

**Impact of the invasive amphipod**  
***Dikerogammarus villosus* on trophic interactions**  
**under field conditions**

by

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In der Wissenschaft gleichen wir alle nur den Kindern, die am Rande des Wissens hie und da einen Kiesel aufheben, während sich der weite Ozean des Unbekannten vor unseren Augen erstreckt.

*(Sir Isaac Newton, 1643-1727)*

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The following parts of this thesis are published:

**Chapter II:** René Gergs (RG) considered the application of this method to investigate freshwater food webs. Silke Claßen provided the majority of specimens for the spectrum of 130 taxa. Meike Koester (MK) established the majority of primers (diploma thesis: 16, doctoral thesis: 5). Sample processing and optimisation of laboratory protocols were exclusively performed by MK. The first author wrote the first draft. All authors contributed to the final version of the manuscript.

Koester, M., Claßen, S. & Gergs, R. (2013) Establishment of group-specific PCR primers for the identification of freshwater macroinvertebrates. *Conservation Genetics Resources*, 5, 1091-1093.

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**Chapter IV:** MK and RG designed the study. Field sampling and sample processing were done by MK. Processing of stable isotope samples was mainly performed by Bastian Bayer. Statistical analyses of the data were conducted partly by the second author and mainly by MK. The first author wrote the first draft. All authors contributed to the final version of the manuscript.

Koester, M., Bayer, B. & Gergs, R. (2015) Is *Dikerogammarus villosus* (Crustacea, Gammaridae) a ‘killer shrimp’ in the River Rhine system? *Hydrobiologia*, 768, 299-313.

**Chapter V:** The study was designed by RG and Ralf Schulz. MK contributed to the field sampling and data analyses. Robert S. Schulz processed the majority of stable isotope samples. The first author wrote the first draft. All authors contributed to the final version of the manuscript.

Gergs, R., Koester, M., Schulz, R.S. & Schulz, R. (2014) Potential alteration of cross-ecosystem resource subsidies by an invasive aquatic macroinvertebrate: implications for the terrestrial food web. *Freshwater Biology*, 59, 2645-2655.

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## Chapter I

### General Introduction

#### Invasive species in freshwater ecosystems

Biological invasions are known to have an effect upon various levels of ecological organisations (Elton, 1958) and have been recognized to be one of the major threats to native biodiversity (Sala *et al.*, 2000, Chandra & Gerhardt, 2008). The introduction of species can either be deliberate or unintentional, for instance due to escape or contamination over transport goods (Hulme *et al.*, 2008). Once established, these species can spread rapidly dismissing geopolitical boundaries, thus the invasion of alien species is of local as well as global concern (Chandra & Gerhardt, 2008). In Europe 11 % of the ca 12,000 alien species are considered to be invasive (Caffrey *et al.*, 2014). Invasive species cause environmental as well as economic and social damage with estimated annual costs of €12 billion (Gallardo & Aldridge, 2013, Caffrey *et al.*, 2014). The use of several terms like ‘non-indigenous’, ‘alien’ or ‘invasive’ is not uniform in invasion biology (Kolar & Lodge, 2001). In this thesis the term ‘alien species’ refers to species introduced to regions beyond their native range after 1492 either directly or indirectly by human activity (= non-native species = non-indigenous species). Alien species that established self-sustaining populations, spread from the point of introduction (secondary spread) and became abundant elsewhere, thereby modifying invaded ecosystems, are referred to as ‘invasive (alien) species’ (IAS).

Freshwater ecosystems have been strongly altered not only by human land use and the modification of riparian zones, which inter alia lead to elevated inputs of contaminants, nutrients and sediments but also because waterways are intensively used for the transportation of goods, the disposal of sewage and as water source (Sala *et al.*, 2000). Due to high levels of such human disturbance and the high intrinsic dispersal ability of species, freshwater systems are in particular vulnerable regarding the introduction of IAS (Gherardi, 2007). Nowadays, a number of roughly 262 alien animal species is established in European freshwater systems (Gherardi *et al.*, 2009). The introduction and dispersal of these alien species in aquatic systems strongly benefited from the interconnection of running waters for merchant shipping (Bij de Vaate *et al.*, 2002,

Galil, Nehring & Panov, 2007). For instance, in the River Rhine, one of the European inland waterways with the highest number of alien species, the yearly average number of newly recorded alien species strongly increased after the opening of the Rhine-Main-Danube Canal in 1992 (Leuven *et al.*, 2009). In Central Europe, many of the freshwater invaders originate from the Ponto-Caspian area (Bollache *et al.*, 2008) and nowadays an average of one Ponto-Caspian species a year invades the River Rhine system via the Rhine-Main-Danube Canal (Baur & Schmidlin, 2007). By changing habitat conditions and availability of food resources these alien species strongly altered community structures and food webs of invaded and adjusted systems (e.g. Vander Zanden, Casselman & Rasmussen, 1999, Ricciardi & MacIsaac, 2000, Gergs, Rinke & Rothhaupt, 2009), thereby potentially representing a threat to native biodiversity (Sala *et al.*, 2000, Chandra & Gerhardt, 2008).

### **Invasion history of *Dikerogammarus villosus* in Europe**

One of the most successful invaders in European water systems is the amphipod *Dikerogammarus villosus* (Sowinsky 1894) (DAISIE, 2014). Originating from the Ponto-Caspian area, the species invaded Central European water systems via the Main-Danube Canal (Bij de Vaate *et al.*, 2002) and rapidly spread throughout Europe (Rewicz *et al.*, 2014). Besides, not long after the invasion *D. villosus* was already found in high densities (e.g. Rey, Ortlepp & Küry, 2005) and therefore was strongly relevant for the system.

In 1976 *D. villosus* was first recorded from the middle reaches of the River Danube, in Slovakia and Hungary (Russev, 1979), but it was not found in the upper reaches of the Danube in Austria until 1992 (Nesemann, Pöckl & Wittmann, 1995). With the opening of the Rhine-Main-Danube Canal, connecting the rivers Danube and Rhine, in 1992, the consistency of the so called ‘southern migration corridor’ was gained (Bij de Vaate *et al.*, 2002). After colonising the canal in 1993, *D. villosus* reached the River Main in 1994 (Schöll, Becker & Tittizer, 1995) and was found in the Lower Rhine in the Netherlands in the same year (Bij de Vaate & Klink, 1995). However, the species, despite yearly monitoring of navigable parts, was not found in the German part of the River Rhine until 1995 (Schöll *et al.*, 1995). Therefore, it had to be actively transported to the Netherlands, likely attached to the shell of ships that used the Main-Danube Canal as direct interconnection between the Black Sea region and the big sea harbours in Rotterdam. By 1997 *D. villosus* was already common in the whole River Rhine

downstream of the city Basel (Bollache *et al.*, 2004) and was found the first time in the French River Saône, which is directly connected to the former via canals (Bollache *et al.*, 2004). Until 2003 *D. villosus* had invaded all major rivers in France (Bollache *et al.*, 2004).

In 1998 *D. villosus* was first detected in the Midland Canal, in the Elbe-Havel Canal as well as in the rivers Weser and Elbe (Grabow, Eggers & Martens, 1998). One year later (1999), the species had colonised the River Moselle (Tittizer *et al.*, 2000, Devin *et al.*, 2001). Until 2008 *D. villosus* had been reported from the rivers Oder (Grabowski, Jazdzewski & Konopacka, 2007b), Drava (2007; Žganec, Gottstein & Hudina, 2009), Dnieper (2006; Mastitsky & Makarevich, 2007), Vltava (Berezina & Ďuriš, 2008) and Warta as well as from the North Sea basin and the Baltic Sea basin (Rewicz *et al.*, 2014). Additionally, *D. villosus* was even discovered in 12 lakes in the alpine region, including Lake Zürich (Rewicz *et al.*, 2014).

More recently, *D. villosus* extended its range expansion outside mainland Europe in Great Britain, where it was first detected in 2010 (MacNeil *et al.*, 2010) and can be expected to continue its spread (Gallardo, Errea & Aldridge, 2012). As happened with other Ponto-Caspian invaders, *D. villosus* is expected to further expand beyond Europe eventually reaching North American freshwaters like the Great Lakes (Ricciardi & MacIsaac, 2000).

### **Potential reasons for the colonisation success of *D. villosus***

For an amphipod, *D. villosus* possesses several traits virtually making the species predestined to be a successful invader (Grabowski, Bacela & Konopacka, 2007a). The high tendency of *D. villosus* to drift (Van Riel, Van der Velde & Bij de Vaate, 2011), which probably enables the species to colonise rivers in downstream direction, might be one potential reason for its fast spreading (Rewicz *et al.*, 2014). Furthermore, *D. villosus* has a wide ecophysiological tolerance towards parameters such as temperature, oxygen content, salinity (Bruijs *et al.*, 2001, Maazouzi *et al.*, 2011) and pollution (Sroda & Cossu-Leguille, 2011, Bundschuh *et al.*, 2013). Combined with its ability to colonise diverse types of substrates (Devin *et al.*, 2003), this wide ecophysiological tolerance makes the species capable to invade nearly all freshwater ecosystems. Rapid growth (Piscart *et al.*, 2003) and the high reproductive potential of *D. villosus*, due to early sexual maturity, long breeding periods, large number of comparatively small eggs in the brood pouch and short embryonic development time (Pöckl, 2007, 2009), enable the

species to establish sustainable populations in invaded systems within a short time period making it a strong competitor for space and food. Additionally, unspecialised mouthparts facilitating various modes of feeding, including carnivory and predation, may also be reasons for the invasion success of *D. villosus* (Mayer *et al.*, 2008).

Furthermore, *D. villosus* has a high tolerance towards air exposure as it was reported to survive outside the water at least six days embedded in zebra mussel clusters covering boats (Martens & Grabow, 2008), up to five days within folds of a diving suite (Bączela-Spychalska *et al.*, 2013) as well as up to six days within piles of roots and macrophytes (Rewicz *et al.*, 2014). Moreover, the species enhances survival when exposed to air without shelter due to grouping behaviour (Poznańska *et al.*, 2013). The ability to cope with air exposure is suggested to increase the potential for overland transport of *D. villosus*, enabling not only the invasion of isolated water bodies, but also a rapid range expansion (Rewicz *et al.*, 2014).

### **Impacts on invaded systems**

*D. villosus* is intimidating the native diversity and ecosystem functioning (Bollache *et al.*, 2008, MacNeil *et al.*, 2010, Piscart, 2010) and altering food webs (Van Riel *et al.*, 2006). In many invaded waters, the establishment of the species was associated with a decline of previously prevalent native and non-native macroinvertebrate taxa, including other amphipod species (e.g. Piscart *et al.*, 2011b, MacNeil *et al.*, 2013, Gergs & Rothhaupt, 2015). Laboratory studies have revealed a strong predatory impact of *D. villosus* on other macroinvertebrates, as chironomid, mayfly and dragonfly larvae, isopods, other amphipods and juvenile crayfish (e.g. Dick & Platvoet, 2000, Dick, Platvoet & Kelly, 2002, Krisp & Maier, 2005, MacNeil & Platvoet, 2005, Buřič *et al.*, 2009). However, little is known about the relevance of predation by *D. villosus* in the field, since natural conditions are much more complex than laboratory conditions (Kinzler *et al.*, 2009). Moreover, using fatty acids as biomarkers Maazouzi *et al.* (2009) found minor importance of predation in the diet of *D. villosus* in the Mirgenbach Reservoir, in north-eastern France.

It is also known that *D. villosus* affects leaf litter decomposition and energy flow not only indirectly by decline of shredders, but also directly (MacNeil *et al.*, 2011, Piscart *et al.*, 2011b, Truhlar, Dodd & Aldridge, 2014). The fact that *D. villosus* was found consuming even unconditioned leaf material could cause a time-shift in availability of fine particular organic matter, leading to a lack of this resource for species tending to



emerge later in autumn, resulting in changes of the overall community assemblage (Truhlar *et al.*, 2014). No matter if *D. villosus* is directly or indirectly affecting aquatic insect larvae and thus the densities of insects emerging to the terrestrial environment, the species thereby also has the potential to alter cross-ecosystem resource flows and might therefore even have impacts on terrestrial food webs.

Since most of the knowledge about used food resources of *D. villosus* was gained from laboratory experiments they are not necessarily of the same relevance under field conditions and impacts of the species by feeding activities might be misjudged. Therefore, to predict the impact of *D. villosus* on natural communities, knowledge about trophic positioning of the species within natural food webs is essential. However, even though many studies have been conducted regarding the impact of *D. villosus*, only few studies investigated the feeding behaviour or trophic positioning of *D. villosus* in the field (Van Riel *et al.*, 2006, Maazouzi *et al.*, 2009, Hellmann *et al.*, 2015). This is partially because tracking trophic linkages in complex systems using conventional methods is difficult. But within the last decades alternative approaches enabling the assessment of feeding interactions in the field have been established (e.g. Traugott *et al.*, 2013).

### **Food web analyses in natural communities**

A nowadays frequently used method to characterise aquatic food webs is the analysis of stable isotope ratios ( $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$ ) as a time-integrating natural tracer of predator–prey interactions (e.g. Bearhop *et al.*, 1999, Davis *et al.*, 2012). These analyses rely on different trophic fractionation of the isotopes when transferring organic matter to higher trophic positions (Brauns, von Schiller & Gergs, 2012). As the proportion of the stable nitrogen isotope ( $^{15}\text{N}$ ) is enriched in consumers relative to their diet, on average 2.3 – 3.4 ‰ per trophic level (e.g. Post, 2002, McCutchan *et al.*, 2003), it can be used to estimate trophic positions of organisms relative to a known baseline (Peterson & Fry, 1987, Kling, Fry & O’Brian, 1992, Cabana & Rasmussen, 1996, Post, 2002). By contrast, the stable carbon isotope ( $^{13}\text{C}$ ) is usually less enriched with increasing trophic level (< 1 ‰ in most cases), but varies between different carbon sources (Peterson & Fry, 1987, Post, 2002). This fact enables to determine the origin of carbon, such as littoral and pelagic primary production (France, 1995, Hardy *et al.*, 2010). Therefore, stable isotope metrics enable the determination of trophic structures at the community-level (Layman *et al.*, 2007a). For instance, mixing models, based on Bayesian

estimations taking account of uncertainties in the sources and trophic enrichment factors, allow quantifying the relative contribution of resources to the diet of a consumer with regard to natural variability (Brauns *et al.*, 2012). Furthermore, individual variations in  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  within populations can provide additional insights in their trophic ecology (Bearhop *et al.*, 2004, Layman *et al.*, 2007b). To this end, metrics like the convex hull area or standard ellipse area occupied by a species in  $\delta^{13}\text{C}$ - $\delta^{15}\text{N}$  isotopic space representing trophic diversity can be used as a quantitative indication of their niche space (Layman *et al.*, 2007b, Jackson *et al.*, 2011). Therefore, properly applied, stable isotope analyses are a powerful tool for evaluating invasion effects on the food web (Vander Zanden *et al.*, 1999, Jackson *et al.*, 2012).

However, an exact definition of predator–prey interactions can be difficult to obtain using stable isotopes since it requires a comprehensive knowledge about all potential food sources and their appropriate isotopic signature (Hardy *et al.*, 2010). The latter is difficult to achieve because of potential overlapping isotopic values from different prey species (Carreon-Martinez & Heath, 2010). Therefore, gut content analysis might be necessary to identify single prey species of a consumer. Most common such analyses are visual and require a consolidated knowledge about morphologic diversity from prey organisms. Visual gut content analyses miss soft bodied prey-organisms and, in some cases, the physical process of digestion makes it difficult (Redd *et al.*, 2008). Invertebrate consumers, like *D. villosus*, intensively comminute their food before ingestion, so that visual definition of prey species in gut contents is impossible (Gergs, 2009). Due to this, molecular analyses, such as a technique using group-specific primers for genetic gut content analyses to amplify only DNA regions of particular target groups and exclude non-target species (Jarman, Deagle & Gales, 2004), are more auspicious here. Yet, such genetic analyses are not without limitations. For instance, gut content analysis only reflect a snapshot of feeding behaviour and provide no information about food basis of prey-organisms. Thus, combining these two methods, can lead to a better understanding of food webs and their relationship to nutrient or energy fluxes (Carreon-Martinez & Heath, 2010, Hardy *et al.*, 2010).

### **Aims of this study**

Like already mentioned above, up to know, the knowledge about the feeding behaviour of *D. villosus* under natural conditions is only remote. But, as *D. villosus* is predicted to even further increase its range expansion (Devin *et al.*, 2003) and thereby potentially

threatens their biodiversity (Dick & Platvoet, 2000), knowledge of its trophic positioning is essential to predict the impact of this invader on natural communities in newly invaded systems. Thus, the general aim of my thesis is to assess potential trophic impacts of *D. villosus* on food webs and community structures under field conditions and potential propagating effects to adjacent habitats. Thereby, my major hypothesis is that *D. villosus* is not mainly a predator in the field. For my investigations, I chose the River Rhine system as study area because of its importance as the so-called “global highway” for aquatic invasive species (e.g. Leuven *et al.*, 2009) and decided to use a combination of stable isotope and molecular gut content analyses like suggested by Carreon-Martinez & Heath (2010) and Hardy *et al.* (2010). Hence, genetic analyses suitable for prey detection in *D. villosus* gut contents had to be established initially. Therefore, based on my diploma thesis, I further developed and established group-specific primers for several potential macroinvertebrate prey species of *D. villosus* that are common in the River Rhine system (**Chapter II**).

Combining genetic gut content analyses, with one of these newly established primers, and stable isotope analyses, I examined the importance of intraguild predation (IGP), i.e. predatory interactions between members of the same taxonomic guild (Polis, Myers & Holt, 1989), by *D. villosus* under natural conditions at an invasion front (**Chapter III**). Frequently found in laboratory studies, IGP is often assumed to be the key driver for the displacement of other amphipod species (e.g. Dick & Platvoet, 2000, Kinzler *et al.*, 2009), but has not been verified in the field. However, I hypothesised, if IGP is relevant in the field it would be intensively marked at an invasion front. Studying stored field samples from an invasion front of the species in Switzerland, I determined and compared the stable carbon ( $\delta^{13}\text{C}$ ) and nitrogen ( $\delta^{15}\text{N}$ ) isotope signatures of *D. villosus* and co-occurring native amphipod species and genetically tested gut contents of *D. villosus* using a group-specific primer for gammarid amphipods to detect recent predation on native gammarids.

Because the impact on native fauna as well as the feeding strategy of *D. villosus* might differ between habitats (Hesselschwerdt, Necker & Wantzen, 2008, Hesselschwerdt, 2010), I also studied the predatory impact of *D. villosus* on other macroinvertebrates in various sites of the River Rhine system covering a broad range of common microhabitats (**Chapter IV**). Stable isotope analyses of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  were thereby used to determine the position of *D. villosus* in the food web in question and the width of the respective isotopic niche occupied by the species. Furthermore, genetic gut

content analyses using 16 group-specific primers, established within my thesis, were conducted to test for recently ingested macroinvertebrate prey.

In which way ever, the establishment of *D. villosus* has changed aquatic food webs. As rivers and their catchments are linked by fluxes of matter, energy and organisms, the question arises if impacts of *D. villosus* on the benthic community and food web have repercussions on adjacent terrestrial habitats. Therefore, in **Chapter V** I focus on potential cross-ecosystem effects of *D. villosus*. In this chapter, we assessed the indirect impact of the species on the feeding behaviour of two riparian spider taxa as different contributions of aquatic insects to the spiders' diet in presence of different densities of *D. villosus*. Using stable isotope analyses of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  the contribution of aquatic and terrestrial prey to the diet of the spiders was determined via a stable isotope mixing model.

## Chapter II

### **Establishment of group-specific PCR primers for the identification of freshwater macroinvertebrates**

*Meike Koester, Silke Claßen and René Gergs*

Conservation Genetic Resources (2013) 5: 1091-1093

Due to copyright issues, the text of this chapter was replaced by the reference information and its web link to the journal publication. The interested reader is kindly asked to read the published paper via the following reference:

Koester, M., Claßen, S. & Gergs, R. (2013) Establishment of group-specific PCR primers for the identification of freshwater macroinvertebrates. Conservation Genetics Resources, 5, 1091-1093.

[Click here to see the paper on the publisher's website.](#)

#### **Supplementary material**

Additional supplementary material for this chapter may be found in the section ‘Supplementary material’ of this thesis.

**Table II-S1:** Results from all combinations of the 21 primer sets with the 130 taxa included into our test for specificity

**Table II-S2:** Accession numbers of obtained sequences from GenBank

**Table II-S3:** Species targeted by the group-specific primers and their corresponding accession numbers (EMBL Nucleotide Sequence Database; EMBL-Bank).

## Chapter III

### **No evidence for intraguild predation of *Dikerogammarus villosus* (Sowinsky, 1894) at an invasion front in the Untere Lorze, Switzerland**

*Meike Koester and René Gergs*

Aquatic Invasions (2014) 9: 489-497

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## Chapter IV

### **Is *Dikerogammarus villosus* (Crustacea, Gammaridae) a 'killer shrimp' in the River Rhine system?**

*Meike Koester, Bastian Bayer & René Gergs*

Hydrobiologia (2015) 768: 299-313

Due to copyright issues, the text of this chapter was replaced by the reference information and its web link to the journal publication. The interested reader is kindly asked to read the published paper via the following reference:

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[Click here to see the paper on the publisher's website.](#)

#### **Supplementary material**

Additional supplementary material for this chapter may be found in the section 'Supplementary material' of this thesis.

**Table IV-S1:** Details of the 2 batches of 16 group-specific primer pairs amplifying regions of the 18S or 28S rDNA from 16 target groups of aquatic macroinvertebrates.

**Table IV-S2:** Sex (m, male; f, female), size, stable isotope signature ( $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ ) and results of the genetic gut content analyses of 226 *Dikerogammarus villosus* individuals from the ten sampling sites.

**Table IV-S3:** Wilcox-Mann-Whitney test of mean mean  $\delta^{15}\text{N}$  values of *Dikerogammarus villosus* and the respective primary consumers of the 10 study sites.

**Table IV-S4:** Correlation analyses between the mode  $\text{SEA}_B$  ( $\text{MdSEA}_B$ ) and biotic and abiotic parameters.

**Table IV-S5:** Correlation analyses between the size of *Dikerogammarus villosus* individuals and their isotopic signature ( $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ ) for each of the 10 sites. \* = significance level 0.05, \*\* = significance level 0.01, \*\*\* = significance level 0.001.

**Table IV-S6:** Regression analysis ( $n = 10$ ) of mean size of tested *Dikerogammarus villosus* individuals and proportion of gut contents in which and number of groups from which DNA was detected. \* = significance level 0.05.

**Figure IV.S1:** Stable isotope bi-plot illustrating the isotopic niche of *Dikerogammarus villosus* at sampling site 1. The stable isotope signature of single *D. villosus* individuals ( $n = 20$ ) and the standard ellipse area ( $\text{SEA}_c$ ) for *D. villosus* are shown. Mean  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  values  $\pm$  SD of other macroinvertebrates and primary producers are given.

**Figure IV.S2:** Stable isotope bi-plot illustrating the isotopic niche of *Dikerogammarus villosus* at sampling site 2. The stable isotope signature of single *D. villosus* individuals ( $n = 20$ ) and the standard ellipse area ( $\text{SEA}_c$ ) for *D. villosus* are shown. Mean  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  values  $\pm$  SD of other macroinvertebrates and primary producers are given.

**Figure IV.S3:** Stable isotope bi-plot illustrating the isotopic niche of *Dikerogammarus villosus* at sampling site 3. The stable isotope signature of single *D. villosus* individuals ( $n = 20$ ) and the standard ellipse area ( $\text{SEA}_c$ ) for *D. villosus* are shown. Mean  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  values  $\pm$  SD of other macroinvertebrates and primary producers are given.

**Figure IV.S4:** Stable isotope bi-plot illustrating the isotopic niche of *Dikerogammarus villosus* at sampling site 4. The stable isotope signature of single *D. villosus* individuals ( $n = 20$ ) and the standard ellipse area ( $\text{SEA}_c$ ) for *D. villosus* are shown. Mean  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  values  $\pm$  SD of other macroinvertebrates and primary producers are given.

**Figure IV.S5:** Stable isotope bi-plot illustrating the isotopic niche of *Dikerogammarus villosus* at sampling site 5. The stable isotope signature of single *D. villosus* individuals ( $n = 20$ ) and the standard ellipse area ( $\text{SEA}_c$ ) for *D. villosus* are shown. Mean  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  values  $\pm$  SD of other macroinvertebrates and primary producers are given.



**Figure IV.S6:** Stable isotope bi-plot illustrating the isotopic niche of *Dikerogammarus villosus* at sampling site 6. The stable isotope signature of single *D. villosus* individuals ( $n = 21$ ) and the standard ellipse area ( $SEA_c$ ) for *D. villosus* are shown. Mean  $\delta^{15}N$  and  $\delta^{13}C$  values  $\pm$  SD of other macroinvertebrates and primary producers are given.

**Figure IV.S7:** Stable isotope bi-plot illustrating the isotopic niche of *Dikerogammarus villosus* at sampling site 7. The stable isotope signature of single *D. villosus* individuals ( $n = 23$ ) and the standard ellipse area ( $SEA_c$ ) for *D. villosus* are shown. Mean  $\delta^{15}N$  and  $\delta^{13}C$  values  $\pm$  SD of other macroinvertebrates and primary producers are given.

**Figure IV.S8:** Stable isotope bi-plot illustrating the isotopic niche of *Dikerogammarus villosus* at sampling site 8. The stable isotope signature of single *D. villosus* individuals ( $n = 21$ ) and the standard ellipse area ( $SEA_c$ ) for *D. villosus* are shown. Mean  $\delta^{15}N$  and  $\delta^{13}C$  values  $\pm$  SD of other macroinvertebrates and primary producers are given.

**Figure IV.S9:** Stable isotope bi-plot illustrating the isotopic niche of *Dikerogammarus villosus* at sampling site 9. The stable isotope signature of single *D. villosus* individuals ( $n = 20$ ) and the standard ellipse area ( $SEA_c$ ) for *D. villosus* are shown. Mean  $\delta^{15}N$  and  $\delta^{13}C$  values  $\pm$  SD of other macroinvertebrates and primary producers are given.

**Figure IV.S10:** Stable isotope bi-plot illustrating the isotopic niche of *Dikerogammarus villosus* at sampling site 10. The stable isotope signature of single *D. villosus* individuals ( $n = 21$ ) and the standard ellipse area ( $SEA_c$ ) for *D. villosus* are shown. Mean  $\delta^{15}N$  and  $\delta^{13}C$  values  $\pm$  SD of other macroinvertebrates and primary producers are given.

**Figure IV.S11:** Large-scale map overview showing the River Rhine including Lake Constance (dark blue) and a selection of further 1st order water bodies (light blue). Approximate locations of the ten sites are indicated by red dots and the respective site numbers (for coordinates of each site see Table IV.1).

**Figure IV.S12:** Apportionment of A) positively tested group-specific primers and B) filling category of the gut ( $1 \leq 10\%$ ,  $2 = 11-25\%$ ,  $3 = 26-50\%$ ,  $4 = 51-75\%$ ,  $5 > 75\%$ ; e.g. Table IV-S2) to four size categories of *D. villosus* individuals investigated from the 10 sites.

## Chapter V

### **Potential alteration of cross-ecosystem resource subsidies by an invasive aquatic macroinvertebrate: implications for the terrestrial food web**

*René Gergs, Meike Koester, Robert S. Schulz & Ralf Schulz*

Freshwater Biology (2014) 59: 2645-2655

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Gergs, R., Koester, M., Schulz, R.S. & Schulz, R. (2014) Potential alteration of cross-ecosystem resource subsidies by an invasive aquatic macroinvertebrate: implications for the terrestrial food web. *Freshwater Biology*, 59, 2645-2655.

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#### **Supplementary material**

Additional supplementary material for this chapter may be found in the online version of this article.

**Table V-S1:** Abiotic and biotic environmental parameters, and different type of aquatic (midges and other aquatic taxa) and terrestrial emerging daily biomass of insects at the nine investigated study sites.

**Table V-S2:** Results of stable isotope analyses of the aquatic and terrestrial emerging insects per study site.

**Table V-S3:** Results of stable isotope analyses of the two spiders, *Tetragnatha* sp. and *Pirata piraticus*, at the nine study site.

## Chapter VI

### General Discussion and Perspectives

As outlined in the introduction, *Dikerogammarus villosus* nowadays colonised most of the major European inland rivers (e.g. Rewicz *et al.*, 2014), often associated with a decline of other macroinvertebrates (e.g. MacNeil *et al.*, 2013, Gergs & Rothhaupt, 2015). The observed displacement effects are often assumed to be caused by the strong predatory potential of the species revealed by laboratory studies (e.g. Dick & Platvoet, 2000, Kinzler *et al.*, 2009). Therefore, in recent years *D. villosus* is often called 'killer shrimp'. However, my main hypothesis was that *D. villosus* is not mainly a predator in the field and with this thesis I clearly show, that *D. villosus*, at least in the River Rhine system, is rather an opportunistic omnivore than a predator. Thus, assumptions based on the results of laboratory studies might have overestimated the impact of *D. villosus*, which is why a more general knowledge of its trophic positioning in the field is essential to predict its impact on natural communities. Furthermore, the results of this thesis give reason to assume that not only trophic positioning of populations but rather individual variation in the feeding behaviour might be important for the invasion success of *D. villosus*.

#### Methodological developments

Initially, I established group-specific primers for freshwater taxa (**Chapter II**), suitable to detect DNA of respective prey taxa out of mixed sources to enable detection of direct predator–prey interactions out of gut contents from field samples of *D. villosus*. As prey DNA is more intensively degraded during the process of digestion, the length of amplified fragments was kept as short as possible to increase the detection efficiency (e.g. King *et al.*, 2008). For the screening of gut contents of field samples for prey taxa not only the specificity of primers but also the detection efficiency and accuracy are important. Agarose gel electrophoresis is a common and inexpensive tool to visualise DNA fragments and determine their approximate length (Mülhardt, 2013). But, the visual resolution is strongly dependent on the amount DNA and the staining dye (Lee & Bahaman, 2012). While visualisation usually is no problem whenever working with

pure DNA samples, like I did for the establishment of the primers (**Chapter II**), a potentially very low amount of prey DNA in the gut content of an omnivore can strongly complicate the scoring of agarose electrophoresis results (personal experience M. Koester). Nevertheless, for the screenings of a low number of gut content samples of consumer organisms from the field for one particular prey group, as in **Chapter III**, this detection method is still feasible. But, complication in the scoring of agarose gel electrophoresis results makes the screening of a higher number of samples for multiple prey taxa, as in **Chapter IV**, extremely time intensive and thus impracticable. Automated fragment analysis via capillary electrophoresis upon an automated sequencer is a more sensitive detection method and in addition allows determining the exact length of fragments (e.g. Wang *et al.*, 2009). Moreover, the use of different fluorescent dyes as label enables not only the detection of a very low amount of DNA (Mülhardt, 2013), but also the parallel detection and determination of different fragments of comparable length by automated fragment analysis, as demonstrated in several microsatellite based studies (e.g. Baric *et al.*, 2006, Olafsson *et al.*, 2010, Gemmer & Gergs, 2013). Thus, I developed a screening method enabling the parallel screening for DNA fragments of each eight different prey taxa using automated fragment analysis in order to increase the detection efficiency and facilitate the scoring. Using this approach I screened 206 gut content samples of *D. villosus* individuals from the field for 16 prey taxa (**Chapter IV**). Regardless of the frequency with which prey DNA from different taxa was detected, the results proved the efficiency of this genetic approach for the detection of direct predator–prey interactions from multiple gut content samples of specimen collected in the field.

### **Role of predation by *D. villosus* in the field**

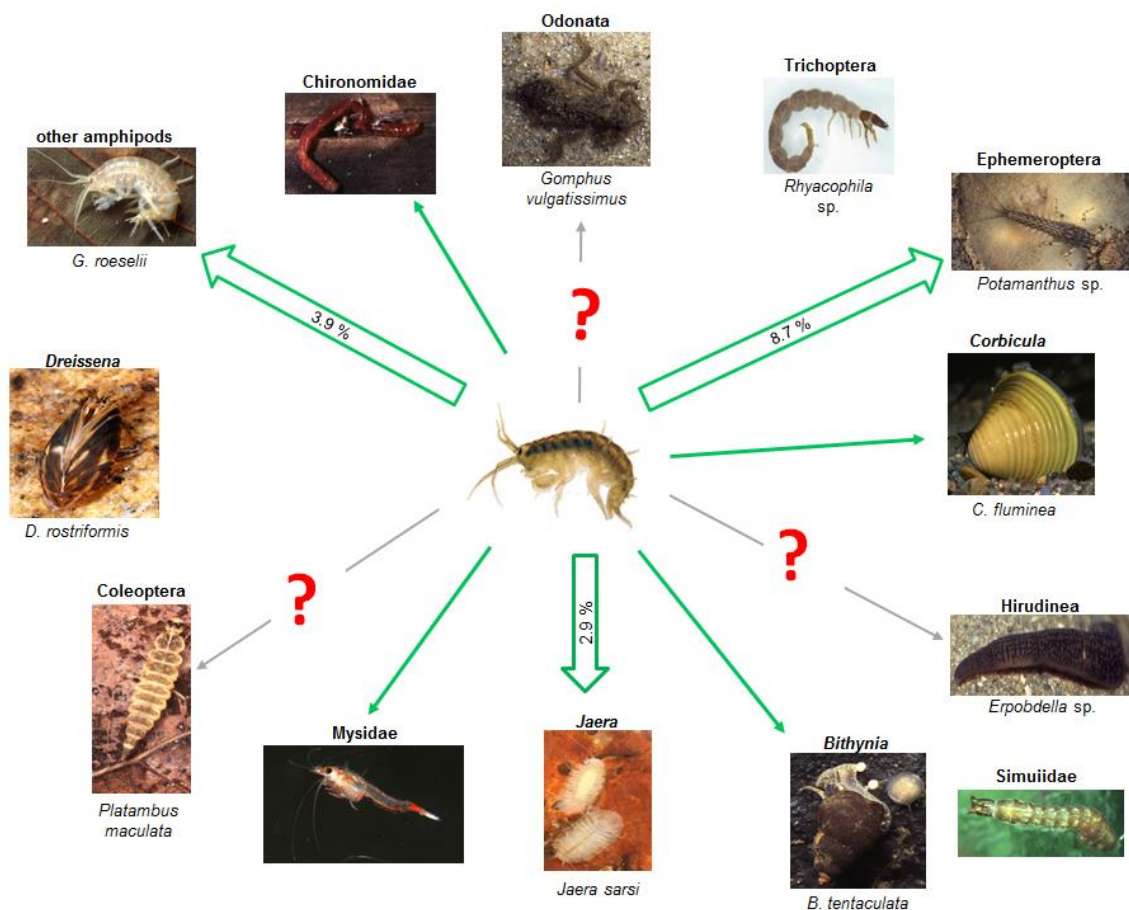
As outlined in the introduction, gut content analyses in general, and therefore also the genetic approach established in this thesis, only show a snapshot of the feeding behaviour. To overcome such disadvantages of particular methods, I combined this genetic approach and stable isotope analyses (as a time-integrated tracer) for the same specimens to investigate the importance of predation by *D. villosus* under field conditions in the River Rhine system (**Chapter III** and **Chapter IV**). In ecological studies individual variation is often sacrificed to reduce noise and clarify the target pattern, but in my opinion, knowledge about such individual variation in the feeding behaviour of a species is necessary to better understand its impact on food webs. Thus,

for my thesis, I used analyses of the Stable Isotope Bayesian Ellipses in R (SIBER) as a measure of the core isotopic niche of *D. villosus* (Jackson *et al.*, 2011), which enable to keep information regarding individual variation.

As strong intraguild predation (IGP) by *D. villosus*, observed in laboratory studies, is often assumed to be the key driver of the observed displacement of native amphipod species (e.g. Dick & Platvoet, 2000, Kinzler *et al.*, 2009), I investigated its importance in the field hypothesising that, if at all relevant in the field, IGP should be intensively marked at an invasion front. Analysing stored samples from an invasion front of *D. villosus* in Switzerland, I showed that, even though earlier studies have shown a strong predatory impact from *D. villosus* on *G. pulex* and *G. fossarum* (Kinzler & Maier, 2003, MacNeil & Platvoet, 2005, Kinzler *et al.*, 2009), IGP seems to be of low importance for the displacement of native amphipod species during this particular *D. villosus* invasion (**Chapter III**). Instead, overlapping isotopic niches of *D. villosus* and the native amphipods rather indicated competition of these species for the same food resources. Besides this, the fact that  $\delta^{15}\text{N}$  values of *D. villosus* were not higher than that of the well-defined consumer I *A. fluviatilis* indicated an overall sparsely predacious feeding behaviour of the species. This was somewhat surprising, because if *D. villosus* is mainly a predator in the field, I would have expected it to be notably predacious during an ongoing invasion in order to create space for itself. But despite my expectation, it might also be exactly reverse and *D. villosus* could be more predacious once it has become established in a system and adapted to its environmental conditions. Moreover, the impact on native fauna as well as the feeding behaviour of *D. villosus* are supposed to differ between habitats (Hesselschwerdt *et al.*, 2008, Hesselschwerdt, 2010) and this study was only conducted at a few sampling sites of one river, which is why these results might be specific to the investigated water body.

This led me to investigate the role of predation by *D. villosus* at multiple sites of the River Rhine system, covering a broad range of microhabitats (**Chapter IV**). There was indication of some predatory impact of *D. villosus* at three (out of ten) sites, because mean  $\delta^{15}\text{N}$  values of *D. villosus* were significantly higher than those of the primary consumers. But, differences in the mean  $\delta^{15}\text{N}$  values between *D. villosus* and the respective primary consumer in none of the cases exceeded one trophic level (TEF animal diet 2.29 ‰; Hellmann *et al.*, 2015). Additionally, genetic gut content analyses detected DNA of macroinvertebrate prey taxa in a few *D. villosus* individuals (33 out of 206). Of course, not all potential prey known from laboratory studies (reviewed by

Rewicz et al. 2014) was covered by the 16 group-specific primers used within this thesis (e.g. Figure VI.1). But, among the macrozoobenthos prey listed by Rewicz et al. (2014), only three groups were not covered by group-specific primers (see Figure VI.1). Instead, the genetic analyses additionally covered mysids, each one gastropod and blackfly taxon, as well as each two taxa of bivalves and caddisflies (e.g. Table IV-S1). Even though DNA of most of macrozoobenthos taxa I tested for was found in a few field samples, the frequency of detected prey DNA was very low (see Fig VI.1). Furthermore, prey DNA in the gut content could also originate from feeding on dead animal material instead of active predation. Thus, in keeping with the results of **Chapter III**, *D. villosus* seems to be less predacious in the overall River Rhine system than suggested by laboratory studies (reviewed by Rewicz et al. 2014).

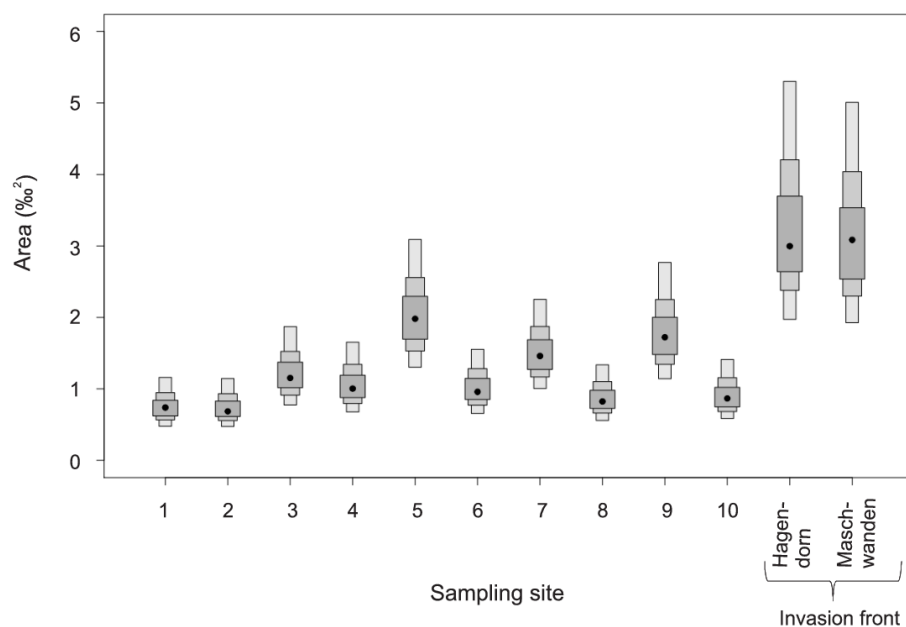


**Figure VI.1** Diagram showing macrozoobenthos taxa *Dikerogammarus villosus* is supposed to prey upon (e.g. Rewicz et al. 2014) and genetically tested for within this thesis. All existing relationships are displayed by arrows. Green arrows represent single and green-rimmed arrows indicate infrequently findings of DNA (exact percentages are given within the arrows) within gut content samples, whereas grey arrows with red question marks show that the respective prey groups were not covered by the 16 primer sets used in this thesis. Depicted species are just exemplary for prey groups (given in bold). Pictures have been provided by L. Richter & S. Worischka (*D. villosus*), C. Hellmann (*Rhyacophila*) and K. Grabow (all others).

Instead of predation, results of my thesis indicated strong intraspecific variations in the feeding habits of *D. villosus*, even within the same microhabitat during the ongoing invasion (**Chapter III**) as well as after the establishment of the species (**Chapter IV**). These results endorse studies showing that *D. villosus* is not only a predator but rather an unspecialised omnivore with a flexible feeding behaviour (Mayer *et al.*, 2008, Platvoet *et al.*, 2009).

### Feeding behaviour during invasion and after establishment

Comparisons of the niche width of *D. villosus* between the ten sites of **Chapter IV** and the two foremost sites from the invasion front in Switzerland (**Chapter III**) showed that the intraspecific variation seems to be highest at the invasion front (Figure VI.2), indicating an even more opportunistic feeding behaviour of the species during an ongoing invasion. However, the analysed data originate from only one newly invaded river and might not represent a general pattern. But, comparably to this, *Neogobius melanostomus* populations that had recently invaded the upper Danube showed greater plasticity in feeding behaviour than populations in areas they had invaded more than a decade ago (Brandner *et al.*, 2013).



**Figure VI.2** Density plot showing the confidence intervals of the standard ellipse area for *Dikerogammarus villosus* at the ten different microhabitats in the Rhine system (**Chapter IV**) and the two foremost sites from an invasion front in Switzerland (**Chapter III**). Black points correspond to the mean standard ellipse area. Boxes shaded from dark to light grey represent the 50%, 75% and 95% confidence intervals.

From the ecological point of view a reduction of trophic niche width during the invasion process seems at least imaginable, because the invading species probably needs to adapt to its new environment before being able to switch to a reduced spectrum of preferred food. On the contrary, Jackson *et al.* (2012) found an inverse relationship between the degrees of interspecific competition a species experienced and the isotopic niche space it occupied. According to these findings, a reduction in niche space occupied by *D. villosus* might seem unlikely, because the establishment of the species often was observed to coincide with a decline in densities of competing macroinvertebrates (e.g. MacNeil *et al.*, 2013, Gergs & Rothhaupt, 2015). But, the reverse relationship between interspecific competition and isotopic niche width was found between two invasive omnivores (Jackson *et al.*, 2012) and might not reflect a general pattern.

### **Impact of *D. villosus* on terrestrial food webs**

As *D. villosus* is known to outcompete and displace a wide range of aquatic macroinvertebrate taxa (Dick & Platvoet, 2000, Bollache *et al.*, 2004), it is likely that the species also affects aquatic-terrestrial energy fluxes, for instance due to its impact on the biomass of emerging insects. While such a reduction of the water to land energy flow has been shown for invasive trout (Baxter *et al.*, 2004, Benjamin *et al.*, 2013), potential effects of invasive amphipods like *D. villosus* on the terrestrial food web had never been addressed before. Based on SIAR mixing model results the contribution of aquatic resources to the diet of the web-building spider *Tetragnatha* sp. significantly decreased with increasing density of the *D. villosus*, which corresponded with the lowered subsidy flux of emerging midges (**Chapter V**). As midge larvae are considered a major prey of *D. villosus* (Dick *et al.*, 2002) and nitrogen stable isotope values from macroinvertebrates in the Rhine from earlier studies indicated that midges contribute to the diet of the species (Van Riel *et al.*, 2006), assuming that reduced emergence is due to predation by *D. villosus* on midge larvae might seem obvious. But, investigations within my thesis revealed a low importance of predation on midge larvae by *D. villosus* in the field (e.g. **Chapter IV**). Therefore, it seems more likely that *D. villosus* affected aquatic emerging midges indirectly by causing a time shift in the availability of fine particular organic matter due to the consumption of unconditioned leaf leading to a lack of this resource for the midges (e.g. Truhlar *et al.*, 2014). However, **Chapter V** showed, that effects of *D. villosus* are not only restricted to invaded ecosystems but potentially extend to adjacent terrestrial ecosystems.



## Perspectives

Even though *D. villosus* has been intensively studied there is still a lot unknown. My thesis clearly showed the significance of investigating invasive species under field conditions and strongly indicated that assumptions about the key role of predation by *D. villosus* for its invasion success as well as the displacement of species should be reconsidered.

An opportunistic feeding behaviour, like found in this thesis, might even be beneficial for the invasion success of a species. Particularly during the invasion of various rivers, alien species need to cope with different resource availabilities, and omnivory is assumed to be the best feeding strategy for this purpose (e.g. Arbačiauskas *et al.*, 2013). The invasion success of a species can be separated into three main stages: 1) the introduction of a species in a region outside its natural range, 2) the establishment of self-sustaining, reproductive populations and 3) population growth and further spreading (García-Berthou *et al.*, 2005). While the introduction stage mainly depends on the passive and active dispersal capacity of a species and its tolerance towards various environmental conditions, the establishment and further spread are strongly influenced by the fitness of the population (growth rates and reproductive potential) and traits of the species (e.g. Hänfling, Edwards & Gherardi, 2011). Both, growth and reproduction of many macroinvertebrates, are affected by the food consumed (Willoughby & Sutcliffe, 1976, Fuller, Fry & Roelofs, 1988, Söderström, 1988). For instance, it is well known, that the consumption of low-quality food (e.g. leaf litter) can lead to a stoichiometric mismatch between diet and consumer which can strongly affect growth and reproduction (Frost & Elser, 2002, Fink *et al.*, 2006). In keeping with this knowledge Gergs and Rothhaupt (2008) found reduced growth of *D. villosus* in a laboratory experiment when fed leaf litter. But up to now it is unknown how the physiological fitness of *D. villosus* is influenced by a minor predacious feeding behaviour under different field conditions and how the species copes with uncomfortable conditions. However, intraspecific variation in the feeding behaviour of individuals, as found in this thesis, reduces intraspecific competition (e.g. Brandner *et al.*, 2013) and thereby potentially increases the fitness of a population.

Aside from that, the intraspecific variation found within sites (**Chapter III** and **Chapter IV**) could be explained by two different types of omnivory at the individual level, which could affect physiological fitness differently: 1) single individuals being

facultative specialists (individual specific specialisation) or 2) generalist feeding on different proportions of prey items (flexible omnivory; e.g. Barnes *et al.*, 2008). In case of the former, if at all only individuals feeding specialised on low-quality food would suffer from reduced physiological fitness, while in the case of flexible omnivory either all or none of the individuals would be affected since they all use the same pool of food sources. Due to the fact that a high number of offspring can even be produced within one clutch by only one large *D. villosus* female, a few individuals might be able to establish a population (Pöckl, 2007). Thus, even if the reproductive potential of single individuals would be reduced due to the consumption of low-quality food, single individuals temporary feeding specialised on food with higher quality could found a sustainable population within the newly invaded system. Nevertheless, directional selection towards individuals feeding permanently specialised on high quality animal food could be prevented by constantly changing conditions in flowing waters that alternately favour different feeding habits.

Knowledge to which extend opportunistic feeding behaviour in general, and individual specific specialisation or flexible omnivory in particular contribute to the invasion success of an omnivorous species would be essential to predict its impact on newly invaded systems. *D. villosus* is predicted to further increase its range expansion on a global scale (Devin *et al.*, 2003) and therefore remains an interesting organism for research as a model for omnivorous macroinvertebrate invaders.

## Summary

The establishment of aquatic alien species can strongly affect community and food web structure of the invaded systems and thus represents a major threat to native biodiversity. One of the most important aquatic invasive species in European rivers is the Ponto-Caspian amphipod *Dikerogammarus villosus*. The species invaded most of the major European waterways within two decades, often associated with a decline of many other macroinvertebrate species, including other amphipods. Based on laboratory results predation by the so called ‘killer shrimp’ is often regarded as the key driver for observed displacement effects, but recent studies indicated a minor relevance of predation by *D. villosus* in the field. To allow the determination of exact predator-prey interactions from field samples, I established 22 group-specific rDNA primers for freshwater taxa suitable for prey species identification in dietary samples (**Chapter II**) and an approach for the screening of *D. villosus* gut contents using 16 of these primers. Combining genetic gut content analyses, with one of these primers, and stable isotope analyses, I examined the importance of intraguild predation (IGP) by *D. villosus*, which is often assumed the key driver for the displacement of native amphipod species, at an invasion front of the species in Switzerland (**Chapter III**). The results of this study revealed a low importance of IGP during this particular *D. villosus* invasion and indicated an overall sparsely predacious feeding behaviour of the species. As the feeding behaviour of *D. villosus* is supposed to differ between habitats and this study was only conducted at a few sampling sites of one river, I also investigated the role of predation by *D. villosus* at multiple sites of the River Rhine system, covering a broad range of microhabitats (**Chapter IV**). In keeping with the results from the invasion front results of this study strongly indicated a sparsely predacious feeding but rather a flexible feeding behaviour of *D. villosus* even within the same microhabitat.

However, established populations of *D. villosus* have changed aquatic food webs and can be expected to affect aquatic-terrestrial energy fluxes. In **Chapter V** of my thesis, I present a field study investigating the impact of *D. villosus* on the diet of two riparian spider taxa. The results of this study indicate an effect of *D. villosus* on the terrestrial food web via cross-ecosystem resource flow.

In conclusion, *D. villosus* influences terrestrial food webs by altering cross-ecosystem resource fluxes, but it is rather an opportunistic omnivore than a predator in the field.

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## Supplementary material

Due to copyright issues, the text of this chapter was replaced by the reference information and the web links to supplementary material published by the respective journals. The interested reader is kindly asked to download the supplementary material via the following reference:

**Chapter II:** Koester, M., Claßen, S. & Gergs, R. (2013) Establishment of group-specific PCR primers for the identification of freshwater macroinvertebrates. *Conservation Genetics Resources*, 5, 1091-1093.

**Table S1:** Results from all combinations of the 21 primer sets with the 130 taxa included into our test for specificity

**Table S2:** Accession numbers of obtained sequences from GenBank

**Table S3:** Species targeted by the group-specific primers and their corresponding accession numbers (EMBL Nucleotide Sequence Database; EMBL-Bank).

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**Chapter IV:** Koester, M., Bayer, B. & Gergs, R. (2015) Is *Dikerogammarus villosus* (Crustacea, Gammaridae) a 'killer shrimp' in the River Rhine system? *Hydrobiologia*, 768, 299-313.

**Table S1:** Details of the 2 batches of 16 group-specific primer pairs amplifying regions of the 18S or 28S rDNA from 16 target groups of aquatic macroinvertebrates.

**Table S2:** Sex (m, male; f, female), size, stable isotope signature ( $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ ) and results of the genetic gut content analyses of 226 *Dikerogammarus villosus* individuals from the ten sampling sites.

**Table S3:** Wilcox-Mann-Whitney test of mean mean  $\delta^{15}\text{N}$  values of *Dikerogammarus villosus* and the respective primary consumers of the 10 study sites.

**Table S4:** Correlation analyses between the mode  $SEA_B$  ( $MdSEA_B$ ) and biotic and abiotic parameters.

**Table S5:** Correlation analyses between the size of *Dikerogammarus villosus* individuals and their isotopic signature ( $\delta^{13}C$  and  $\delta^{15}N$ ) for each of the 10 sites. \* = significance level 0.05, \*\* = significance level 0.01, \*\*\* = significance level 0.001.

**Table S6:** Regression analysis ( $n = 10$ ) of mean size of tested *Dikerogammarus villosus* individuals and proportion of gut contents in which and number of groups from which DNA was detected. \* = significance level 0.05.

**Figure S1:** Stable isotope bi-plot illustrating the isotopic niche of *Dikerogammarus villosus* at sampling site 1. The stable isotope signature of single *D. villosus* individuals ( $n = 20$ ) and the standard ellipse area ( $SEA_c$ ) for *D. villosus* are shown. Mean  $\delta^{15}N$  and  $\delta^{13}C$  values  $\pm$  SD of other macroinvertebrates and primary producers are given.

**Figure S2:** Stable isotope bi-plot illustrating the isotopic niche of *Dikerogammarus villosus* at sampling site 2. The stable isotope signature of single *D. villosus* individuals ( $n = 20$ ) and the standard ellipse area ( $SEA_c$ ) for *D. villosus* are shown. Mean  $\delta^{15}N$  and  $\delta^{13}C$  values  $\pm$  SD of other macroinvertebrates and primary producers are given.

**Figure S3:** Stable isotope bi-plot illustrating the isotopic niche of *Dikerogammarus villosus* at sampling site 3. The stable isotope signature of single *D. villosus* individuals ( $n = 20$ ) and the standard ellipse area ( $SEA_c$ ) for *D. villosus* are shown. Mean  $\delta^{15}N$  and  $\delta^{13}C$  values  $\pm$  SD of other macroinvertebrates and primary producers are given.

**Figure S4:** Stable isotope bi-plot illustrating the isotopic niche of *Dikerogammarus villosus* at sampling site 4. The stable isotope signature of single *D. villosus* individuals ( $n = 20$ ) and the standard ellipse area ( $SEA_c$ ) for *D. villosus* are shown. Mean  $\delta^{15}N$  and  $\delta^{13}C$  values  $\pm$  SD of other macroinvertebrates and primary producers are given.

**Figure S5:** Stable isotope bi-plot illustrating the isotopic niche of *Dikerogammarus villosus* at sampling site 5. The stable isotope signature of single *D. villosus* individuals ( $n = 20$ ) and the standard ellipse area ( $SEA_c$ ) for *D.*

*villosus* are shown. Mean  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  values  $\pm$  SD of other macroinvertebrates and primary producers are given.

**Figure S6:** Stable isotope bi-plot illustrating the isotopic niche of *Dikerogammarus villosus* at sampling site 6. The stable isotope signature of single *D. villosus* individuals (n = 21) and the standard ellipse area (SEA<sub>c</sub>) for *D. villosus* are shown. Mean  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  values  $\pm$  SD of other macroinvertebrates and primary producers are given.

**Figure S7:** Stable isotope bi-plot illustrating the isotopic niche of *Dikerogammarus villosus* at sampling site 7. The stable isotope signature of single *D. villosus* individuals (n = 23) and the standard ellipse area (SEA<sub>c</sub>) for *D. villosus* are shown. Mean  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  values  $\pm$  SD of other macroinvertebrates and primary producers are given.

**Figure S8:** Stable isotope bi-plot illustrating the isotopic niche of *Dikerogammarus villosus* at sampling site 8. The stable isotope signature of single *D. villosus* individuals (n = 21) and the standard ellipse area (SEA<sub>c</sub>) for *D. villosus* are shown. Mean  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  values  $\pm$  SD of other macroinvertebrates and primary producers are given.

**Figure S9:** Stable isotope bi-plot illustrating the isotopic niche of *Dikerogammarus villosus* at sampling site 9. The stable isotope signature of single *D. villosus* individuals (n = 20) and the standard ellipse area (SEA<sub>c</sub>) for *D. villosus* are shown. Mean  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  values  $\pm$  SD of other macroinvertebrates and primary producers are given.

**Figure S10:** Stable isotope bi-plot illustrating the isotopic niche of *Dikerogammarus villosus* at sampling site 10. The stable isotope signature of single *D. villosus* individuals (n = 21) and the standard ellipse area (SEA<sub>c</sub>) for *D. villosus* are shown. Mean  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  values  $\pm$  SD of other macroinvertebrates and primary producers are given.

**Figure S11:** Large-scale map overview showing the River Rhine including Lake Constance (dark blue) and a selection of further 1st order water bodies (light blue). Approximate locations of the ten sites are indicated by red dots and the respective site numbers (for coordinates of each site see Table IV.1).

**Figure S12:** Apportionment of A) positively tested group-specific primers and B) filling category of the gut ( $1 \leq 10\%$ ,  $2 = 11-25\%$ ,  $3 = 26-50\%$ ,  $4 = 51-75\%$ ,  $5 > 75\%$ ; e.g. Table IV-S2) to four size categories of *D. villosus* individuals investigated from the 10 sites.

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**Chapter V:** Koester, M., Bayer, B. & Gergs, R. (2015) Is *Dikerogammarus villosus* (Crustacea, Gammaridae) a 'killer shrimp' in the River Rhine system? *Hydrobiologia*, 768, 299-313.

**Table S1:** Abiotic and biotic environmental parameters, and different type of aquatic (midges and other aquatic taxa) and terrestrial emerging daily biomass of insects at the nine investigated study sites.

[Click here to download Table S1 from the publisher's website.](#)

**Table S2:** Results of stable isotope analyses of the aquatic and terrestrial emerging insects per study site.

[Click here to download Table S2 from the publisher's website.](#)

**Table S3:** Results of stable isotope analyses of the two spiders, *Tetragnatha* sp. and *Pirata piraticus*, at the nine study site.

[Click here to download Table S3 from the publisher's website.](#)

## Declaration

I hereby declare that I autonomously conducted the work presented in this PhD thesis entitled “Impact of the invasive amphipod *Dikerogammarus villosus* on trophic interactions under field conditions”. All used assistances and involved contributors are clearly declared. They are co-authors of, or are acknowledged in, the respective publication.

This thesis has never been submitted elsewhere for an exam, as a thesis or for evaluation in a similar context to any department of this University or any scientific institution. I am aware that a violation of the aforementioned conditions can have legal consequences.

Koldenz, den 19.02.2016

Heike Koester

Place, Date

Signature



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2011 Diploma thesis entitled “Development of group-specific primers for genetic gut content analyses” conducted at the Institute for Environmental Sciences, University of Koblenz-Landau under supervision of Dr. René Gergs and Prof. Dr. Ralf Schulz

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Teaching	2014 – Bachelor thesis Bastian Bayer “Nahrungsspektrum des invasiven Amphipoden <i>Dikerogammarus villosus</i> - eine Studie im Rhein anhand stabiler Isotopenanalyse”
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## Publications

### *Articles in preparation*

**Koester, M.**, Schneider, M., Hellmann, C., Becker, J., Winkelmann, C. & Gergs, R. (in preparation) *Dikerogammarus villosus* is not the driving factor for the benthic community structure of the River Rhine system!

### *Peer-reviewed articles*

Gergs, R., **Koester, M.**, Grabow, K., Schöll, F., Thielsch, A. & Martens, A. (2015) *Theodoxus fluviatilis*' re-establishment in the River Rhine: a native relict or a cryptic invader? *Conservation Genetics*, **16**, 247-251.

Gergs, R., **Koester, M.**, Schulz, R.S. & Schulz, R. (2014) Potential alteration of cross-ecosystem resource subsidies by an invasive aquatic macroinvertebrate: implications for the terrestrial food web. *Freshwater Biology*, **59**, 2645-2655.

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**Koester, M.** & Gergs, R. (2014) No evidence for intraguild predation of *Dikerogammarus villosus* (Sowinsky, 1894) at an invasion front in the Untere Lorze, Switzerland. *Aquatic Invasions*, **9**, 489-497.

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Martin, P., **Koester, M.**, Schynawa, L. & Gergs, R. (2015) First detection of prey DNA in *Hygrobatas fluviatilis* (Hydrachnidia, Acari): a new approach for determining predator-prey relationships in water mites. *Experimental and Applied Acarology*, **67**, 373-380.