

Interactions between invasive and native crustaceans: differential functional responses of intraguild predators towards juvenile hetero-specifics

Åsa M. Kestrup · Jaimie T. A. Dick ·
Anthony Ricciardi

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Abstract Intraguild predation (IGP) between invasive and native species can lead to species exclusions or co-existence, dependent on the direction and strength of the interaction. Recently, derivation of ‘functional responses’ has been identified as a means of comparing the community impacts of invasive and native species. Here, we employ a novel use of this functional response methodology to evaluate any IGP asymmetries between the invasive Ponto-Caspian amphipod *Echinogammarus ischnus* and the North American native *Gammarus fasciatus*. The direction and magnitude of intraguild predation of adult males on hetero-specific adult females has previously been shown to reverse across a water conductivity gradient. This partially explains field patterns, but does not predict the co-existence of the two species observed in many habitats and locations. Here, we compared intraguild predation by both species on each other’s juveniles in high- and low- conductivity water.

G. fasciatus has a higher type II functional response towards *E. ischnus* juveniles compared to the reciprocal interaction. Conductivity did not influence the predation rate on juveniles of either *E. ischnus* or *G. fasciatus*. Thus, the male/female IGP advantage to the native *G. fasciatus* in low conductivity water is compounded by a juvenile IGP asymmetry, which also counteracts the male/female IGP advantage to *E. ischnus* in high conductivity waters, helping to explain field patterns of exclusion and co-existence. Thus, complex asymmetries in mutual IGP associated with inherent species differences, environmental modulation, and life-history effects can help us understand and predict the population and community level outcomes of species invasions.

Keywords Amphipods · Conductivity · *Echinogammarus* · Exotic species · Functional response · Intraguild predation

Å. M. Kestrup · A. Ricciardi (✉)
Redpath Museum, McGill University, 859 Sherbrooke
Street West, Montreal, QC H3A 2K6, Canada
e-mail: tony.ricciardi@mcgill.ca

Å. M. Kestrup
e-mail: asa.kestrup@mcgill.ca

J. T. A. Dick
School of Biological Sciences, Queen’s University
Belfast, MBC, 97 Lisburn Road, Belfast BT9 7BL,
Northern Ireland, UK
e-mail: j.dick@qub.ac.uk

Introduction

Intraguild predation (IGP; Polis et al. 1989) is increasingly recognized as a powerful force in structuring biological communities and determining the outcomes of species invasions (Arim and Marquet 2004; Dick 2008; Hatcher et al. 2008). Where IGP is mutual between two species, any biotic or abiotic mediation of the interaction, or inherent asymmetries

in the interaction, can profoundly influence patterns of species exclusion and co-existence. For example, many amphipod species replacements are caused by asymmetrical engagement in IGP (Dick 2008), while parasitism of such IGP participants can determine species co-existence (MacNeil et al. 2003; Hatcher et al. 2008). Recently, it has also been demonstrated that environmental factors, such as water chemistry, can modulate IGP (Kestrup and Ricciardi 2009; Piscart et al. 2009). Thus, resolving the strength and direction of IGP in various environmental contexts should help us understand and predict the structuring of communities and the outcomes of invasions.

Bollache et al. (2008) showed that the functional response (*sensu* Holling 1959) of an introduced species can be used to quantify and compare its effect on prey populations with that of native species. This involves interspecific comparisons of the relationship between prey density and prey consumption. Such an approach can help forecast the community-level impacts of invaders (Bollache et al. 2008; Dick et al. 2010). Here, we took the novel approach of using functional responses in an IGP context, deriving and comparing the functional responses of co-occurring native and invader amphipods towards each others' juveniles under differing environmental regimes, in order to understand spatial variation in the population and community level outcomes of the invasion.

Amphipod crustaceans feature as aquatic invaders throughout much of the world, frequently resulting in the displacement of native species and previously established invaders (e.g., Dick and Platvoet 2000; Kelly et al. 2003; Dick 2008). Many invasive amphipods are highly predatory and feed on a broad range of small invertebrates, including other amphipods; some of these species can thereby reduce the diversity and biomass of benthic communities (Dick and Platvoet 1996; Kelly et al. 2002a, 2003, 2006; Krisp and Maier 2005; Kestrup and Ricciardi 2009).

The Ponto-Caspian invader *Echinogammarus ischnus* has displaced the native *Gammarus fasciatus* on hard substrate throughout much of the lower Great Lakes (Dermott et al. 1998). The invader may be more carnivorous than *G. fasciatus* (Limen et al. 2005) and appears to be replacing the latter through mutual but asymmetric IGP by adult males on females (Kestrup and Ricciardi 2009). However, these two species continue to co-exist in a variety of habitats (e.g. in the St. Lawrence River; Kestrup and

Ricciardi 2009), even a decade after invasion, in contrast to other asymmetrical amphipod IGP systems where complete replacements have been rapid (Dick et al. 1993; Dick and Platvoet 2000; Dick 2008). One factor contributing to the complex pattern of co-existence is the lower tolerance of *E. ischnus* to water of low ionic content, such that it is the dominant intraguild predator only at sites with high conductivity (i.e. $\geq 300 \mu\text{S}/\text{cm}$). In contrast, the roles are reversed in ion-poor waters (175–200 $\mu\text{S}/\text{cm}$), in which *G. fasciatus* males are the dominant intraguild predators (Kestrup and Ricciardi 2009). However, this pattern implies that the species should not co-exist, since even small asymmetries in IGP can lead to species exclusions (Dick et al. 1993; Dick 2008; Hatcher et al. 2008).

The vulnerability of a species to IGP may vary with life history stage (Polis et al. 1989). Generally, larger amphipod individuals prey on smaller hetero-specifics, particularly males on females, and the asymmetric loss of females from the population of the inferior IGP participant reduces population size and recruitment (e.g. Dick et al. 1993). However, juvenile amphipods are also subject to IGP by adults and any asymmetries in this interaction will clearly have implications for population recruitment and the dynamics of co-existence. Thus, in the present invasion scenario, it is necessary to examine the intraguild predatory pressure of the two species on each other's juveniles under different water conductivities, to gain a more complete understanding of this interaction. We therefore compare the functional responses of *E. ischnus* and *G. fasciatus* towards hetero-specific juvenile prey in ion-rich and ion-poor waters, in order to assess the magnitude and any asymmetry of such IGP.

Methods

In August and September 2009, *E. ischnus* (invader) and *G. fasciatus* (native) were collected at Chateauguay West (45°21.80 N, 73°47.20 W), a site south of the Island of Montreal that receives ion-rich water from the St Lawrence River. High-conductivity water (290 $\mu\text{S}/\text{cm}$, 26 mg Ca^{2+}/L) was collected from this site and low-conductivity water (98 $\mu\text{S}/\text{cm}$, 13 mg Ca^{2+}/L) from Place St-Louis (45°25.03 N, 73°52.68 W), a site on the north shore

of Lake St. Louis that receives water from the Ottawa River, in clean plastic buckets. Water for the two experimental treatments was high-conductivity (HC) water, and intermediate-conductivity (IC) water (175 $\mu\text{S}/\text{cm}$, 15 mg Ca^{2+}/L), the latter a mixture of the two source waters. Conductivity was measured using an electronic meter (YSI# 85-25-FT), while the calcium concentration was analysed using a LaMotte hardness kit (model PHT-CM-DR-LT).

In the laboratory (20°C and 10:14 h L:D), animals were treated in a bath of 15 ppm Malachite green in filtered source water (11 μm filter paper) for 15 min to reduce the risk of fungal infection (Melendre et al. 2006). The species were kept separately in aquaria with filtered source water and cobble and fed ad libitum with dried winter squash (*Cucurbita maxima*), which was readily consumed. Emerging juveniles were collected from gravid females held individually in plastic cups with 150 ml filtered source water and stored for 3 days in trays with food. Juvenile length (tip of rostrum to tip of telson) was then measured on a sample of juveniles ($n = 20$ per species) using a stereo microscope and micrometer eyepiece, and the mean sizes of juveniles of the two species were compared by a *t*-test. We selected similar-sized adult males of the two species (measured after the experiment; mean body length of the two species in both experimental conductivities examined by ANOVA) and starved them for 24 h in either HC or IC water before use in the experiment. Individual males of the two species were then presented with hetero-specific juveniles in both HC and IC water at nine prey densities (4, 6, 8, 10, 16, 20, 30, 60, 90; $n = 4$ per density) or until an asymptote was reached; *G. fasciatus* males were therefore also offered a density of 120 juveniles. Four replicates of each prey density in both HC and IC water without adult amphipods acted as controls. Replicates were examined after 24 and 40 h.

The mean number of juvenile prey eaten was examined in a five-factor ANOVA with respect to predator status (i.e. adults present/absent), predator species, prey density, time (repeated measure) and water conductivity type. While there are mixed views as to which functional response models are appropriate in cases in which prey are not replaced as they are eaten (see Juliano 2001), we take the view that the simpler Holling's type equations are sufficiently robust in cases where the primary purpose is an

interspecific comparison of functional responses. Thus, functional responses were modelled in Sigma-Plot v. 10.0 using a Monod function $y = ax/(1 + bx)$, which provided estimates of *a* (the scale parameter), *b* (the saturation parameter), the maximum feeding rate (given by the asymptote $a/(bh)$, where *h* is experimental time), and the R^2 values for the fitted curves. Mean maximum feeding rate estimates were examined with respect to predator species by a *t*-test. All analyses were conducted with SPSS 17.0 for Windows (release 12.0.0).

Results

E. ischnus juveniles were marginally, if consistently, smaller in length than *G. fasciatus* juveniles (1.5 mm \pm 0.02 SE vs. 1.7 mm \pm 0.02 SE, $t_{38} = -11.9$, $P < 0.001$). Experimental adult males of the two species did not differ significantly in length (*E. ischnus* IC water = 7.6 mm \pm 0.10 SE and HC water = 7.7 \pm 0.07 SE; *G. fasciatus* IC water = 7.8 mm \pm 0.06 SE and HC water = 7.9 \pm 0.07 SE; $F_{3,151} = 2.6$, N.S). Survival of control juveniles at 24 and 40 h was, respectively, 98.4 and 96.8% for *E. ischnus* in HC water, 98.2 and 95.2% for *G. fasciatus* in HC water, 98.3 and 97.3% for *E. ischnus* in IC water, and 98.2 and 95.9% for *G. fasciatus* in IC water. Predation was thus concluded to be the principal cause of juvenile mortality in the predator treatments, and this activity was indeed frequently observed.

The presence of adults significantly increased juvenile mortality ($F_{1,288} = 898.8$, $P < 0.001$), with significantly more hetero-specific juvenile prey eaten by the native *G. fasciatus* than the invader *E. ischnus* ($F_{1,288} = 140.1$, $P < 0.001$; Fig. 1). Significantly more prey were consumed as prey density increased ($F_{8,288} = 647.2$, $P < 0.001$) and over time ($F_{1,288} = 149.2$, $P < 0.001$; Fig. 1). However, there was no significant difference in predation between the two water conductivities ($F_{1,288} = 0.06$, NS; Fig. 1). All two- and three-way interactions were significant ($P < 0.001$), except for those including water conductivity type.

Since the Monod models achieved high goodness of fit (R^2 values, Table 1), the functional responses of *E. ischnus* and *G. fasciatus* (Fig. 1) can be described as type II (see also Bollache et al. 2008; Dick et al. 2010). In addition, maximum predation rate (see

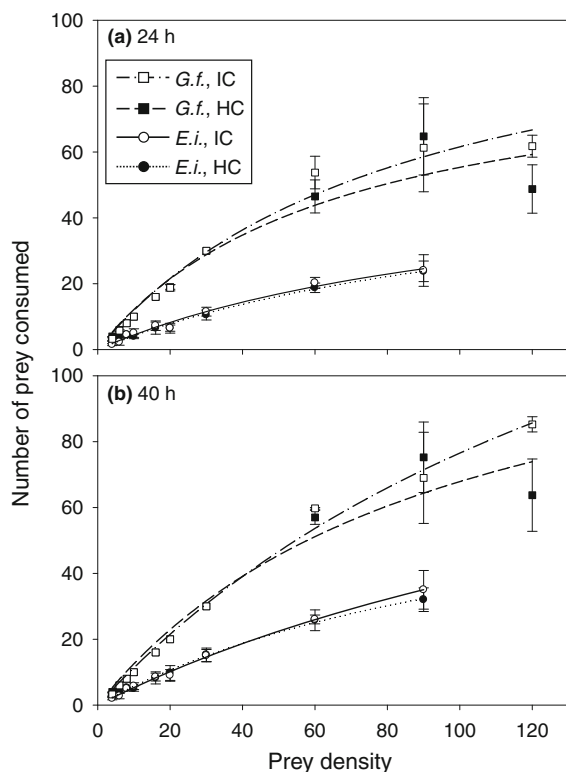


Fig. 1 Relationship between prey density and the number of prey consumed (the functional response) by *G. fasciatus* (*G.f.*) and *E. ischnus* (*E.i.*) in water of high and intermediate conductivities (HC and IC, respectively), after **a** 24 h and **b** 40 h

Table 1) was significantly higher for *G. fasciatus* than for *E. ischnus* ($t_6 = 3.82$, $P < 0.01$).

Discussion

In its invasion of North American freshwaters, the Ponto-Caspian amphipod *E. ischnus* is disadvantaged

at low and intermediate water conductivities, both through its lower tolerance to ion-poor waters in terms of survival and growth, and to the asymmetry in IGP on adult females that favours the native *G. fasciatus* under such conditions (Kestrup and Ricciardi 2009). The present study shows clearly that *E. ischnus* suffers another differential predation pressure—that of a higher predatory impact on its juveniles from *G. fasciatus* compared to the reciprocal interaction, as revealed through our derivation of functional responses. This is fully consistent with field patterns, where the invader is excluded or exists in very low abundance alongside *G. fasciatus* in low and intermediate conductivity waters (Kestrup and Ricciardi 2009). Co-occurrences of the two species in ion-poor waters may be explained by immigration of *E. ischnus*, a situation found in another amphipod invasion scenario by Dick (1996). In contrast, *E. ischnus* is the stronger intraguild predator with respect to adult male/female predation in high conductivity waters, and indeed is successful in invading areas of high *G. fasciatus* abundance (Dermott et al. 1998; Palmer and Ricciardi 2004; Kestrup and Ricciardi 2009). However, the present experiment helps explain why the invader does not always entirely replace the native in high conductivity waters, since the native retains its IGP advantage over *E. ischnus* juveniles under such conditions, counteracting the IGP asymmetry on females favouring *E. ischnus*. Thus, the field patterns of exclusion and co-existence are much better understood when the asymmetries in IGP, in relation to water conductivity, are resolved for a number of life-history stages.

In the experiment, *E. ischnus* juveniles were slightly smaller than those of *G. fasciatus*. However, the difference in prey size was insignificant compared

Table 1 Functional response parameters with goodness of fit (R^2) for each species/water (conductivity)/time combination and estimated mean maximum feeding rate, $a/(bh)$

| Adult predators | Juvenile prey | Conductivity ($\mu\text{S}/\text{cm}$) | Time | a | b | R^2 | $a/(bh)$ |
|---------------------|---------------------|--|------|-------|-------|-------|----------|
| <i>G. fasciatus</i> | <i>E. ischnus</i> | 290 | 24 | 1.402 | 0.015 | 0.803 | 3.82 |
| | | | 40 | 1.384 | 0.010 | 0.857 | 3.33 |
| <i>G. fasciatus</i> | <i>E. ischnus</i> | 175 | 24 | 1.329 | 0.012 | 0.867 | 4.77 |
| | | | 40 | 1.195 | 0.006 | 0.924 | 5.34 |
| <i>E. ischnus</i> | <i>G. fasciatus</i> | 290 | 24 | 0.452 | 0.008 | 0.864 | 2.38 |
| | | | 40 | 0.617 | 0.008 | 0.881 | 1.93 |
| <i>E. ischnus</i> | <i>G. fasciatus</i> | 175 | 24 | 0.483 | 0.009 | 0.817 | 2.34 |
| | | | 40 | 0.556 | 0.005 | 0.878 | 2.95 |

to the difference in predation rate and it therefore seems unlikely that a small size discrepancy alone explains the large difference in functional responses between these species. Further, the adult males of the two species were matched for size in the experiment. However, since *G. fasciatus* generally grows larger than *E. ischnus* (Dermott et al. 1998; Kestrup and Ricciardi unpublished data), the species differences in functional responses shown here are most likely conservative. Additionally, at the population level, the effect of the higher functional response of *G. fasciatus* towards juvenile *E. ischnus* as compared to the reciprocal interaction may be enhanced by the lower fecundity of the latter. Even though the size-specific fecundity of the two species is similar, the reproductive output of *G. fasciatus* females is higher due to their larger size (Dermott et al. 1998; Kestrup and Ricciardi unpublished data). Indeed, Dick and Platvoet (1996) showed that a reversal in species dominance can occur with changes in the balance of IGP and reproductive output.

There is a growing body of evidence that local environmental factors are key to understanding variation in IGP interactions and hence patterns of species exclusions and co-existence. Dick and Platvoet (1996) and MacNeil et al. (2004) showed that patterns of dominance by either *G. pulex*, *G. tigrinus* or *G. duebeni celticus* are partially driven by the changing balance of IGP under different water qualities, while an unknown feature of water chemistry reduced IGP asymmetries and hence slowed the replacement of *G. duebeni celticus* by *G. pulex* in one Irish river (Piscart et al. 2009). With respect to the current North American invasion by *E. ischnus*, we predict (1) its expansion into high conductivity and polluted waters (such as parts of the Mississippi and the Missouri Rivers; USGS Water Quality Watch 2009), (2) the persistence of the native species in low conductivity and more pristine waters (such as rivers draining the Canadian Shield, including the Ottawa River and northshore tributaries to the St Lawrence River; Rondeau 1993), and (3) its co-existence with natives in intermediate conductivity waters such as Lake Champlain and the Richelieu River (Jokela and Ricciardi 2008; Vermont Department of Environmental Conservation 2009a, b). Further, the range of parasites that these species harbour can modulate IGP asymmetries (MacNeil et al. 2003; Hatcher et al. 2008), such that species exclusions, reversals of such

exclusions, and complex patterns of co-existence are now being unravelled (Dick 2008).

It should be noted that we did not examine the influence of any anti-predator behaviour of juveniles, such as phototaxis (Hunte and Myers 1984), which may have an influence on the relative vulnerability of juveniles to predation. In addition, substrate heterogeneity, oxygen levels, alternative prey and other factors may alter functional responses (see Bollache et al. 2008; Dick et al. 2010) and require further investigation in the present context.

With regards to the wider aquatic community, predation is the primary mechanism associated with invasive amphipod impacts (Kelly et al. 2003; Kelly and Dick 2005; van Riel et al. 2006). The invasion of Northern Ireland by *G. pulex* resulted not only in a replacement of the similar-sized native *G. duebeni celticus*, but also in a reduction in the abundance and diversity of other benthic invertebrates, owing to the invader's voracious feeding habits (Kelly et al. 2002b, 2003; Kelly and Dick 2005; Dick et al. 2010). Similarly, the predatory *Dikerogammarus villosus* has had a substantial impact on invaded food webs in Europe (Dick et al. 2002; van Riel et al. 2006; Platvoet et al. 2009). By contrast, while the displacement of *G. fasciatus* by *E. ischnus* in the lower Great Lakes is well documented, the impact of *E. ischnus* on other benthic invertebrates is largely unknown. It would be informative to compare functional responses of these amphipods on different individual or multiple prey species.

Nonetheless, the differences in functional responses revealed by our study tentatively suggest that the replacement of *G. fasciatus* by *E. ischnus*, where it occurs, may alter amphipod predation rates in benthic food webs. Given that *E. ischnus* may have a lower per-capita effect than *G. fasciatus* on small invertebrate prey (as suggested by the results of this study), its total predation pressure per unit area in the upper St. Lawrence River should be low compared to the native amphipod. As *E. ischnus* rarely reaches high abundances in the upper St. Lawrence River, where the benthic community is often dominated locally by *G. fasciatus*, its impact on benthic food webs might be low in this area. However, in areas of the lower Great Lakes where the invader thrives, high local abundances may overcome the low per-capita effect, resulting in a larger total impact (as observed for in *G. pulex* in Ireland; Kelly et al. 2003; Bollache et al.

2008). This requires pre- and post-invasion monitoring of the composition of the benthic community.

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