

Invading predatory crustacean *Dikerogammarus villosus* eliminates both native and exotic species

Jaimie T. A. Dick^{1*} and Dirk Platvoet²

¹*School of Biology and Biochemistry, The Queen's University of Belfast, Medical Biology Centre, Belfast BT9 7BL, UK*

²*Institute for Systematics and Population Biology, University of Amsterdam, 1090 GT Amsterdam, The Netherlands*

As the tempo of biological invasions increases, explanations and predictions of their impacts become more crucial. Particularly with regard to biodiversity, we require elucidation of interspecific behavioural interactions among invaders and natives. In freshwaters in The Netherlands, we show that the invasive Ponto-Caspian crustacean amphipod *Dikerogammarus villosus* is rapidly eliminating *Gammarus duebeni*, a native European amphipod, and *Gammarus tigrinus*, until now a spectacularly successful invader from North America. In the laboratory, survival of single (unguarded) female *G. duebeni* was significantly lower when male *D. villosus* were free to roam as compared with isolated within microcosms. In addition, survival of paired (guarded) female *G. duebeni* was significantly lower when male *D. villosus* as compared with male *G. duebeni* were present. *D. villosus* killed and consumed both recently moulted and, unusually, intermoult victims. Survival of *G. tigrinus* was significantly lower when *D. villosus* were free to roam as compared with isolated within microcosms and, again, both moulted and intermoult victims were preyed upon. Male *D. villosus* were significantly more predatory than were females, while female *G. tigrinus* were significantly more often preyed upon than were males. Predation by *D. villosus* on both species occurred over a range of water conductivities, an environmental feature previously shown to promote amphipod coexistence. This predatory invader is predicted to reduce further the amphipod diversity in a range of freshwater habitats in Europe and North America.

Keywords: amphipods; interspecific interactions; invasions; microcosms; predation

1. INTRODUCTION

Invading species may interact with the fauna of new host locations in a variety of ways, for example, by competition (Human & Gordon 1986), predation (Zaret & Paine 1973), hybridization (Capelli & Capelli 1980) and disease transmission (Dogiel *et al.* 1970). Linking invasion patterns with interspecific processes is often difficult, but such information is crucial in the prediction of the impacts of invaders on the biodiversity of new host locations (Dick 1996a; Moyle & Light 1996; Holway & Suarez 1999; Williamson 1996, 1999). Successful invaders often show spectacular population increases and consequent eliminations of native faunas in short time-spans (Elton 1958; Diamond & Case 1986; di Castri *et al.* 1990; Kinzelbach 1995; Williamson 1996, 1999). In this study, a species invasion was investigated in its phase of rapid geographical expansion and population explosion. In addition, there is growing realization that proximate causes of invasion success may be illuminated by considering behavioural characteristics of the species involved (Holway & Suarez 1999). In the present study, experimental laboratory assessment of individual interactions among the invader and natives was undertaken during the invasion, thus allowing details of the suspected mechanism of species interaction to be linked to the ongoing field-displacement patterns.

Dikerogammarus villosus is an amphipod crustacean native to the Ponto-Caspian region of eastern Europe/Ukraine, particularly the Danube River system (Nesemann *et al.* 1995). This species has invaded western Europe via the Main–Danube canal (Tittizer 1996), appearing in the

River Rhine at the German–Dutch border in 1994–1995 (Bij de Vaate & Klink 1995). This is one of a suite of Ponto-Caspian organisms predicted to have an impact in Europe and North America (Ricciardi & Rasmussen 1998). We discovered *D. villosus* on the western shores of the Markermeer at Schardam, north of Amsterdam, in July 1998 (figure 1). This Dutch water body has received much attention as regards amphipod species diversity due to previous invasions by exotic amphipods and their interactions with native species (Pinkster *et al.* 1992; Dick & Platvoet 1996).

Gammarus duebeni is native and widespread in western Europe, although replaced over parts of its range by previous invaders such as the North American *Gammarus tigrinus* (Pinkster *et al.* 1992). Since 1984, the Dutch and German sections of the River Rhine have seen dramatic explosions in the distribution and abundance of *G. tigrinus*, probably introduced via ship ballast water (Pinkster *et al.* 1992; Van der Velde *et al.* 2000). This invader is now, however, in sharp decline, coincidental with the invasion of *D. villosus* (Van der Velde *et al.* 2000). Both *G. duebeni* and *G. tigrinus* are found along rocky shorelines and sheltered vegetated bays of the Markermeer and IJsselmeer (figure 1), although *G. tigrinus* favours the latter habitat type and *G. duebeni* the former (J. T. A. Dick and D. Platvoet, unpublished data). Crucially, *D. villosus* can occupy a range of habitats and has wide environmental tolerances as regards temperature and salinity (Van der Velde *et al.* 2000) and is thus able to colonize the preferred habitats of both these native and exotic species, with resultant interaction.

Stable isotope analyses have shown that *D. villosus* is on the same trophic level as some predatory fish species (Marguillier 1998), while a review of the trophic ecology

*Author for correspondence (j.dick@qub.ac.uk).

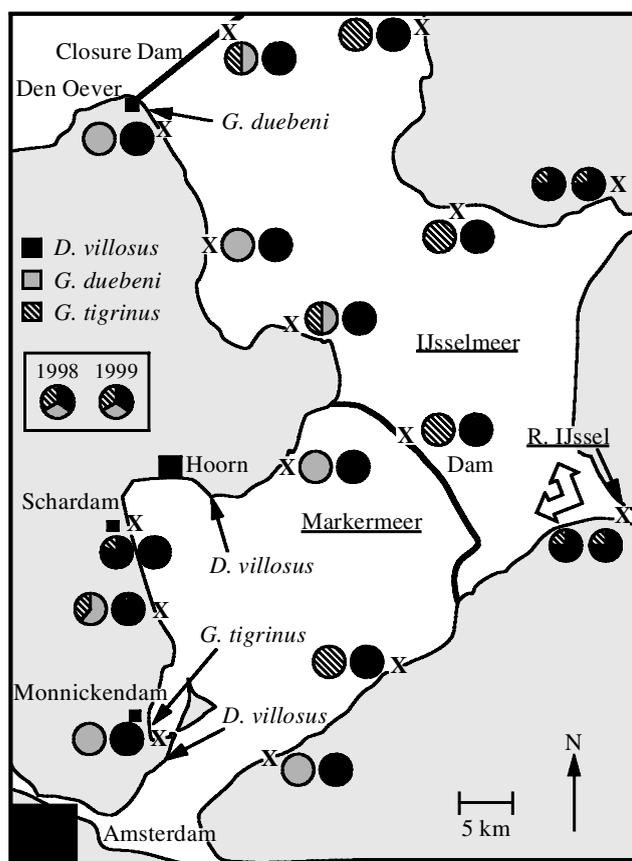


Figure 1. The Markermeer and IJsselmeer of Holland showing invasion and expansion by the Ponto-Caspian amphipod *D. villosus* in 1998 and 1999 and the elimination and replacement of the native, *G. duebeni*, and previous invader from North America, *G. tigrinus*. Pies show relative species' abundances based on at least 100 individuals collected per site (see §2). The double arrow shows the likely *D. villosus* invasion route from the River IJssel, which connects with the River Rhine. Sampling stations arrowed are those from which animals were collected for use in the 1998 microcosm experiments.

of *Gammarus* and related genera indicates that their traditionally designated role as detritivores and herbivores belies a predatory disposition (MacNeil *et al.* 1997). We thus suspected that the rapid expansion of *D. villosus* and its devastating impact on related genera may involve intraguild predation (IGP) (Polis *et al.* 1989), rather than interspecific competition as the likely mechanism operating within this ecological guild. In order to test this hypothesis, a sampling programme and three laboratory experiments were designed to establish any link between field patterns of invasion and elimination with any predatory disposition of *D. villosus* towards *G. duebeni* and *G. tigrinus*. Further, we argue that the resultant data, alongside other studies of the biological characteristics of *D. villosus*, may be used to make predictions regarding the future impacts of this invader on amphipod diversity.

2. METHODS

(a) Study area and field sampling

Sampling of the Markermeer and IJsselmeer (figure 1) was conducted once in late June–early July 1998 and at the same sites

again in late June 1999. Sampling entailed using kick nets to sweep vegetation, while large rocks or boulders and debris were disturbed and the net swept over the area. Sampling continued until approximately 100 individual amphipods were caught. Amphipod species presence and relative abundances were recorded on site.

(b) Laboratory microcosm experiments

Three experiments, run concurrently, took place at the University of Amsterdam in September 1998. We collected *D. villosus* from near Hoorn and Monnickendam (figure 1). This is a relatively large amphipod, males in the present experiments ranging from 50 to 85 mg and females from 35 to 65 mg (live weight). *G. duebeni* were collected from near Den Oever (figure 1), males ranging from 35 to 50 mg and females from 15 to 25 mg. *G. tigrinus* were collected from near Monnickendam (figure 1). This is a considerably smaller amphipod, although size range is highly variable throughout the year. In the present study, male *G. tigrinus* ranged from 8 to 12 mg and females from 3 to 5 mg.

In the laboratory, water temperatures were maintained at 15–17 °C and in a 16L:8D cycle, in accordance with field conditions. Experiments took place in aerated aquaria ('microcosms') of 15 cm × 9 cm × 5 cm supplied with 4 cm depth of water from the Markermeer/IJsselmeer. Water from Hoorn was of relatively low conductivity, approximately 900 $\mu\text{S cm}^{-1}$, whereas water from Den Oever was of higher conductivity, approximately 1700 $\mu\text{S cm}^{-1}$. This difference reflects proximity to the sea. Habitat heterogeneity and food were supplied in the form of pieces of terracotta plant pot (which provided numerous sizes of crevice), two pieces of 1 cm × 2 cm cuttings of reed and six pellets of food designed for catfish. Plastic vials of 3 cm diameter with 20 small holes in their sides and gauze mesh around the interior were constructed as the 'isolators' for *D. villosus*. These isolators were present in all aquaria and *D. villosus* were either inside (i.e. 'isolated' from the other species) or outside (i.e. 'free' to interact with the other species).

Pilot trials indicated that adult *D. villosus* were predatory towards both adult *G. duebeni* and adult *G. tigrinus*, but the latter two species did not kill the former. In particular, *D. villosus* killed and consumed intermoult victims, whereas all previously reported instances of IGP in amphipods has involved the consumption of victims at the vulnerable time of moult, when the new exoskeleton is still soft (Dick 1996b; Dick & Platvoet 1996; MacNeil *et al.* 1997). The experiments were thus designed to characterize and quantify the degree of *D. villosus* predation on both species in replicated microcosms, simulating patches of habitat within which individuals may interact. Such experiments go some way to balance the scale at which interactions can be monitored yet be meaningful in extrapolation to field patterns (Dick *et al.* 1999).

(c) *D. villosus* versus *G. duebeni*

Experiments 1 and 2 aimed to assess predation by *D. villosus* on the native *G. duebeni*. Adult male *D. villosus* were used, as male amphipods may be both cannibalistic and predatory, particularly towards reproductive females (MacNeil *et al.* 1997). Adult, ovigerous female *G. duebeni* were used as the 'target' of predation, as the killing of these individuals would have the greatest impact on populations. Females occur as 'singles' and 'pairs', the latter occurring when conspecific males take hold of females in 'precopulatory guarding' a few weeks prior to female moult and subsequent copulation (Dick 1989).

Experiment 1 was designed to assess predation in one-on-one interspecific encounters, since individuals are likely to encounter one another in such a way in microhabitats such as crevices in rocks. This design also allowed sufficient experimental replication with limited numbers of *G. duebeni*, which is increasingly rare (see below). Thus, 28 aquaria were supplied with a 50:50 mix of Hoorn and Den Oever water (approximately $1300\ \mu\text{S cm}^{-1}$) and a single (i.e. unpaired) female *G. duebeni* carrying eggs in the early stage of development. Such females are several weeks from moult and have hardened exoskeletons (Dick 1989). In half the aquaria, a male *D. villosus* was isolated, whereas in the other half a male *D. villosus* was free to interact with the female (see §2(b)). Each replicate was examined twice daily and the experiment was allowed to run for five days. Comparison of frequencies of death of female *G. duebeni* between these groups allows for discrimination between active predation by male *D. villosus* and deaths of females followed by scavenging.

Experiment 2 was designed to assess any protection afforded to females by being in the precopulatory guarding phase and to compare levels of intraspecific killing (cannibalism) with interspecific killing (predation). In addition, the remaining populations of *G. duebeni* are mostly found in areas of high water conductivity such as Den Oever (figure 1); however, the availability of pairs is limited (see below). Thus, 40 aquaria were supplied with high-conductivity water (Den Oever water, approximately $1700\ \mu\text{S cm}^{-1}$) and a pair of *G. duebeni*. Such females carry well-developed embryos and are closer to moult than single, unguarded females (Dick 1989). Half of these aquaria were supplied with a second male *G. duebeni* and the other half with a male *D. villosus*. Each replicate was examined twice daily and the experiment allowed to run for five days. Comparison of frequencies of death of female *G. duebeni* between these groups allows, first, assessment of the strength of predation by male *D. villosus* compared with female deaths and/or cannibalism by male *G. duebeni* and, second, assessment of whether mate-guarding protects female *G. duebeni* from male *D. villosus* predation. In addition, the high-conductivity water used in this second experiment assessed the ability of *D. villosus* to both survive and prey upon *G. duebeni* in environmental conditions which have favoured *G. duebeni* populations and may be its last refuge from invasion and replacement (Pinkster *et al.* 1992).

(Ethical/practical note: although not protected under any legislation, *G. duebeni* populations are increasingly endangered in freshwaters due, principally, to replacement by invasive species (Pinkster *et al.* 1992; Dick *et al.* 1999). This raises an ethical issue with regards to destructive sampling of this species and practical problems in terms of sufficient replication for meaningful experiments. Thus, the present two experiments, which were designed individually to answer a range of questions and run concurrently, aimed to balance information gain with the number of replicates ethically justifiable and practically feasible with the dwindling availability of *G. duebeni* in these Dutch water bodies.)

(d) *D. villosus* versus *G. tigrinus*

Experiment 3 was run concurrently with experiments 1 and 2 and aimed to assess predation by *D. villosus* on the North American invader *G. tigrinus*. The very dense field populations of the relatively small *G. tigrinus* led to an experimental design different from that with *G. duebeni* (and see the ethical/practical note above). We simulated the invasion scenario of limited numbers of *D. villosus* individuals encountering very abundant populations of *G. tigrinus* by placing four precopulatory guarding pairs of *G. tigrinus* in each of 38 aquaria (supplied with habitat, food and

isolators) and monitoring their survival under all combinations of the following: (i) a *D. villosus* individual was either isolated within the aquarium or free to interact with the *G. tigrinus*; (ii) the *D. villosus* individual was either an adult male or adult female; and (iii) the water of the aquarium was either of low conductivity (approximately $900\ \mu\text{S cm}^{-1}$, from Hoorn) or high conductivity (approximately $1700\ \mu\text{S cm}^{-1}$, from Den Oever). This experiment thus allows for assessment of the predatory impact of *D. villosus* (both males and females) on the reproductively active individuals of relatively abundant populations of *G. tigrinus*. As with experiments 1 and 2, the design allows for discrimination between active predation and deaths followed by scavenging. This experiment also assesses the ability of *D. villosus* to overcome the ability of *G. tigrinus* to avoid predation to a greater degree in high-conductivity water, as occurs when in the presence of *Gammarus pulex* (Dick & Platvoet 1996). Each replicate was examined twice daily and full counts were made after five and ten days. Numbers of surviving male and female *G. tigrinus* after five days were arcsine transformed for statistical analyses (Sokal & Rohlf 1995). A four-factor ANOVA was conducted using SuperANOVATM (Abacus Concepts 1989), the factors being (i) to (iii) above, with the fourth factor 'sex of *G. tigrinus*' entered as a 'repeated measure' in the analysis due to the non-independence of these data, both sexes of *G. tigrinus* being present in each replicate.

In the experiments, female *G. duebeni* and male and female *G. tigrinus* in the '*D. villosus*-isolated' replicates were monitored closely for moult, such that the moult frequency of animals in the '*D. villosus*-free' groups could be estimated. Moulting is evidenced in amphipods by the shed exoskeleton and clean appearance of the new exoskeleton.

3. RESULTS

In late June–early July 1998, *D. villosus* was found in the River IJssel (which links to the River Rhine) and in an inland pond north of that site (figure 1). A population with precopula pairs in abundance was also found at Schardam on the west bank of the Markermeer (figure 1). There was also a small proportion of *G. duebeni* and *G. tigrinus* at the Schardam site at this time, this site for the previous several years having an abundant and relatively stable mix of the latter two species (D. Platvoet and J. T. A. Dick, unpublished data). Thus, in 1998, *D. villosus* had invaded and perhaps begun replacing *G. duebeni* and *G. tigrinus*, although these latter species held most ground at this time (figure 1). In 1999, however, *D. villosus* had replaced both species almost completely at all sampling stations (figure 1). This process was extremely rapid; for example, at a site near Monnickendam, *G. duebeni* was the sole species present in June–July 1998 and was observed there again in September 1998 (J. T. A. Dick, unpublished data), but this *G. duebeni* population had been entirely replaced by *D. villosus* by June 1999 (see figure 1).

In experiment 1, there was zero *D. villosus* mortality over the five day period. However, 86% of single female *G. duebeni* survived when the male *D. villosus* was isolated, whereas only 28% survived when the male *D. villosus* was free ($p < 0.005$, Fisher's exact test) (figure 2). Typically, female *G. duebeni* at first appeared to have escaped from aquaria where male *D. villosus* were free; however, the remains of those females were detected when the aquarium water was examined closely, often under a binocular

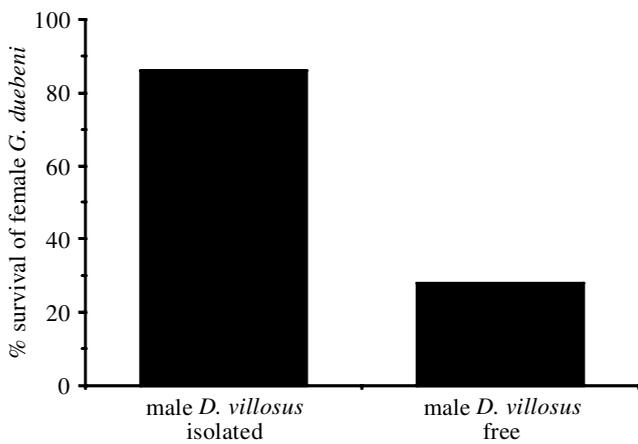


Figure 2. Percentage survival of single intermoult female *G. duebeni* when male *D. villosus* were free to roam as opposed to isolated within experimental microcosms.



Figure 3. Percentage survival of precopula guarded female *G. duebeni* when male *D. villosus* were present compared with when conspecific males were present.

microscope. In one case, for example, the presence of the alimentary canal of the *G. duebeni*, plus assorted legs and pieces of exoskeleton, was proof that the female had been shredded and consumed. As expected with single females, there were no moults during the time-span of this experiment and thus all females must have been killed in the hard intermoult state.

In experiment 2, there was again no *D. villosus* mortality over the five day period. No male *G. duebeni* were killed during this experiment. However, 80% of paired female *G. duebeni* survived when a second conspecific male was present, whereas only 45% of paired females survived when a male *D. villosus* was present ($p < 0.02$, Fisher's exact test) (figure 3). Thus, male *D. villosus* predation of female *G. duebeni* is significantly greater than female mortality and/or cannibalism and, further, mate guarding does not prevent significant killing of females. These females were in precopula and thus closer to moult than those in experiment 1. Thus, as expected, a small proportion (15%) of females in the 'conspecific male present' group moulted. Clearly, then, the male *D. villosus* in experiment 2 must have killed intermoult as well as recently moulted female *G. duebeni*. This experiment also confirms that *D. villosus* is capable of

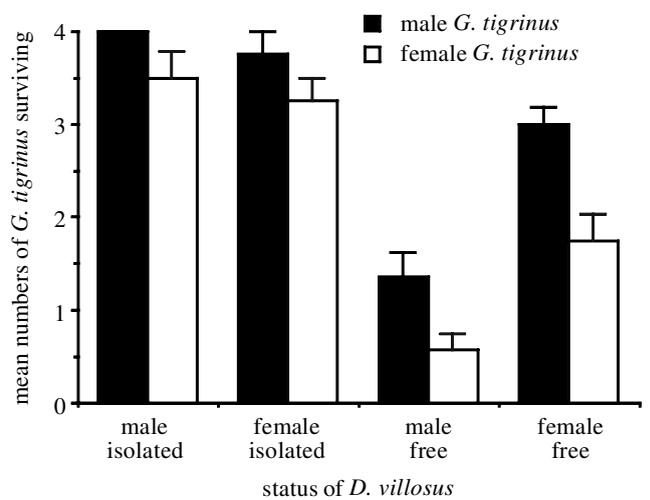


Figure 4. Mean numbers (s.e.) surviving of *G. tigrinus* when *D. villosus* individuals were free to roam compared with those isolated within experimental microcosms.

surviving in high-conductivity waters and killing *G. duebeni* females under such conditions, which are typical of the last refuges of the latter species (Pinkster *et al.* 1992).

In experiment 3, there was no *D. villosus* mortality over the ten days. When *D. villosus* were isolated and thus unable to interact with *G. tigrinus*, survival of the latter after five days was high (figure 4); some cannibalism of females by males is likely to account for the slight drop in female survival in this group (figure 4). On the other hand, the presence of free *D. villosus* in the microcosms was characterized by significant reductions in survival of *G. tigrinus* ($F_{1,30} = 47.9$, $p < 0.0001$) (figure 4), whose remains, which consisted of legs, antennae and assorted pieces of exoskeleton, littered the floors of the aquaria. Male *D. villosus* were significantly more predatory than were females ($F_{1,30} = 4.7$, $p < 0.05$) (figure 4), while female *G. tigrinus* were significantly more often preyed upon than were males ($F_{1,30} = 14.4$, $p < 0.001$) (figure 4). Indeed, after ten days, 27% of replicates with free *D. villosus* had total elimination of *G. tigrinus*, whereas 100% of replicates with isolated *D. villosus* had at least one male and one female *G. tigrinus* surviving. In those replicates with free male *D. villosus*, there were no surviving female *G. tigrinus* after ten days. We estimated that 30–40% of females in the 'D. villosus isolated' replicates moulted within the five day period. Males do not moult when in precopula (Dick 1989). Thus, male *D. villosus* predation of 80–90% of females and 60–75% of males (figure 4) indicates that intermoult as well as moulted individuals were killed and consumed. There was no significant difference in survival of *G. tigrinus* in low compared with high-conductivity waters ($F_{1,30} = 0.8$, n.s.).

4. DISCUSSION

Microcosms containing *D. villosus* and *G. duebeni* were characterized by high frequencies of predation by males of the former species on females of the latter. Male *D. villosus* were clearly able to overcome the hard intermoult exoskeleton of female *G. duebeni* and devour them,

rather than being restricted to the vulnerable time of moult when most crustacean cannibalism and predation occurs (Dick 1996a; Dick & Platvoet 1996; MacNeil *et al.* 1997). Thus, the predatory impact of *D. villosus* is not restricted to the short (approximately 12 h (Dick 1989)) period of post-moult vulnerability, facilitating rapid eliminations of all stages of reproductive females. Both single females and those held in the precopulatory mate-guarding position were vulnerable to *D. villosus* predation, even though guarding male amphipods may attempt to aggressively repel intruding conspecifics and heterospecifics (Dick & Elwood 1990; Dick *et al.* 1995). Thus, female *G. duebeni* carrying embryos and the future of the population may be eliminated rapidly in the face of *D. villosus* invasion. Interestingly, no male *G. duebeni* were killed during experiment 2, indicating that males, being larger, are more able to fend off any predatory attack, although this may not be the case at moult (see Dick 1996b). Indeed, the large size of *D. villosus* relative to other freshwater amphipods is in part likely to explain its successful predatory behaviour.

In addition, male *D. villosus* were able to survive and effectively prey upon female *G. duebeni* in the relatively high-conductivity water typical of the IJsselmeer at Den Oever (figure 1), a northern site not (by September 1998) colonized by *D. villosus*. Thus, we predict that *G. duebeni* populations will be unable to resist invasion by *D. villosus* even in traditionally 'safe' areas of raised conductivity to which the former species is optimally adapted (Pinkster *et al.* 1992). Indeed, the 1999 data from the Closure Dam at Den Oever show that *G. duebeni* is unable to resist replacement by *D. villosus* in high-conductivity waters (figure 1). We believe that the population of *G. duebeni* used in the present experiments (figure 1) has only persisted due to the physical enclosure of this site by dykes and a sluice gate at the seaward margin.

D. villosus also has the ability to eliminate large numbers of the North American *G. tigrinus* through predation in short time-spans and, in particular, remove the reproductive females from the population. In addition, it is known that high conductivities reduce predation by *G. pulex* on *G. tigrinus*, possibly due to the latter hardening its exoskeleton more effectively under such conditions (Dick & Platvoet 1996). Whatever the mechanism, this environmental modification of the strength of the predatory interaction facilitates the coexistence of these species (Dick & Platvoet 1996). However, the predatory impact of *D. villosus* on *G. tigrinus* is not alleviated in high-conductivity conditions, indicating that *D. villosus* will eliminate *G. tigrinus* regardless. *G. tigrinus* does, however, have a very high reproductive rate and forms extremely dense populations. Thus, the apparent persistence of a small proportion of *G. tigrinus* in some sites invaded by *D. villosus* (e.g. the east coast of the IJsselmeer) (figure 1) may reflect this ability of *G. tigrinus* to maintain itself in the face of predation pressures. However, the rapidity with which *D. villosus* eliminated *G. tigrinus* in microcosms, plus the rapidly diminishing sources of *G. tigrinus* to populate areas by immigration (figure 1), suggests that eventually *G. tigrinus* populations will succumb to *D. villosus* predation.

Prediction of the identity and ecological consequences of biological invaders has been a long-sought yet elusive

goal of ecologists (Elton 1958; Diamond & Case 1986; Mooney & Drake 1986; Vitousek *et al.* 1986; di Castri *et al.* 1990; Kinzelbach 1995; Moyle & Light 1996; Holway & Suarez 1999; Williamson 1996, 1999). A major problem with prediction is that general features of successful invasions, for example, in terms of the intrinsic attributes of invading species (e.g. high dispersal rate) and community type (e.g. disturbed and/or low diversity) may be useful as general predictors, yet so many exceptions exist that prediction of the outcome of any specific invasion is difficult (Lodge 1993). However, the accumulation of case studies of species attributes, together with linkage of processes of interspecific interaction with ecological pattern, particularly in laboratory microcosms (as proposed by Lodge (1993) and Holway & Suarez (1999)), may be major routes to refining explanations and predictions of the identity and impacts of invaders. Although the use of microcosms in ecological experimentation is contested (e.g. see debate among Drenner & Mazumder (1999), Carpenter (1999) and Huston (1999)), particularly in extrapolation from laboratory to field, microcosms have been recognized as fruitful routes to identifying and making tractable the proximate mechanisms behind successful invasions (Holway & Suarez 1999), particularly where different scales and approaches are combined (Huston 1999). In the present study, the rapid field pattern of exclusion of both native and previously successful invading species by *D. villosus* appears from microcosm studies to be linked with the predatory behaviour of this species. This link is supported by other types of study, such as the finding of Marguillier (1998) from isotope analyses that *D. villosus* is on the same trophic level as some predatory fish species. In addition, Mordukhai-Boltovskoi (1949) described the cannibalistic propensity of *D. villosus*, a characteristic which generally accompanies a propensity for IGP (Polis *et al.* 1989). Thus, accumulated evidence, and in the present study the bridging of scales of investigation by the use of microcosms, tends to support the link between the predatory behaviour of *D. villosus* and its exclusion of both native and exotic species.

While predation between member species of different ecological guilds has often been linked to the elimination of natives by invaders (Diamond & Case 1986), in many invasion scenarios mechanisms are often inferred incorrectly, such as the assumed role of interspecific competition within amphipod guilds (Dick & Platvoet 1996). With amphipods and many other arthropods, intraguild predation (IGP) has been increasingly recognized as a potent force in structuring communities (Polis *et al.* 1989; Holt & Polis 1997) and may override interspecific competition (Dick *et al.* 1993; Dick & Platvoet 1996). In the present case, IGP appears to be the mechanism responsible for rapid species exclusions. In addition, however, the present study has illustrated important details of the nature of predation by *D. villosus*, such as the killing of intermoult victims, that may explain its rapid and decisive impact on populations of native and other exotic species. These predatory features of *D. villosus*, together with its wide habitat requirements and tolerances to temperature and salinity, high reproductive rate (Van der Velde *et al.* 2000) and ability to disperse by anthropogenic means, particularly boats (Nesemann *et al.* 1995), leads us

to predict that this invader will further reduce amphipod diversity in western Europe and elsewhere. Indeed, other European and Ponto-Caspian invaders such as the zebra mussel *Dreissena polymorpha*, the cladoceran *Bythotrephes cederstroemi* and the amphipod *Echinogammarus ischnus* have reached and impacted upon the ecology of the North American Great Lakes (Morton 1997; Witt *et al.* 1997; Dermot *et al.* 1998). We predict that this trend will continue (see also Ricciardi & Rasmussen 1998), with *D. villosus* likely to impact severely on both native and previously successful invading species in such regions.

We thank the British Council for financial support through their UK–Dutch Joint Scientific Research Programme. We are grateful to Anita Kirkpatrick, Alex Portig, Roberta Bailey, David Kelly, Fred Schram, Ian Montgomery, Bob Elwood and Calum MacNeil for a variety of helpful input. We also thank the three referees for comments that greatly aided in the revision of the manuscript.

REFERENCES

- Abacus Concepts 1989 *SuperANOVA*. Berkeley, CA: Abacus Concepts.
- Bij de Vaate, A. & Klink, A. G. 1995 *Dikerogammarus villosus* Sowinsky (Crustacea: Gammaridae) a new immigrant in the Dutch part of the Lower Rhine. *Lauterbornia* **20**, 51–54.
- Capelli, G. M. & Capelli, J. F. 1980 Hybridization between crayfish of the genus *Orconectes*: morphological evidence (Decapoda, Cambaridae). *Crustaceana* **39**, 121–132.
- Carpenter, S. R. 1999 Microcosm experiments have limited relevance for community and ecosystem ecology: reply. *Ecology* **80**, 1085–1088.
- Dermot, R., Witt, J., Um, Y. M. & Gonzalez, M. 1998 Distribution of the Ponto-Caspian amphipod *Echinogammarus ischnus* in the Great Lakes and replacement of native *Gammarus fasciatus*. *J. Great Lakes Res.* **24**, 442–452.
- Diamond, J. & Case, T. J. 1986 Overview: introductions, extinctions, exterminations and invasions. In *Community ecology* (ed. J. Diamond & T. J. Case), pp. 65–79. New York: Harper & Row.
- di Castri, F., Hansen, A. J. & Debussche, M. 1990 *Biological invasions in Europe and the Mediterranean basin. Monographiae Biologicae* 65. Dordrecht, The Netherlands: Kluwer.
- Dick, J. T. A. 1989 Assessments and decisions during mate choice in *Gammarus pulex* (Crustacea: Amphipoda). PhD thesis, The Queen's University of Belfast, UK.
- Dick, J. T. A. 1996a Animal introductions and their consequences for freshwater communities. In *Disturbance and recovery of ecological systems* (ed. P. S. Giller & A. A. Myers), pp. 47–58. Dublin: Royal Irish Academy.
- Dick, J. T. A. 1996b Post-invasion amphipod communities of Lough Neagh, N. Ireland; influences of habitat selection and differential predation. *J. Anim. Ecol.* **65**, 756–767.
- Dick, J. T. A. & Elwood, R. W. 1990 Symmetrical assessment of female quality by male *Gammarus pulex* (Amphipoda) during struggles over precopula females. *Anim. Behav.* **40**, 877–883.
- Dick, J. T. A. & Platvoet, D. 1996 Intraguild predation and species exclusions in amphipods: the interaction of behaviour, physiology and environment. *Freshwat. Biol.* **36**, 375–383.
- Dick, J. T. A., Montgomery, I. & Elwood, R. W. 1993 Replacement of the indigenous amphipod *Gammarus duebeni celticus* by the introduced *G. pulex*: differential cannibalism and mutual predation. *J. Anim. Ecol.* **62**, 79–88.
- Dick, J. T. A., Elwood, R. W. & Montgomery, W. I. 1995 The behavioural basis of a species replacement: differential aggression and predation between the introduced *Gammarus pulex* and the native *G. duebeni celticus* (Amphipoda). *Behav. Ecol. Sociobiol.* **37**, 393–398.
- Dick, J. T. A., Montgomery, W. I. & Elwood, R. W. 1999 Intraguild predation may explain an amphipod replacement; evidence from laboratory populations. *J. Zool. Lond.* **249**, 463–468.
- Dogiel, V. A., Petrushevski, G. K. & Polyanski, Yu. I. 1970 *Parasitology of fishes*. Leningrad University Press 1958. (Translation Oliver Boyd Ltd, 1970.)
- Drenner, R. W. & Mazumder, A. 1999 Microcosm experiments have limited relevance for community and ecosystem ecology: comment. *Ecology* **80**, 1081–1085.
- Elton, C. S. 1958 *The ecology of invasions by animals and plants*. London: Methuen.
- Holt, R. D. & Polis, G. A. 1997 A theoretical framework for intraguild predation. *Am. Nat.* **149**, 745–764.
- Holway, D. A. & Suarez, A. V. 1999 Animal behavior: an essential component of invasion biology. *Trends Ecol. Evol.* **14**, 328–330.
- Human, K. G. & Gordon, D. M. 1996 Exploitation and interference competition between the invasive Argentine ant, *Linepithema humile*, and native ant species. *Oecologia* **105**, 405–412.
- Huston, M. A. 1999 Microcosm experiments have limited relevance for community and ecosystem ecology: synthesis of comments. *Ecology* **80**, 1088–1089.
- Kinzelbach, R. 1995 Neozoans in European waters—exemplifying the worldwide process of invasion and species mixing. *Experientia* **51**, 526–538.
- Lodge, D. M. 1993 Biological invasions: lessons for ecology. *Trends Ecol. Evol.* **8**, 133–137.
- MacNeil, C., Dick, J. T. A. & Elwood, R. W. 1997 The trophic ecology of freshwater *Gammarus* (Crustacea: Amphipoda); problems and perspectives concerning the functional feeding group concept. *Biol. Rev.* **72**, 349–364.
- Marguillier, S. 1998 Stable isotope ratios and food web structure of aquatic ecosystems. PhD thesis, University of Brussels.
- Mooney, H. A. & Drake, J. A. 1986 *Ecology of biological invasions of North America and Hawaii. Ecological studies*, vol. 58. New York: Springer.
- Mordukhai-Boltovskoi, F. D. 1949 Life cycle of some Caspian gammarids. *Dokl. Akad. Nauk SSSR* **46**, 997–999.
- Morton, B. 1997 The aquatic nuisance species problem: a global perspective and review. In *Zebra mussels and aquatic nuisance species* (ed. F. M. D'Itri), pp. 1–54. Chelsea, MI: Ann Arbor Press.
- Moyle, P. B. & Light, T. 1996 Biological invasions of fresh water: empirical rules and assembly theory. *Biol. Conserv.* **78**, 149–161.
- Nesemann, H., Pöckl, M. & Wittmann, K. J. 1995 Distribution of epigeic Malacostraca in the middle and upper Danube (Hungary, Austria, Germany). *Miscnea. Zool. Hung.* **10**, 49–68.
- Pinkster, S., Scheepmaker, M., Platvoet, D. & Broodbakker, N. 1992 Drastic changes in the amphipod fauna (Crustacea) of Dutch inland waters during the last 25 years. *Bijdr. Dierk.* **61**, 193–204.
- Polis, G. A., Myers, C. A. & Holt, R. D. 1989 The ecology and evolution of intraguild predation: potential competitors that eat each other. *A. Rev. Ecol. Syst.* **20**, 297–330.
- Ricciardi, A. & Rasmussen, J. B. 1998 Predicting the identity and impact of future biological invaders: a priority for aquatic resource management. *Can. J. Fish. Aquat. Sci.* **55**, 1759–1765.
- Sokal, R. R. & Rohlf, F. J. 1995 *Biometry. The principles and practice of statistics in biological research*. New York: W. H. Freeman & Co.
- Tittizer, T. 1996 Main–Danube canal now a short cut for fauna. *Danube Watch* **2**, 7–8.
- Van der Velde, G., Rajagopal, S., Kelleher, B., Musko, I. B. & Bij de Vaate, A. 2000 Ecological impact of crustacean invaders: general considerations and examples from the Rhine

- river. In *Proceedings of the Fourth International Crustacean Congress, Amsterdam, The Netherlands, July 20–24, 1998*, vol. 2 (ed. J. C. von Vaupel Klein & F. R. Schram), pp. 3–34. Rotterdam, The Netherlands: Balkema.
- Vitousek, P. M., D'Antonio, C. M., Loope, L. L. & Westbrooks, R. 1996 Biological invasions as global environmental change. *Am. Sci.* **84**, 468–478.
- Williamson, M. 1996 *Biological invasions*. London: Chapman & Hall.
- Williamson, M. 1999 Invasions. *Ecography* **22**, 5–12.
- Witt, J. D. S., Hebert, P. D. N. & Morton, W. N. 1997 *Echinogammarus ischnus*: another crustacean invader in the Laurentian Great Lakes basin. *Can. J. Fish. Aquat. Sci.* **54**, 264–268.
- Zaret, T. M. & Paine, R. T. 1973 Species introduction in a tropical lake. *Science* **182**, 449–455.

As this paper exceeds the maximum length normally permitted, the authors have agreed to contribute to production costs.