates its energy into production of few (10-35 eggs as opposed to >100 in *Dikerogammarus* spp.) but large eggs which could be beneficial at sites where food is scarce (Kley and Maier 2006). This might give it a competitive advantage to other Ponto Caspian invaders (Grabowski et al. 2007a). *E. ischnus* reproduces in summer (until September) generating 2-3 generations per year, females bear < 20 eggs and predates on small ostracods (Kohn and Waterstraat 1990).

HABITAT PREFERENCE

E. ischnus generally inhabits fresh and brakish waters. It occurs in several inshore Black Sea lakes (Jazdzewski 1980), in large Ponto-Caspian rivers, lagoons and dam reservoirs (Grabowski et al. 2007b). As an eurohalyne species, *E. ischnus* prefers large slow moving waters and prevals in downstream sites (Khon and Waterstraat 1990). In the Wloclawek Dam reservoir, it preferred sites distant from shore, rocky habitats overgrown by macrophytes or covered by mussel shells (Zytkowicz et al. 2008).

INTERATION WITH OTHER PONTO CASPIAN SPECIES

The introduction of *E. ischnus* is particulalrly favoured by the physical structure of dreissenids (Van der Ploeg et al. 2002, bij de Vaate et al. 2002). This positive relationship has been confirmed both in Europe (e.g. Lake Kummerow, Germany, Köhn and Waterstraat 1990) and North America (e.g. Great Lakes, bij de Vaate et al. 2002). *E. ischnus* may co-occur with other Ponto Caspian invaders, such as *D. villosus* and *D. bispinosus* in the Danube-Rhine (Kley and Maier 2006, Grabowski et al. 2007b), because swimming in the water column enable *E. ischnus* to minimise its encounters with other amphipods (van Riel et al. 2009). However, *E. ischnus* was replaced by *P. robustoides* and *D. haemobaphes* in the Vistula river (Jazdzewski et al. 2004, Zytkowicz et al. 2008).

DISPERSAL

Dispersal of *E. ischnus* has been associated to intentional introduction in Ukraine lakes (Alexandrov et al. 2007) and the construction of canals such as the Pripet-Bug canal between the Vistula and Dnieper (Jazdzewski 1980, Berezina et al. 2007). The rapid dispersal of *E. ischnus* through the canal systems of Europe together with its high abundance in drift samples suggest that this species is very active in the water column (Nalepa et al. 2001, Godard et al. 2012). Furthermore, upstream dispersal reached 4000 km from their native area in the Volga (Lyakhov 1958). Howevere, in the River Rhine, only low numbers of *E. ischnus* were found drifting (van Riel et al. 2011). *E. ischnus* has been also transported in ballast water to North America (Witt et al. 1997).

ENVIRONMENTAL IMPACTS

E. ischnus replaced *G. fasciatus* in North America and became the dominant species in rocky habitats of the Great Lakes and rivers St. Clair, Detroit, Niagara and Ontario and Erie lakes (Dermott et al. 1998, Nalepa et al. 2001, van Overdijk 2003). In Europe, displacement of native *G. pulex* and *G. varsoviensis* has also been noted in the Vistula River, Poland (Jazdzewski et al. 2004).

ENVIRONMENTAL CONSTRAINS

Oxygen: The species has been observed at well oxygentaed waters (94-125% oxygen saturation) in the Danube-Rhine (Kley and Maier 2006). Under low oxygen concentration (0.1-0.3 mg/L), it is able to become motionless (Mordukhai-Boltovskoi, 1960).

Salinity and ionic elements: The species has been observed at 442-521 µS/cm in the Danube-Rhine (Kley and Maier 2006).

Nutrients: The species has been observed at 36-69 µg/L phosphate, 0.1-2.6 mg/L nitrate in the Danube-Rhine (Kley and Maier 2006).

Temperature and pH: The species has been observed at 9.2-24.6 ˚C in the Danube-Rhine (Kley and Maier 2006).

YEAR REPORTED IN GREAT BRITAIN AND THE NETHERLANDS

The species arrived in the lower Rhine in 1989 (Schöll 1990) and in 1991 in the Rhine delta.

ECHINOGAMMARUS TRICHIATUS, MARTYNOV, 1932

Taxonomic classification: Crusctacea/ Amphipoda/ Gammaridea
Type of organism: Gammarid

BIOLOGICAL TRAITS

Relatively short life span and generation time, protection of juveniles, omnivore feeding, with a broad variety of ecological living conditions including a wide range of salinities (bij de Vaate et al. 2002).

HABITAT PREFERENCE

Outside its native area, *E. trichiatus* has been recorded in the Upper Danube and Lower Rhine, likely spreading through the Main-Danube canal (Holdich et al. 2007). E. trichiatus can inhabit artificial ripraps as well as near-natural gravel banks, reeds and stones (Borza 2009).

INTERATION WITH OTHER PONTO CASPIAN SPECIES

In the Rhine, *E. trichiatus* co-occurs with *E. ischnus, D. villosus, D. haemobaphes* and *C. robustum* (Labat et al. 2011)

DISPERSAL

E. trichiatus was intentionally introduced along with other Ponto Caspian gammarids in Ukraine lakes to improve fish stocks (Alexandrov et al. 2007). This gammarid is abundant in drift samples of the river Rhine (van Riel et al. 2011) although a rather patchy distribution with gaps in the Danube suggest human-mediated dispersal.

ENVIRONMENTAL IMPACTS

E. trichiatus is an intermediate host of metazoan parasites, although their environmental effect is unknown (Emde et al. 2012). No significant impacts were detected in the Danube (Borza 2009).

ECONOMIC IMPACTS

Not reported

ENVIRONMENTAL CONSTRAINS

Not reported

YEAR REPORTED IN GREAT BRITAIN AND THE NETHERLANDS

Podraza et al. (2001) found the species in the middle and lower Rhine River in 2000 and the delta in 2001 (bij de Vaate et al. 2002)

HEMIMYSIS ANOMALA, G.O. SARS, 1907

English name: Bloody-red shrimp
Taxonomic classification: Crustacea/ Mysida/ Mysidae
Type of organism: Mysid

BIOLOGICAL TRAITS

Relatively short life span and generation time, protection of juveniles, gregarious behaviour, suspension feeding, omnivorous feeding, with a broad variety of ecological living conditions including a wide range of salinities (bij de Vaate et al. 2002). *H. anomala* can change in colour depending on habitat, an important anti-predation strategy (Bacescu 1954). According to Komarova (1991), *H. anomala* breeds from April to October, with two broods per year and an average brood size of 10-15 eggs (Bacescu 1954, Ketelaars et al. 1999).

HABITAT PREFERENCE

Preferring lentic conditions, *H. anomala* has been observed in the coastal regions of the Caspian, Black, and Azov seas, in adjacent lagoons, and up to 50 km upstream in the lower, slow-flowing reaches of the Don, Dniester, Dnieper, Pruth, and Danube rivers (Bacescu 1954, Komarova 1991, Borza 2008). Since *H. anomala* is a poor swimmer, its ability to spread against currents characteristic for the upper river sections is very limited (Wittmann 2007).

H. anomala is essentially a nocturnally active semi-pelagic species, seeking shelter by day. Because it avoids light, it is usually a deep water species although it can be observed in shallower areas where it can use natural or artificial structures for shelter (Stubbington et al. 2008). For instance, riparian reed belts can provide suitable shelter for the species, given the water is relatively deep and well-oxygenated (Borza 2009). Harbours also offer suitable habitats for the species (de Lafontaine et al. 2012). In lake Ontario it was most abundant in near shore habitats with cobble-rubble substrate (Fitzsimons et al. 2012), whereas in the Danube it was located in rip-raps with moderate currents (Borza et al. 2011).

INTERATION WITH OTHER PONTO CASPIAN SPECIES

Not reported

DISPERSAL

Mysids such as *H. anomala* have been massively introduced in Lithuanian and Ukraine lakes to improve fish stocks, from where they seems to have spread to multiple locations in the Baltic and North Sea basins (Alexandrov et al. 2007, Arbaciauskas et al. 2010).

Since all *H. anomala* observations were made in the vicinity of the international ports, its introduction has been related to ballast water transfer (vij de Vaate et al. 2002), and natural spread along the Baltic coast (kotta and Kotta 2010).

The recent acceleration of mysid dispersions is mainly attributed to waterway construction and small boat movement (Ricciardi and Rasmussen 1998, Wittmann 2007). Certainly, in France important range extensions of Ponto Caspian species were facilitated by the extensive network of canals followed by downstream drift (Wittmann and Ariani 2009). However, considering that *H. anomala* is a weak swimmer and that the main French water courses are interrupted by weirs with locks, most of the observed upstream expansions probably reflect passive transport by ships (Wittmann and Ariani 2009).

The likely vector of introduction in UK is considered to be private boat or light commercial boat traffic using rivers and canals, deliberate release into ponds as live food for fish, accidental transfer in water involved in the stocking of imported fishes, or in imports of aquatic plants (Brooking et al. 2010, Minchin and Boelens 2010). *H. anomala* has the potential to spread through England's canal network and could colonize the lower reaches and estuaries of rivers including the River Thames and River Severn (Stubbington et al. 2008).

Other potential modes of overland transfer of mysids that have strongly increased since the early 1990s are: increasing aquarist use of mysids including internet trade (Piepiorka and Walter 2006), fish stocking (e.g., Borza et al. 2011), and natural downstream drift (e.g. Rhine River, van Riel et al. 2011).

ENVIRONMENTAL IMPACTS

There is limited information on ecological impacts of *H. anomala* (Godard et al. 2012). The species is an opportunistic omnivore, feeding primarily on zooplankton, but also preying on benthic invertebrates, and scavenging dead animal matter (Godard et al. 2012). For instance, the invasion of Dutch reservoirs by *H. anomala* dramatically affected grazing Ostracoda and Rotifera but did not result in cascading effects on algal density, pressumably because younger individuals feed mainly on phytoplankton (Ketelaars et al. 1999, Borcherding et al. 2006).

On the other hand, *H. anomala* is considered an energy-rich food source for planktivorous fish species (Kipp and Ricciardi 2007). For instance it was found to be an important prey item of alewife in the Great Lakes (Lantry et al. 2010). In this line, studies in the River Rhine suggest that *H. anomala* may become an important link between primary/secondary production and higher trophic levels (Borcherding et al. 2006), and similar concerns have been expressed about potential impact to food webs in the Great Lakes of North America (Walsh et al. 2010).

Other impacts include increased concentration of surface water nutrients due to the production of fecal pellets (Ricciardi 2007), enhanced bioaccumulation of contaminants, new pathways of parasite transmission to fishes, and altered nutrient cycling (Ricciardi et al. 2012).

ECONOMIC IMPACTS

Introduced as fish food, *H. anomala*'s contribution to young of the year perch in the river Rhine range from 20 to 100%, which may have important economic outcomes (Borcherding et al. 2006).

ENVIRONMENTAL CONSTRAINS

Salinity and ionic elements: From fresh water to 19‰ salinity (Bacescu 1954).

Temperature and pH: Preferred temperature 9-20 ˚C (Ioffe 1973, Kipp and Ricciardi 2007).

YEAR REPORTED IN GREAT BRITAIN AND THE NETHERLANDS

The first observation in the Rhine basin (Neckar River) is from 1997 (Schleuter et al. 1998). The species was later located in the Humber river in 2004 (Stubbington et al. 2008).

HYPANIA INVALIDA, GRUBE, 1960

Taxonomic classification: Annelida/ Canalipalpata/ Ampharetidae
Type of organism: Polychaete worm

BIOLOGICAL TRAITS

Relatively short life span and generation time, euryhalinity, filter and deposit feeding (feeds on algae and diatoms) (bij de Vaate et al. 2002). *H. invalida* reproduces by males discharging their sperm into the water column while eggs are retained and fertilised in the female dwelling tubes. Fecundity *of H. invalida* ranged between 60 and 260 eggs per clutch and is increased by iteroparity (i.e. multiple cycles of oogenesis and egg-laying per specimen). Offspring are brooded for about 2 weeks before they leave the maternal dwelling tubes and disperse in the water column, once they settle they reach maturity within only 12 weeks (Norf et al. 2010).

HABITAT PREFERENCE

H. invalida invades both fresh and marine waters (estuaries). The species prefers a muddy bottom with reduced flow velocity and turbulence (Filinova et al. 2008, Norf et al. 2010), although it may also inhabit sandy bottomed areas covered by zebra mussel beds, and even stones, but its aggregations on those substrates are not as dense as those on muddy substrates (Yakovlev and Yakovleva 2010, Norf et al. 2010).

INTERATION WITH OTHER PONTO CASPIAN SPECIES

H. invalida is usually found within dreissenid communities (both *D. polymorpha* and *D. r. bugensis*),whose products provide food and structural material for polychaete tube-huts (Shcherbina 2001). For instance, in the Upper Volga river, *H. invalida* was registered in a biocenosis of the zebra mussel on silty sands of the reservoirs' channel zone. *H. invalida* also co-occurs with *C. curvispinum* (Vanden Bossche et al. 2002), *D. haemobaphes* (Yakovlev and Yakovleva 2010), and serves as prey for gobiids such as *N. melanostomus* (Yakovlev and Yakovleva 2010).

DISPERSAL

H. invalida was purposefully introduced into newly constructed dam reservoirs on the Volga and the Dnepr in the 1960s (Mordukhai-Boltovskoi 1964). After the formation of the dam lake Portile de Fier (Romania), the polychaete has extended its proliferation area and the density as well as the biomass have increased (Popescu-Marinescu 1992).The initially slow dispersal of the species changed to a rapid invasion once the Rhine–Main–Danube Canal was opened in 1992 (Wozniczka et al. 2011). *H. invalida* is capable of establishing dense populations exclusively via settlement of the drifting juveniles (Van Riel et al. 2011). This way, using relatively small refuges, the species can rapidly colonize new areas and recolonize those it had to abandon (e.g. as a result of drying-out). Although this way of dispersal facilitates easy downstream colonization, *H. invalida* is also capable of colonizing upstream areas by taking advantage of inland shipping as a vector of spread (e.g. ballast water) (Norf et al. 2010).

ENVIRONMENTAL IMPACTS

H. invalida feeds on algae, thus it might provoke bottom up food web changes. It can also enhance water quality by reducing the amount of organic matter in the water and sediment and aireating the sediment, which in turn fosters the activity of aerobic bacteria that decompose organic compounds (Surugiu 2005).

ECONOMIC IMPACTS

Not reported

ENVIRONMENTAL CONSTRAINS

Depth: Present in the shoreline and up to 400 m deep (Norff et al. 2010), although usually found at depths > 5 m (Yakovlev and Yakovleva 2010).

Oxygen: Observed at 6.4-6.5 mg/L in the Meuse River (Belgium) (Vanden Bossche et al. 2002).

Salinity and ionic elements: In its native range, *H. invalida* supports a wide range (0-12‰) of salinity (Norff et al. 2010). It was observed at 443-586 µg/L conductivity in the Meuse (Belgium) (Vanden Bossche et al. 2002)

Temperature and pH: In its native range, *H. invalida* supports 2 to 25 ˚C (Norff et al. 2010). It was observed at 19.5-24.2 ˚C in the Meuse River (Belgium) (Vanden Bossche et al. 2002)

YEAR REPORTED IN GREAT BRITAIN AND THE NETHERLANDS

H. invalida was recorded in the Dutch section of the Rhine in 1995 (Klink and Bij de Vaate 1996). In Great Britain, *H. invalida* was first detected in 2008 in samples from the river Thames (Trevor Renals, personal communication).

JAERA ISTRI, VEUILLE, 1979

Taxonomic classification: Crustacea/ Isopoda/ Janiridae
Type of organism: Isopod

BIOLOGICAL TRAITS

Relatively short life span and generation time, protection of juveniles, omnivorous feeding, with a broad variety of ecological living conditions including a wide range of salinities (bij de Vaate et al. 2002). The food of this small (1.98 mm) isopod, which can reach mean densities of 2,814 ind/m^2, and highest maximum densities of 5,110 ind/m^2 (Kelleher et al. 2000), consists of algae, plant remains, and detritus. The life history and reproductive behaviour have not been studied.

HABITAT PREFERENCE

The lithophilous isopod *J. istri* inhabits the littoral zones of the lower reaches and estuaries of large rivers discharging into the Black and Caspian seas (Tittizer 1997). It is restricted to the tidal part of the river Meuse (Josen et al. 2005). In contrast to other *Jaera*, *J. istri* is adapted to freshwaters, it prefers high flows and does not invade tributaries (Nesseman et al. 1995).

INTERATION WITH OTHER PONTO CASPIAN SPECIES

It has been found to co-occur with *C. curvispinum* in Lake Balaton (Musko et al. 2007).

DISPERSAL

Settlement of the drifting juveniles in the water column allows the spread of *J. istri*, as evidenced its abundance in drift samples from the river Rhine (van Riel et al. 2011). Leuven et al. (2008) repored spread velocity of 109 km/year (31-185 km/year) for *J. istri* in the Rhine.

ENVIRONMENTAL IMPACTS

J. istri is an intermediate host of parasites for the eel. For instance, in the German part of the Rhine, nine metazoan species hosted by *J. istri* were found to infest eels (Sures et al. 1999).

ECONOMIC IMPACTS

Not reported

ENVIRONMENTAL CONSTRAINS

Not reported

YEAR REPORTED IN GREAT BRITAIN AND THE NETHERLANDS

The Rhine delta was colonized in 1997 (Kelleher et al. 2000), where it inhabits solid substrates.

LIMNOMYSIS BENEDENI, CZERNIAVSKY, 1882

Taxonomic classification: Crustacea/ Mysida/ Mysidae
Type of organism: Mysid

BIOLOGICAL TRAITS

Relative short life span and generation time, protection of juveniles, gregarious behaviour, omnivore feeding, with a broad variety of ecological living conditions including a wide range of salinities (bij de Vaate et al. 2002). *L. benedeni* feeds mainly on small particles, such as detritus, epilithon and phytoplankton (bij de Vaate et al. 2002, Gergs et al. 2008). Assmann et al. (2009) showed that leaf litter can be an important part of its diet. Mysids protect themselves against predation by forming swarms (Lindén 2007).

HABITAT PREFERENCE

L. benedeni is endemic to the coastal waters of the Black, Azov and Caspian seas and can be found several hundred kilometres upstream in rivers discharging into both seas (Bacescu 1954). Since they are poor swimmers, their ability to spread against currents characteristic for the upper river sections is very limited (Wittmann 2007). It inhabits lentic environments relatively shallow, with aquatic vegetation or other types of hard substrate such as roots, stones or zebra mussels (Wittmann 1995, Kelleher et al. 1999, Gergs et al. 2008).

INTERATION WITH OTHER PONTO CASPIAN SPECIES

Not reported

DISPERSAL

Genetic evidence suggest several invasion waves from *L. benedeni*'s native range (Audzijonyte et al. 2009). Downstream drift may be a common dispersal mechanism for this species (Wittmann and Ariani 2009, Van Riel et al. 2011), whereas upstream expansions probably reflect passive transport by ships (Wittmann and Ariani 2009). This is in line with the recent acceleration of mysid dispersions being mainly attributed to waterway construction and small boat movement (Ricciardi and Rasmussen 1998, Wittmann 2007).

Other potential modes of overland transfer of mysids that have strongly increased since the early 1990s sare: increasing aquarist use of mysids including internet trade (Piepiorka and Walter 2006), fish stocking (e.g., fishing lakes inHungary, Borza et al. 2011), fauna improvement (e.g. Lithuanian and Ukraine lakes, Alexandrov et al. 2007, Arbaciauskas et al. 2010), and natural downstream drift (e.g. Rhine River, van Riel et al. 2011).

Records of *L. benedeni* in numerous isolated recreational fishing ponds (reservoirs and gravel-pit lakes) in Hungary suggest the functioning of an effective dispersal mechanism independent of navigation, possibly fish stocking (Borza et al. 2011).

ENVIRONMENTAL IMPACTS

As an omnivorous feeder, *L. benedeni* consumes small benthic and pelagic particles, and can potentially change nutrient cycles (Hanselmann et al. 2013). Mesocosm experiments demonstrated selective predation on components of the zooplankton, leading to reduced densities of cladocerans, rotifers and copepod nauplii (Fink et al. 2012). On the other hand, *L. benedeni* is preyed upon fish like *Perca fluvialitis*, playing an important role in trophic food webs (Hanselmann et al. 2011).

ECONOMIC IMPACTS

Not reported

ENVIRONMENTAL CONSTRAINS

Salinity and ionic elements: Euryhaline species, 6.5‰ salinity is tolerated (Wittmann 1995).

YEAR REPORTED IN GREAT BRITAIN AND THE NETHERLANDS

It was detected in the Middle Rhine River and the Rhine delta in 1998 (Kelleher et al. 1999, Ketelaars et al. 1999)

LITHOGLYPHUS NATICOIDES, PFEIFFER, 1828

English name: Gravel snail
Taxonomic classification: Mollusca/ Gastropoda / Hydrobiidae
Synonym: *Paludina naticoides*
Type of organism: Mollusc

BIOLOGICAL TRAITS

In the Saône river, *L. naticoides* is an annual species: spawning occurs from March to June and the juveniles that generally appear in May grow rapidly during the summer then spawn and disappear in the spring of the following year (Mouthon 2007). In the Kuibyshev reservoir, the species showed a one year life cycle, reproducing mostly in July (Yakovlev et al. 2010).

HABITAT PREFERENCE

L. naticoides prefers gravel, slowly flowing waters like those in the downstream parts of rivers, canals, and lakes (Gittenberger et al. 1998). The species is also found in large and medium sized lowland rivers in Poland (Piechocki 1979). In the Kuibyshev reservoir, *L. naticoides* inhabited all biotopes except deep waters (> 20 m), with highest abundance at 10 m (Yakovlev et al. 2010).

INTERATION WITH OTHER PONTO CASPIAN SPECIES

L. naticoides co-exists with *D. polymorpha* in Poland.

DISPERSAL

Construction of shipping canals and transport of materials (e.g. firewood) from Russia into Western Europe appears to have facilitated the dispersal fo this snail (Karatayev et al. 2008).

ENVIRONMENTAL IMPACTS

As a suspension-feeder, *L. naticoides* may affect the availability of organic matter and significantly increase water clarity.
It is preyed upon water birds, and may thereby affect their occurrence.
An intermediate host of the highly pathogenic trematode *Apophallus muehlingi, L. naticoides* formed an unusually dense population (up to 8800 individuals per m^2) soon after its invasion of the Volga River Delta (Biserova 1990). This, in combination with the high prevalence of infection with *A. muehlingi*, could have lead to production and release by the snails of enormous numbers of the parasite's cercariae, resulting in the documented 80% mortality rate among young cyprinid fishes (Biserova 1990).
L. naticoides has been reported to transmit other Nematodes such as *Apophallus* sp. and *Nicolla* sp. to fish (Tyutin and Slynko 2010).

ECONOMIC IMPACTS

Not reported

ENVIRONMENTAL CONSTRAINS

Not reported

YEAR REPORTED IN GREAT BRITAIN AND THE NETHERLANDS

The species has been present in The Netherlands since the 19th century.

NEOGOBIUS GYMNOTRACHELUS, KESSLER, 1857

English name: Racer goby
Taxonomic classification: Vertebrata/ Perciformes/ Gobiidae
Synonym: *Mesogobius gymnotrachelus*
Type of organism: Fish

BIOLOGICAL TRAITS

N. gymnotrachelus forages mainly on benthos and has a nocturnal feeding activity. It displays great plasticity and opportunism in its feeding habits, taking a variety of prey types and usually choosing the most abundant food organisms, mainly amphipods and chironomid larvae, and to a lesser extent chironomid pupae, ceratopogonida larvae, oligochaets, dipteran and fish larvae (Kostrzewa and Grabowski 2003, Grabowska and Grabowski 2005). Specialized reproductive behaviour (nest construction and parental care of eggs), an extended spawning period, and high fecundity (e.g. 952 eggs per female in the Vistula River) increase the probability that racer goby can successfully establish self-sustaining populations in novel environments.

HABITAT PREFERENCE

In its native range, *N. gymnotrachelus* inhabits the brackish lagoons of the Black and the Caspian Seas and lower courses of their rivers: Danube and its larger tributaries, the Dniester drainage, Boh (known also as Southern Bug or Eastern Bug), Dnieper and Don (Copp et al. 2005). *N. gymnotracehlus* has been reported from the Danube (Kautman 2001), the lower River Vistula (Kostrzewa and Grabowski, 2001)

INTERATION WITH OTHER PONTO CASPIAN SPECIES

Not reported

DISPERSAL

Spread of gobiids such as *N. gymnotrachelus* is mainly associated to shipping and canal construction. The species has a very high upstream dispersal potential, of up to hundreds of kilometres (Ahnelt et al. 1998).

ENVIRONMENTAL IMPACTS

N. gymnotrachelus juveniles are an important food source for perch, pike and pikeperch, which can stimulate considerable changes in local food webs (Plachocki et al. 2012).

ECONOMIC IMPACTS

Not reported

ENVIRONMENTAL CONSTRAINS

Not reported

NEOGOBIUS MELANOSTOMUS, PALLAS, 1814

English name: Round goby
Taxonomic classification: Vertebrata/ Perciformes/ Gobiidae
Synonym: *Mesogobius melanostomus, Apollonia melanostoma*
Type of organism: Fish

BIOLOGICAL TRAITS

Invasive populations of *N. melanostomus* have fewer species of parasites and lower infection rates, are smaller, mature earlier, have a male biased operational sex ratio and are more short-lived compared with round gobies from marine (native) habitats (Corkum et al. 2004). Initial slow population growth was observed in the Gulf of Gdansk, followed by a gradual increased until it becomes the dominant species in shallow areas (Sapota 2005).

HABITAT PREFERENCE

N. melanostomus is more abundant in gravel beds and rip-raps, with lower density in sand (Eros et al. 2005). In the gulf of Gdansk it initially colonized stony and rock habitats but later it also occupied sandy bottoms (Sapota et al. 2004). Habitats devoid of predatory fish and with mollusk beds (which dominate England) are most vulnerable to *N. melanostomus* invasion (Skora and Rzeznik 2001).

INTERATION WITH OTHER PONTO CASPIAN SPECIES

Ponto-Caspian shrimps and quagga mussels are important preys to *N. melanostomus* and thus facilitate its introduction both in Europe (Van der Ploeg et al. 2002) and the Great lakes of North America (e.g. Lake Erie, Campbell et al. 2009). In lake Ontario dressenids were the most common prey of *N. melanostomus* (Fitzsimons et al. 2012).

DISPERSAL

Spread of gobiids such as *N. melanostomus* is associated to shipping, ballast water from Black and Caspian seas, and bait bucket transfer (Jude 2001).

The secondary movements between sites has potentially been facilitated by abandoned eggs in nests deposited in crevices on freight vessels moving from port to port (Ray and Corkum 2001).

Once the gobies have become established in a new area, the fish are likely to disperse naturally (Ray and Corkum 1997; Ray & Corkum 2001; Sapota and Skora 2005). Actually, upstream dispersal might be of hundreds of kilometers (Ahnelt et al. 1998).

ENVIRONMENTAL IMPACTS

N. melanostomus mainly feeds on chironomids, ostracods and amphipods during the first year; and mussels and crustaceans during the second year (Rakauskas et al. 2008). Predation of native species can lead to algal blooms (Kuhns and Berg 1999), as well as bottom up changes in the food web which are likely to occur through the transfer of energy and contaminants (Morrison et al. 2000). In the gulf of Gdansk, the most significant effects of *N. melanostomus* invasion were decreases of area covered by plants (macroalgae and vascular plants) and decreases in the number of arthropods, correlated with increases in the number and areas covered by bivalves (Zmudzinski and Osowiecki 1991).

On the other hand, *N. melanostomus* is one of the main prey of predatory cod, perch and even cormorants in the Gulf of Gandsk, becoming the most important energetic pathway from mussels to top predators (Bzoma 1998, Almqvist et al. 2010).

Transmission of disease can also be related to *N. melanostomus*, such as the Acanthocephala *Pomphorhynchus tereticollis*, present in 90% of *N. melanostomus* in the river Rhine (Emde et al. 2012).

ECONOMIC IMPACTS

Not reported

ENVIRONMENTAL CONSTRAINS

Not reported

YEAR REPORTED IN GREAT BRITAIN AND THE NETHERLANDS

Located in the Netherlands in 2004.

OBESOGAMMARUS CRASSUS, G.O. SARS, 1894

Taxonomic classification: Crustacea/ Amphipoda/ Pontogammaridae
Type of organism: Gammarid

BIOLOGICAL TRAITS

Relatively short life span and generation time, protection of juveniles, nonspecific food preference, with a broad variety of ecological living conditions including a wide range of salinities (bij de Vaate et al. 2002). *O. crassus* may have a limited invasion potential because of its smaller size, low fecundity, brood size limited by brood pouch size and small size of females (average 8.81 mm versus 11.39 of *D. villosus*, or 12.65 mm of *P. robustoides*) (Grabowski et al. 2007a).

HABITAT PREFERENCE

O. crassus occurs in the coastal Caspian Sea and lower courses of its rivers and brackish coastal waters of Poland (Arbaciauskas et al. 2010). In the Black Sea it lives in lagoons, entering the lower sections of the Kuban, Don, Dnieper, Ingulec, Boh, Dniester and the Danube as far as Serbia (Dudich 1947, Jażdżewski 1980)

INTERATION WITH OTHER PONTO CASPIAN SPECIES

The Ponto-Caspian species *O. crassus*, although at low numbers, is capable of long-term survival with *P. robustoides* in the same habitats of lakes or water reservoirs (Arbaciauskas 2005). Both species have similar salinity tolerance and are found in the more saline parts of the Vistula and Oder deltas, Szczecin Lagoon, brakish coastal lakes and lagoons of Poland (Jazdzewski et al. 2005). The ecological mechanism of such co-occurrence still remains unknown. *O. crassus* has been also reported to co-occur with *D. haemobaphes, E. ischnus* and *D. villosus* in Belarus.

DISPERSAL

Dispersal in Russia, Lithuanian and Ukraine is associated to intentional introductions to improve fish stocks (Alexandrov et al. 2007, Arbačiauskas and Gumuliauskaitė 2007, Berezina et al. 2007, Arbaciauskas et al. 2010).
Westward dispersal has been the result of offshore transportation (in ballast water) via the Baltic Sea (bij de Vaate et al. 2002)

ENVIRONMENTAL IMPACTS

Reduced species richness, community diversity and biomass of native invertebrates are expected from the invasion of *O. crassus* (Arbaciauskas et al. 2010).

ECONOMIC IMPACTS

Not reported

ENVIRONMENTAL CONSTRAINS

Oxygen: A lethal dissolved oxygen minimum concentration of 0.262 mg/L has been reported for *O. crassus* (Arbačiauskas and Gumuliauskaitė, 2007).

Salinity and ionic elements: Can tolerate between 1 and 6‰ in the Vistula Lagoon (Konopacka and Jażdżewski 2002). Experiments showed 100% mortality in sea water, although it survived up to 24 h (Santagata et al. 2008).

OBESOGAMMARUS OBESUS, G.O. SARS, 1894

Taxonomic classification: Crustacea/ Malacostraca/ Amphipoda/ Pontogammaridae
Type of organism: Gammarid

BIOLOGICAL TRAITS

Relatively short life span and generation time, protection of juveniles, omnivore feeding, with a broad variety of ecological living conditions including a wide range of salinities (bij de Vaate et al. 2002)

HABITAT PREFERENCE

O. obesus originates from the lower sections of large Ponto-Caspian rivers (Volga, Don, Dnieper, Dniester, and Danube rivers) as well as from some inland brackish and freshwater lakes around the Black Sea (Jazdzewski 1980). Outside its native area, it has been found in the Austrian and Bavarian Danube as well as in the Rhine (Holdich and Pöckl 2007). As many other Ponto Caspian invasive species, it is only found in the main river channel and not in tributaries. The species occupies deeper areas of southern rivers but adapted to shallower areas with favourable trophic, oxygen and temperature conditions in reservoirs of Russia, migrating into deeper water during storms or substrate drying (Berezina et al. 2007).

INTERATION WITH OTHER PONTO CASPIAN SPECIES

Not reported

DISPERSAL

Dispersal of *O. obesus* is associated to the construction of canals such as Main-Danube conecting the Danube and Rhine (van der Velde et al. 2000). Upstream dispersal reached 500 km in the Volga from 1958 to 1972 (i.e. 35 km per year, Shakhmatova and Antonov 1988). This species is mainly distributed in the lower stretchs of native rivers, and apparently not able to move upstream as much as other crustaceans.

ENVIRONMENTAL IMPACTS

Not reported

ECONOMIC IMPACTS

Not reported

ENVIRONMENTAL CONSTRAINS

Not reported

PONTOGAMMARUS ROBUSTOIDES, G.O. SARS, 1894

Taxonomic classification: Crustacea/ Amphipoda/ Pontogammaridae
Type of organism: Gammarid

BIOLOGICAL TRAITS

P. robustoides displays omnivore feeding and a very high reproductive potential due to its high fecundity, early maturity, and multiple reproduction cycles per year (Grabowski et al. 2007a). *P. robustoides* breeds from April to October, with up to 3 generations per year during warm years, but only two during cold years in the Baltic sea (Berezina and Gubelit 2012). High abundance of up to 2100-3300 ind./m^2 were reported in Lithuanian Dusia and Elektenai Lakes. Effective predator, starts to predate at a young age (body length of 6–7 mm), attacking the larvae of chironomids, isopods, aquatic insects and oligochaetes, which results in a significant decrease in their density (Berezina and Panov 2003, Berezina et al. 2007). Environmental resistance may also explain the invasion success of *P.robustoides*. As way of example, in a drying experiment *P. robustoides* was most resistant to substratum drying and was the only species burying into the substratum in comparison with other Ponto Caspian species (Poznanska et al. 2013).

HABITAT PREFERENCE

P. robustoides occurs in the lower courses of large Ponto-Caspian rivers (e.g. Volga, Don, Dnieper, Dniester and Danube), as well as in some freshwater and brackish coastal lakes and Black Sea lagoons (Jażdżewski 1980), the brackish mouth of rivers in Latvia and onshore lakes of the Baltic basin.
Choice tests have shown certain habitat partition between juveniles, who preferred natural substratum and plants with small elements such as *Miriophyllum spitacum* and *Ceratophyllum demersum*, and adults showing no preference for natural/artificial substrate (Czarnecka et al. 2010). In the Wloclawek Dam reservoir, it is present in shallow (< 1 m) sandy bottom near the shore, its abundance decreasing with distance from the shore, where it showed higher affinity for plants (Zytkowicz et al. 2008). In the Eastern Baltic Sea, *P. robustoides* migrates to deeper water zones during winter and back to shallower areas from April to October to reproduce (Berezina and Gubelit 2012).

INTERATION WITH OTHER PONTO CASPIAN SPECIES

P. robustoides co-occurs with *O. crassus* (Arbaciauskas 2005) although it may replace other alien amphipods through competition and intraguild predation (Berezina et al. 2007). Such is the case of *D. haemobaphes* (Jazdzewskiet al. 2002), although in some cases both species have been reported to co-occur, for instance in Lucieńskie Lake located in the Vistula valley (Grabowski and Bącela 2005).

DISPERSAL

The dispersal of *P. robustoides* is almost exclusively human-mediated since it is not able to disperse through lotic environments where it is only located downstream infested reservoirs (Arbačiauskas and Gumuliauskaitė 2007). Dispersal in Russia, Lithuania, Latvia, Estonia and Ukraine was associated to intentional introductions and shipping (Gasjunas 1972, Alexandrov et al. 2007, Arbačiauskas and Gumuliauskaitė 2007, Berezina et al. 2007, Arbaciauskas et al. 2010), whereas dispersal towards western Europe was associated to the construction of the Pripet-Bug canal between the Vistula and Dnieper rivers (Jazdzewski, 1980). The construction of reservoirs may also play a relevant role in its dispersal: after construction of the Dnepropetrovsky Reservoir on the Dnieper River, *P. robustoides* colonized the reservoir and became one of the dominant species (Mordukhai-Boltovskoi, 1960). Its subsequent spread through Europe is attributed to a combination of shipping, probably attached to fouling organisms on hulls, and natural dispersal assisted by newly created canals (Jazdzewski et al. 2002, Mastitsky and Makarevich 2007).

ENVIRONMENTAL IMPACTS

P. robustoides displaces native species (e.g. *Gammarus* sp., *Asellus* sp.), reducing the overall abundance, biomass, richness and diversity of native communities (Gumuliauskaite and Arbaciauskas 2008, Berezina and Gobelit 2012). As an omnivorous feeder, *P. robustoides* reduced the abundance of chironomids and plants (Cladophora sp.) in the Gulf of Findland, while in some lakes of Lithuania *P. robustoides* contributed to algae dissapearance in only 5 years (Berezina et al. 2007). On the other hand, *P. robustoides* can represent an important prey for fishes.

P. robustoides can also be a vector of parasitic microsporidia (e.g. *Nosema pontogammari*) and gregarines (e.g. *Uradiophora ramosa, U. longissima, Thelohania* sp. and *Cephaloidophora mucronata*) (Ovcharenko et al. 2006, 2009), although threre are no reports of transference to other species.

ECONOMIC IMPACTS

Not reported

ENVIRONMENTAL CONSTRAINS

Oxygen: Dissolved oxygen > 0.209 mg/L migt be lethal for this species (Arbačiauskas and Gumuliauskaitė 2007).

Salinity and ionic elements: Salinity < 3–4‰ can be tolerated by this species (Arbačiauskas and Gumuliauskaitė 2007). In experiment designs, it survived full strengh sea water (Santagata et al. 2008), but it was not able to reproduce successfully in water with potassium concentration < 10–15 mg/L (Berezina and Panov 2003).

***PROTERORHINUS MARMORATUS*, PALLAS, 1814**

English name: Tubenose goby
Taxonomic classification: Vertebrata/ Perciformes/ Gobiidae
Synonyms: *Gobius marmoratus, G. quadricapillus, G. macropterus, G. rubromaculatus, G. blennioides*
Type of organism: Fish

BIOLOGICAL TRAITS

P. marmoratus breeds from late spring to midsummer. It lays its eggs of average 2.5 x 1.3 mm, on underside of shells and stones. *P. marmoratus* is sexually mature at 1 year.
Crustaceans and chironomids constitute the most important food source for P. marmoratus, followed by ostracods, planktonic crustaceans, caddisfly and mayfly (Adámek et al. 2007).

HABITAT PREFERENCE

P. marmoratus is native to estuaries and brackish waters of the Black Seas (Godard et al. 2012)

INTERATION WITH OTHER PONTO CASPIAN SPECIES

It has been shown to predate on *C. curvispinum,* although in very low quantities (Adámek et al. 2007).
A significant partitioning for prey has been reported among *N. melanostomus*, *N. fluviatilis*, and P. marmoratus that allows their coexistence (Simonovic et al., 2001).

DISPERSAL

Introduced via ballast water thanks due to its resistance to variable salinity levles. The spread of *P. marmoratus* is slow when compared with other Ponto Caspian species such as *N. melanostomus* pressumably because it doesn't feed on zebra mussels (Van der Ploeg et al. 2002). Upstream dispersal high potential of up to hundreds of kilometres (Ahnelt et al. 1998).

ENVIRONMENTAL IMPACTS

Gobies such as P. marmoratus are expected to impact directly other benthic fishes, such as sculpins (*Cottus* spp.), darters (*Etheostoma* spp.), and logperch (*Percina caprodes*), and in turn act as prey for walleye (*Stizostedion vitreum*) (Jude et al. 1992). Approximately 30% of P. marmoratus's collected in St. Claire River (US) carried up to six different parasites including *Sphaeromixa sevastopoli* and *Ichthyocotylurus pileatus* (Pronim et al. 1997).

ECONOMIC IMPACTS

Not reported

ENVIRONMENTAL CONSTRAINS

Salinity: The species tolerates a wide range of high salinities (from 12 to 16 mgNaCl/L) but does not survive 8-fold gradual dilution of water, dying because of excessive loss of sodium by the organism (Martemyanov and Borisovskaya, 2012)

YEAR REPORTED IN GREAT BRITAIN AND THE NETHERLANDS

The species is present in The Netherlands since 2002.

PROTERORHINUS SEMILUNARIS, HECKEL, 1837

English name: Freshwater tubenose goby

Taxonomic classification: Vertebrata/ Perciformes/ Gobiidae

Type of organism: Fish

BIOLOGICAL TRAITS

The species has been considered for some time a synonym of *P. marmoratus*. However, following genetic results, Stepien and Tumeo (2006) have validated the existence of the two species: *P. semilunaris* as a freshwater species and *P. marmoratus* as a marine one.

P. semilunaris is a small-bodied fish reaching its sexual maturity quite early (1–2 years), spawning several times within a season, and the male guards the eggs (Ruesink, 2005).

P. semilunaris feeds on invertebrates such as ephemeropterans, trichopterans, dipterans, crustaceans, chironomids and occasionally zooplankton (ostracods, copepods) and larval fish (French and Jude 2001). In the Mušov reservoir on the Dyje River (the Danube basin, Czech Republic), Adàmek et al (2010) reported Chironomid larvae and waterlouse (*Asellus aquaticus*) constitutes 40 and 30% of *P. semilunaris* diet respectively.

HABITAT PREFERENCE

P. semilunaris displays a quite large habitat tolerance (Eros et al., 2005); it is found in lakes, estuaries, rivers, lentic streams, canals and in side arms (Kottelat and Freyhof, 2007). It seems to prefer shallow (less than 5 m depth), slow-moving, nearshore environments. The species prefers areas with abundant aquatic macrophytes, but can also be found in sandy areas (Jude and Deboe 1996).

INTERATION WITH OTHER PONTO CASPIAN SPECIES

Van Riel et al. (2006) suggested the introduction of *C. curvispinum* in the Rhine facilitated other invasive species including *P. semilunaris*.

DISPERSAL

P. semilunaris is a native of the Black Sea basin and of the Maritza and Struma drainages in the eastern Aegean basin (Kottelat and Freyhof, 2007). It spread out its native range as far as the Netherlands in Europe in 2002 and in the Great Lakes in North America in 1991.

Although its rate of spread has proved to be slower than that of the round goby, *P. semilunaris* has expanded its range up the Danube in recent decades, facilitated by the digging of the “Rhine-MainDanube” canal in 1992 (Freyhof, 2003), but its use as live bait (Prášek and Jurajda, 2005). Its colonisation of the North American Great Lakes is due to its transport viaships’ ballasts (Jude and DeBoe, 1996). Transoceanic transport in ballast water is assumed to be responsible for its arrival in North America (Wonham et al. 2000). It can also be spread by transport of egg clutches on the hulls of ships, and by accidental stocking with other fish species (von Landwüst 2006). Its recent arrival in the Czech Republic is attributed to use as live bait fish by anglers (Prášek and Jurajda 2005), and it has been suggested that this vector could explain its discontinuous range in Lake Erie (Kocovsky et al. 2011). Natural dispersal has been attributed to drift associated with nocturnal vertical migration of larvae (Kocovsky et al. 2011). Manné and Poulet (2008) documented a spread velocity of 25 km/year in Germany.

ENVIRONMENTAL IMPACTS

According to Godard et al. (2012), *P. semilunaris* could potentially compete with a number of native fish species for food and space. In the Great Lakes, there is substantial overlap in diet and habitat with the rainbow darter *Etheostoma caeruleum*, and potential competition with the johnny darter *E. nigrum* for spawning sites on the underside of rocks (French and Jude 2001, Kocovsky et al. 2011). In Europe, particular concern has been expressed about the possible impact on bullheads *Cottus* spp., following observations of a decline in European bullhead *Cottus gobio* population density in the Slovak River Danube after invasion by several goby species in the 1990s (Jurajda et al. 2005). *C. gobio* were also absent from the headwater of a weir populated by *P. semilunaris* on the River Moselle (von Landwüst 2006), with preliminary experiments suggesting that *C. gobio* may be outcompeted for shelter, moving to less optimal habitats (van Kessel et al. 2011).

P. semilunaris has been also identified as a paratenic host of *Anguillicola crassus*, an eel parasite with severe pathological effects with, nevertheless, a low prevalence (Koubková and Baruš, 2000).

ECONOMIC IMPACTS

Not reported

ENVIRONMENTAL CONSTRAINS

Not reported

YEAR REPORTED IN GREAT BRITAIN AND THE NETHERLANDS

The species is present in The Netherlands since 2008.

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APPENDIX E Statistics from species distribution models (SDM). PP: precipitation, T= temperature, HII: Human Influence Index.

Name	Training samples	Test samples	Test gain	Test AUC	Altitude	Annual PP	PP driest month	PP seasonality	Annual T	T seasonality	Maximum T	Minimum T	Geology	TOTAL ENVIRONMENTA	HII	Land use	Human population	Port closeness	Road closeness	TOTAL SOCIO-ECONOMIC	Entropy	Prevalence	MaxTSS threshold
C.curvispinum	160	372	3.24	0.99	7.74	0.66	1.08	0.60	56.85	13.35	1.28	9.62	1.24	92.41	4.60	0.15	0.01	0.18	2.65	7.59	6.09	0.02	0.15
C.pengoi	48	110	3.99	0.99	5.20	0.00	0.05	4.11	10.43	21.80	0.00	56.36	0.11	98.05	0.32	1.61	0.00	0.01	0.02	1.95	5.46	0.01	0.06
C.robustum	10	22	3.52	0.99	1.51	0.91	0.00	40.58	0.88	0.01	0.00	47.33	0.42	91.64	0.20	0.61	0.00	7.55	0.00	8.36	6.33	0.03	0.22
C.sowinskyi	19	43	3.80	0.99	9.67	13.57	0.00	28.77	0.27	0.00	0.05	36.71	0.86	89.91	6.38	0.80	1.64	1.12	0.14	10.09	5.97	0.02	0.19
C.warpachowski	31	70	3.64	0.99	58.33	0.00	1.61	10.48	1.58	1.53	0.00	5.46	0.08	79.06	0.68	0.06	0.00	1.50	18.69	20.94	5.72	0.01	0.43
D.bispinosus	7	16	3.32	0.99	13.96	0.32	0.00	0.57	13.41	0.00	0.00	59.28	0.66	88.20	0.00	0.00	0.09	10.85	0.86	11.80	6.31	0.03	0.45
D.bugensis	58	134	3.95	0.99	3.41	9.52	4.34	1.26	20.46	0.00	0.68	56.86	0.08	96.62	1.57	0.32	0.01	1.25	0.24	3.38	5.49	0.01	0.12
D.haemobaphes	58	133	3.18	0.98	5.63	5.87	6.49	0.16	40.14	7.39	0.59	27.76	0.46	94.49	2.84	0.70	0.15	0.92	0.91	5.51	6.16	0.02	0.12
D.villosus	99	229	3.58	0.99	2.31	1.68	3.45	0.89	0.43	17.8	5.52	66.8	0.05	99.0	0.73	0.02	0.00	0.20	0.00	0.95	5.79	0.02	0.08

										9		4		5									
E.ischnus	18	40	3.72	0.99	4.11	2.24	0.00	1.00	38.80	0.00	0.13	36.69	2.34	85.31	0.83	0.42	0.00	10.21	3.24	14.69	6.16	0.02	0.41
E.trichiatus	24	55	4.20	0.99	2.27	0.48	0.00	6.06	9.35	1.96	0.00	64.03	0.57	84.70	0.15	0.03	0.40	14.72	0.00	15.30	5.17	0.01	0.24
H.anomala	55	127	3.73	0.99	2.82	1.28	0.00	1.79	12.69	0.00	0.00	75.56	0.23	94.36	0.15	0.08	0.04	5.29	0.08	5.64	5.74	0.01	0.10
H.invalida	**60**	**137**	**3.98**	**0.99**	**4.44**	**4.00**	**9.59**	**0.02**	**19.22**	**8.33**	**0.00**	**52.91**	**0.54**	**99.05**	**0.24**	**0.00**	**0.03**	**0.41**	**0.26**	**0.95**	**5.37**	**0.01**	**0.04**
J. istri	23	51	4.01	0.99	1.17	2.62	0.00	1.55	13.44	0.00	0.00	70.34	0.06	89.16	1.22	0.16	0.08	8.49	0.89	10.84	5.56	0.01	0.18
L.benedeni	89	205	3.75	0.99	5.35	2.60	1.27	1.02	5.60	5.36	1.57	74.09	1.27	98.12	1.80	0.02	0.00	0.04	0.02	1.88	5.70	0.01	0.14
L.naticoides	54	123	3.32	0.99	13.21	0.89	0.68	0.10	31.12	8.89	0.03	42.25	2.13	99.30	0.17	0.02	0.02	0.42	0.08	0.70	5.76	0.02	0.08
N.gymnotrachelus	11	24	3.01	0.98	7.86	13.47	4.04	0.24	6.23	0.00	0.00	27.98	2.92	62.73	0.12	0.00	0.00	9.09	28.06	37.27	6.83	0.04	0.42
N.melanostomus	24	53	3.24	0.98	24.69	2.90	0.17	4.06	2.49	5.22	0.28	51.42	0.41	91.64	0.62	0.02	0.26	6.76	0.70	8.36	5.59	0.01	0.17
O.crassus	36	83	3.56	0.99	8.91	9.15	1.07	0.65	17.49	7.15	0.00	53.15	0.08	97.66	0.23	0.49	0.00	0.73	0.90	2.34	5.68	0.01	0.14

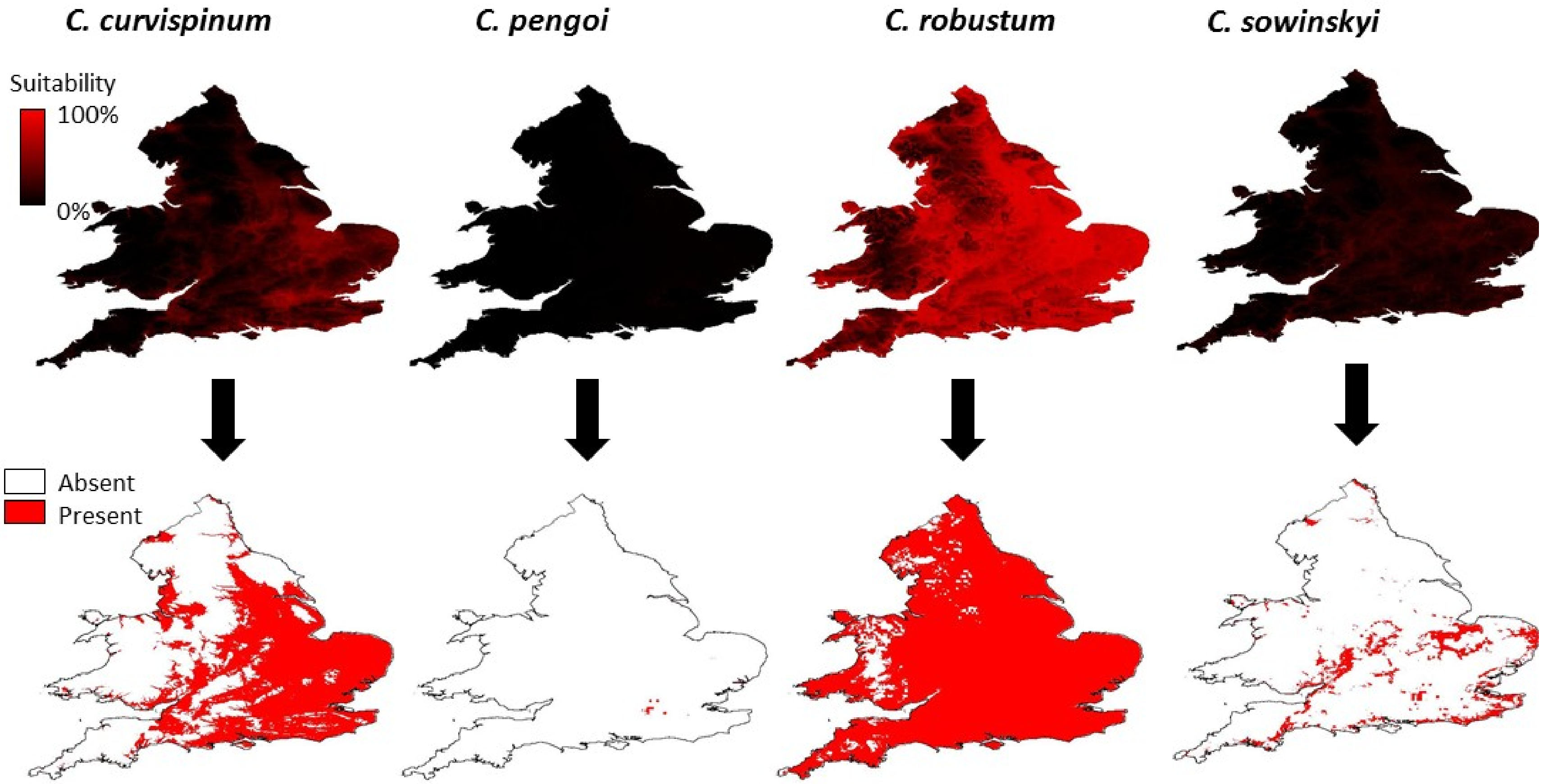
O.obesus	26	59	3.33	0.99	0.81	6.19	2.67	30.33	0.08	7.23	0.00	28.80	0.23	76.33	2.94	0.93	0.00	0.00	19.80	23.67	6.29	0.03	0.08
P.marmoratus	33	74	2.86	0.98	2.46	1.07	0.00	2.39	8.65	6.02	0.00	59.85	1.39	81.85	0.04	0.00	0.00	17.87	0.24	18.15	6.59	0.03	0.23
P.robustoides	56	130	3.47	0.99	8.17	0.00	0.47	2.89	16.28	7.00	0.12	54.56	0.15	89.63	1.86	1.64	0.00	6.83	0.04	10.37	5.78	0.02	0.04
P.semilunaris	45	102	3.75	0.99	2.41	4.32	5.76	0.00	12.33	0.84	0.27	72.89	0.84	99.66	0.24	0.02	0.01	0.06	0.00	0.34	5.85	0.02	0.10
TOTAL	**45.39**	**104.00**	**3.57**	**0.99**	**8.54**	**3.64**	**1.86**	**6.07**	**14.71**	**5.22**	**0.46**	**49.16**	**0.74**	**90.39**	**1.21**	**0.35**	**0.12**	**4.54**	**3.38**	**9.61**	**5.89**	**0.02**	**0.18**

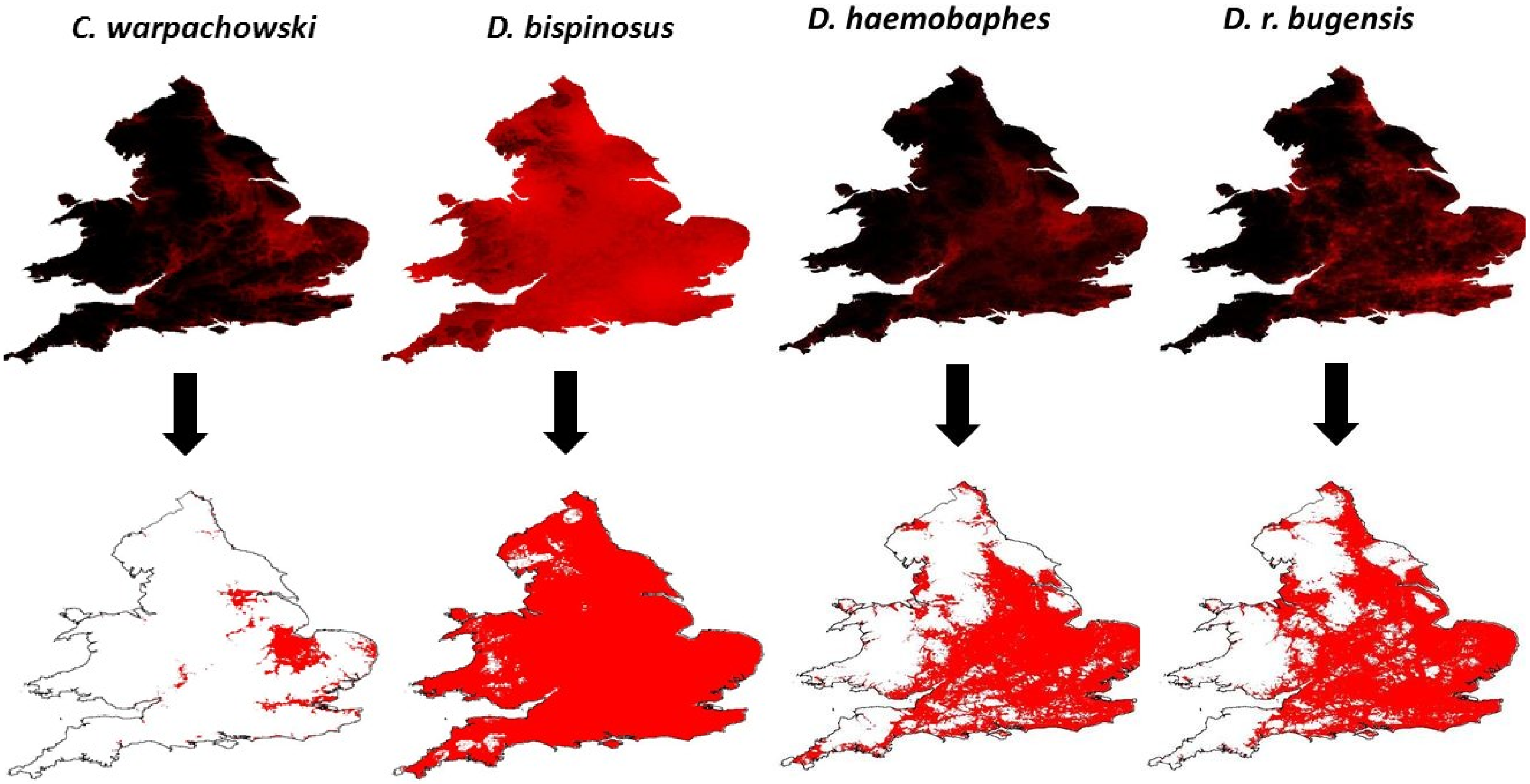
Definition of terms (modified from MaxEnt's tutorial in http://www.cs.princeton.edu/~schapire/maxent/):

Name: Scientific name of the species
Training samples: Number of presence records used for training the model (70% of the total).
Test samples: Number of presence records used for testing the model (30% of the total).
Test gain: Model gain calculated from presence records held out to test the model.
Test AUC: Area Under the ROC curve calculated using test data. A model that performs no better than random will have a test AUC of 0.5 whereas a model with perfect discrimination will score 1.
VARIABLE: The permutation importance of each variable to the model is calculated as follows: for each environmental variable in turn, the values of that variable on training presence and background data are randomly permuted. The model is reevaluated on the permuted data, and the resulting drop in training AUC is shown in the table, normalized to percentages. The % contribution and permutation importance of variables represent different methodologies to calculate the relevance of each variable in the model that provide slightly different results. Variable permutation importance should be interpreted with caution when the predictor variables are correlated.

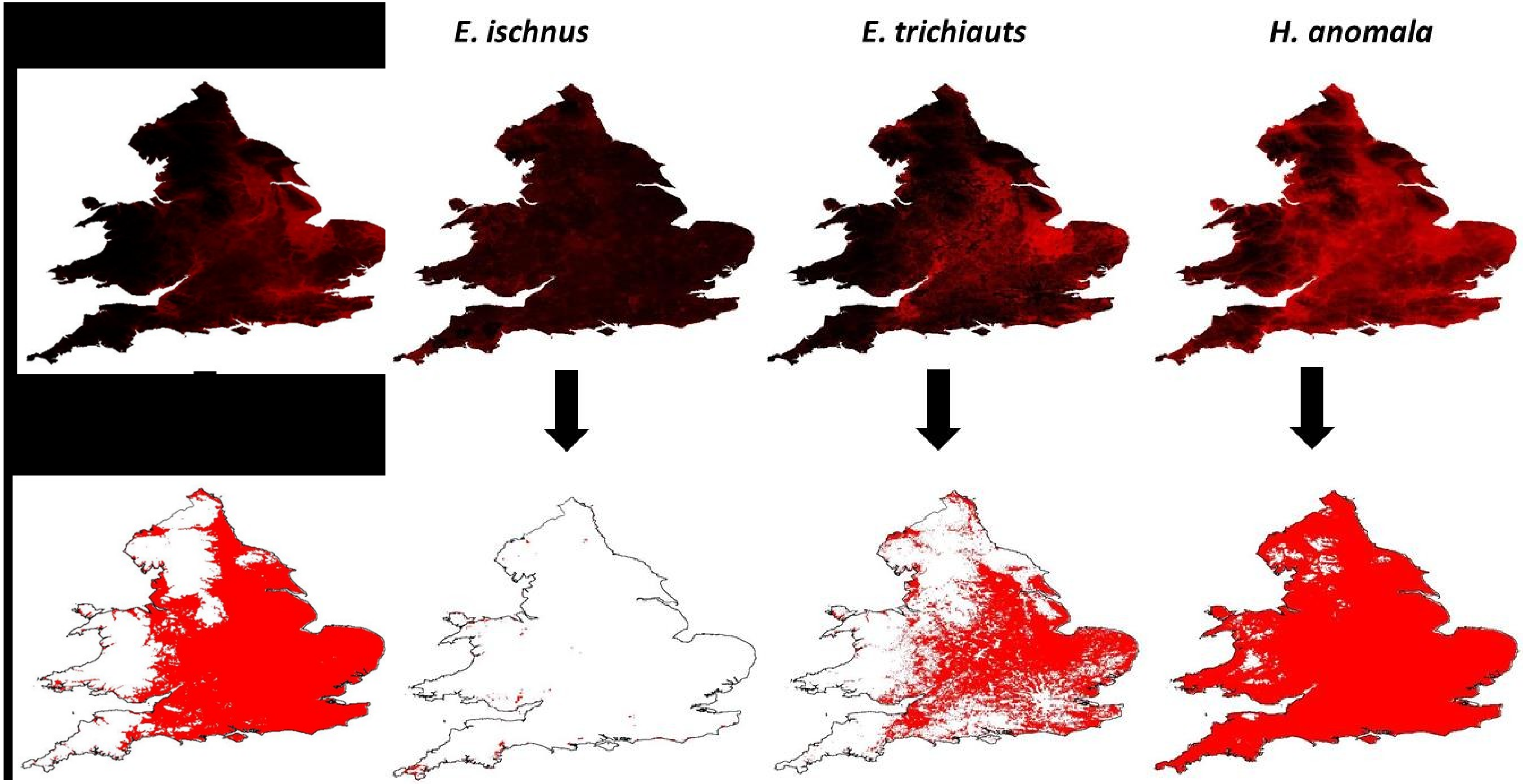
TOTAL ENVIRONMENTAL: Sum of the permutation importance of all environmental variables.
TOTAL SOCIO-ECONOMIC: Sum of the permutation importance of all socio-economic variables.
Entropy: Measure of the disorder in the species distribution.
Prevalence: Ratio of presence to background samples.
MaxTSS threshold: Maximum training sensitivity plus specificity threshold used for transforming continuous (0-100%) into binary (0-1) predictions.

APPENDIX F Results from Species Distribution Models (SDM) performed between the occurrence of 23 invasive Ponto-Caspian species in Europe and a set of 14 predictors. For each species, two suitability maps are provided: continuous prediction (from 0%-conditions unsuitable for the species, to 100% perfect match with the species range) and thresholded prediction (predicted presence/absence, using the threshold maximizing the sensibility and specificity of the model). For more details on model calibration and projection, consult section 2.4).





C. warpachowski   *D. bispinosus*   *D. haemobaphes*   *D. r. bugensis*



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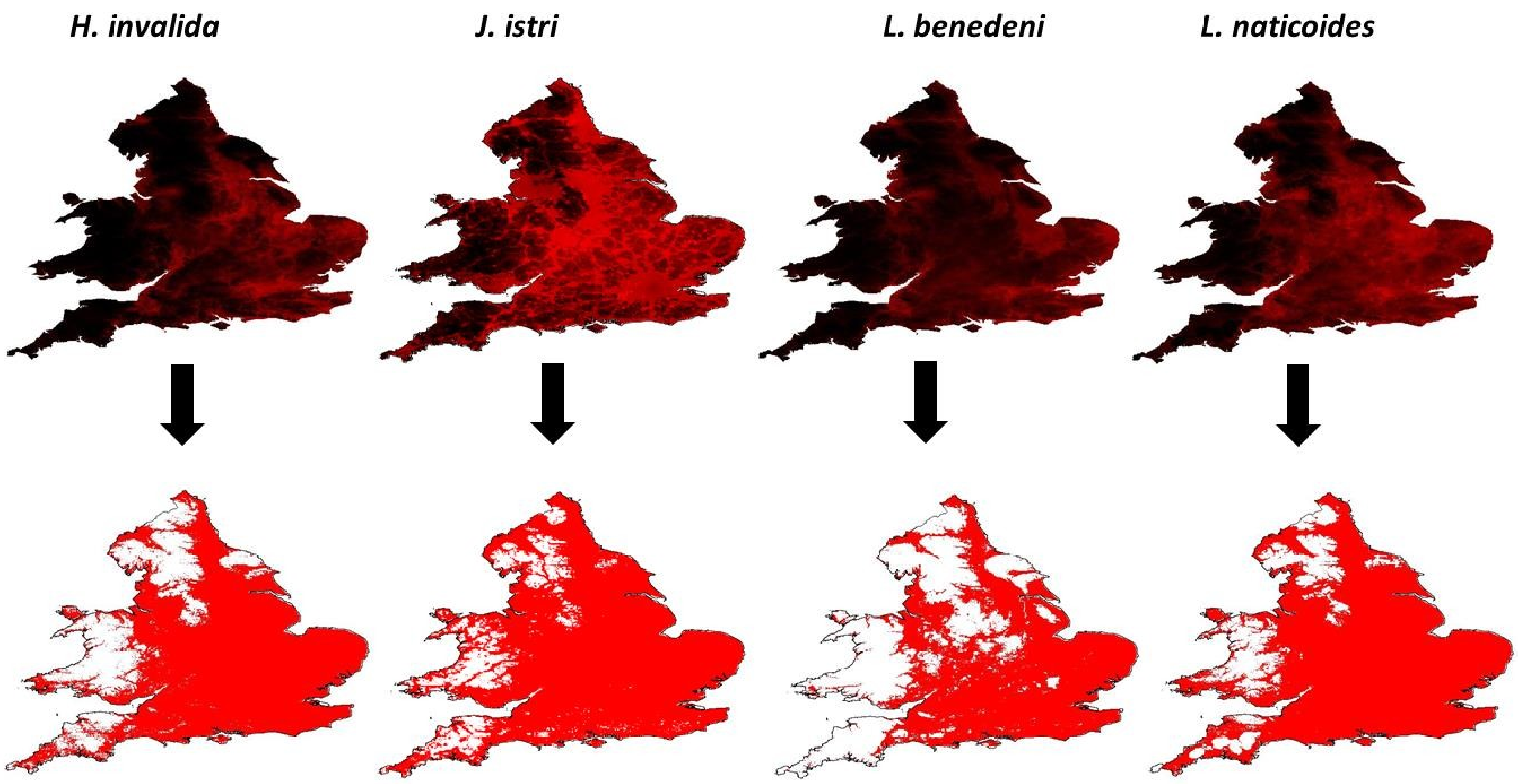
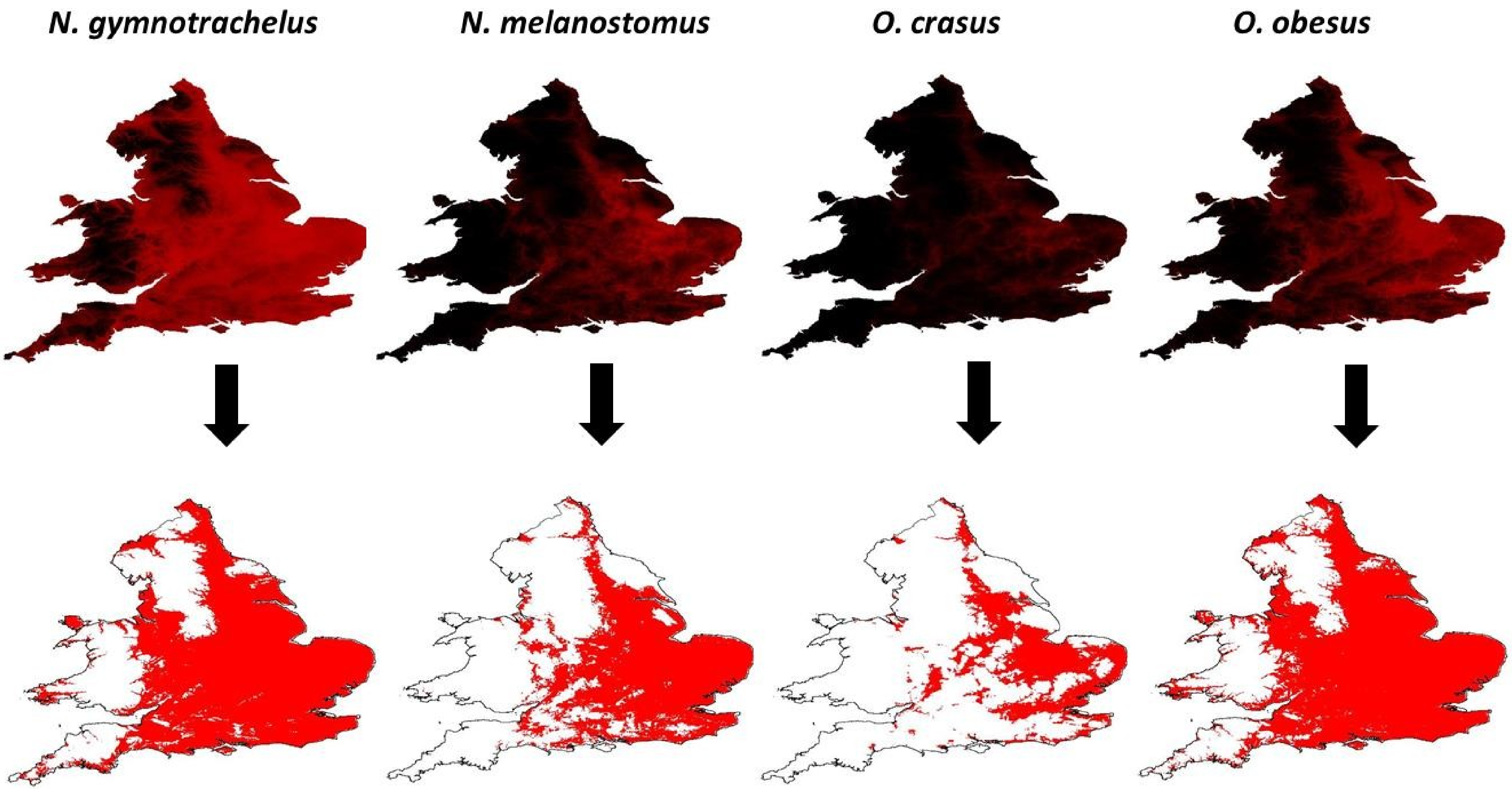


H. invalida *J. istri* *L. benedeni* *L. naticoides*


N. gymnotrachelus
N. melanostomus
O. crasus
O. obesus